



## THE EARLY CRETACEOUS MESOFOSSIL FLORA OF CATEFICA, PORTUGAL: ANGIOSPERMS

ELSE MARIE FRIIS<sup>1,2,\*</sup>, PETER R. CRANE<sup>3,4</sup>, KAJ RAUNSGAARD PEDERSEN<sup>1</sup>, MÁRIO MIGUEL MENDES<sup>5,6</sup>, JIŘÍ KVAČEK<sup>7</sup>

<sup>1</sup> Department of Geoscience, University of Aarhus, Høegh-Guldbergs Gade 2, DK-8000 Aarhus C, Denmark; e-mail: else.marie.friis@geo.au.dk.

<sup>2</sup> Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.

<sup>3</sup> Oak Spring Garden Foundation, 1776 Loughborough Lane, Upperville, Virginia 20184, USA.

<sup>4</sup> Yale School of Environment, Yale University, New Haven, Connecticut 06511, USA.

<sup>5</sup> University of Coimbra, MARE – Marine and Environmental Sciences Centre / ARNET – Aquatic Research Network, Largo Marquês de Pombal, 3030-790 Coimbra, Portugal.

<sup>6</sup> Fernando Pessoa University, Praça 9 de Abril 349, Porto 4249-004, Portugal.

<sup>7</sup> National Museum, Václavské náměstí 68, 110 00 Praha 1, the Czech Republic.

\*corresponding author

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**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 (Magnoliales, 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., *Endressistemon 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

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### 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, Horikx 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, Catefica, 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. Associated with these early angiosperm mesofossils is also a diverse assemblage of chlamydospermous seeds assigned to the Bennettitales-Erdtmanithecates-Gnetales group (BEG; Friis et al. 2007, 2009b, 2013, 2019e, Mendes et al. 2020) that were clearly an important component of the ecosystems that included early angiosperms, as is also suggested from the increase in the diversity of ephedroid pollen in Early to mid-Cretaceous palynofloras (Crane and Lidgard 1989, Lupia et al. 2000). The mesofossil assemblages are also rich in other plant fragments including diverse megaspore assemblages, ferns and remains of conifers (e.g., Friis et al. 2019a).

While many of the taxa in the mesofossil floras from Portugal remain to be studied in detail, numerous individual taxa have already been described (see references above). However, the only comprehensive account of a whole mesofossil assemblage is that from Torres Vedras, which is currently the oldest mesofossil flora containing well-preserved angiosperm flower, fruit and seed remains (Friis et al. 2019a). At the Torres Vedras locality angiosperms account for more than 60 % of all the species recognized, but their relationships to extant taxa are highly constrained. Most species are most closely related to extant 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).

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 Catefica in western Portugal, ca. 40 km north of Lisbon. Several angiosperm and non-angiosperm taxa based on mesofossils have been described previously from Catefica (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 Catefica mesofossil flora, together with the bryophytes and pteridophytes, will be provided in later accounts.

Like the slightly older Torres Vedras mesofossil flora, the Catefica mesofossil flora is dominated by well-preserved fossils of early angiosperms, among which, ANA-grade and magnoliid angiosperms, including a variety of chloranthoids, are the most prominent. The Catefica mesofossil flora provides further important insights into some of the earliest plant communities in which angiosperm were a significant component and a valuable point of comparison with the assemblage of angiosperm fossils from Torres Vedras, and from other Early Cretaceous mesofossil floras.

## Material and methods

The Catefica 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 Catefica 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 Catefica 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 Catefica 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 Catefica exposure, and consideration of its sedimentological setting is provided in several previous studies of fossils from the Catefica 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).

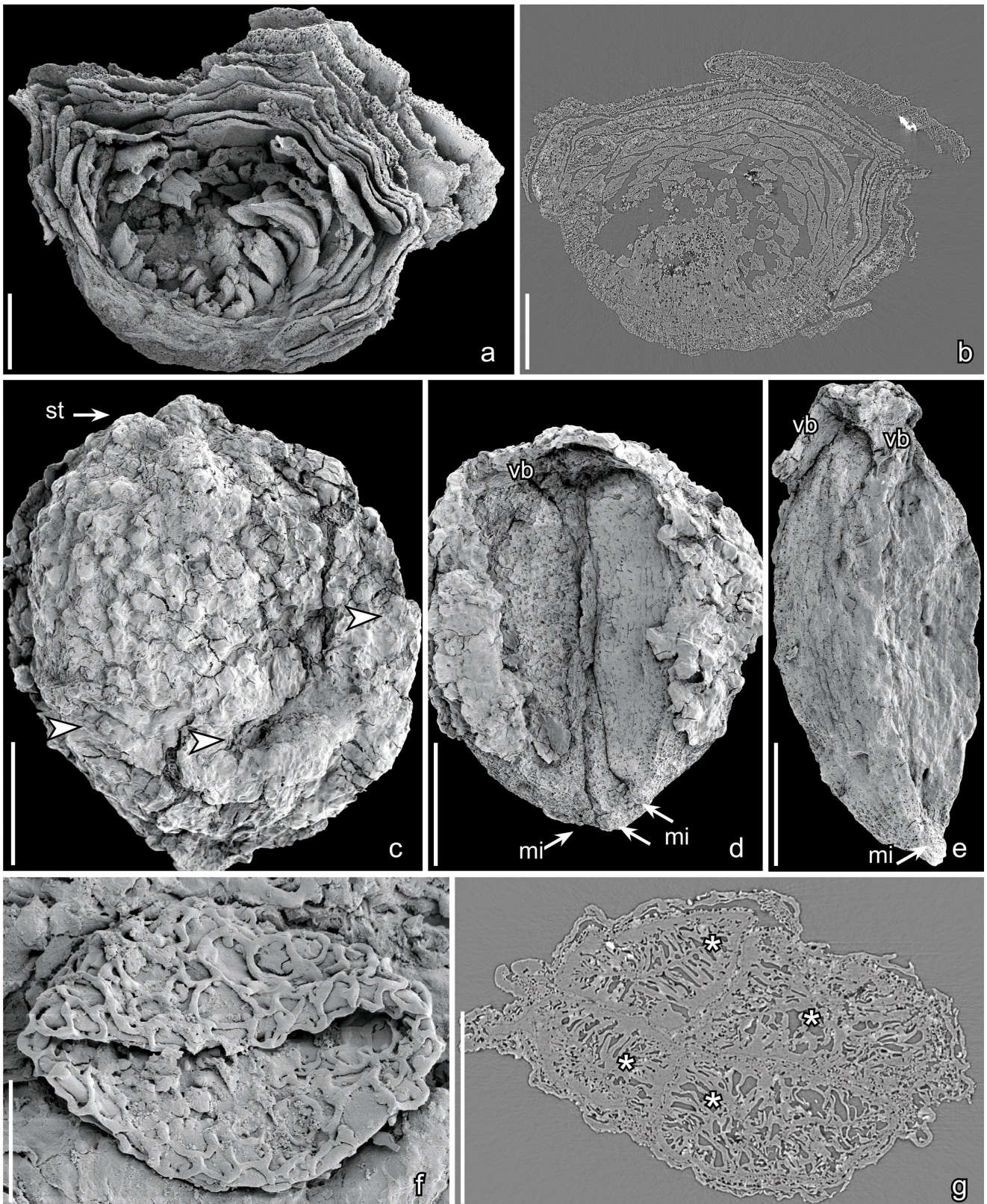


**Text-fig. 1.** The Catefica exposure along the road between Catefica and Mugideira photographed in 1989 when the mesofossil flora was discovered. The exposed strata are mainly cross-bedded light colored sands, darker horizons of clay and dark lenses with mesofossils. The most productive sample, Catefica sample 49, was collected in the basal part of the exposed sequence (arrow head). One of the authors (PRC) exploring the middle part of the section. Photo K. R. Pedersen.

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 charcoalfications, 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; note the remains of the apical vascular bundles (vb); 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 JSM 840 scanning electron 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 (Stampanoni 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 with 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.

showing the long colpus and coarse reticulum; g) Transverse section (orthoslice xy0705) through a fruit showing four seeds all with radially elongated endothelium cells formed from the inner epidermis of the tegmen (asterisks). Specimens, Catefica 150-S174254 (a, b), Catefica 49-S170377 (c), Catefica 49-S170372 (d), Catefica 50-S170401 (e), Catefica 50-S170404 (f), Catefica 50-S174906 (g). Scale bars = 300 µm (a–e, g), 6 µm (f).

**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	Aperture:diameter grain	Muri, ornamentation	Muri, width
<i>Canrightia resinifera</i>	2c–g	flower/fruit/seed	?	15.8–21.0 µm	monocolpate	1:1	smooth	
<i>Canrightia foveolata</i>	3a–f, 4a–i	flower/fruit/seed	?	?	?	?	?	?
<i>Canrightia</i> sp.	5a, b	flower/fruit/seed	?	?	?	?	?	?
<i>Canrightiopsis crassitesta</i>	6a–c, g, h	flower/fruit/seed	?	12–14 µm	monocolpate	1:1	beaded, 1 row	0.25 µm
<i>Canrightiopsis intermedia</i>	6d–f	flower/fruit/seed	?	?	?	?	?	?
<i>Canrightiopsis</i> sp.		flower/fruit/seed	?	?	?	?	?	?
<i>Hedyflora crystallifera</i>	7a–f	flower/fruit/seed	?	22 µm	tetrachotomocolpate	2:3	beaded, two rows	0.3 µm
<i>Proencistemon portugallicus</i>	8a–f, 9a–g	inflorescence/stamen	0.55 mm	12.5–16 µm	trichotomocolpate	2:3	beaded, 2–3 rows	0.2 µm
<i>Proencistemon</i> sp.	9h–j	inflorescence/stamen	0.8 mm	16 µm	trichotomocolpate	2:3	beaded, 2 rows	0.3 µm
<i>Clavatipollenites</i> type pollen sp. 1	10a–d	stamen	1.3 mm	17–20 µm	monocolpate	2:3	beaded, 1 row	0.2–0.4 µm
<i>Clavatipollenites</i> type pollen sp. 2	11a–e	stamen	1.3 mm	24–26 µm	monocolpate	1:3	beaded, 1–2 rows	0.5 µm
<i>Clavatipollenites</i> type pollen sp. 3	12a–e	stamen	0.5 mm	15–17 µm	monocolpate	?	beaded, 1–2 rows	0.4 µm
<i>Clavatipollenites</i> type pollen sp. 4	13a–d	stamen	0.5 mm	14–17 µm	monocolpate	2:3	beaded, 1–2 rows	0.3 µm
<i>Asteropollis</i> type pollen sp. 1	14a–e	stamen	0.4 mm	20–24 µm	tetrachotomocolpate	2:3	beaded, 2 rows	0.5 µm
<i>Asteropollis</i> type pollen sp. 2	15a–e	stamen	0.9 mm	15–18 µm	pentachotomocolpate	2:3	beaded, 2 rows	0.4 µm
<i>Asteropollis/Clavatipollenites</i> sp. 1	16a–c	stamen	1 mm	17–20 µm	?	?	beaded-perforated, 1–2 rows	0.3 µm
<i>Asteropollis/Clavatipollenites</i> sp. 2	16d–f	stamen	1.4 mm	22 µm	?	?	beaded, 2 rows	0.5 µm
<i>Asteropollis/Clavatipollenites</i> sp. 3	16g–i	stamen	0.8 mm	16 µm	?	?	beaded, 2 rows	0.8 µm

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 (Friis and

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, Catefica, 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 Catefica 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 Catefica mesofossil flora (Tab. 1). Pollen grains similar to those observed on the *Canrightia* fruits are present, however, in palynological samples analyzed from the Catefica locality and in other palynofloras 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.KVAČEK sp. nov.**  
Text-figs 3a–f, 4a–i

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

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

**Paratypes.** S175179, S265998, S266057, S266107 (Catefica sample 49), S266042 (Catefica sample 154), S175178 (Catefica 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.** 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).

**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 Famalicão locality, while fruits of *C. resinifera* from the Catefica 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.

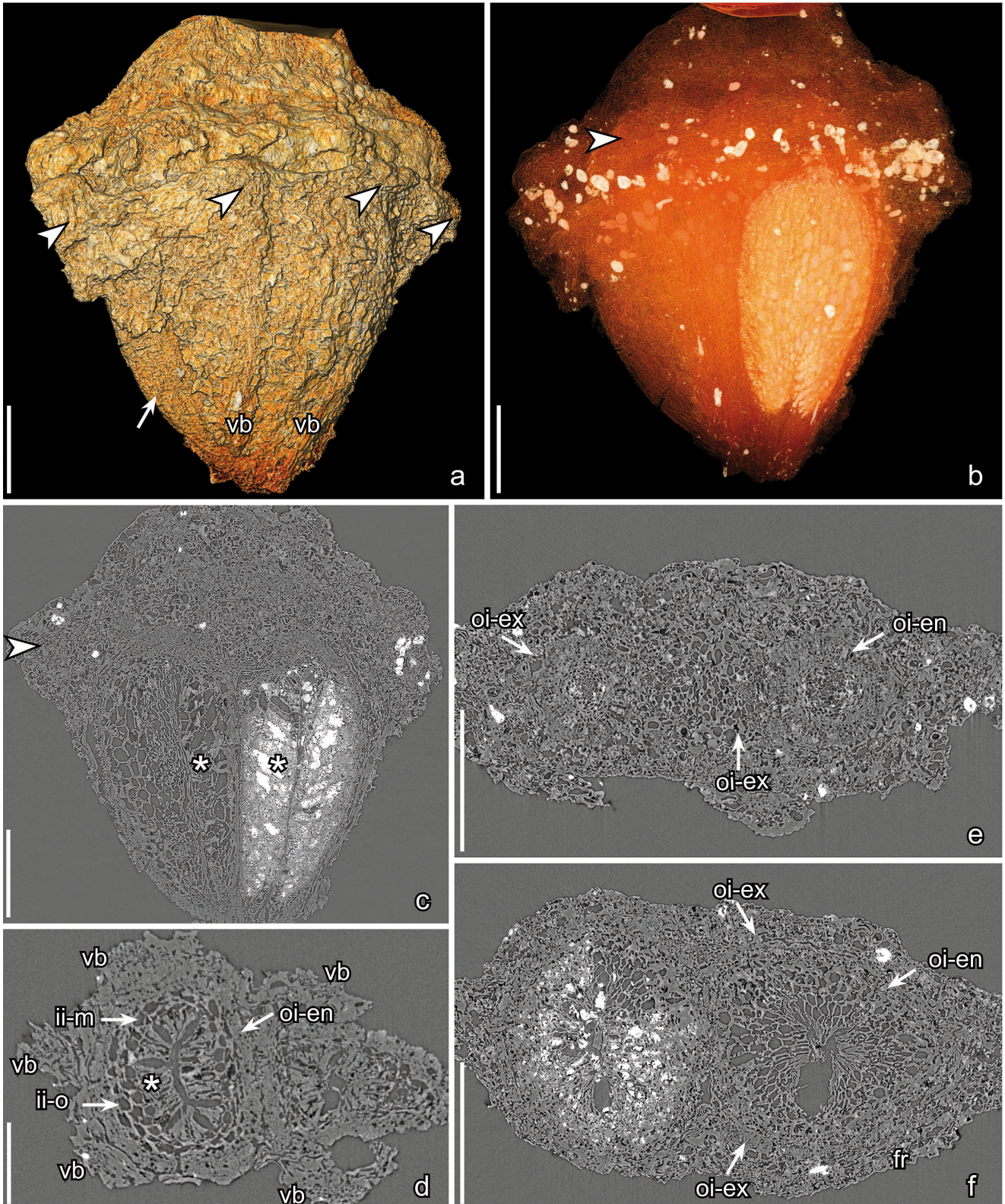
A pitted surface of the endotesta is also present in seeds of *Canrightiopsis* E.M.FRIIS, G.W.GRIMM, M.M.MENDES et K.R.PEDERSEN and *Kvacekispermum* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN, two other extinct genera of chloranthoid affinity (Friis et al. 2015a, 2018b), but both of these genera have one-seeded 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, c, e). 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 towards 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 *C. foveolata*. 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 Catefica 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 endothelium 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).

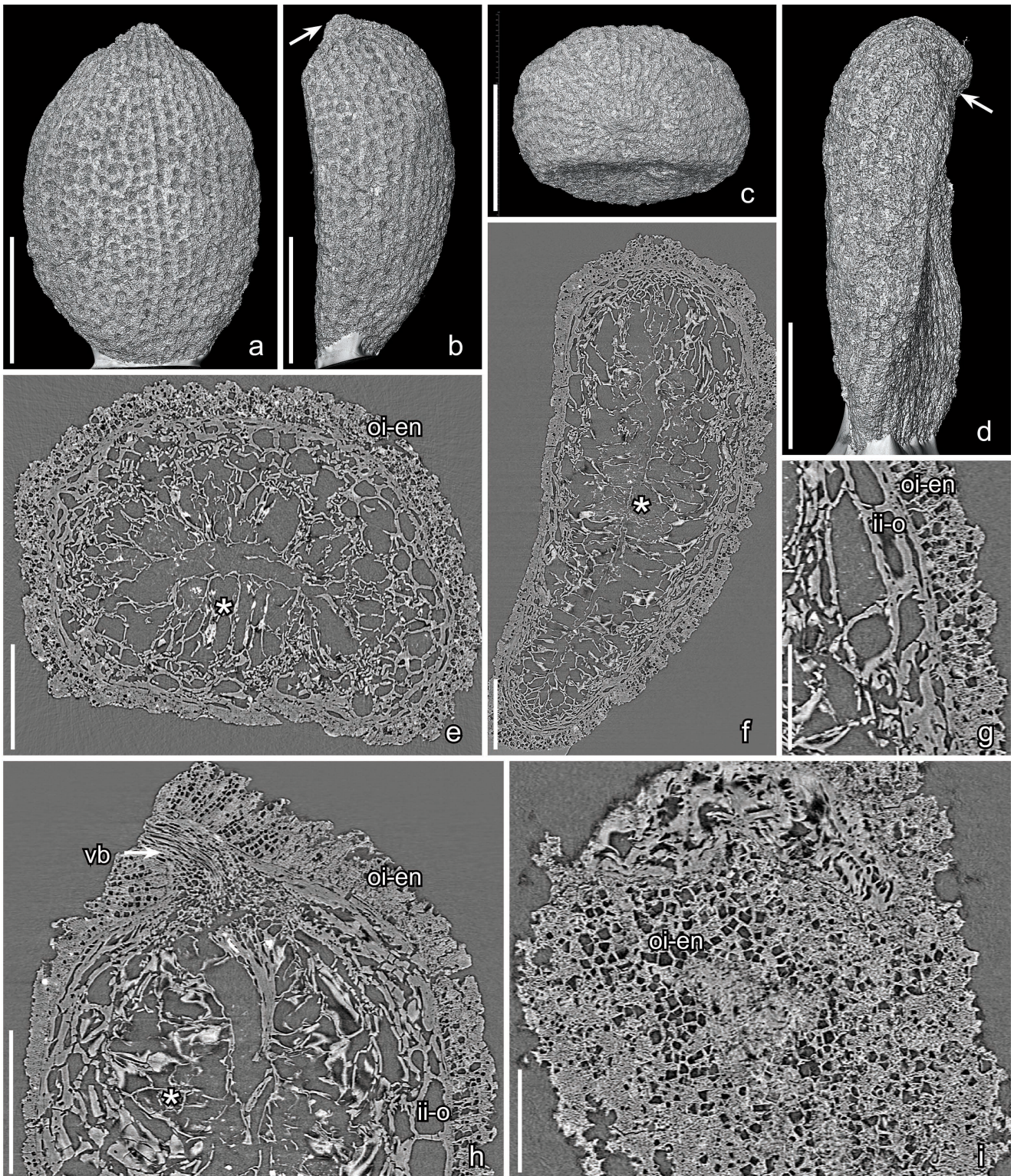
**Affinity and other occurrences.** Analysis of the phylogenetic relationships of *Canrightiopsis* placed the genus in the Chloranthaceae as part of the *Ascarina* J.R.FORST. et G.FORST.-*Sarcandra* GARDNER-*Chloranthus* Sw. clade, particularly close to *Sarcandra* and *Chloranthus* (Friis et al. 2015a), 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. dinisii* E.M.FRIIS, G.W.GRIMM, M.M.MENDES et K.R.PEDERSEN. Only *C. crassitesta* and *C. intermedia* are present in the Catefica 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 Catefica studied using SEM are typical *C. crassitesta*, while only one specimen is a distinct *C. intermedia*. Other specimens from Catefica for which internal features are unknown are referred to as *Canrightiopsis* sp. (Friis et al. 2015a).

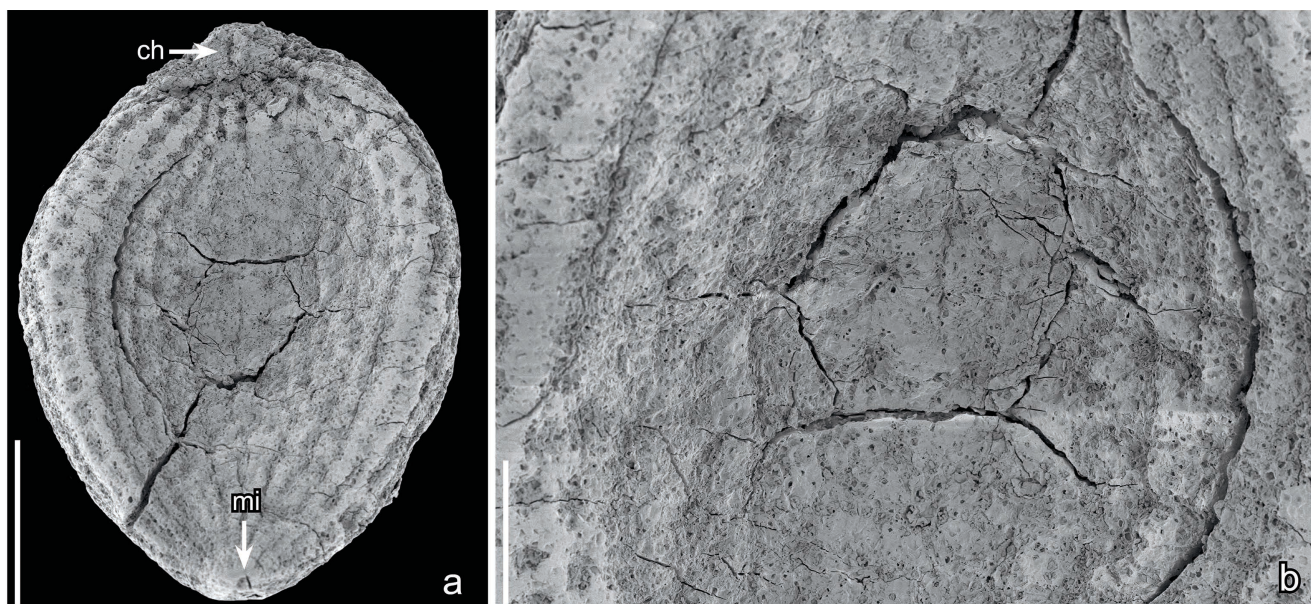
Fruits and seeds of *Canrightiopsis* are particularly common in the mesofossil flora from Famalicão, but are also reported from the Arazede, Buarcos, Chicalhão, Vale de Água and Vila Verde mesofossil floras (Friis et al. 2015a). Currently *C. crassitesta* is reported only from the Catefica mesofossil 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 Catefica 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-o) and fruit wall (fr). Specimen, Catefica 49-S174249 (holotype, a–f). Scale bars = 300 µm (a–c, e, f), 100 µm (d).



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  $\mu$ m (a–d), 100  $\mu$ m (e, f, h, i), 50  $\mu$ m (g).



**Text-fig. 5.** Scanning electron microscope images of the seed of *Canrightia* sp.; Catefica locality, Portugal. a) Seed in ventral view showing the slightly protruding chalaza (ch) at the apex, pointed micropyle (mi) at the base and pitted surface of the endotesta; b) Detail of endotesta surface showing larger pits in longitudinal rows and the finer pits created by crystals in the cells of the endotesta. Specimen, Catefica MM158-P0289 (a, b). Scale bars = 300  $\mu$ m (a), 100  $\mu$ m (b).

*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 *Clavatiipollenites*-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.

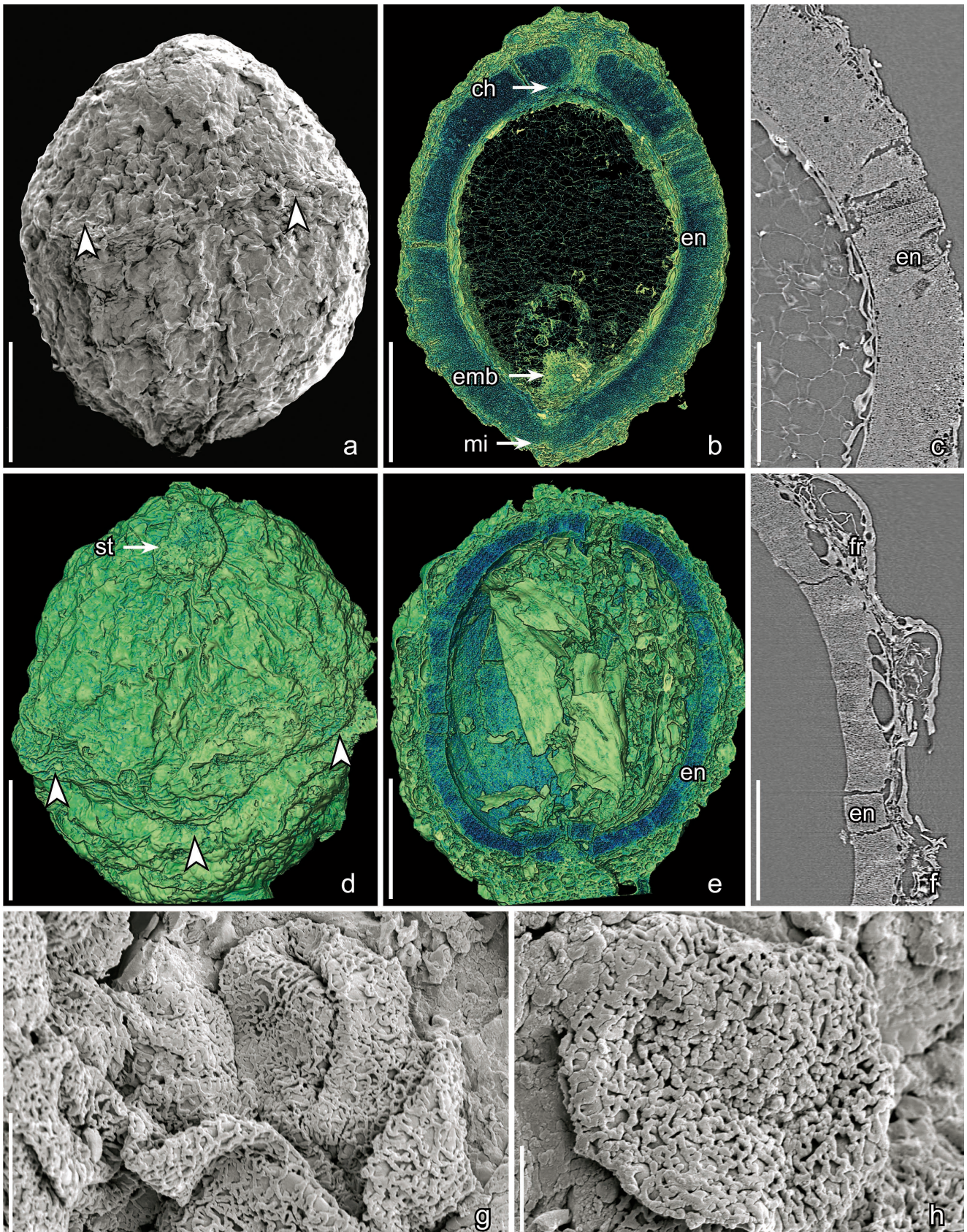
**Genus *Hedyflora* E.M.FRIIS, P.R.CRANE et  
K.R.PEDERSEN, 2019**

***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 crassitesta* (a–c, g, h) and fruit of *Canrightiopsis intermedia* (d–f); Catefica 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 Arazedo, 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.** Staminate 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 suprategmatal ornamentation composed

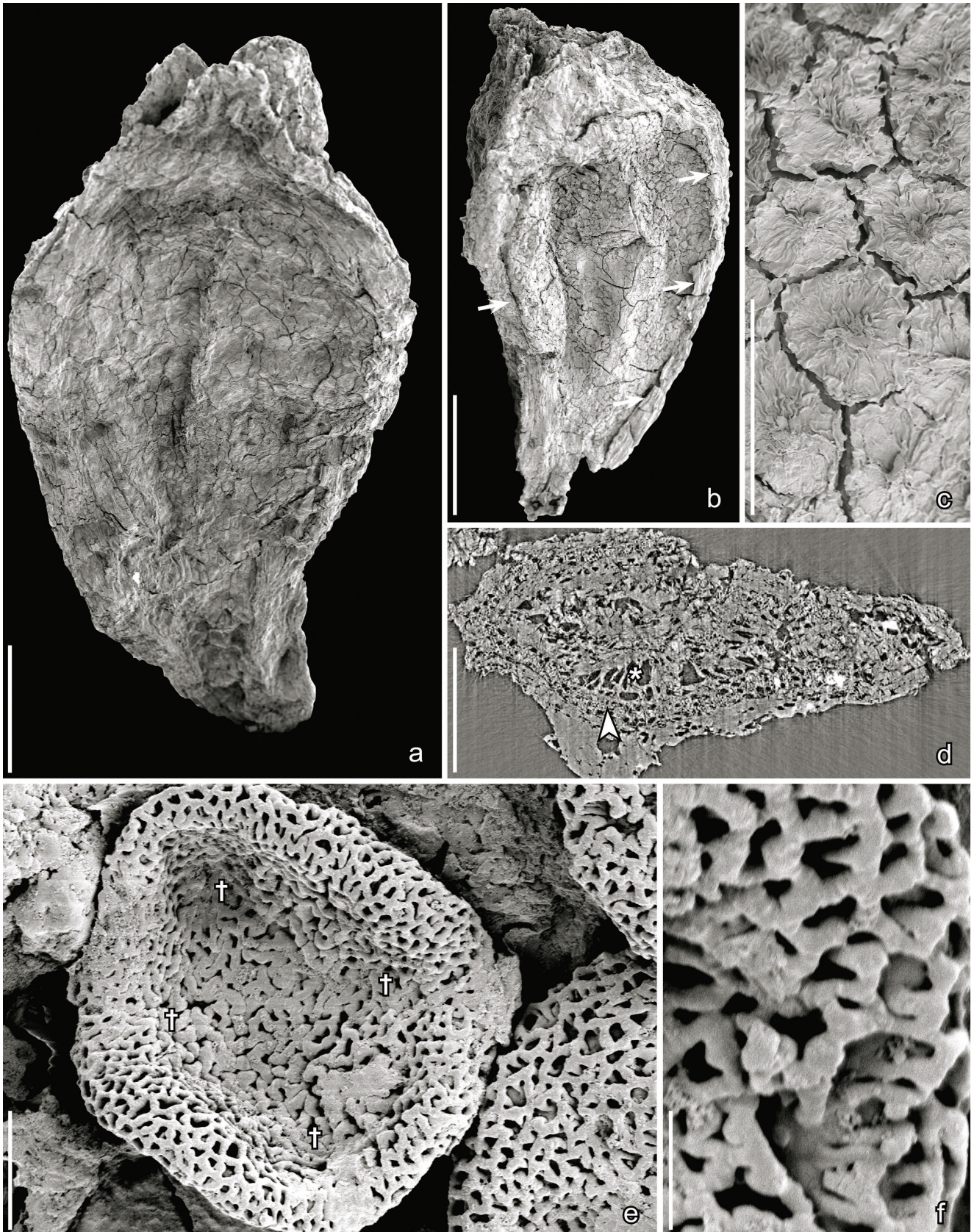
of minute verrucae aligned in two to three longitudinal rows that create poorly defined transverse ridges over the muri. Aperture margin indistinct. Aperture membrane irregularly verrucate. Orbicules spherical with fine verrucate-spiny ornamentation.

**Distinguishing features.** Among extant angiosperms, species of *Ascarina* (Chloranthaceae) are comparable to *Proencistemon* in having staminate 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 suprategmatal 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 staminate 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 staminate 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 staminate 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 tetrachotomo- 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*

longitudinal section of fruit in (d) (cut at orthoslice xz0560) showing the crystalliferous endotesta (en, dark blue) and the inner tissues of the seed; f) Longitudinal section (orthoslice xz0560) through fruit and seed showing the finely crystalliferous endotesta (en) and thin fruit wall (fr); g, h) Pollen grains from apical region of fruit showing poorly defined margin of the single colpus, reticulate tectum and muri ornamented by minute verrucae. Specimens, Catefica 343-S174311 (a), Catefica 49-S174159 (b, c), Catefica 50-S174905 (d–f), Catefica 342-S122089 (g, h). Scale bars = 300 µm (a, b, d, e), 150 µm (c, f), 6 µm (g), 3 µm (h). g, h published with permission from Grana.



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 *Hedyflora 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).

COUPER (Doyle and Robbins 1977) or treated as aff. *Clavatipollenites* (Walker and Walker 1984). Dispersed trichotomocolpate pollen grains from the Early Cretaceous (Aptian) of Patagonia described as *Jusinghipollis ticoensis* M.LLORENS et LOINAZE (Llorens and Perez Loinaze 2015) are closely similar to the in situ pollen of *Proencistemon*, but the reticulum is looser, the muri are narrower, and the ornamentation of the tectum is coarser. The type species of *Jusinghipollis* JANSON. et HILLS, *J. microreticulata* (JUHÁSZ et GÓCZÁN) JANSON. et HILLS, which is based on dispersed pollen from the Albian of Hungary (Juhász and Góczán 1985), also has a trichotomocolpate aperture, but differs from pollen of *Proencistemon* in having longer aperture arms that almost reach to the equator. The aperture margins are also more well defined than the diffuse aperture margins in *Proencistemon* pollen grains.

***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 (Catefica sample MM282; figured Text-fig. 8a, c, d).

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

**Paratypes.** S266015, S266016 (Catefica sample 49), S170393, S170394 (Catefica sample 50), S174257 (Catefica sample 150), S122086 (Catefica 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.** 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 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 Catefica 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.

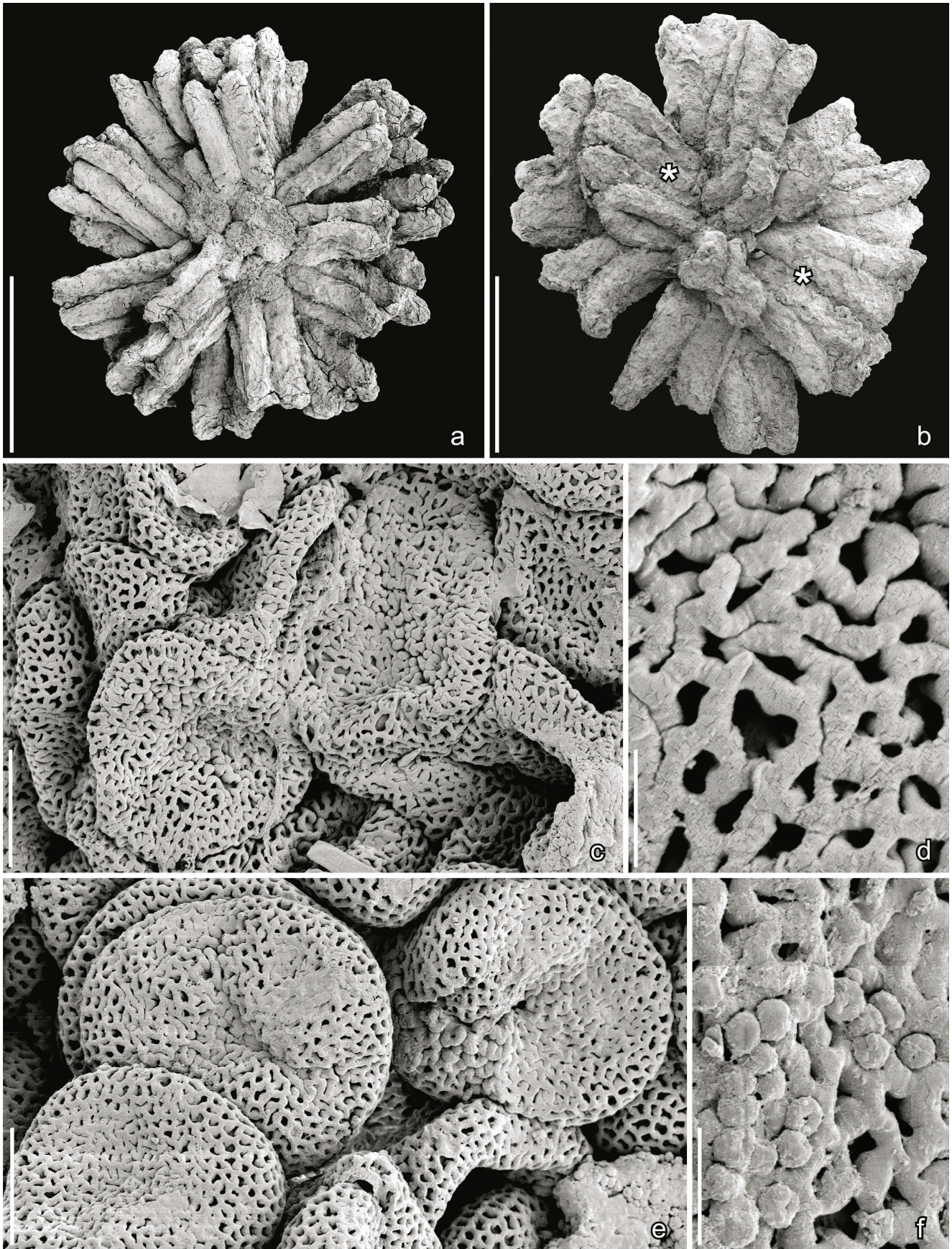
**Dimensions.** Staminate structure (measured on holotype) about 1.5 mm in diameter; stamens 0.55 mm long and 0.25 mm broad; pollen diameter 12.5–16 µm.

**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 charcoallified 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 supracteal ornamentation of minute verrucae that are aligned in two to three longitudinal rows and form poorly defined transverse ridges over the muri (Text-figs 8d, 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  $\mu$ m (a, b), 6  $\mu$ m (c, e), 1.5  $\mu$ m (d, f).



Densely crowded stamens very similar to those of *Proencistemon portugallicus*, 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 portugallicus*). 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 pollen grains are similar to those of *Proencistemon portugallicus* 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.**

Text-fig. 9h–j

**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 portugallicus*.

**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 portugallicus*, 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**

Text-fig. 10a–d

**Description and remarks.** The material comprises two stamen fragments that have a long, narrow, elongated tetrasporangiate 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**

Text-fig. 11a–e

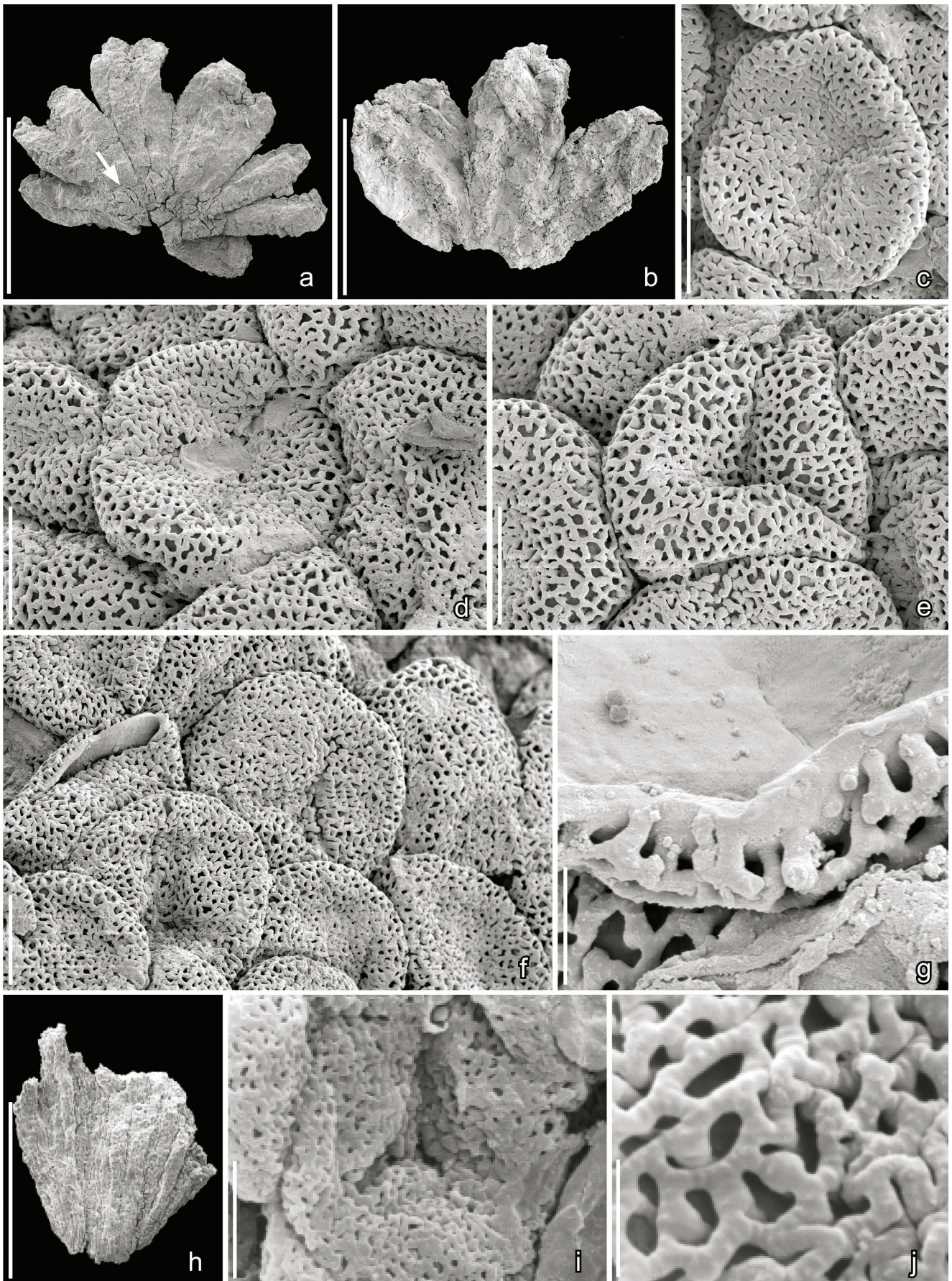
**Description and remarks.** The material comprises a single stamen that has in situ *Clavatipollenites*-type pollen. The anther is tetrasporangiate, elongate and narrow, about 1.3 mm long and 0.3 mm broad (Text-fig. 11a). Pollen is monocolpate and almost circular in equatorial outline, about 24–26 µm 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.

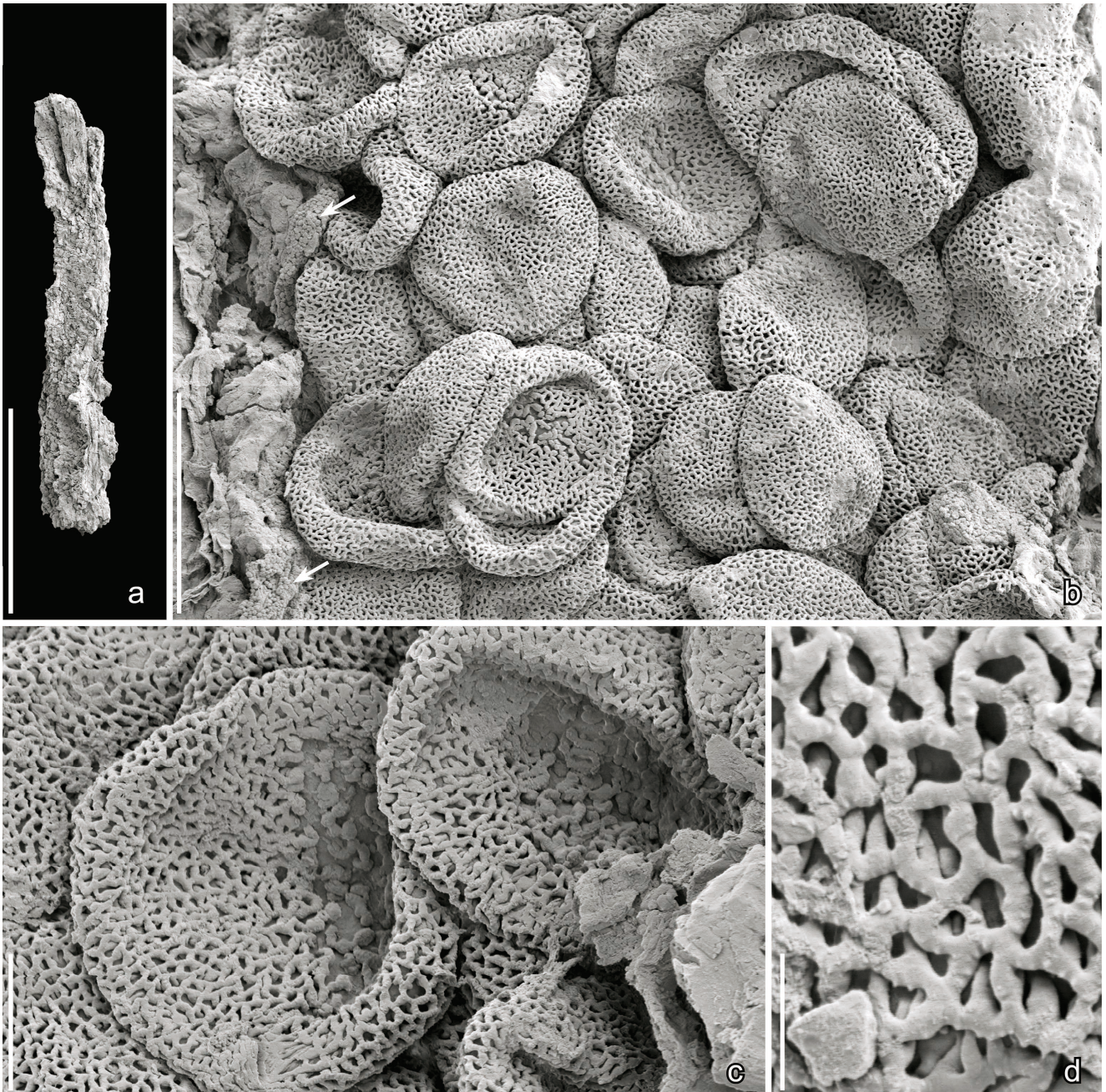
#### **Stamens with monocolpate *Clavatipollenites*-type pollen sp. 3**

Text-fig. 12a–e

**Description and remarks.** The material comprises a single stamen with an elongated, elliptical and tetrasporangiate anther (Text-fig. 12a) that has in situ



Text-fig. 9. Scanning electron microscope (SEM) images of stamens and pollen of *Proencistemon portugallicus* 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

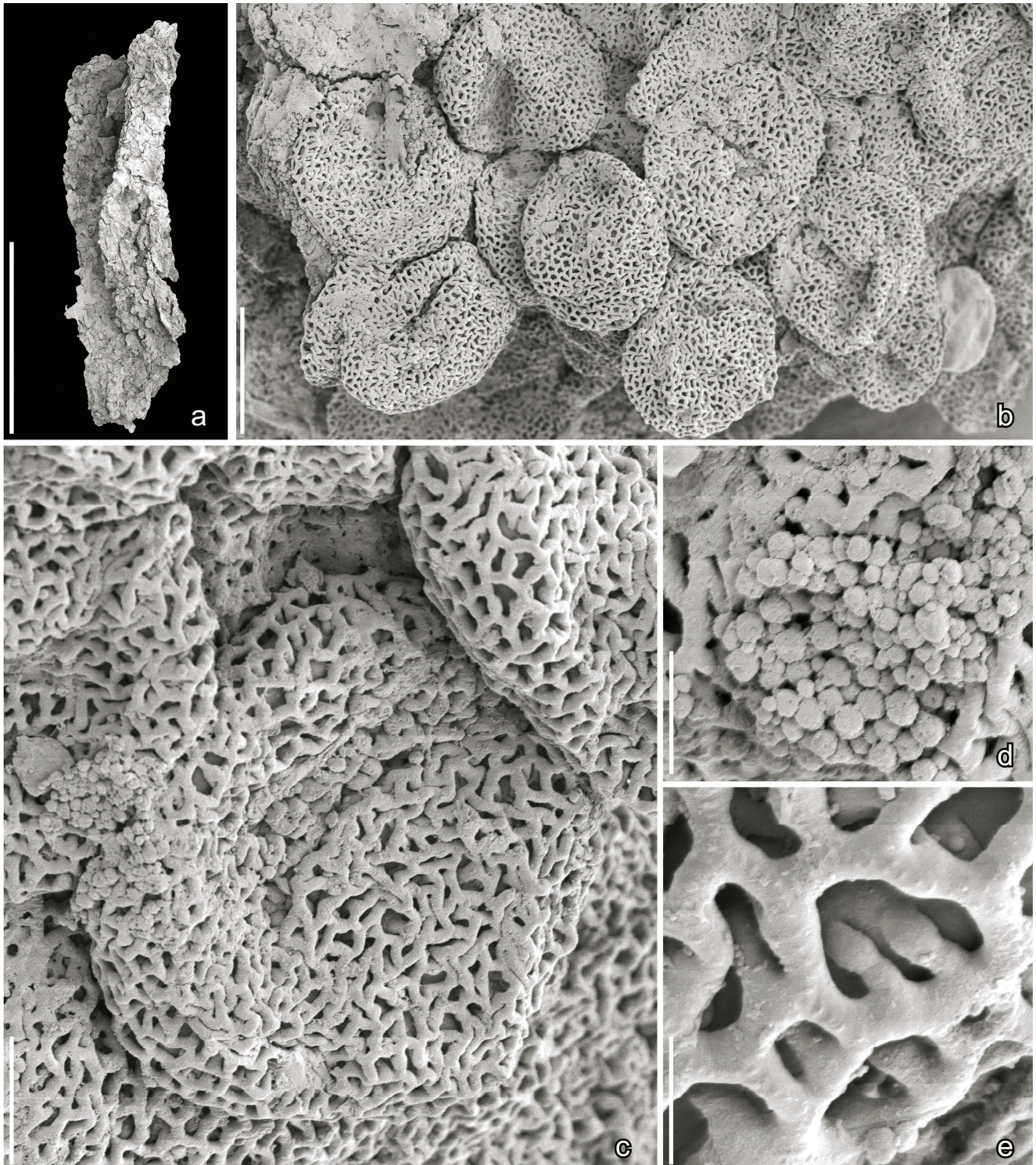


**Text-fig. 10.** Scanning electron microscope (SEM) images of isolated “Stamen fragment with *Clavatipollenites*-type pollen sp. 1”; Catefica locality, Portugal. a) Fragment of tetrasporangiate stamen with pollen in situ; b) Detail from stamen fragment showing distal and proximal surfaces of in situ pollen grains and tiny orbicules on the inner surface of the anther wall (arrows); c) Pollen grains in distal view showing short colpi with irregular margins and aperture membrane with irregular verrucae; d) Detail of pollen wall showing the semitectate-reticulate tectum and long, scattered columellae supporting the narrow muri with finely verrucate supratectal ornamentation. Specimen, Catefica 50-S170387 (a–d). Scale bars = 600  $\mu\text{m}$  (a), 20  $\mu\text{m}$  (b), 6  $\mu\text{m}$  (c), 1.5  $\mu\text{m}$  (d).

*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  $\mu\text{m}$  in diameter. The exine is

semitectate-reticulate with a homobrochate reticulum (Text-fig. 12b–e). Lumina are irregular and up to about 1.5  $\mu\text{m}$  in diameter. Muri are narrow, about 0.4  $\mu\text{m}$  wide and ornamented with verrucae or spines arranged in one to two rows. Columellae are long, about 0.7  $\mu\text{m}$ , and widely

pollen clump showing poorly defined trichotomocolpate aperture, semitectate-reticulate tectum (d–f), and fractured pollen wall with long, scattered columellae supporting narrow muri (g); h) Fragment of staminate inflorescence with narrow, almost sessile, stamens; i, j) Pollen from fragment of staminate inflorescence in (h) showing poorly defined trichotomocolpate aperture (i), semitectate-reticulate tectum (i, j) and long, scattered columellae supporting narrow muri (j). Specimens, Catefica 49-S266015 (a), Catefica 342-S122086 (b, c), Catefica 50-S170394 (d–g), Catefica 49-S107783 (h–j). Scale bars = 600  $\mu\text{m}$  (a, b, h), 6  $\mu\text{m}$  (c–f, i), 1.5  $\mu\text{m}$  (g, j).



Text-fig. 11. Scanning electron microscope (SEM) images of isolated “Stamen fragment with *Clavatipollenites*-type pollen sp. 2”; Catefica locality, Portugal. a) Fragment of tetrasporangiate stamen with pollen in situ; b) Detail from stamen fragment showing distal and proximal surfaces of in situ pollen grains; c) Pollen grain in distal view showing short colpus with irregular margin and aperture membrane covered by irregular verrucae; d) Detail of pollen wall showing tiny spherical orbicules; e) Detail of pollen wall showing the semitectate-reticulate tectum and long, scattered columellae supporting the narrow muri with finely verrucate supracteal ornamentation. Specimen, Catefica 50-S170389 (a–e). Scale bars = 600  $\mu\text{m}$  (a), 20  $\mu\text{m}$  (b), 6  $\mu\text{m}$  (c), 3  $\mu\text{m}$  (d), 1.5  $\mu\text{m}$  (e).

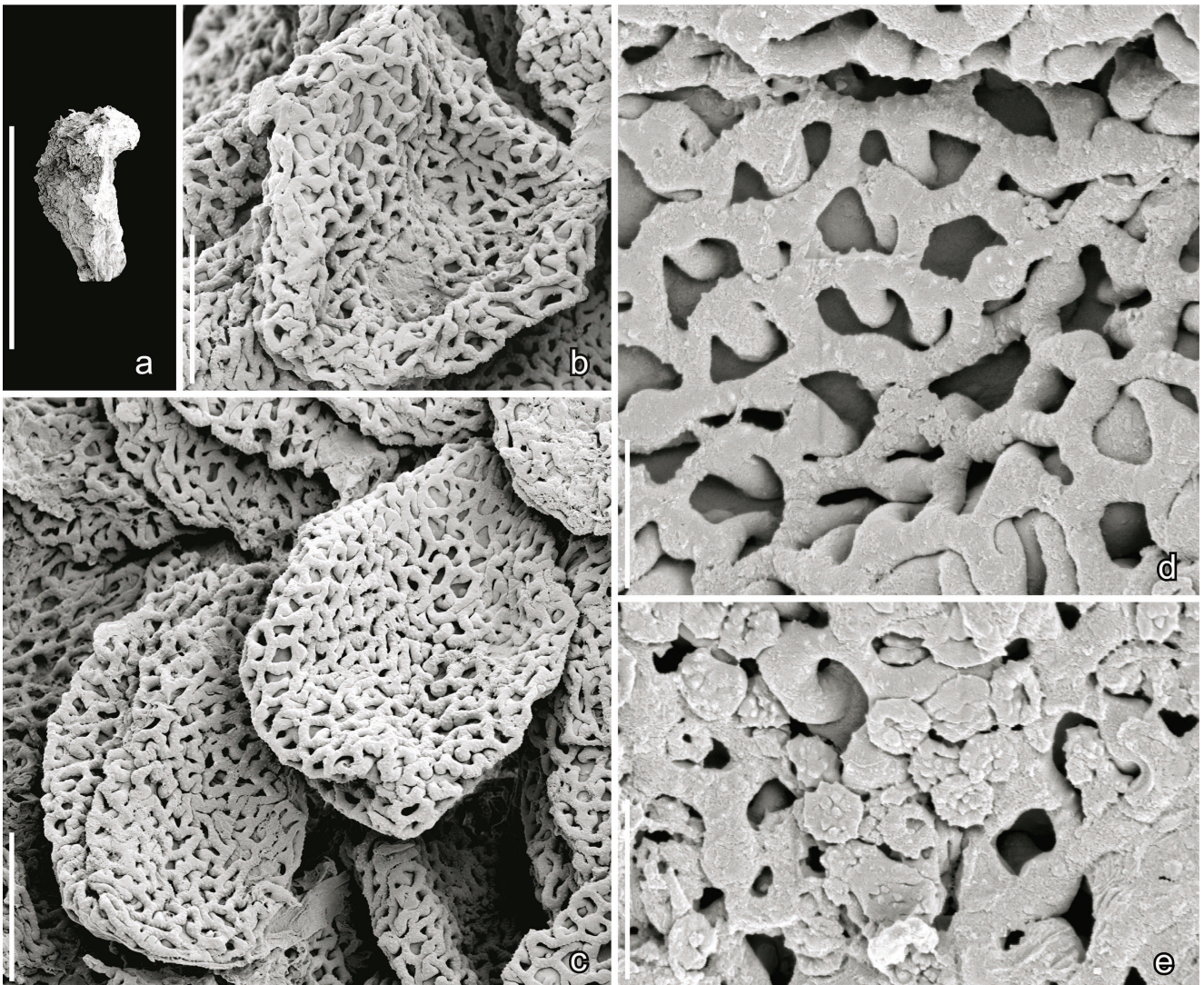
spaced (Text-fig. 12d). Orbicules on the inner surface of the anther wall and on the surface of the pollen grains are tiny, spherical and with fine spines (Text-fig. 12e).

**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*-



**Text-fig. 12.** Scanning electron microscope (SEM) images of isolated “Stamen fragment with *Clavatipollenites*-type pollen sp. 3”; Catefica locality, Portugal. a) Stamen fragment with pollen in situ; b, c) Pollen grains showing the semitectate-reticulate pollen wall and folds (c) indicating a possible monocolpate aperture; d) Detail of pollen wall showing the semitectate-reticulate tectum and long, scattered columellae supporting the narrow muri with finely verrucate supratectal ornamentation; e) Detail of pollen wall showing tiny, spherical, finely spiny orbicules. Specimen, Catefica 50-S170449 (a–e). Scale bars = 600  $\mu\text{m}$  (a), 6  $\mu\text{m}$  (b, c), 1.5  $\mu\text{m}$  (d, e).

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 monoaperturate with a poorly delimited aperture (Text-fig. 13b, c). The grains are about 14–17  $\mu\text{m}$  in diameter. The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 13b–d). Lumina are irregular, up to about 1  $\mu\text{m}$  in diameter. Muri are narrow, about 0.3  $\mu\text{m}$  wide ornamented with minute verrucae arranged in one to two rows. Columellae are long, about 0.7  $\mu\text{m}$ , and widely spaced (Text-fig. 13d). Orbicules were not observed.

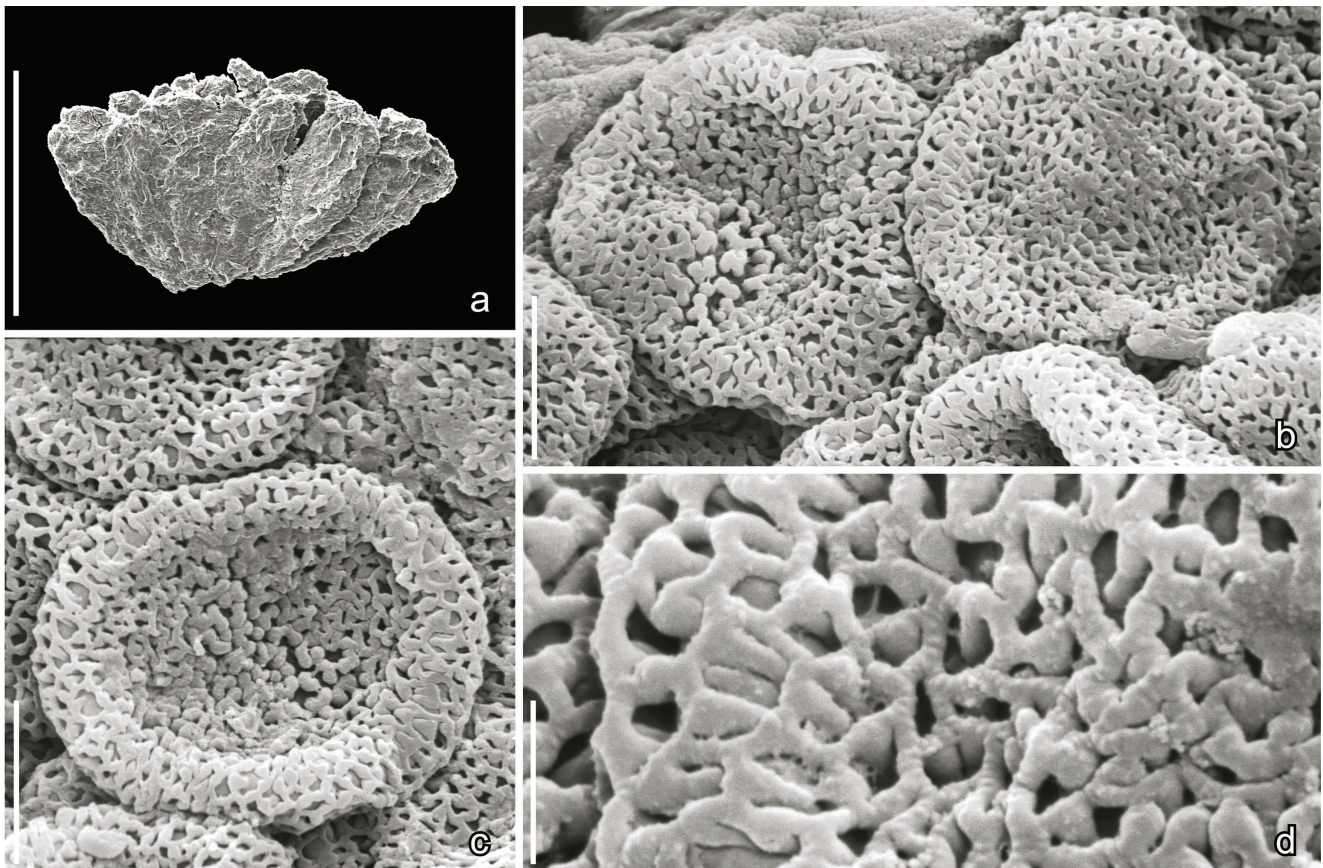
**Affinity and other occurrences.** See comments on “Stamens with monocolpate *Clavatipollenites*-type pollen sp. 1” above. The pollen is closely similar to dispersed fossil grains assigned to the extinct genus *Clavatipollenites*, as well as pollen of extant *Ascarina*. The

stamens are similar to those in the staminate inflorescences of *Proencistemon portugallicus* and *Proencistemon* sp. from Catefica (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



**Text-fig. 13.** Scanning electron microscope (SEM) images of “Staminate inflorescence fragment with *Clavatipollenites*-type pollen sp. 4”; Catefica locality, Portugal. a) Fragment of stamen whorl from staminate inflorescence showing several closely packed, almost sessile stamens that lack a well-developed filament; b, c) Distal and proximal views of pollen grains showing poorly defined aperture with verrucate aperture membrane; d) Detail of pollen wall showing the semitectate-reticulate tectum and long, scattered columellae supporting the narrow muri with finely verrucate supracteal ornamentation. Specimen, Catefica 49-S107782 (a–d). Scale bars = 600  $\mu\text{m}$  (a), 6  $\mu\text{m}$  (b, c), 1.5  $\mu\text{m}$  (d).

and about 20–23  $\mu\text{m}$  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  $\mu\text{m}$  long that become thinner toward the base (Text-fig. 14e). Lumina are irregular in shape, up to about 1.5  $\mu\text{m}$  in diameter. Muri are about 0.5  $\mu\text{m}$  wide with a rounded profile and are ornamented by minute verrucae aligned in two rows along the margins of the muri (Text-fig. 14e).

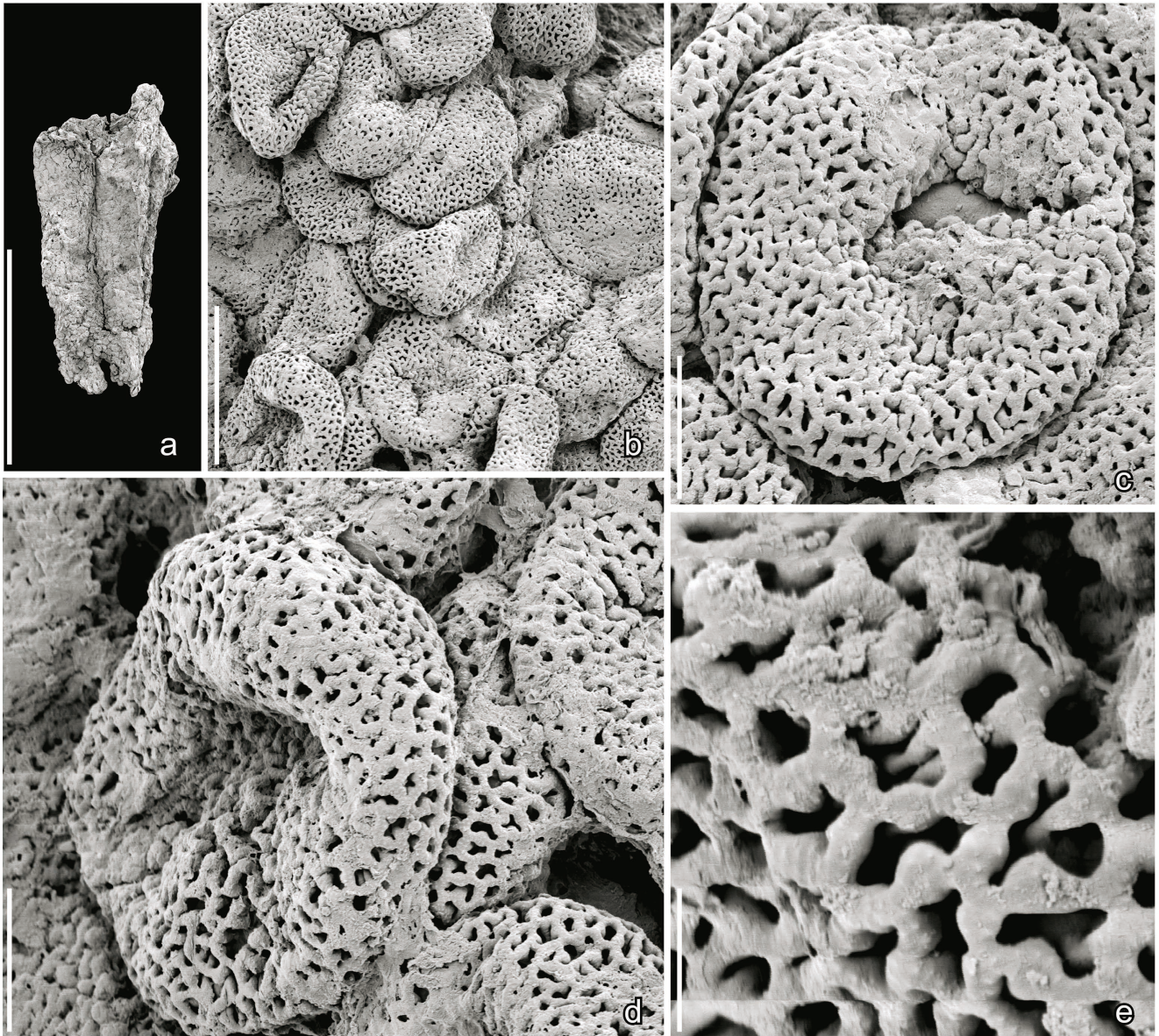
**Affinity and other occurrences.** The in situ pollen grains are closely similar in size, shape and aperture configuration to pollen found attached to the surface of specimens of *Hedyflora crystallifera* from Catefica (above), and also specimens from Buarcos, the type locality for *Hedyflora* (Friis 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  $\mu\text{m}$  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–



**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 columellae supporting the narrow muri; note two irregular rows of minute verrucae ornamenting surface of muri. Specimen, Catefica 50-S170385 (a–e). Scale bars = 600  $\mu\text{m}$  (a), 20  $\mu\text{m}$  (b), 6  $\mu\text{m}$  (c, d), 1.5  $\mu\text{m}$  (e).

d). The exine is semitectate-reticulate, columellate, with short, densely spaced columellae, about 0.8  $\mu\text{m}$  long that diminish in thickness towards the thick foot layer (Text-fig. 15b–e). Lumina are irregular in shape, up to about 1.2  $\mu\text{m}$  in diameter. Muri are about 0.4  $\mu\text{m}$  wide with a rounded profile and are ornamented by minute verrucae aligned in two longitudinal rows that form poorly defined transverse ridges.

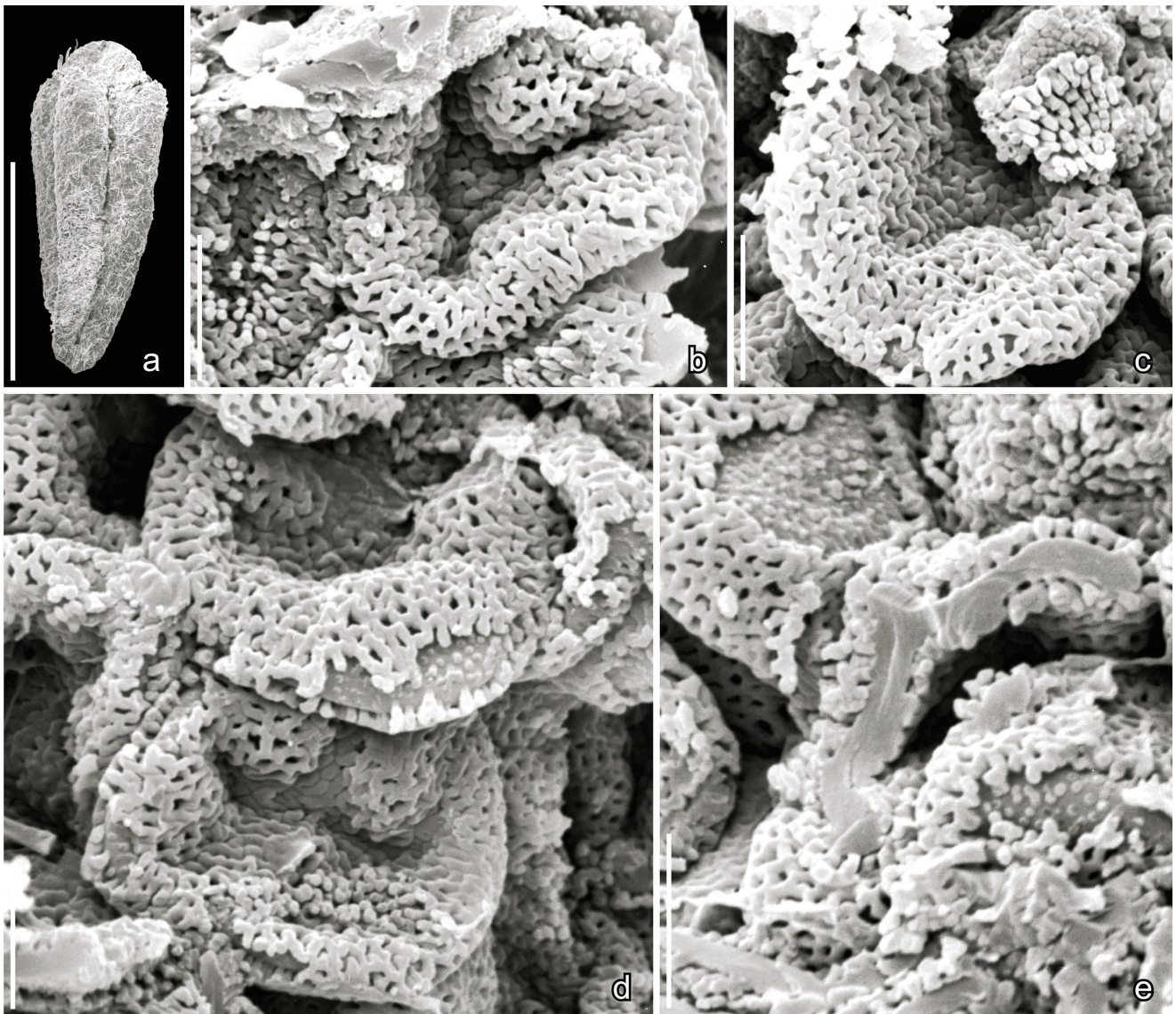
**Affinity and other occurrences.** The in situ pollen grains of *Asteropollis*-type pollen sp. 2 differ from the pollen associated with *Hedyflora crystallifera*, and also pollen of *Asteropollis*-type pollen sp. 1 (above), in their smaller size and in having a mainly pentachotomocolpate aperture configuration 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**

Text-fig. 16a–c

**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. 15.** Scanning electron microscope (SEM) images of stamen with “*Asteropollis*-type pollen sp. 2”; Catefica locality, Portugal. a) Stamen with pollen in situ showing the dome-shaped extension of the connective with hairs; b–d) Pollen in situ in stamen in (a) showing poorly defined pentachotomocolpate (b, d) and possibly tetrachotomocolpate (c) apertures and semitectate-reticulate tectum; e) Detail of broken pollen grains showing the loosely attached reticulum, long scattered columellae and thick foot layer. Specimen, Catefica 49-S101209 (a–e). Scale bars = 600  $\mu\text{m}$  (a), 6  $\mu\text{m}$  (b–e).

monoaperturate. Pollen is circular in equatorial view, about 17–20  $\mu\text{m}$  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  $\mu\text{m}$  in diameter. Muri are narrow, about 0.3  $\mu\text{m}$  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  $\mu\text{m}$ , 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

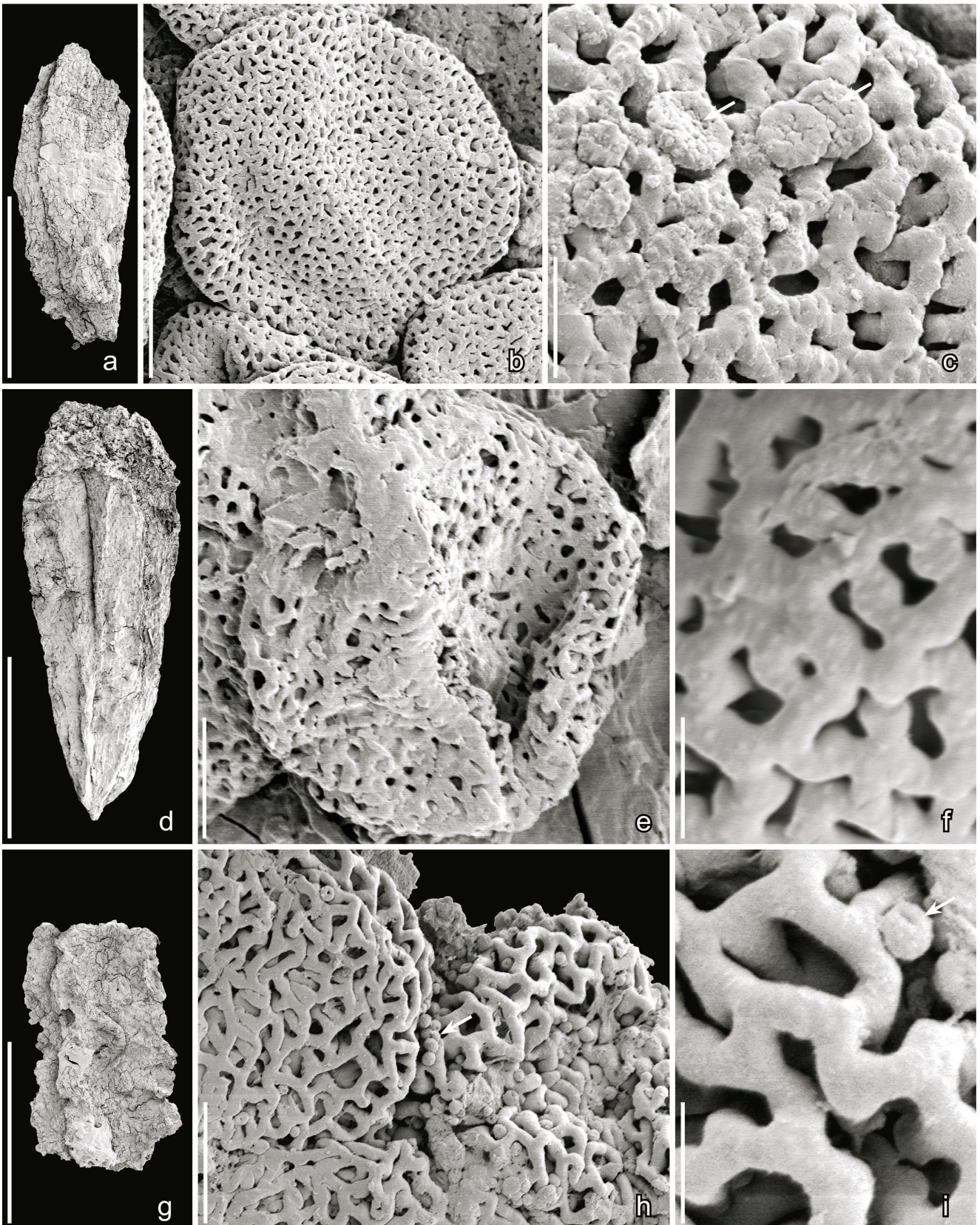
chloranthoid pollen recorded from other mesofossil floras from Portugal, in the line of fine perforations on top of the muri. The distinctiveness of this feature would support the recognition of a separate species, but the lack of information on the aperture configuration precludes closer comparison 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 supracteal 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 columellae and tiny scattered orbicules (arrow). Specimens, Catefica 50-S170395 (a–c), Catefica 49-S172561 (d–f), Catefica 50-S170390 (g–i). Scale bars = 600  $\mu\text{m}$  (a, d, g), 6  $\mu\text{m}$  (b, e, h), 1.5  $\mu\text{m}$  (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  $\mu\text{m}$  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  $\mu\text{m}$  in diameter. Muri are narrow, about 0.5  $\mu\text{m}$  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**

Text-fig. 16g–i

**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 tetrasporangiate. 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  $\mu\text{m}$  in diameter. The exine is semitectate-reticulate with a homobrochate reticulum (Text-fig. 16h, i). Lumina are irregular and up to about 4  $\mu\text{m}$  in diameter. Muri are narrow, about 0.8  $\mu\text{m}$  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 supracteal 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 JUSS. ex BERCHT. et J.PRESL, 1820**

**Genus *Serialis* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN, 2019**

***Serialis communis* E.M.FRIIS, P.R.CRANE et**

**K.R.PEDERSEN, 2019**

Text-fig. 17a

**Description and remarks.** The material includes several fruits with three 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).

**Affinity and other occurrences.** Fruits and seeds assigned to the extinct genus *Serialis* are among the most diverse fossils in Early Cretaceous mesofossil floras from Portugal and nine different species have been recognized (Friis et al. 2019c). Phylogenetic analysis indicates a close relationship of *Serialis* to Magnoliales, but the genus cannot be placed confidently in any extant taxon within the order. The type material of *Serialis communis* is from the Famalicão mesofossil flora where *S. communis* is the most abundant species and more than 2,230 specimens are known. *Serialis communis* is also reported from the Araze de and Vale de Água localities (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 crassitesta* E.M.FRIIS, P.R.CRANE et**

**K.R.PEDERSEN, 2019**

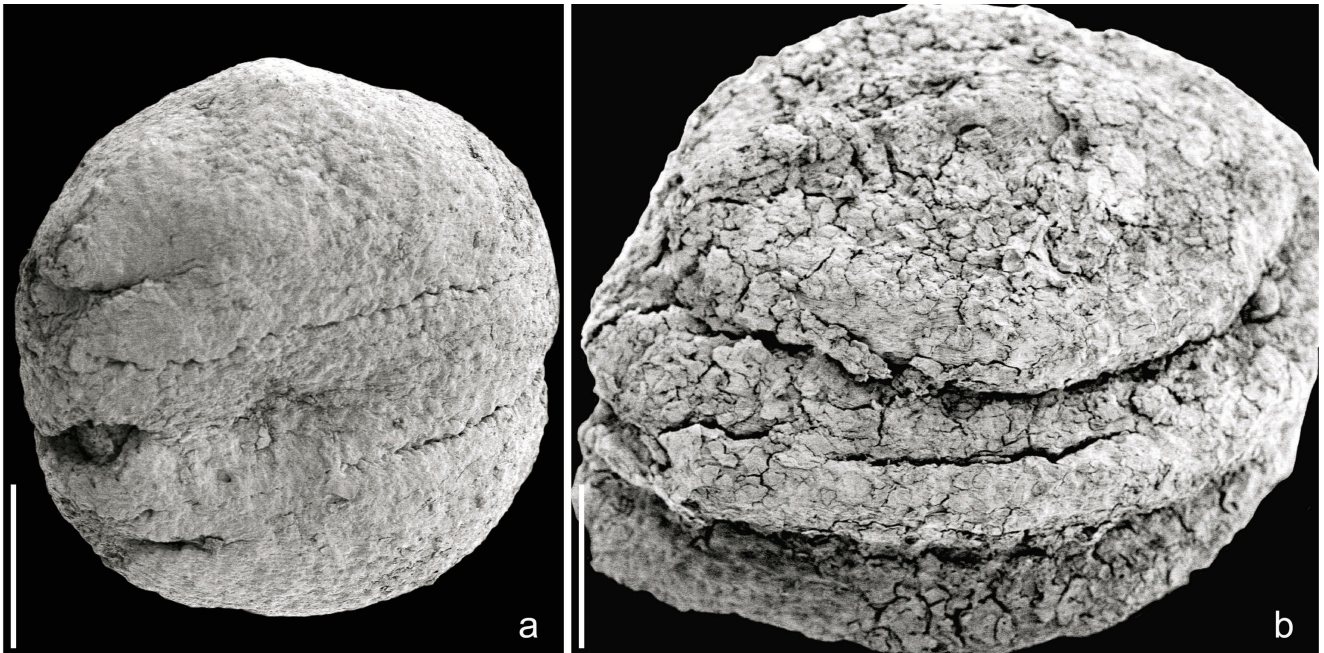
Text-fig. 17b

**Description and remarks.** The material includes several fruits with permanently adhering seeds that are assignable to *Serialis crassitesta* (Text-fig. 17b).

**Affinity and other occurrences.** 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 375 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 present in the Chicalhão (“Fruits with co-adhering seeds in row type 2”; Mendes et al. 2014) and Nossa Senhora da Luz mesofossil floras (“Seeds in row”; Mendes and Friis 2018).

***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).



**Text-fig. 17.** Scanning electron microscope (SEM) images of fruits of *Serialis communis* (a) and *Serialis crassitesta* (b); Catefica locality, Portugal. a) Oblique lateral view of fruit showing three laterally coherent seeds from which the fruit wall has been almost completely lost showing the prominent micropylar region; b) Oblique lateral view of fruit containing three or four laterally coherent seeds with their micropylar regions oriented to the left. Specimens, Catefica MM92-P0167 (a), Catefica MM92-P0169 (b). Scale bars = 300  $\mu\text{m}$  (a, b).

**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 charcoaled 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 charcoaled specimens (Text-fig. 18a, b). The pollen is circular in polar view, about 12  $\mu\text{m}$  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 unilocular, semi-inferior ovary (Text-fig. 18c, d). The pollen is 8–12  $\mu\text{m}$  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 preservable 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 bitegmic with an outer integument (testa) consisting of an outer layer (exotesta) of thin-walled cells and an inner layer (endotesta) of crystalliferous cells. The exotesta is typically abraded and preserved only in patches along the margins of the seed where the abraded palisade-shaped cells form an irregular border around the rest of the seed (Text-fig. 19a). The endotesta 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).

**Family indet.**

**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).



**Text-fig. 18.** Scanning electron microscope (SEM) images of fragmentary flower of *Catanthus dolichostemon* (a, b) and flower of *Saportanthus parvus* (c, d); Catefica locality, Portugal. a, b) Fragment of flower bud showing bulky tepals (te) and fleshy stamens (st) in ventral (a) and lateral (b) views; note the long stamen base and small anther with extrorse anther dehiscence (arrows); c, d) Flower in lateral (c) and oblique apical (d) views showing inferior ovary and eight bulky tepals almost completely enclosing the stamens and styles. Specimens, Catefica MM92-P0159 (a, b), Catefica MM285-P0331 (c, d). Scale bars = 300  $\mu$ m (a–d).

The pollen grains are oblate, circular to elliptical in equatorial outline, about 17  $\mu$ m 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 *Gozania* type has been found on the stigma and surface of *Appomattoxia* fruits in the Torres Vedras mesofossil flora and also on fruits of *Appofructus* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN from Torres Vedras (Friis et al. 2019a). *Gozania*-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 *Appofructus* are both thought to be related to Piperales (Friis et al. 1995, 2019a).

*Goczania rugosa* was first described from the Torres Vedras mesofossil flora (Friis 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 suprategal 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.FRIIS, 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.FRIIS, P.R.CRANE et K.R.PEDERSEN, *A. virginianensis* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN) and from Portugal (*Anacostia portugallica* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN, *Anacostia teixeirae* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN) (Friis et al. 1997). The genus is characterized by its one-seed fruits and exotestal 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 (Friis 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 Buarcos, Famalicão and Vale de Água mesofossil floras where fruits and seeds of *Anacostia* are abundant.

**Genus *Choffaticarpus* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN, 2019**

***Choffaticarpus compactus* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN, 2019**

Text-fig. 19d, e

**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 short 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 SRXTM analyses.

**Affinity and other occurrences.** *Choffaticarpus compactus* was formally described from the Torres Vedras mesofossil flora (Friis et al. 2019a) and compared to pistillate structures of extant *Kadsura* KAEMPF. 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 Buarcos 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.FRIIS, P.R.CRANE, K.R.PEDERSEN, M.M.MENDES et J.KVAČEK gen. nov.**

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

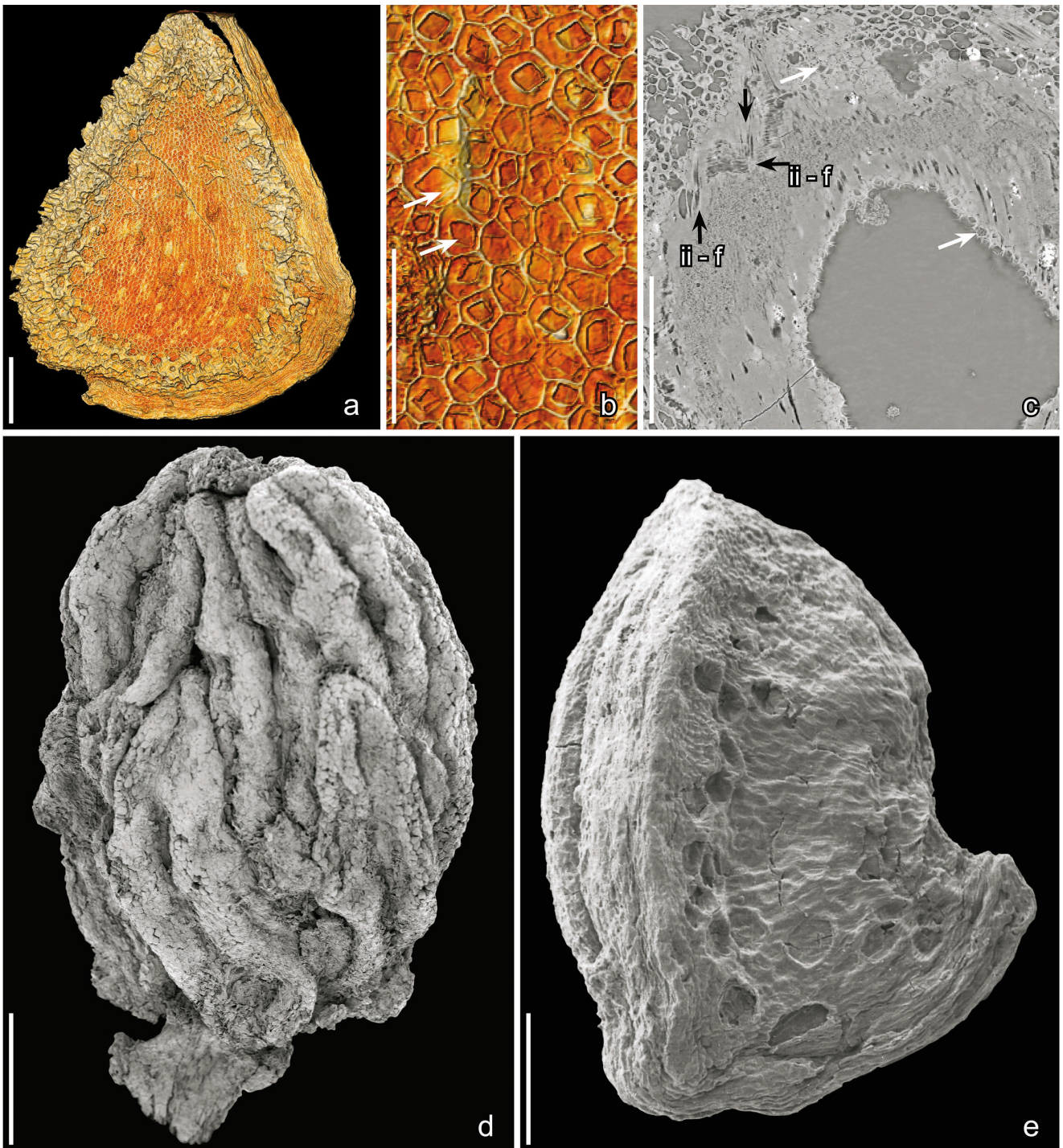
**Plant Fossil Names Registry Number.** PFN0002790 (for new genus).

**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.

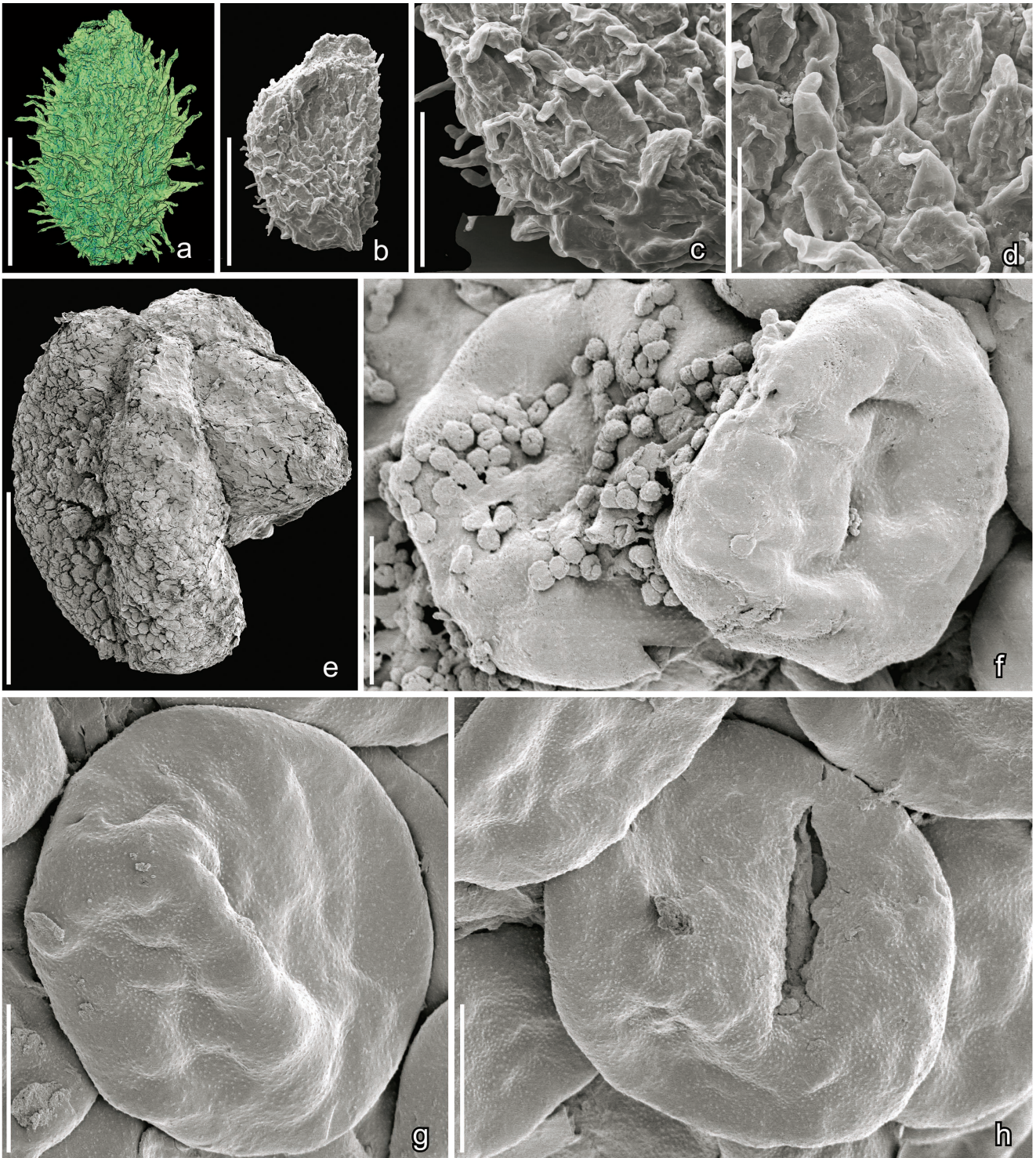
Interpreting the floral structure is not straightforward. One possibility is that the carpel-bearing axis of *Ibericarpus cuneiformis* is a simple, unbranched inflorescence bearing numerous ebracteate pistillate flowers, each consisting of



**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  $\mu\text{m}$  (a, c–e), 100  $\mu\text{m}$  (b).

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 ascidiate 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. 20.** Synchrotron radiation X-ray tomographic microscopy (SRXTM, a) and scanning electron microscope (SEM, b–h) images of fruits of *Appomattoxia* sp. (a–d) and anther and pollen of *Goczania rugosa* (e–h); Catefica locality, Portugal. a) Surface rendering of fruit in lateral view showing densely spaced hairs, some with delicate coiled tips; b) Fruit in lateral view showing short, densely spaced hairs and apical stigmatic region; c, d) Detail of fruit surface and hairs from fruit in (b); e) Fragmentary anther showing four pollen sacs; f) Proximal view of pollen grains from an abraded anther showing microechinate surface of pollen wall and clusters of small, spiny orbicules; g, h) Proximal (g) and distal (h) views of pollen grains from an isolated pollen sac, showing short colpus (h), tectate pollen wall and microechinate surface ornamentation. Specimens, Catefica 49-S174913 (a), Catefica 49-S107794 (b–d), Catefica 50-S170391 (e), Catefica 49-S170138 (f), Catefica 49-S170143 (g, h). Scale bars = 300  $\mu\text{m}$  (a, b, e), 100  $\mu\text{m}$  (c), 50  $\mu\text{m}$  (d), 6  $\mu\text{m}$  (f–h).

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 crystalliferous 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*. *Atlantocarpus* has a very long receptacle and apparently ascidiate carpels that are uniovulate and 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.KVAČEK sp. nov.**

Text-figs 21–23

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

**Plant Fossil Names Registry Number.** PFN002791 (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.** Carpel bearing axis up to about 1.7 mm long and 1.1 mm in diameter; individual carpels up to 1.05 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 to circular 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 DOERENK. (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 Nymphaeales (Nymphaeaceae), Magnoliales (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, Brassicales) (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 psilate-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 *Guatteria* 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-aperture 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 extrorse, 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 magnoliids, 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.

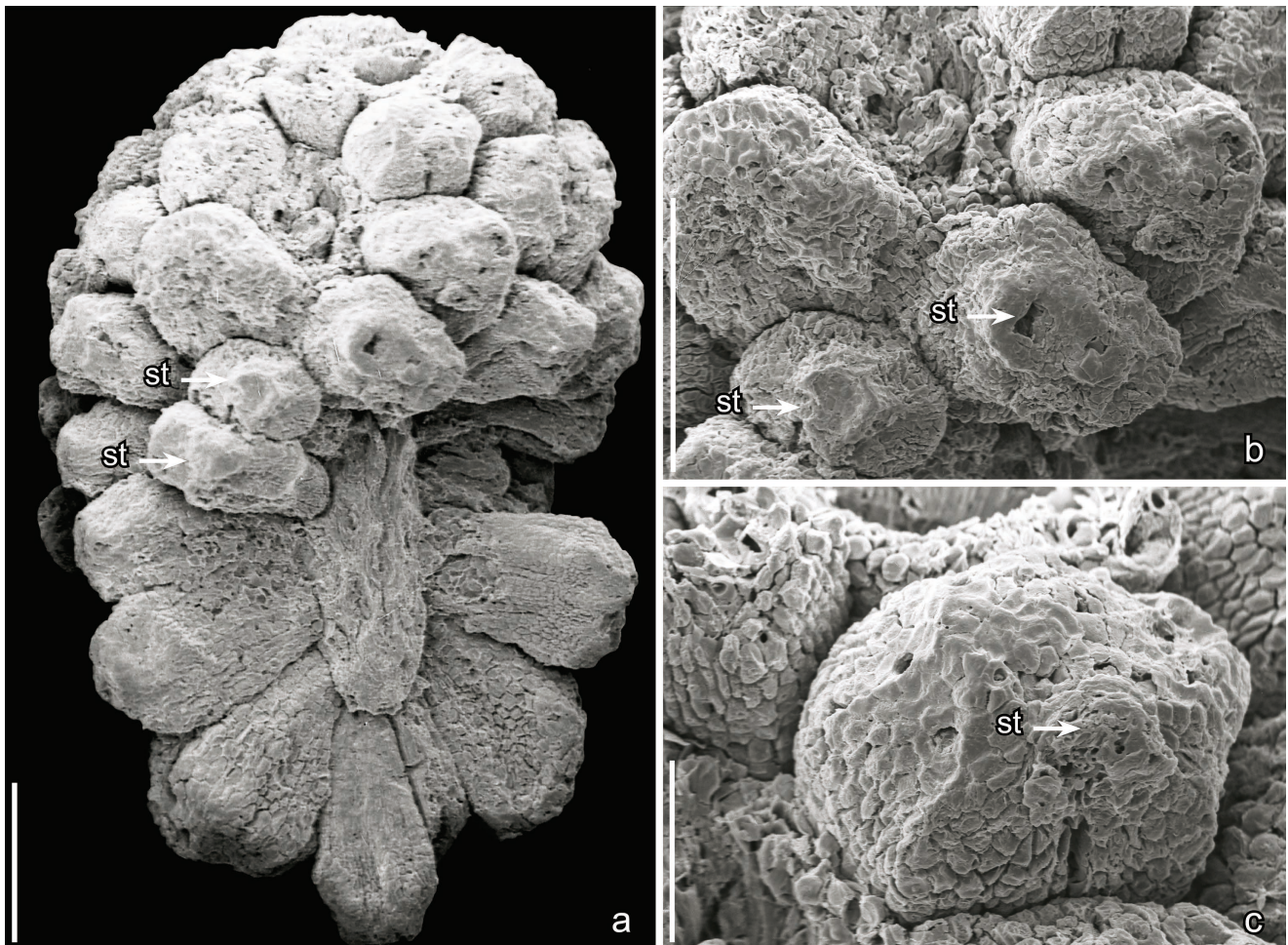
Plant Fossil Names Registry Number. PFN0002792 (for new genus).

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. Staminal 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  $\mu\text{m}$ , 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 infratectal 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 Magnoliales, 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.



Text-fig. 21. Scanning electron microscope (SEM) images of *Ibericarpus cuneiformis* gen. et sp. nov.; Catefica locality, Portugal. a) Fruiting structure in lateral view showing numerous small, helically arranged wedge-shaped fruitlets each with a slightly differentiated apical stigmatic region (st); no bracts or scars from bracts, perianth or stamens were observed associated with the entire structure or with individual carpels; b) Apical portions of fruitlets showing differentiation of the stigmatic region (st); c) Detail of apical portion of fruitlet showing slightly raised stigmatic region (st) and possible ventral suture. Specimen, Catefica 49-S115851 (holotype, a–c). Scale bars = 300  $\mu$ m (a, b), 100  $\mu$ m (c).

*Elasmostemon paisii* E.M.FRIIS, 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.

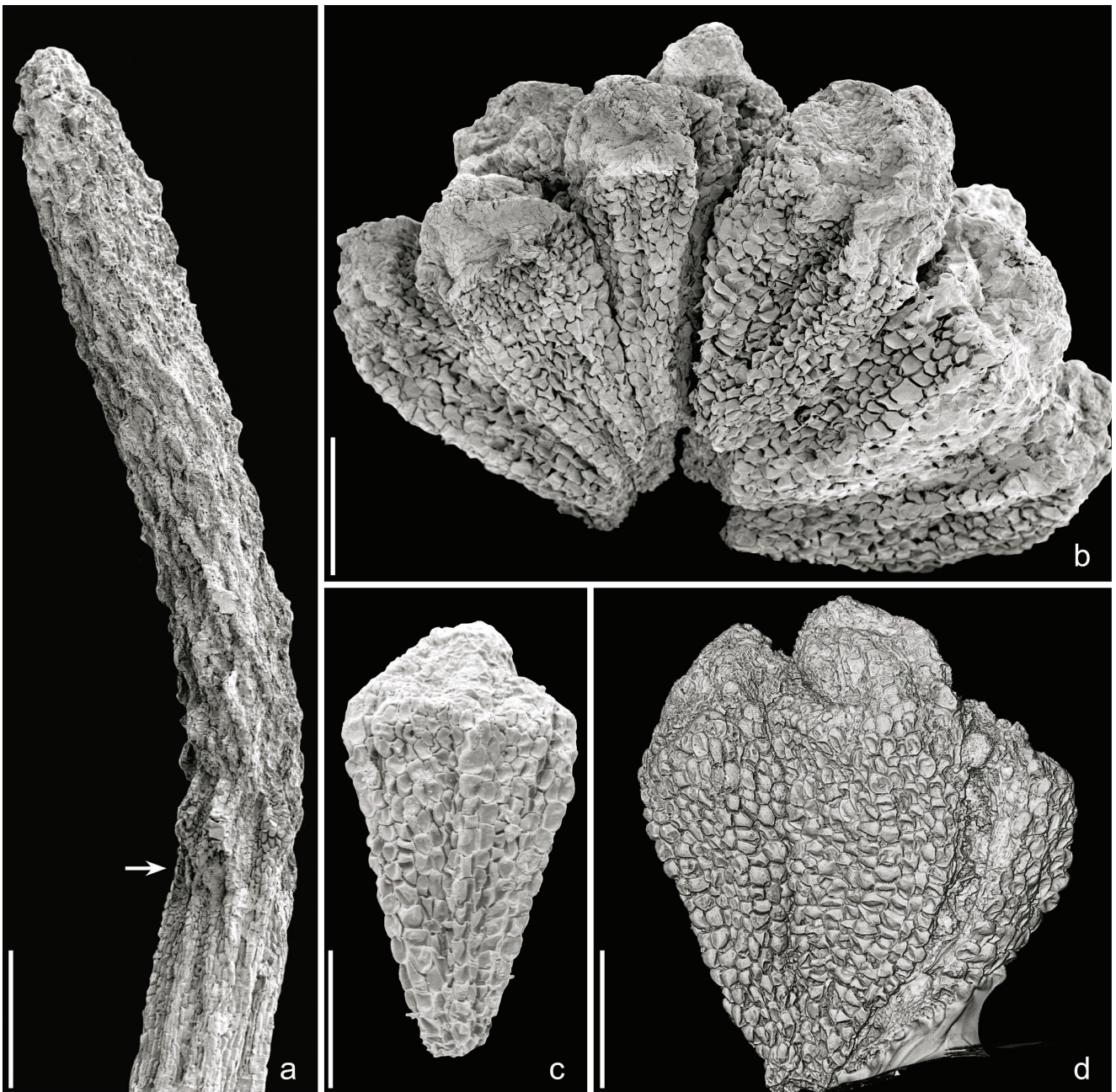
Type stratum and age. Almagem Formation, Early Cretaceous (Aptian–early Albian).

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

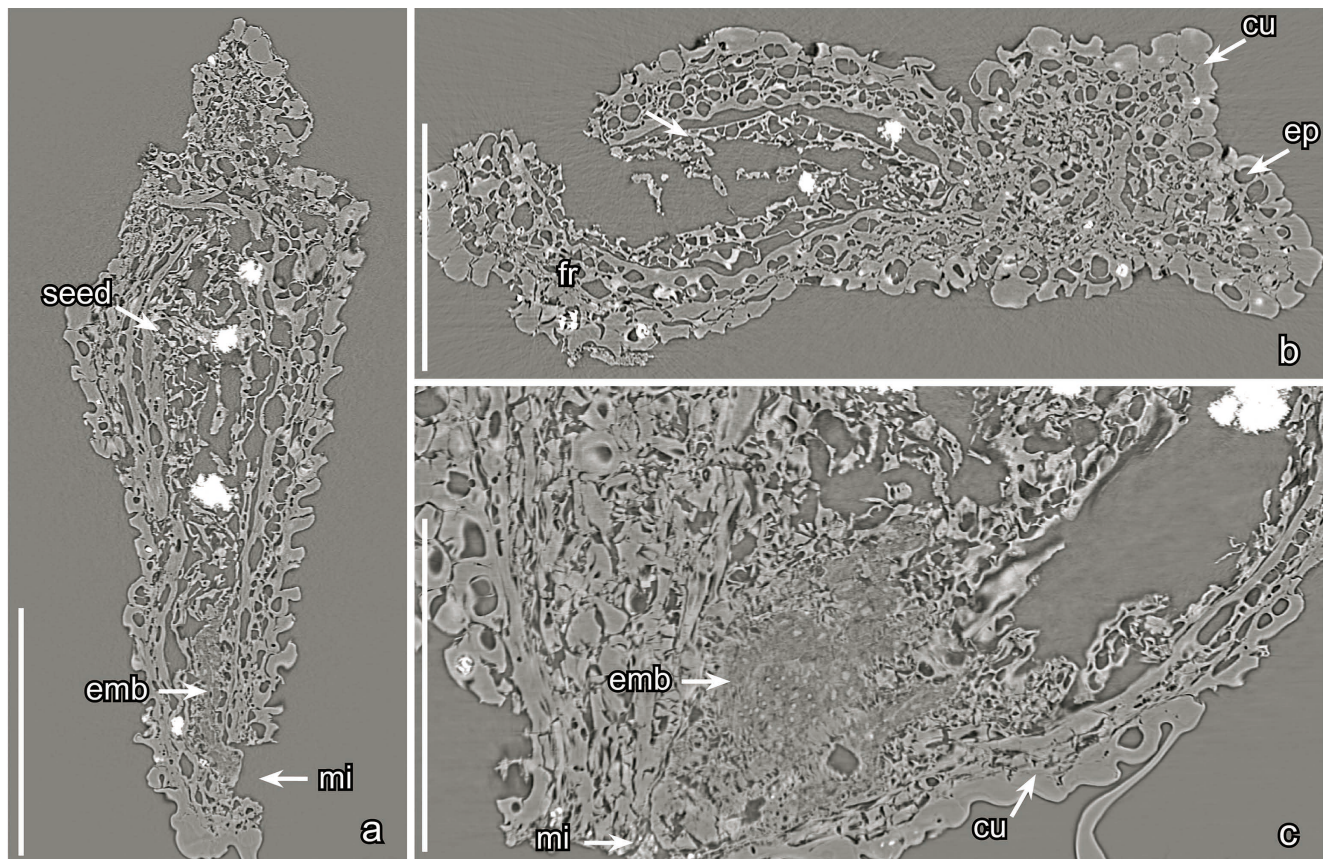


**Text-fig. 22.** Scanning electron microscope (SEM, a–c) and synchrotron radiation X-ray tomographic microscopy (SRXTM, d) images of *Ibericarpus cuneiformis* gen. et sp. nov.; Catefica locality, Portugal. a) Fruiting axis bearing an elongated receptacle with numerous diamond-shaped scars from detached fruitlets; note the absence of scars from bracts, tepals or stamens at the transition to the fruitlet scars and the stalk (arrow); b) Group of ten fruitlets detached from fruiting axis in (a) showing apical stigmatic region and distinctive bulging isodiametric epidermal cells; c) Detached fruitlet showing apical stigmatic region; d) Volume rendering of three adhering fruits showing apical stigmatic region and distinctive bulging isodiametric epidermal cells. Specimens, Catefica MM75-P0477 (a, b), Catefica 49-S115852 (c), Catefica 50-S174907 (d). Scale bars = 300  $\mu\text{m}$  (a–d).

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



**Text-fig. 23.** Synchrotron radiation X-ray tomographic microscopy (SRXTM) images of *Ibericarpus cuneiformis* gen. et sp. nov.; Catefica locality, Portugal. **a)** Longitudinal section (orthoslice yz0827) showing fruitlet with apical stigmatic region and a single seed enclosed within the fruitlet wall that has a thick epidermal cuticle; note the tiny embryo (emb) internal to the micropyle (mi) and oriented toward the base of the fruitlet; **b)** Transverse section through apical part of two fruitlets (orthoslice xy0810) showing the fruitlet wall (fr) composed of small thin-walled cells covered by an epidermis of isodiametric cells (ep) with a thick outer cuticle (cu); **c)** Longitudinal section (orthoslice xz0370) through basal part of fruitlet perpendicular to section in (a) showing the micropyle (mi), embryo (emb) composed of tiny cells, and the thick cuticle (cu) covering the bulging cells of the fruitlet epidermis. Specimen, Catefica 50-S174907 (a–c). Scale bars = 300 µm (a–c).

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 monoaperturate, semitectate-reticulate-foveolate pollen in situ (Text-fig. 26f, g). The stamen is broad and elongate. The anther is basifixed and there is no trace of a filament indicating that the anther may have been sessile (Text-fig. 26d). The anther is tetrasporangiate, 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 fragments assigned above to *Elasmostemon paisii*, especially in the position and orientation of the pollen sacs and the presence of probable ethereal oil cells. 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.KVAČEK gen. nov.**

**Type.** *Valvidistemon globiferus* E.M.FRIIS, P.R.CRANE, K.R.PEDERSEN, M.M.MENDES et J.KVAČEK 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 valvate 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.KVAČEK sp. nov.**  
Text-fig. 27a–d

**Holotype.** S107779 (Catefica 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).

**Etymology.** From Latin in Greek combinations *globifer*, with spherical organ.

**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 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 basifixed 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.FRIIS, P.R.CRANE,  
K.R.PEDERSEN, M.M.MENDES et J.KVAČEK gen. nov.**

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

Plant Fossil Names Registry Number.  
PFN0002796 (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 early diverging angiosperms lineages. Similar prominent apical projections are characteristic of the stamens of many extant Annonaceae (e.g., Endress and Hufford 1989, Van Heusden 1992), but stamens in Annonaceae are always free from each other. The trifid form of the staminal structure is more suggestive of the tripartite androecium of extant *Chloranthus* (Endress 1987) and of the Late Cretaceous *Chloranthistemon* P.R.CRANE, E.M.FRIIS et K.R.PEDERSEN (Crane et al. 1989, Eklund et al. 1997). Both have two lateral and one median stamen typically borne on a common stalk and with the thecae positioned dorsally. However, *Chloranthus* and *Chloranthistemon* have a fully developed, tetrasporangiate median stamen and two bisporangiate lateral stamens, which is the reverse of the situation in *Endressistemon* in which the median axis-like structure appears to lack pollen sacs. The extinct chloranthoid *Canrightiopsis* also has an androecium consisting of three dorsally aligned stamens, but in *Canrightiopsis* the stamen bases are not united.

In the context of the androecia of these living and fossil chloranthoids it is possible that the median structure in *Endressistemon* is a reduced stamen or that the thecae have been torn away during fossilization. Alternatively, the median axis-like structure with its apical projection may be a bract, and the apical projections associated with the lateral stamens may also be derived from a bract fused to the stamens. This interpretation is supported by the tough,

leaf-like nature of the apical projection, the axis-like form of the median structure, and the extension of three separate vascular bundles from the common base into the apical projections, which would be unusual in a typical angiosperm stamen. 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 *Archaeofructus* G.SUN, DILCHER, SHAO L.ZHENG et Z.K.ZHOU also has two or three stamens borne together, but in *Archaeofructus*, 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.FRIIS, 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, e, 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.** Almagem Formation, Early Cretaceous (Aptian-early Albian).

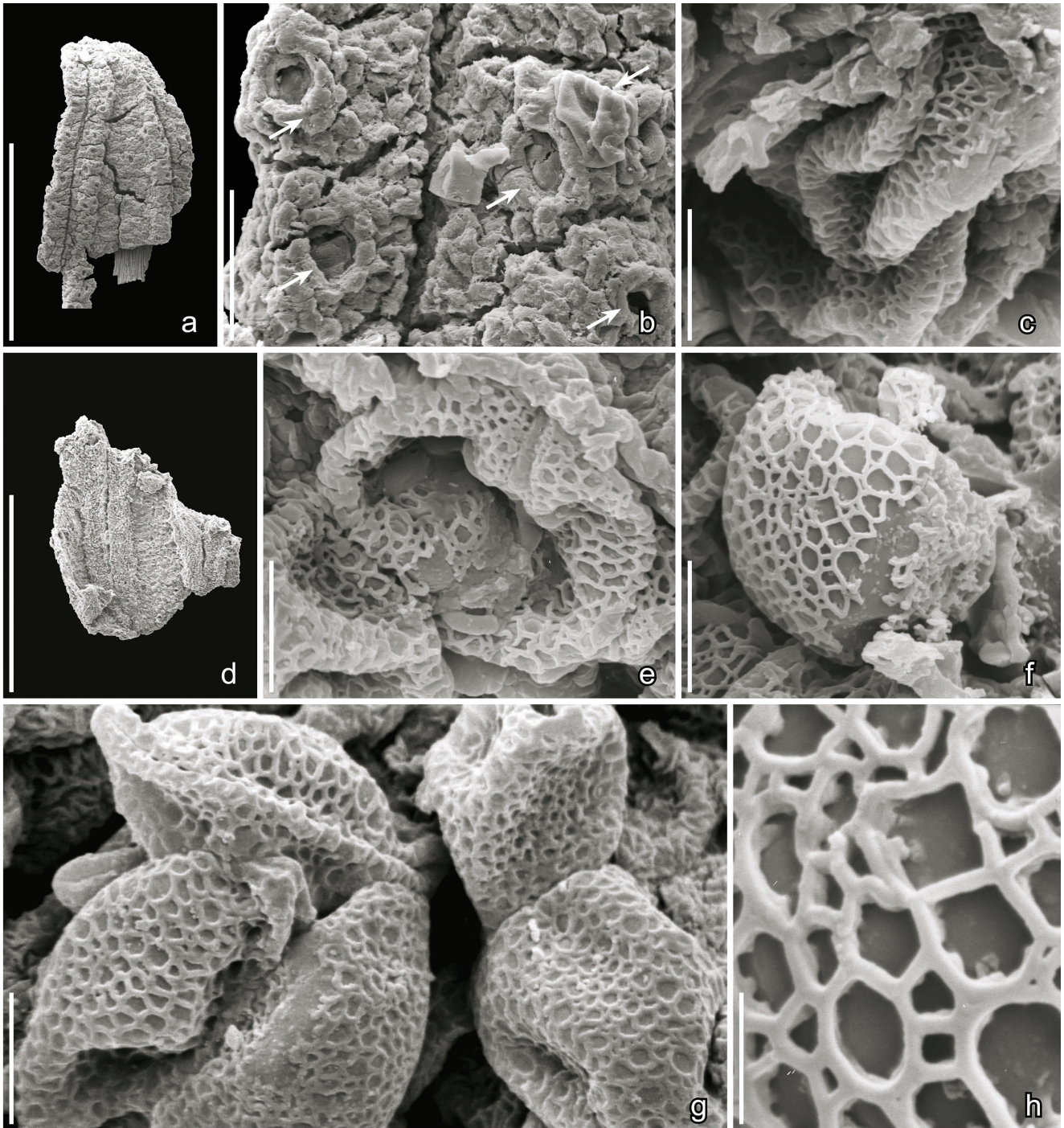
**Specific diagnosis.** As for the genus.

**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).**



**Text-fig. 25.** Scanning electron microscope (SEM) images of stamens and pollen grains of *Elasmotemon paisii* gen. et sp. nov.; Catefica locality, Portugal. a) Stamen fragment showing two pairs of pollen sacs along the margins of the stamen with a broad connective that separates the thecae, except near the apex where the thecae meet; b) Detail of surface of pollen sacs showing larger cells (arrows), interpreted as ethereal oil cells; c) Pollen in situ from specimen in (a); d) Stamen fragment with apical and basal portion missing and surface slightly abraded and compressed obscuring cellular details; note remains of another stamen attached to the underside of the stamen; e–h) Pollen in situ from specimen in (d) showing long aperture (e) and pollen wall with heterobrochate reticulum (e–h); note narrow muri with flatten and smooth surface and short columellae (h). Specimens, Catefica 49-S115859 (a–c), Catefica 151-S105281 (holotype, d–h). Scale bars = 600  $\mu\text{m}$  (a, d), 50  $\mu\text{m}$  (b), 6  $\mu\text{m}$  (c, e–g), 1.5  $\mu\text{m}$  (h).

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 dehiscent 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 stamen from which the stamen base is missing. The anthers are basifixed, 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 *Pennicarpus* E.M.FRIIS, K.R.PEDERSEN et P.R.CRANE, 2000**

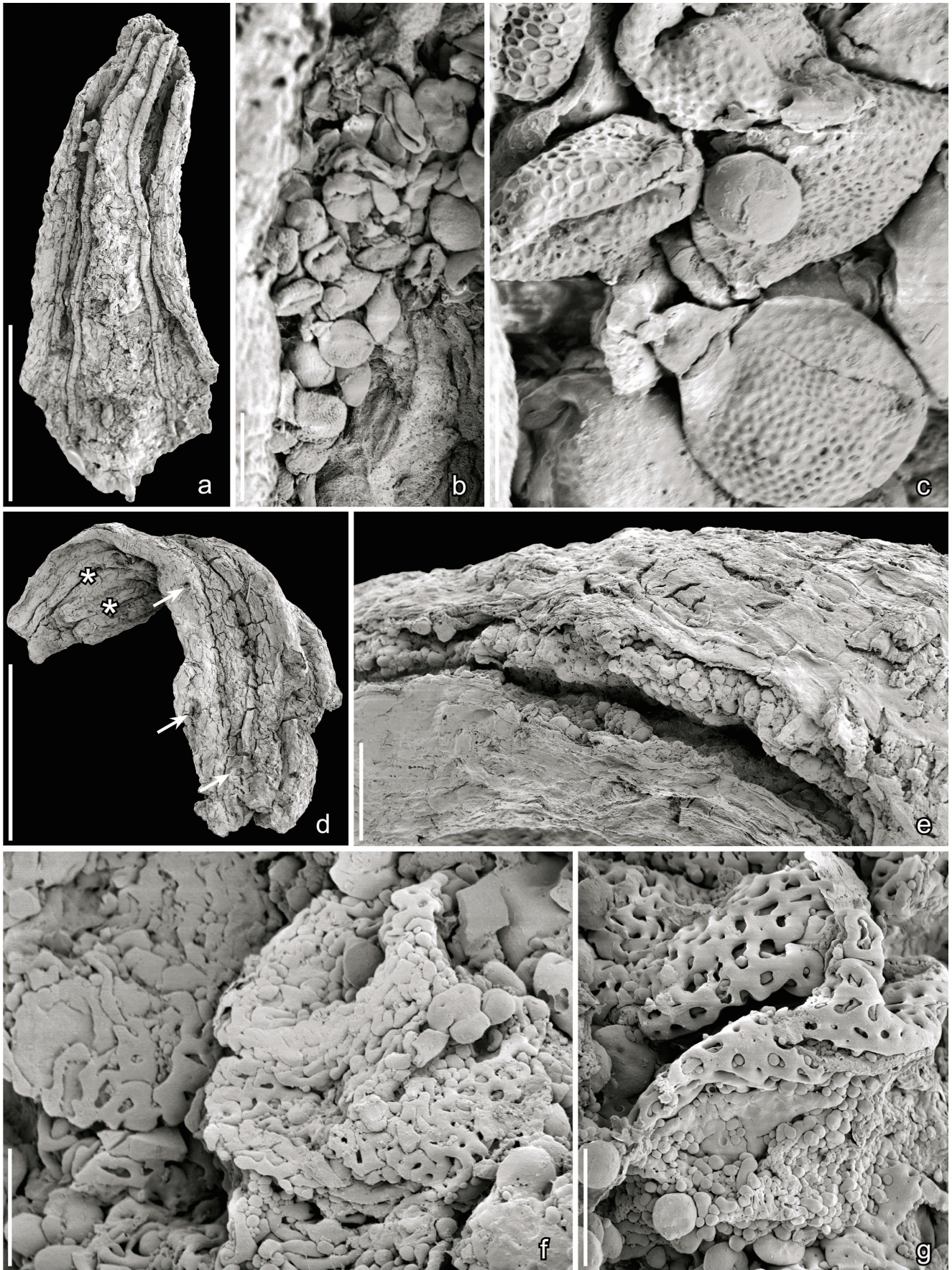
***Pennicarpus tenuis* E.M.FRIIS, K.R.PEDERSEN et P.R.CRANE, 2000**

**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.

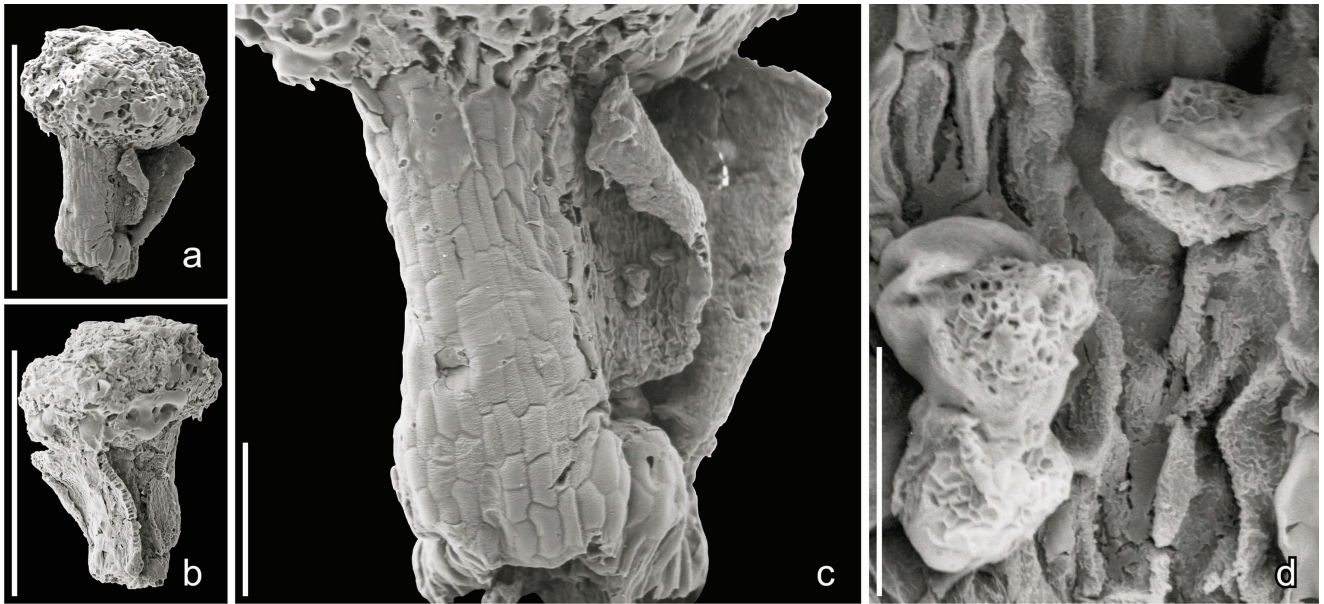
**Affinity and other occurrences.** The fruits are closely similar in size, shape and texture to those of *Pennicarpus tenuis* described from the Vale de Água and Buarcos mesofossil floras (Friis et al. 2000). The fruits from Catefica have not been studied using SEM and it is unknown whether they have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

*Pennicarpus* 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 acolumellate 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 *Elasmotemon 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 dehiscent with the walls of the pollen sacs curled back; b) Pollen grains inside a dehiscent 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



**Text-fig. 27.** Scanning electron microscope (SEM) images of stamens and pollen of *Valvidistemon globiferus* gen. et sp. nov.; Catefica locality, Portugal. a) Stamen in oblique lateral view showing laterally hinged valves, massive connective between the thecae and prominent, globular, apical extension of the connective; b) Stamen in oblique lateral view on the opposite side from (a) showing broken laterally hinged valves and distinct endothecium cells; c) Detail of stamen showing the large, longitudinally aligned cells of the massive connective, broad, poorly defined stamen base, and the laterally hinged valves of one of the thecae; d) Reticulate pollen attached to the inside of the anther wall. Specimen, Catefica 49-S107779 (holotype, a–d). Scale bars = 600  $\mu\text{m}$  (a, b), 100  $\mu\text{m}$  (c), 20  $\mu\text{m}$  (d).

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**  
Text-fig. 30a–f

**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  $\mu\text{m}$  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. 30c). The foot layer is thick, and the endexine is restricted to the apertural region (Text-fig. 30e).

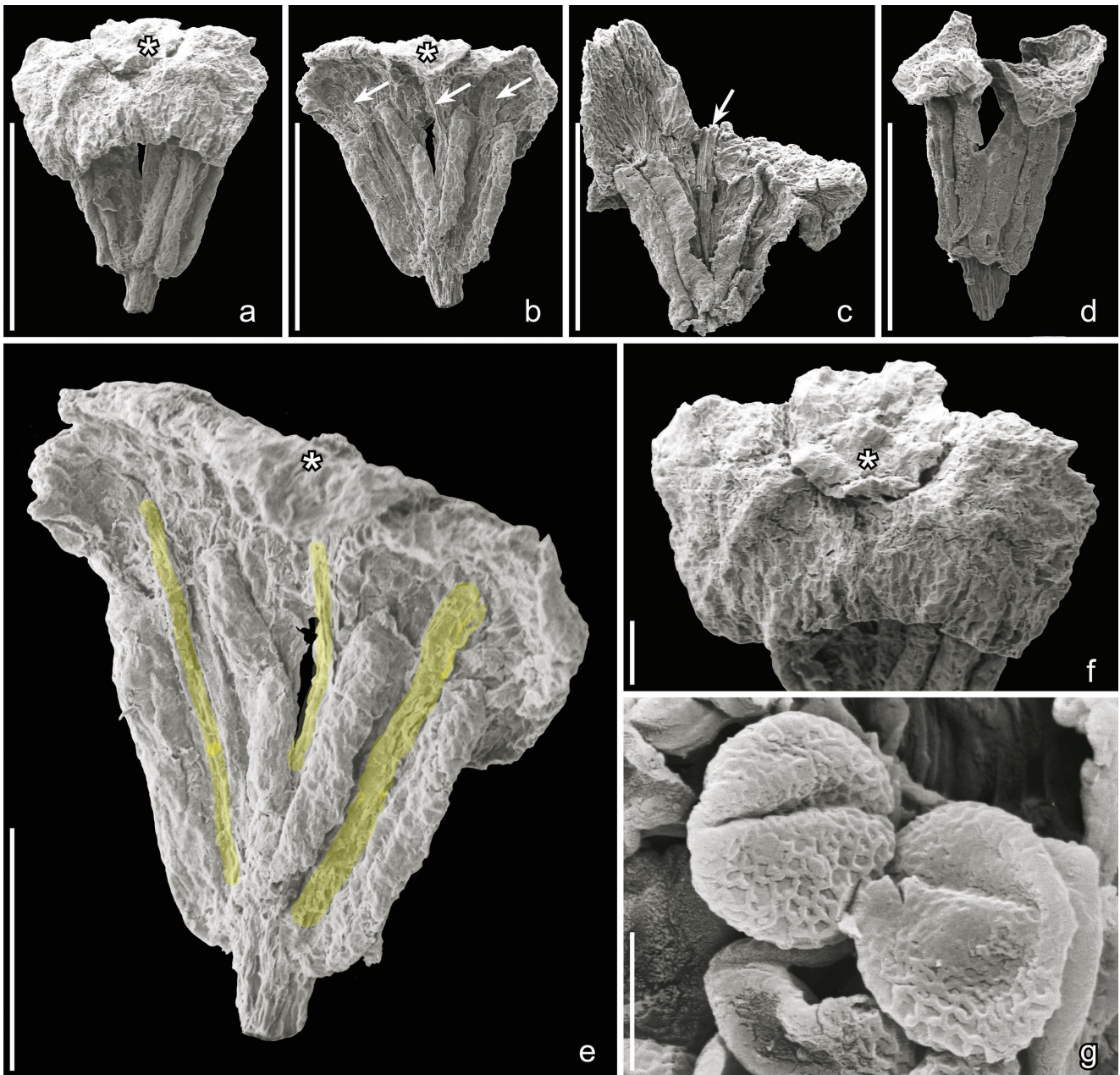
**Affinity and other occurrences.** *Kempia longicolpites* was first described from the Torres Vedras locality (Friis et al. 2019a) and is currently known from only the Torres Vedras and Catefica mesofossil floras.

**Genus *Piercipollis* E.M.FRIIS, P.R.CRANE et K.R.PEDERSEN, 2019**

***Piercipollis* sp.**  
Text-fig. 31a, b

**Description and remarks.** The material comprises two isolated pollen grains, one observed as

**material; d) Stamen with apical and basal part of anther preserved showing two pairs of pollen sacs (asterisks) on the curved, perhaps ventral, surface close to the stamen margin; e) Detail of crack in the anther showing the inner anther wall with densely spaced spherical orbicules that vary greatly in size; f) Pollen exposed in the crack in the anther; note coarsely foveolate to coarsely reticulate pollen wall and densely spaced orbicules; g) Folded pollen grains with reticulate pollen wall and also showing the inner anther wall with densely spaced spherical orbicules that vary greatly in size. Specimens, Catefica 49-S172560 (a–c), Catefica 50-S170384 (d–g). Scale bars = 600  $\mu\text{m}$  (a, d), 20  $\mu\text{m}$  (b, e), 6  $\mu\text{m}$  (c, f, g).**

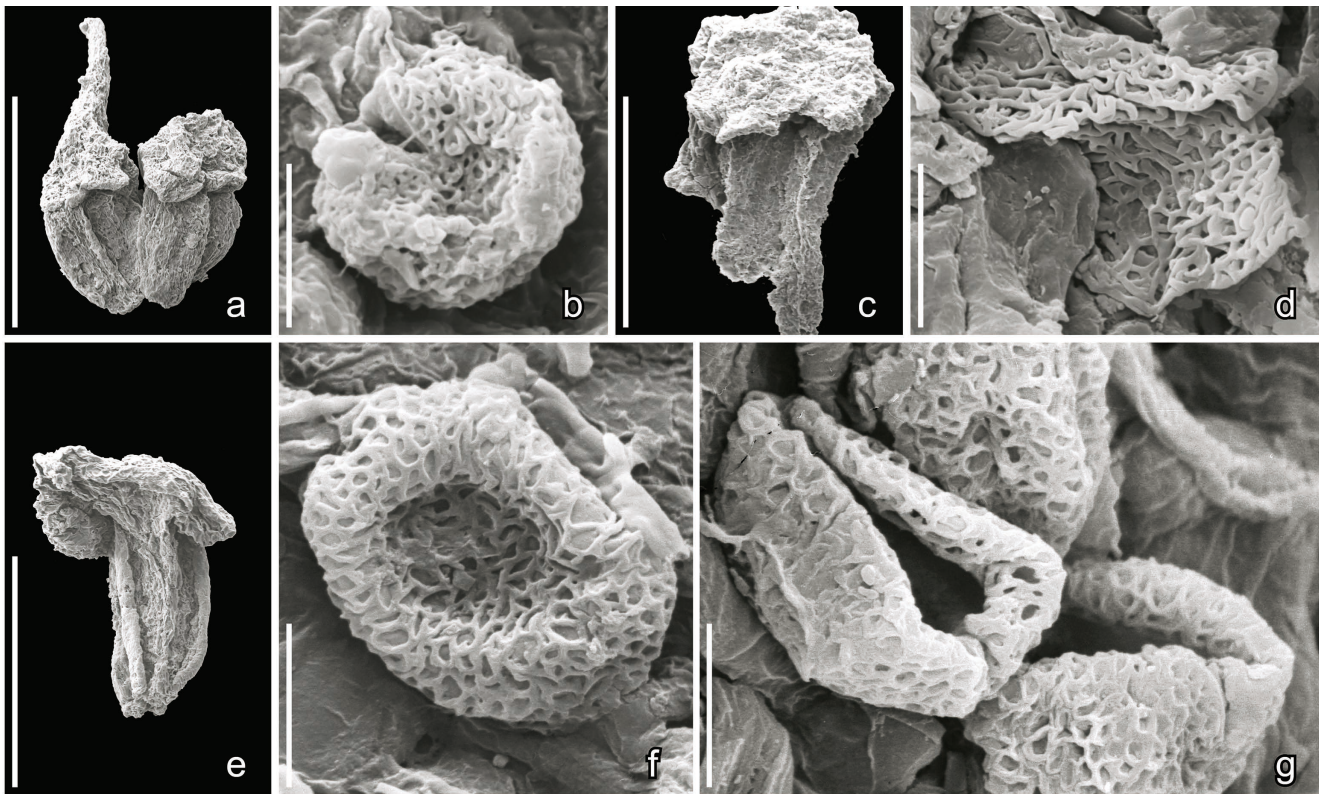


Text-fig. 28. Scanning electron microscope (SEM) images of stamens and pollen of *Endressistemon cateficensis* gen. et sp. nov.; Catefica locality, Portugal. a, b) Staminal structure with two lateral stamens and one median structure seen in ventral and dorsal view (orientation unknown) showing that each stamen has a prominent apical extension and two pairs of pollen sacs separated by a narrow connective; both stamens are borne on a common base together with the median structure and their anthers are sessile on the common stalk; note the apical projection of the median structure (asterisk) between the two stamens and the ribs over probable vascular bundles that extend from the common base into the apical projections of both stamens and the median structure (arrows); c) Staminal structure showing two stamens with prominent apical projections and median axis-like structure between the two stamens (arrow); d) Staminal structure showing two stamens with prominent apical projections borne on a common base; e) Staminal structure in (a) and (b), from the same orientation as (b), showing the ribs over probable vascular bundles (yellow) that extend into the apical projections; f) Detail of staminal structure in (a) and (b) showing the fused or strongly adhering apical projections of the two lateral stamens and the median structure (asterisk); g) Monocolpate, reticulate pollen grains from the pollen sacs of stamen in (d). Specimens, Catefica 49-S107778 (holotype, a, b, e, f), Catefica 49-S107769 (c), Catefica 49-S107751 (d, g). Scale bars = 600  $\mu\text{m}$  (a–d), 300  $\mu\text{m}$  (e), 100  $\mu\text{m}$  (f), 6  $\mu\text{m}$  (g).

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  $\mu\text{m}$  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  $\mu\text{m}$  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.FRIIS,



**Text-fig. 29.** Scanning electron microscope (SEM) images of stamens and pollen grains of cf. *Endressistemon* sp. 1 (a, b), cf. *Endressistemon* sp. 2 (c, d) and cf. *Endressistemon* sp. 3 (e–g); Catefica locality, Portugal. a) Two adhering stamens, each with a long, pointed extension of the connective; b) Monocolpate, reticulate pollen in situ in stamen from stamen pair in (a); c) Fragment of stamen with prominent apical extension of the connective; d) Reticulate, apparently monocolpate, pollen in situ in stamen fragment in (c); e) Stamen with basifixed anther, perhaps sessile, and with prominent, wing-like apical extensions of the connective; note the dehisced thecae with the anther wall curved back; f, g) Monocolpate, reticulate pollen in situ in stamen in (e). Specimens, Catefica 49-S107780 (a, b), Catefica 49-S107784 (c, d), Catefica 49-S107781 (e–g). Scale bars = 600  $\mu\text{m}$  (a, c, e), 6  $\mu\text{m}$  (b, d, f, g).

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.**  
Text-fig. 31c–e

**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  $\mu\text{m}$  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  $\mu\text{m}$  in diameter and that show similar coarse transverse ribbing on the muri (Friis et al. 1999).

**Stamen with monocolpate, reticulate pollen**  
Text-fig. 32a–e

**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  $\mu\text{m}$  in diameter. The aperture is rounded, about 10  $\mu\text{m}$  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  $\mu\text{m}$  in diameter. Muri are narrow, 0.2  $\mu\text{m}$  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 supracteal 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 Catefica 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 Catefica 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 pentamerous 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 whorls 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 supracteal 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.** Pantoporate pollen occurs scattered among all major groups of angiosperms. However, the characters of the pollen combined with the pentamerous 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 Catefica locality. Pollen of *Paisia pantoporata* is also encountered in the palynological strew preparations from Catefica, 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.

### *?Paisia* sp.

Text-fig. 33d

**Description and remarks.** The material comprises a single specimen described previously from the Catefica 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 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).

### *Paisia*-like follicles

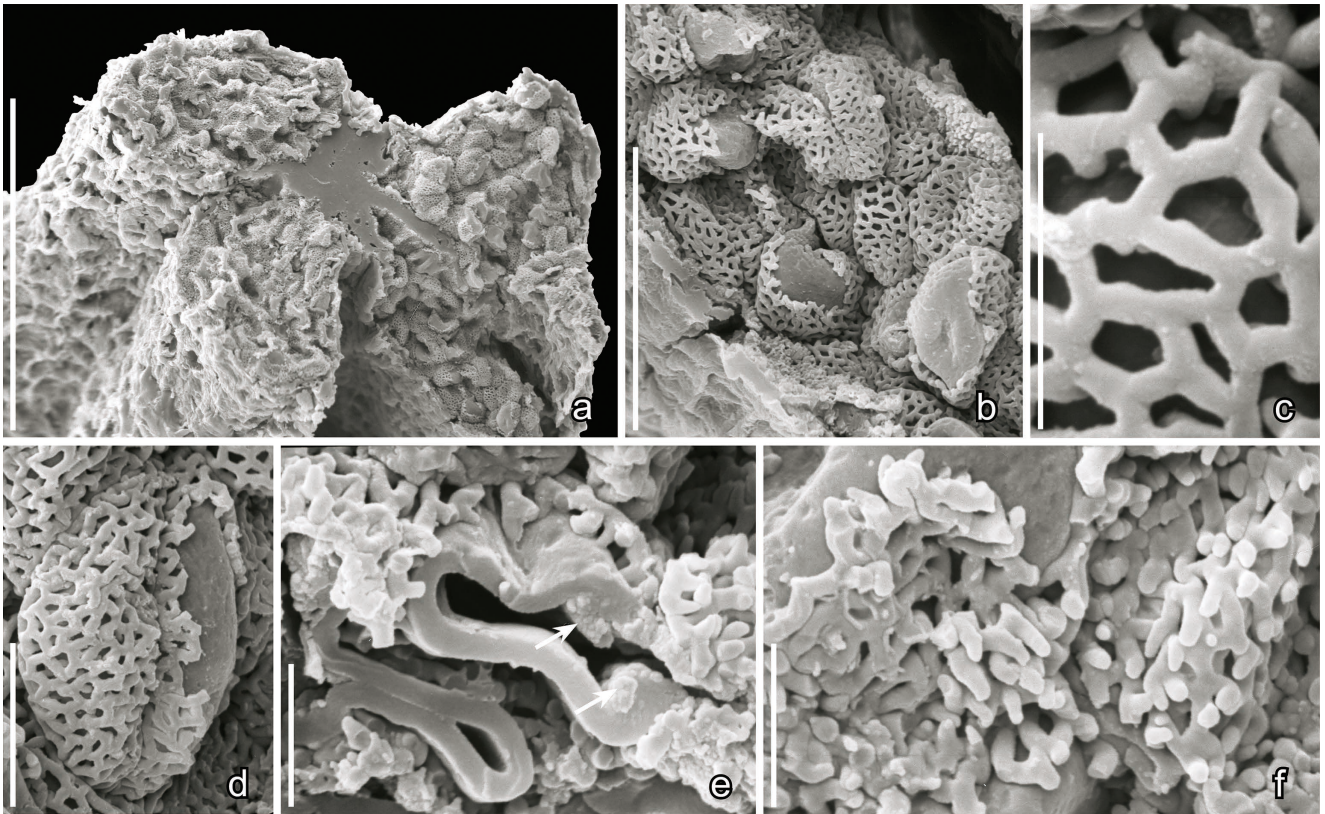
Text-figs 34a–h, 35a–e, 36a–e

**Description and remarks.** 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 decurrent 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 placentae 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





**Text-fig. 30.** Scanning electron microscope (SEM) images of anther and pollen of *Kempia longicolpites*; Catefica locality, Portugal. a) Transverse section through an anther showing the four pollen sacs with in situ pollen; b) Pollen in situ from anther in (a) showing very long colpus and loosely attached reticulum; c) Detail of reticulum showing smooth muri supported by short, scattered columellae; d) Pollen grain from anther in (a) enlarged showing colpus extended beyond the equator and loosely attached reticulum; e) Detail of pollen wall showing thick, homogeneous foot layer, columellae and reticulate tectum; note remains of granular endexine (arrows) in the apertural region of the grain; f) Internal view of reticulum showing the short columellae adhering to the muri detached from the foot layer. Specimen, Catefica 49-S101208 (a–f). Scale bars = 100  $\mu\text{m}$  (a), 20  $\mu\text{m}$  (b), 6  $\mu\text{m}$  (d), 3  $\mu\text{m}$  (c, e, f).

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).

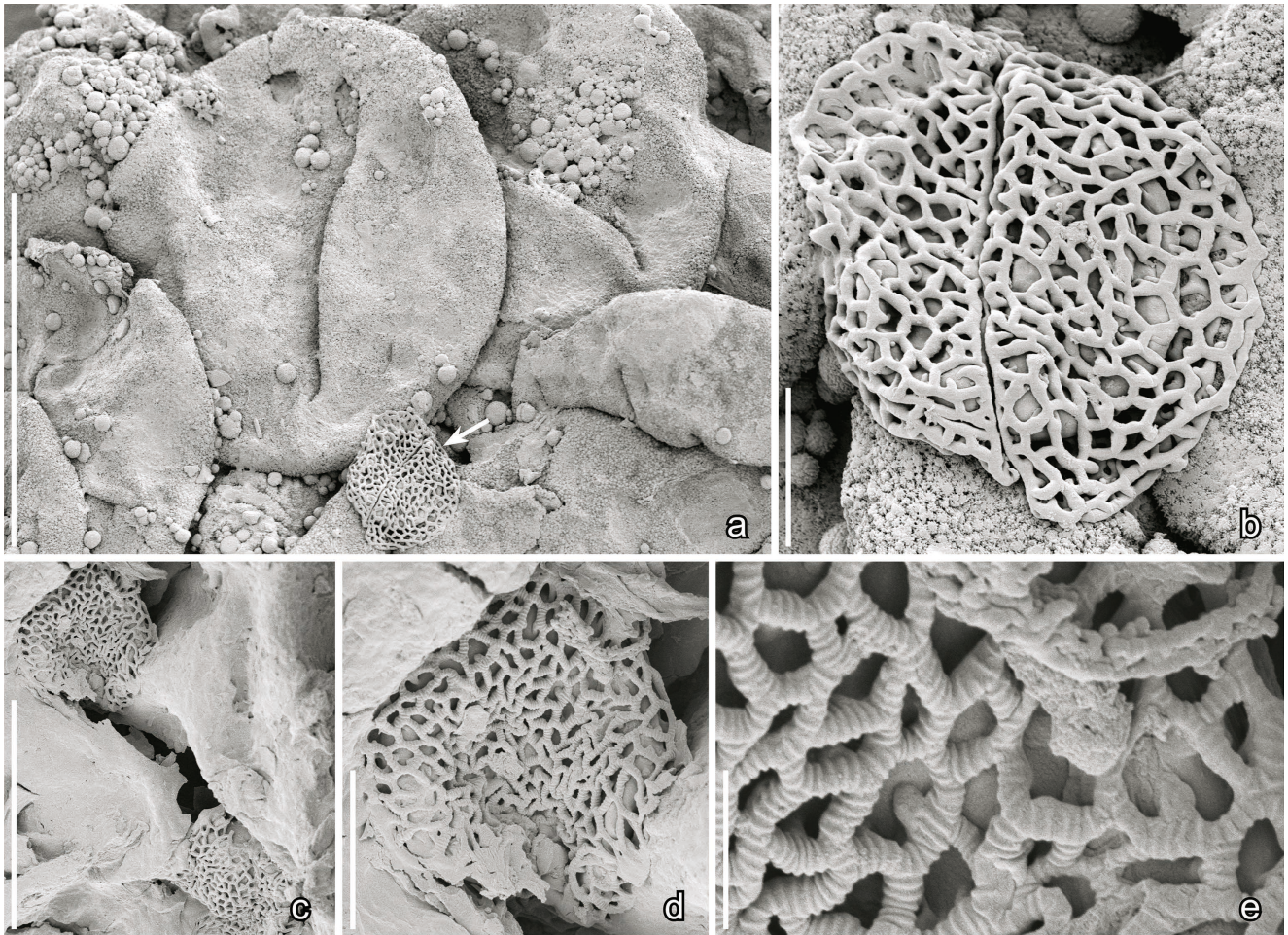
**Affinity and other occurrences.** The follicles are closely similar to the follicles seen in flowers of *Paisia pantoporata* in their elongate shape and in the anatomical details of the follicle wall. However, the carpels in the *Paisia* flowers are immature and the stigmatic zone is indistinct. Other 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, *Psilatricolpites* HAMMEN ex HAMMEN et WYMSTRA, *Retitricolpites* HAMMEN ex HAMMEN et WYMSTRA, *Rhoipites* WODEHOUSE, *Rousea* SAT.K.SRIVAST., or *Striatopollis* 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”.



**Text-fig. 31.** Scanning electron microscope (SEM) images of isolated pollen of *Piercipollis* sp. (a, b) and *Teebacia* sp. (c–e); Catefica locality, Portugal. a) Isolated pollen grain (arrow) adhering to the much larger pollen of *Araucariacites* sp. in fragment of a conifer cone; note the size difference between the angiosperm and conifer pollen that is typical in Early Cretaceous floras; b) Pollen grain in (a) enlarged showing the extended aperture and homobrochate reticulum with smooth muri supported by long, scattered, columellae; c) Isolated pollen grains adhering to the outer surface of a *Saportanthus parvus* flower; d) Pollen grain in (c) enlarged showing the open reticulum and muri ornamented by fine transverse ribs; e) Detail of pollen grain in (d) showing the muri supported by long, scattered columellae; note the fine transverse ribs on the muri. Specimens, Catefica 49-S170139-01 (a, b), Catefica 361-S174322-01 (c–e). Scale bars = 50  $\mu\text{m}$  (a), 20  $\mu\text{m}$  (c), 6  $\mu\text{m}$  (b, d), 1.5  $\mu\text{m}$  (e).

### 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  $\mu\text{m}$  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-reticulate 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  $\mu\text{m}$  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  $\mu\text{m}$  long, irregular in shape and have a solid base of laterally fused spheres with rod-like projections (Text-fig. 37e).

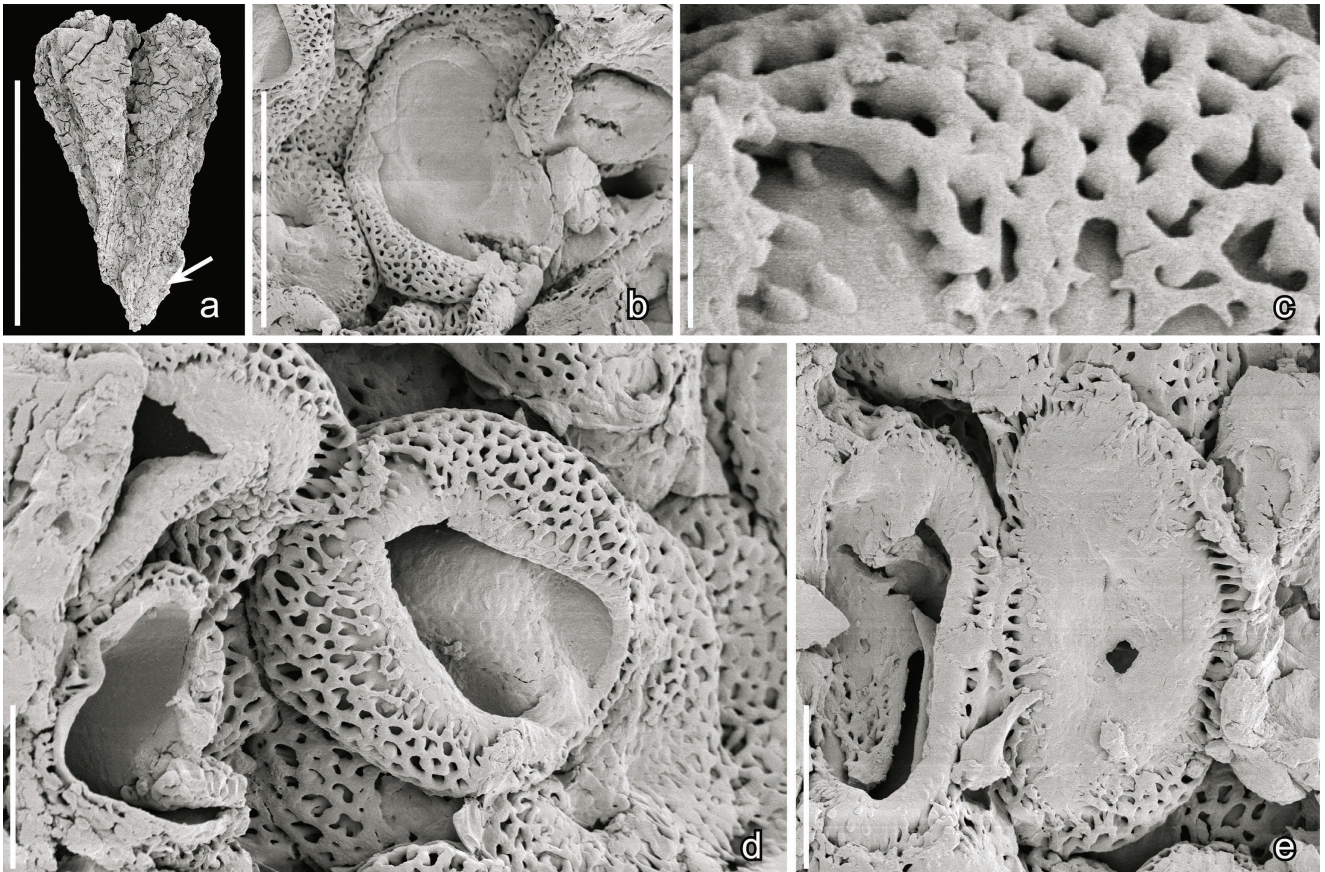
**Affinity and other occurrences.** The triaperturate pollen grains clearly indicate a relationship to eudicots, but relationships to extant taxa within the group are uncertain.

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  $\mu\text{m}$  in diameter, and with an almost circular equatorial amb (Text-fig. 38b, d, e). The apertures are long with irregular margins and a coarsely verrucate aperture membrane (Text-



**Text-fig. 32.** Scanning electron microscope (SEM) images of “Stamen with monocolpate, reticulate pollen”; Catefica locality, Portugal. a) Stamen with four pollen sacs and an adhering bract (arrow); b) Pollen grains from stamen showing the large gaping, almost circular, aperture with a distinct aperture margin; c) Detail of pollen wall showing finely verrucate supracteal ornamentation and bases of broken columellae; d) Pollen grain showing the large gaping, rounded aperture; e) Pollen grains showing large, rounded aperture (left) and abraded reticulum exposing the surface of the foot layer and long columellae (right). Specimen, Catefica 49-S170144 (a–e). Scale bars = 600  $\mu\text{m}$  (a), 20  $\mu\text{m}$  (b), 6  $\mu\text{m}$  (d, e), 1.5  $\mu\text{m}$  (c).

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  $\mu\text{m}$  wide, almost smooth with faint transverse striations and a rounded to flattened profile (Text-fig. 38c). The infracteal 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  $\mu\text{m}$  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  $\mu\text{m}$  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.

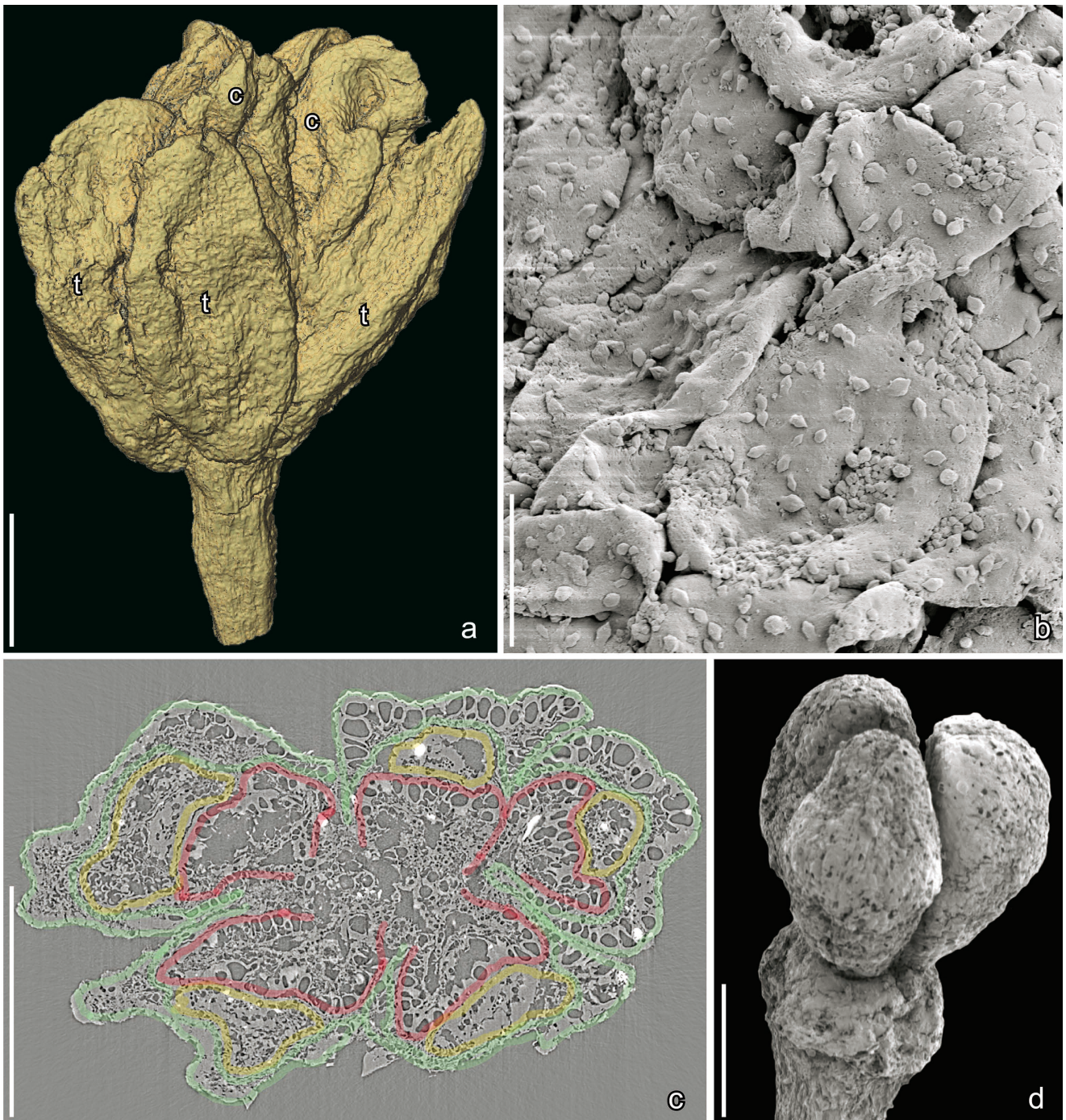
**Affinity and other occurrences.** The triaperturate pollen grains clearly indicate a relationship to eudicots, but relationships to extant taxa within the group are uncertain.

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



**Text-fig. 33.** Synchrotron radiation X-ray tomographic microscopy (SRXTM, a, c) and scanning electron microscope (SEM, b, d) images of *Paisia pantoporata* (a–c) and *?Paisia* sp. (d); Catefica locality, Portugal. a) Lateral view (volume rendering) of flower showing the carpels (c) and the fleshy tepals (t) that have a slightly bulge near the base; b) Pollen grains in situ from stamen showing scattered pores and spiny supracteal ornamentation; c) Transverse section (orthoslice xz1024) through flower showing the pentamerous organization with five tepals (green) five stamens (yellow) and five carpels (red) all on the same radii; d) Lateral view of floral structure with three free carpels borne on the swollen receptacle that has poorly defined facets at the apex indicating the former presence of perianth parts. Specimens, Catefica 49-S101214 (a, c), Catefica 50-S170188 (b), Catefica MM125-P0292 (d). Scale bars = 300  $\mu\text{m}$  (a, c, d), 6  $\mu\text{m}$  (b).

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 it probably is 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  $\mu\text{m}$  long and an equatorial diameter of about 19  $\mu\text{m}$  (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  $\mu\text{m}$  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 *Lusistemon* 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 Catefica. The pollen is distinguished from all other tricolpate pollen from Catefica 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  $\mu\text{m}$  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  $\mu\text{m}$  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 Catefica. The pollen is distinguished from all other tricolpate pollen from Catefica 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 Catefica 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

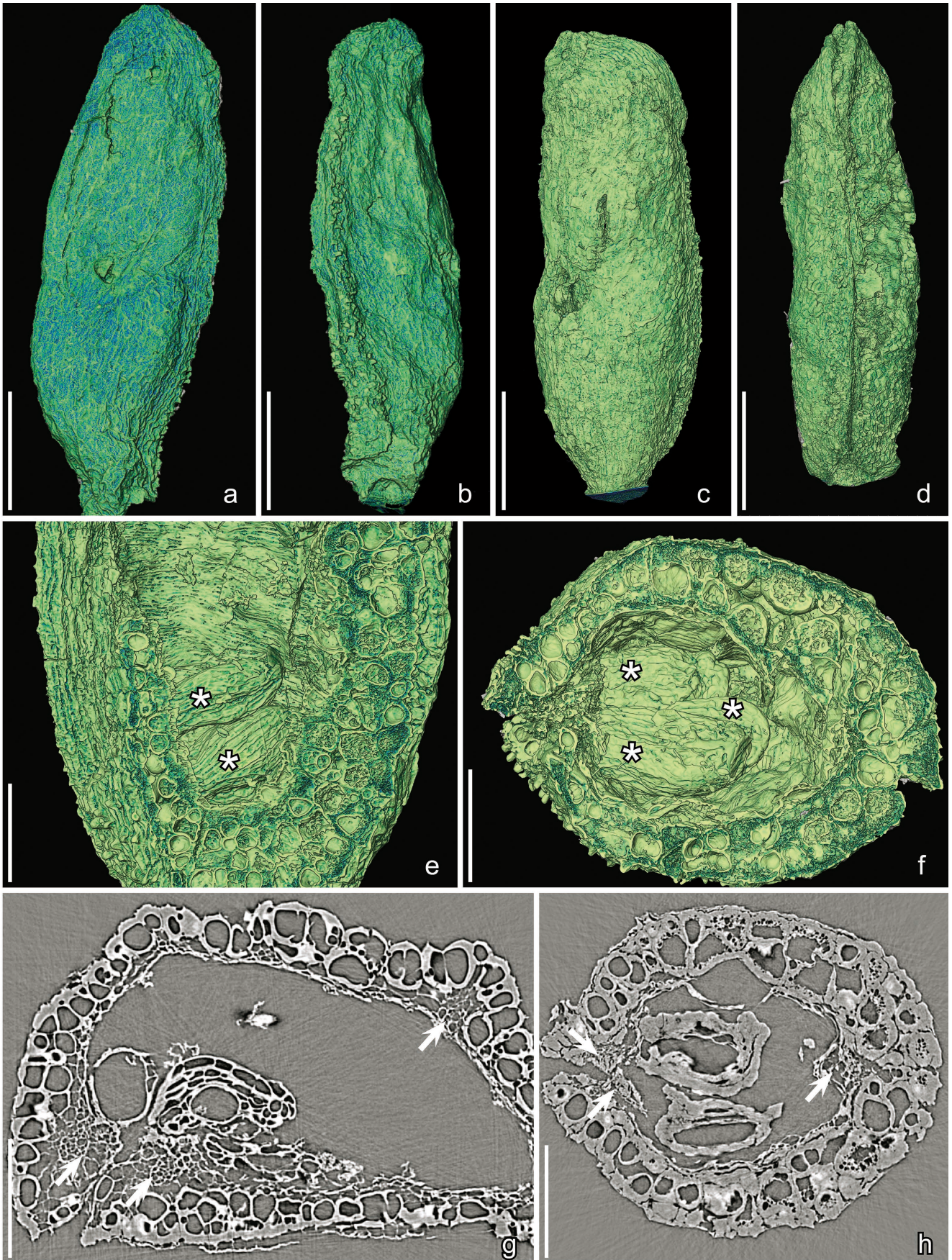
**Description and remarks.** The material comprises several flower buds with an inferior gynoecium (Text-fig. 42a–g). Five specimens were studied using SRXTM, which reveals a trimerous perianth, androecium and gynoecium. The flowers are pedicellate (Text-fig. 42d, e). The perianth apparently consists 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 gynoecium 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 gynoecium is syncarpous, trilobular with axile placentation 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, trilobular gynoecium (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).

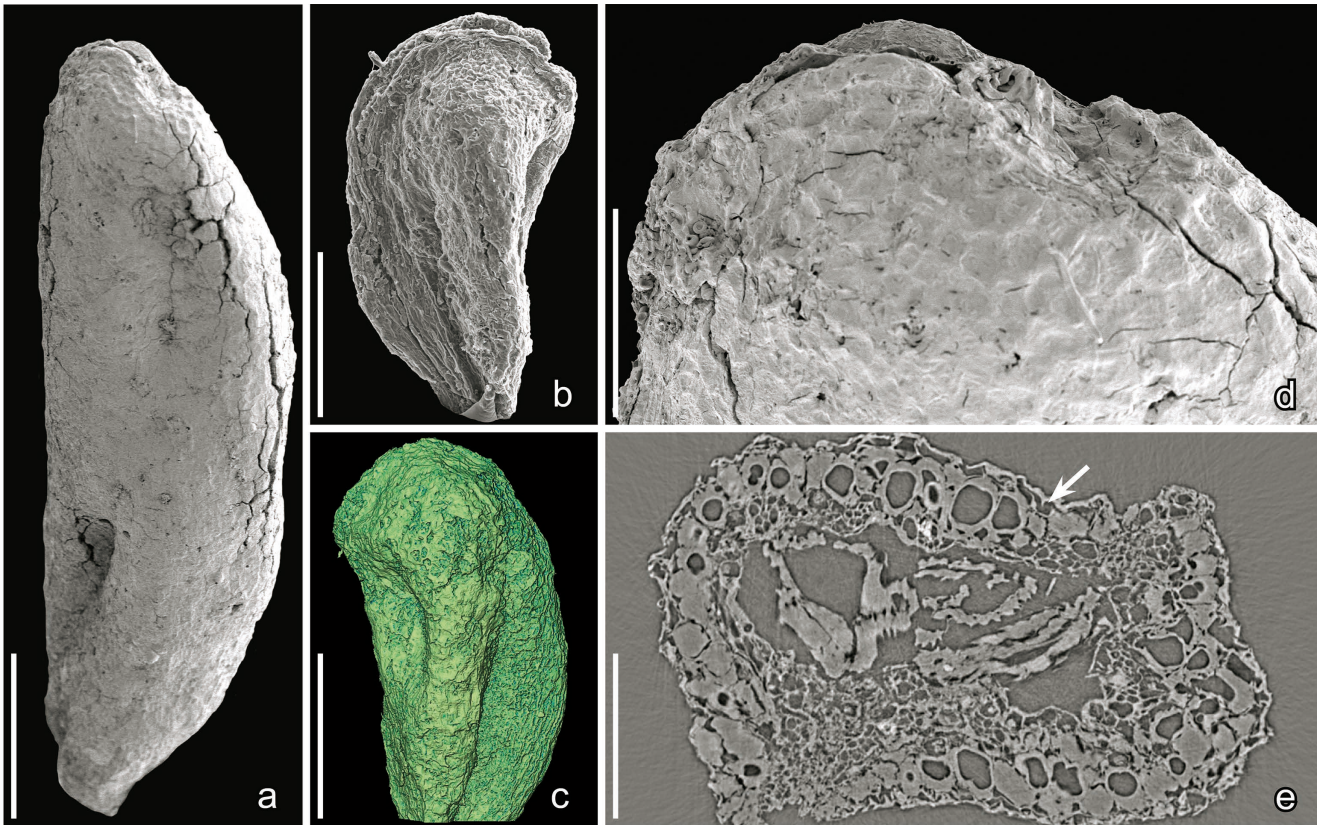
#### **Tricarpellate flower sp. 2**

Text-fig. 43a–e

**Description and remarks.** The material consists of a single flower with a tricarpellate gynoecium 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 hypanthial 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 gynoecium 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



**Text-fig. 35.** Scanning electron microscope (SEM, a, b, d) and synchrotron radiation X-ray tomographic microscopy (SRXTM, c, e) images of “*Paisia*-like follicle”; Catefica locality, Portugal. a) Lateral view of slender follicle with an almost straight ventral margin and a slightly curved dorsal margin; b) Lateral view of small, broad follicle with slightly sinuous ventral margin and rounded dorsal margin; c) Lateral view of small, broad follicle with slightly sinuous ventral margin and rounded dorsal margin; d) Apical part of follicle in (a) showing the slight apical cleft in the probable stigmatic region; e) Transverse section (orthoslice xy0407) of follicle showing ovules and distinct follicle wall with small, thin-walled cells of the outer epidermis (arrow), larger, isodiametric cells of the mesocarp and an inner layer of smaller, thin-walled cells. Specimens, Catefica 50-S171523 (a, d), Catefica 343-S171515 (b), Catefica 49-S174929 (c, e). Scale bars = 300  $\mu\text{m}$  (a–c), 100  $\mu\text{m}$  (d, e).

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

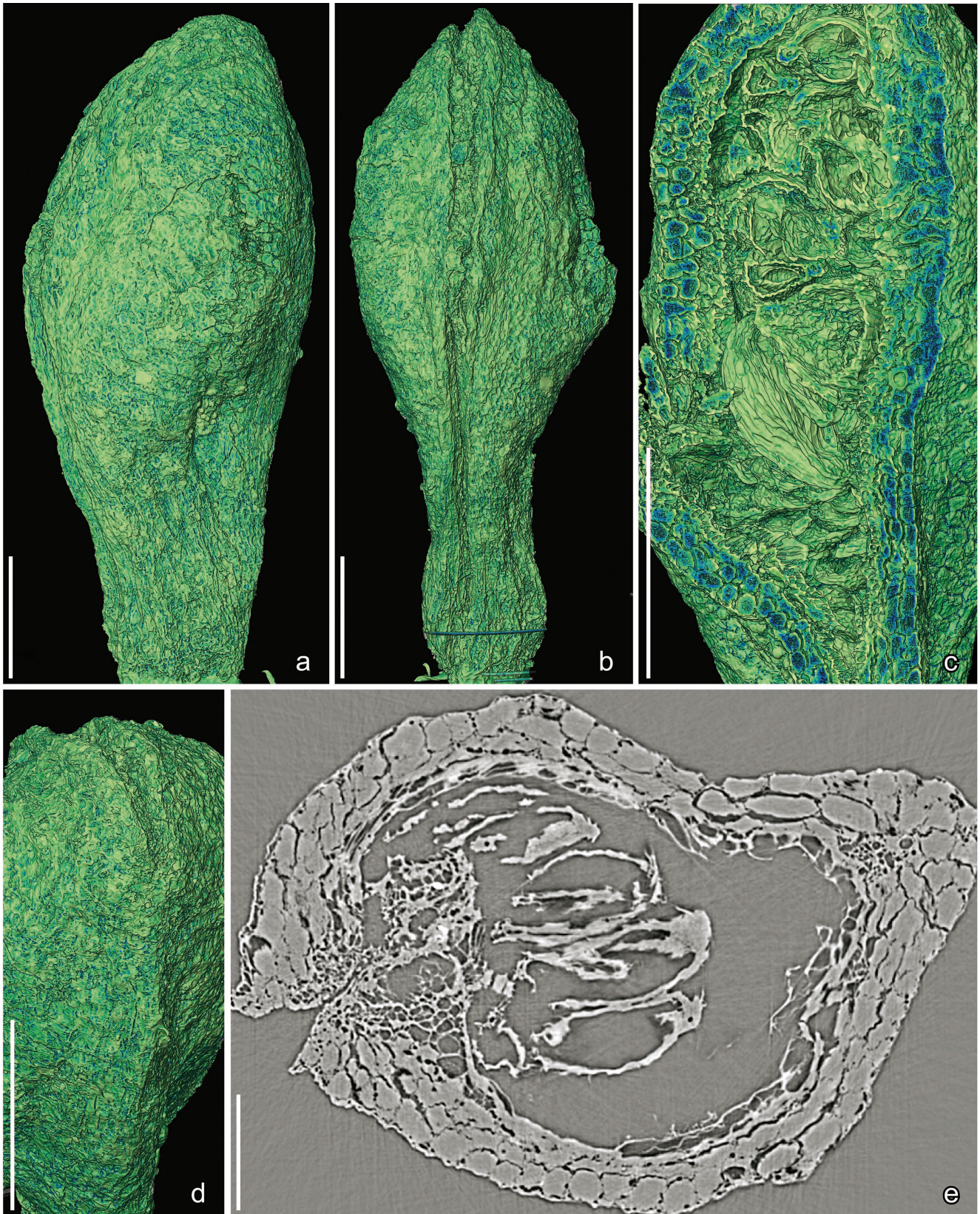
have not been encountered in other Early Cretaceous mesofossil floras and the fossil represents a new genus and species. A detailed description and complete analysis is in preparation (E. M. Friis, P. R. Crane and K. R. Pedersen, work in progress).

### Hexacarpellate flower

Text-fig. 44a–d

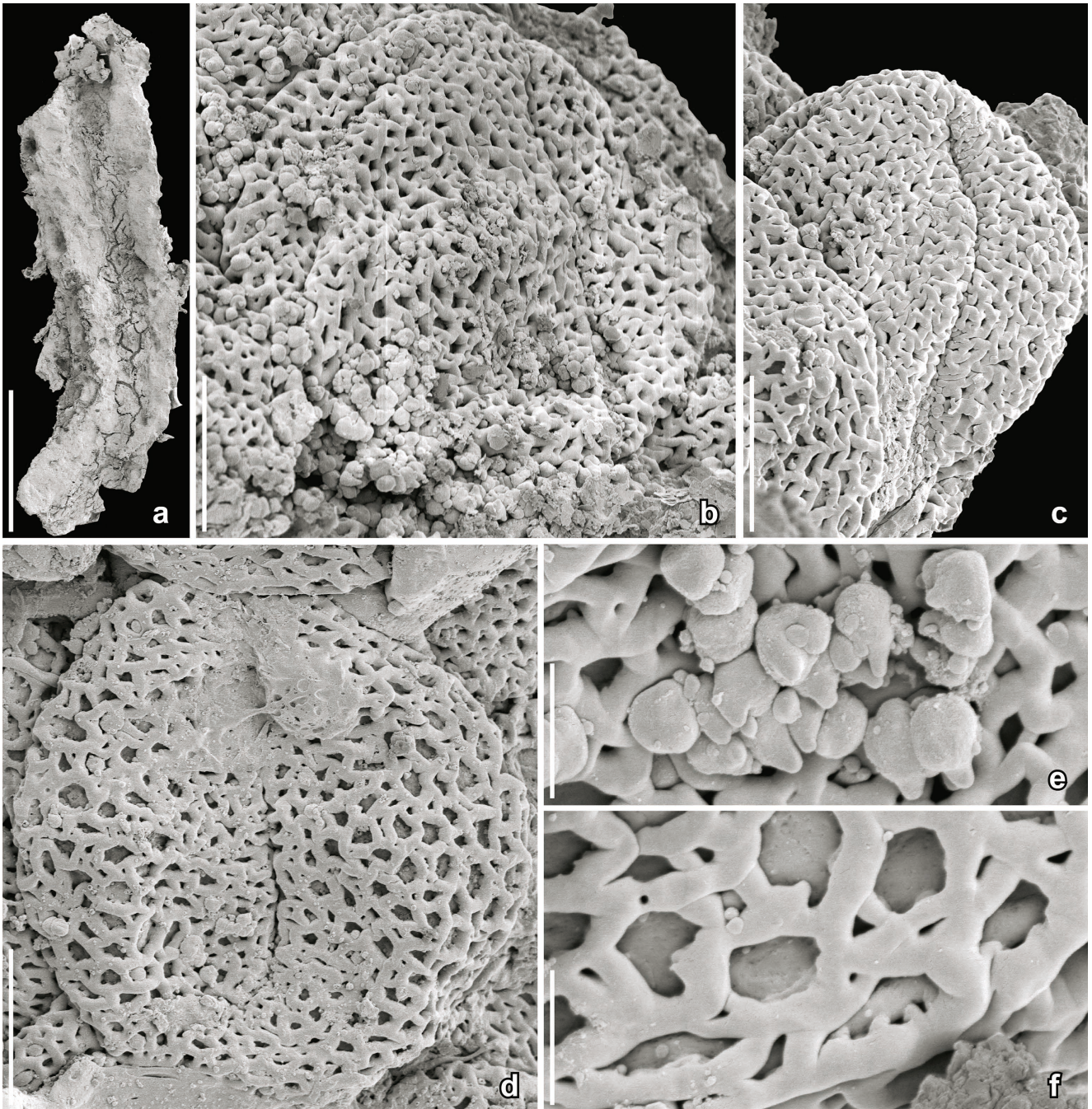
**Description and remarks.** The material comprises a single floral structure, probably preserved around anthesis since the perianth parts are spreading and the ovules are small and do not fill out the locules. The flower is radially symmetrical, epigynous, with six tepals alternating with six carpels (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  $\mu\text{m}$  (a–d), 100  $\mu\text{m}$  (e–h).



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  $\mu\text{m}$  (a–d), 100  $\mu\text{m}$  (e).



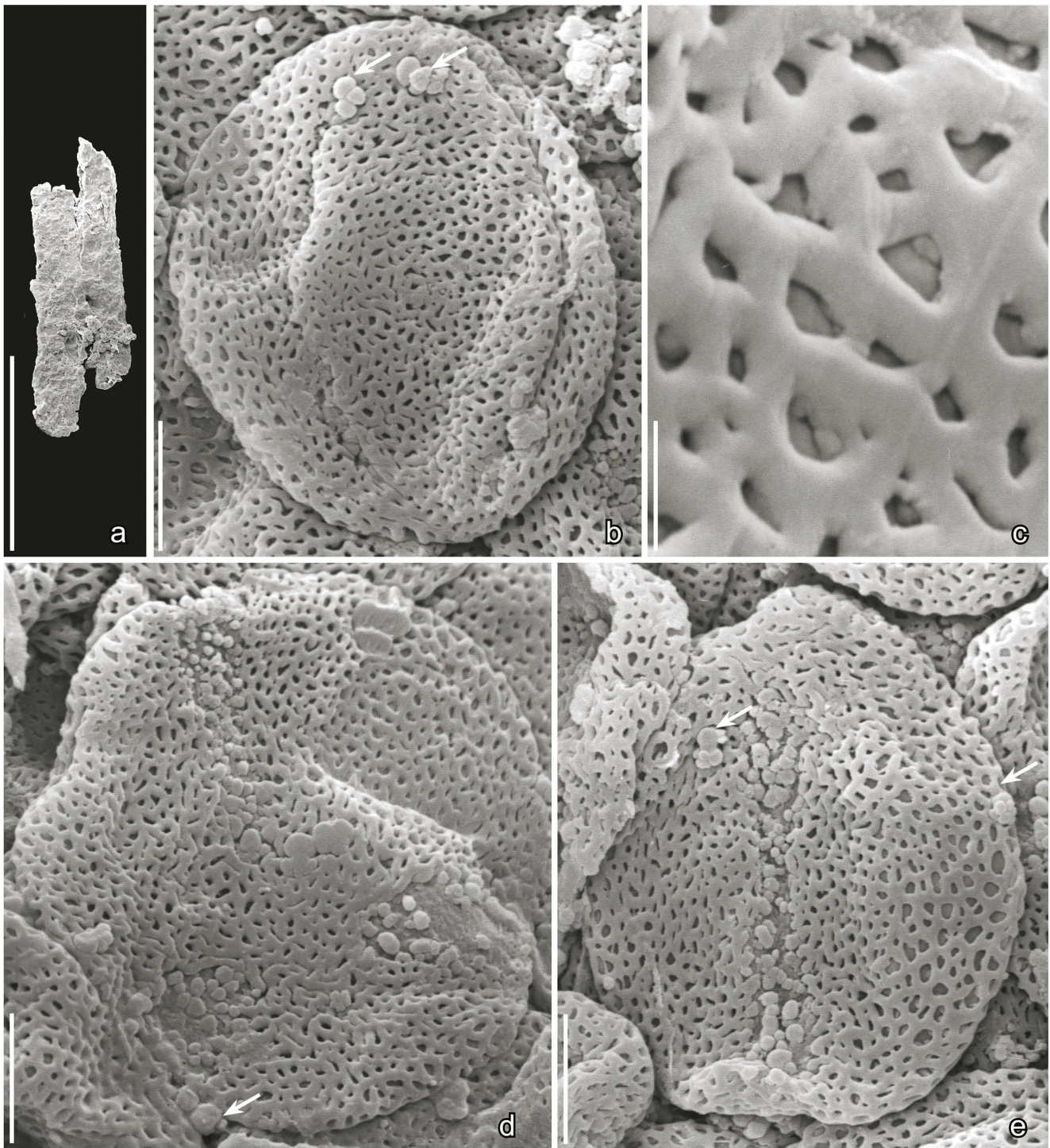


**Text-fig. 37.** Scanning electron microscope (SEM) images of “Stamen with tricolpate pollen sp. 1”; Catefica locality, Portugal. a) Stamen fragment showing the elongate, tetrasporangiate anther but with the base and apex poorly preserved; b–d) Pollen grains from stamen fragment in equatorial view showing 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  $\mu\text{m}$  (a), 6  $\mu\text{m}$  (b–d), 1.5  $\mu\text{m}$  (e, f).

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 remains 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



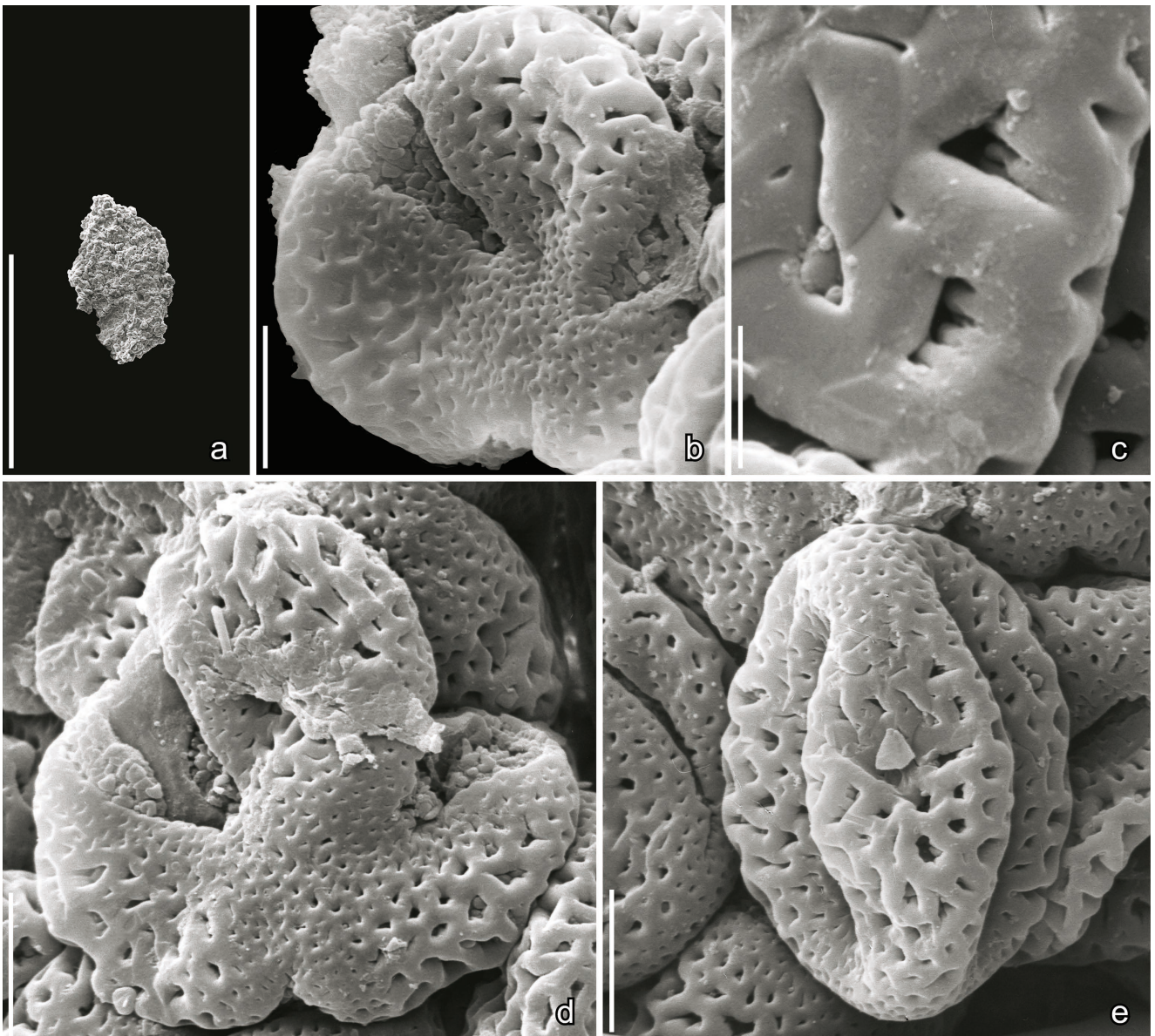
**Text-fig. 38.** Scanning electron microscope (SEM) images of “Stamen with tricolpate pollen sp. 2”; Catefica locality, Portugal. a) Stamen fragment showing the elongate, tetrasporangiate anther but with the base and apex poorly preserved; b, d, e) Pollen grains from stamen fragment in equatorial (b, e) and polar (d) views showing the long colpi with coarsely verrucate aperture membranes and semitectate-microreticulate pollen wall; note small, spherical orbicules scattered on the surface of the tectum (arrows); c) Detail of pollen wall showing smooth muri with very faint transverse striations and a granular to columellate infratectal layer. Specimen, Catefica 153-S105614 (a–e). Scale bars = 600  $\mu\text{m}$  (a), 6  $\mu\text{m}$  (b, d, e), 1  $\mu\text{m}$  (c).

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-

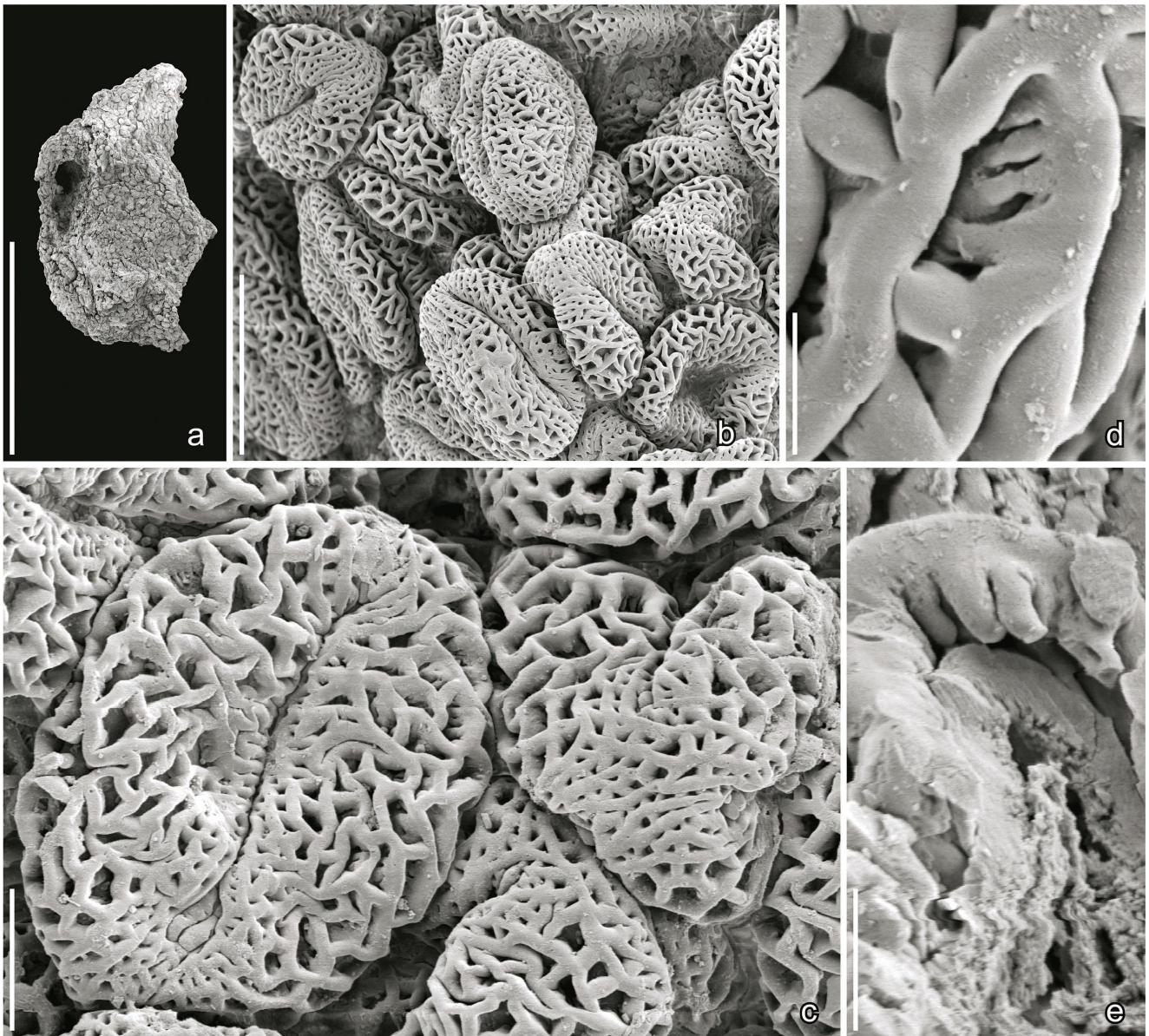


**Text-fig. 39.** Scanning electron microscope (SEM) images of “Pollen clump with tricolpate pollen sp. 3”; Catefica locality, Portugal. a) Pollen clump, probably an anther fragment, containing one kind of pollen; b, d, e) Pollen grains from stamen fragment in polar (b, d) and equatorial (e) views showing the long colpi with coarsely verrucate aperture membranes; note the semitectate-reticulate tectum in the mesocolpium regions and foveolate-punctate tectum in the polar regions and along the aperture margins; c) Detail of pollen wall showing smooth muri and short, densely-spaced columellae. Specimen, Catefica 49-S107785 (a–e). Scale bars = 600  $\mu\text{m}$  (a), 6  $\mu\text{m}$  (b, d, e), 1.5  $\mu\text{m}$  (c).

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.



**Text-fig. 40.** Scanning electron microscope (SEM) images of “Pollen clump with tricolpate pollen sp. 4”; Catefica locality, Portugal. **a)** Pollen clump, probably an anther fragment with one kind of pollen grain; **b)** Detail of pollen clump showing densely packed pollen all of the same kind; **c)** Pollen grains in equatorial (left) and polar (right) views showing the coarse reticulum in the mesocolpium regions, the striate-reticulate tectum over the polar regions, and the microreticulate to foveolate tectum along the aperture margins; **d)** Detail of pollen wall showing smooth muri supported by long, densely-spaced columellae; **e)** Detail of broken pollen wall showing long, densely-spaced columellae detached from the thick foot layer. Specimen, Catefica 50-S170386 (a–e). Scale bars = 600 µm (a), 20 µm (b), 6 µm (c), 1.5 µm (d, e).

### **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.

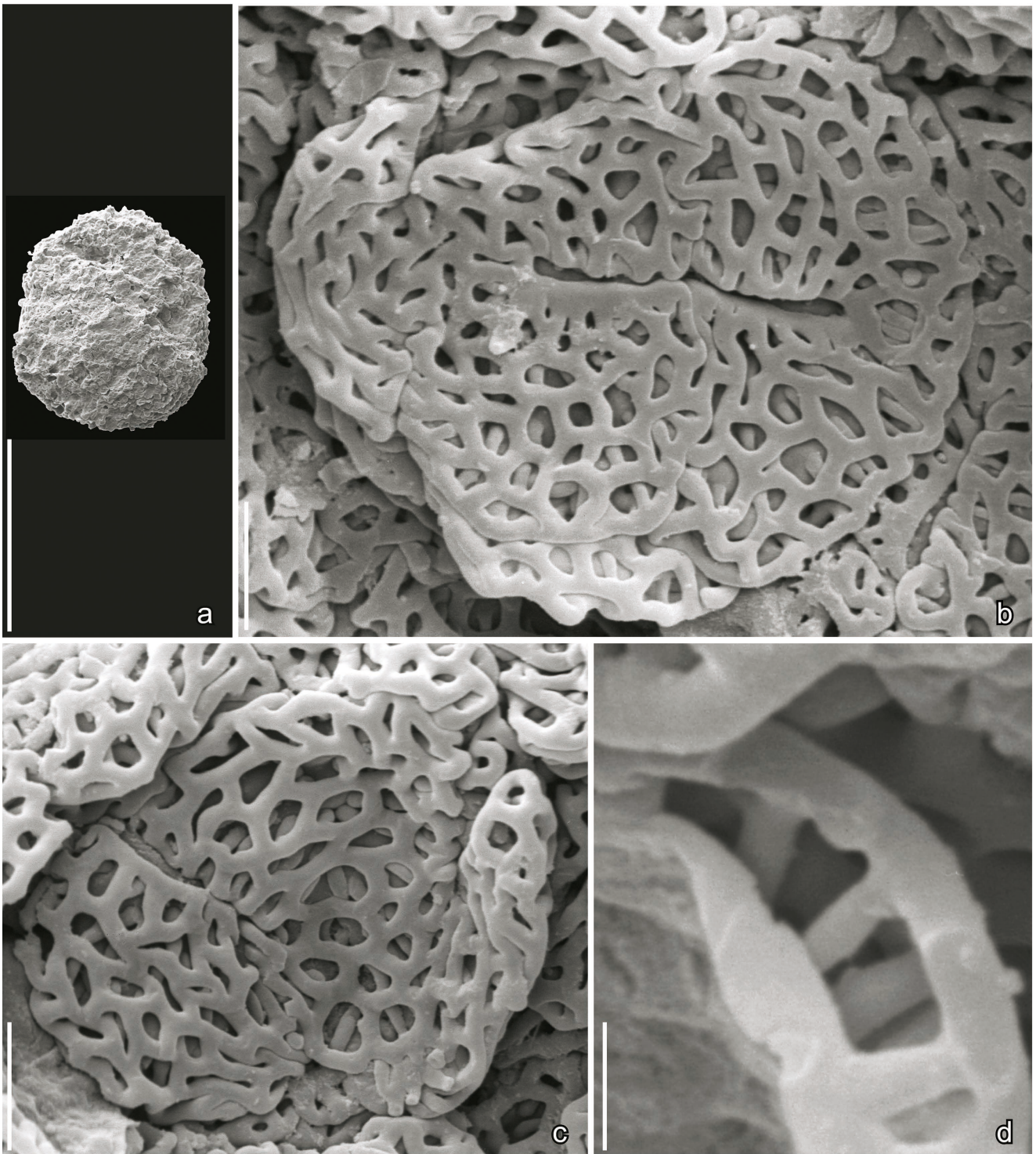
Cells of the outer epidermis have isodiametric facets and are covered by a thick cuticle (Text-fig. 46c). The irregular fruit surface most likely reflects the irregular surface of an endocarp, which is characteristic of many drupaceous fruits and often indicates animal dispersal.

**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

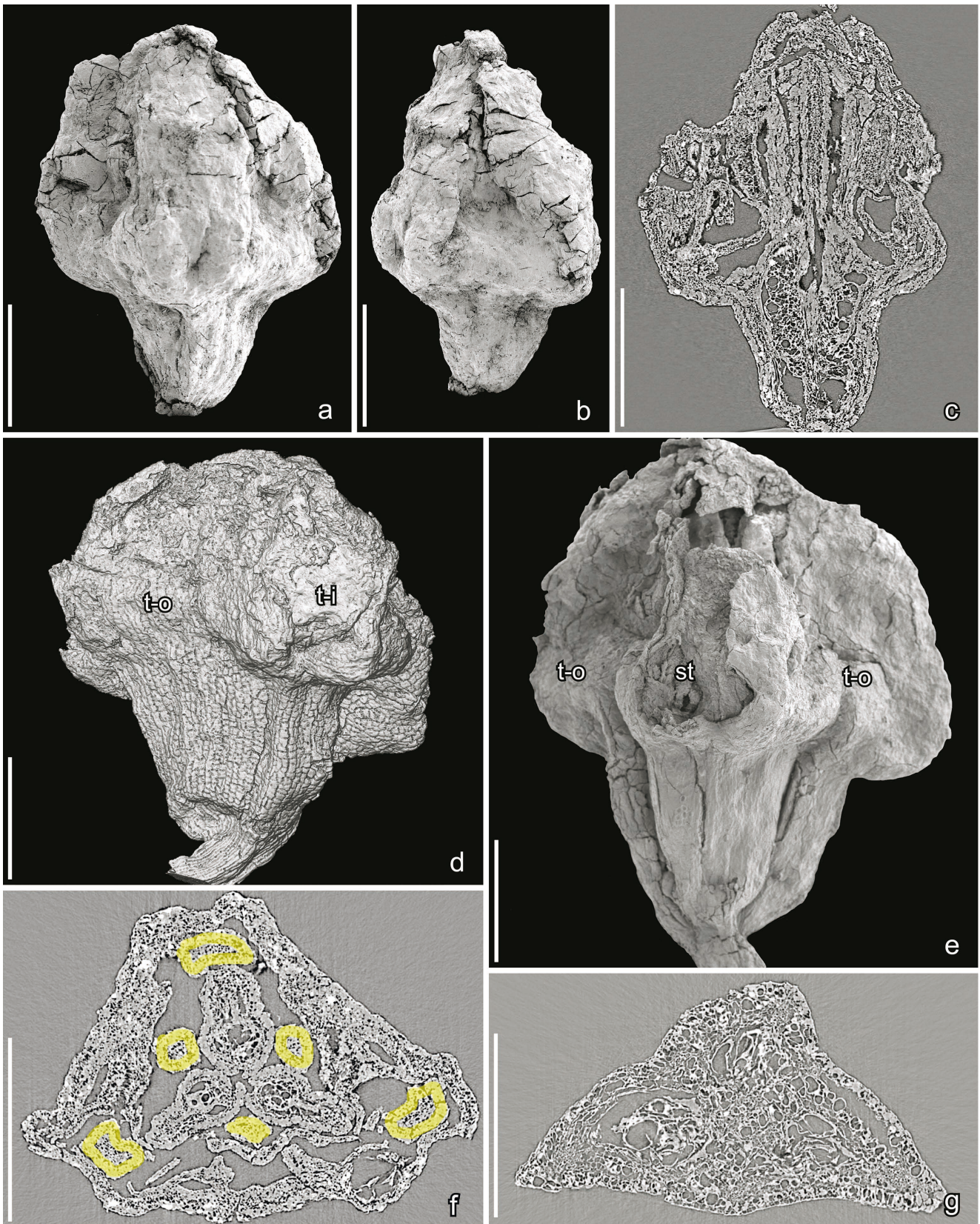
**Description and remarks.** The material includes tiny fruits, each with a single seed that fills out the whole locule (Text-fig. 47a–f). The fruits are about 0.65–



**Text-fig. 41.** Scanning electron microscope (SEM) images of “Pollen clump with tricolpate pollen sp. 5”; Catefica locality, Portugal. a) Pollen clump, probably coprolite but containing one kind of pollen; b, c) Pollen grains from pollen clump in oblique equatorial view (b) and polar view (c) showing the three apertures with a distinct aperture margin and the coarse reticulum; d) Detail of wall of a broken pollen grain showing long straight columellae and a thin foot layer. Specimen, Catefica 50-S115858 (a–d). Scale bars = 600  $\mu\text{m}$  (a), 6  $\mu\text{m}$  (b, c), 1.5  $\mu\text{m}$  (d).

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  $\mu$ m (a–e).

**Affinity and other occurrences.** The fruits and seeds show some similarity 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.

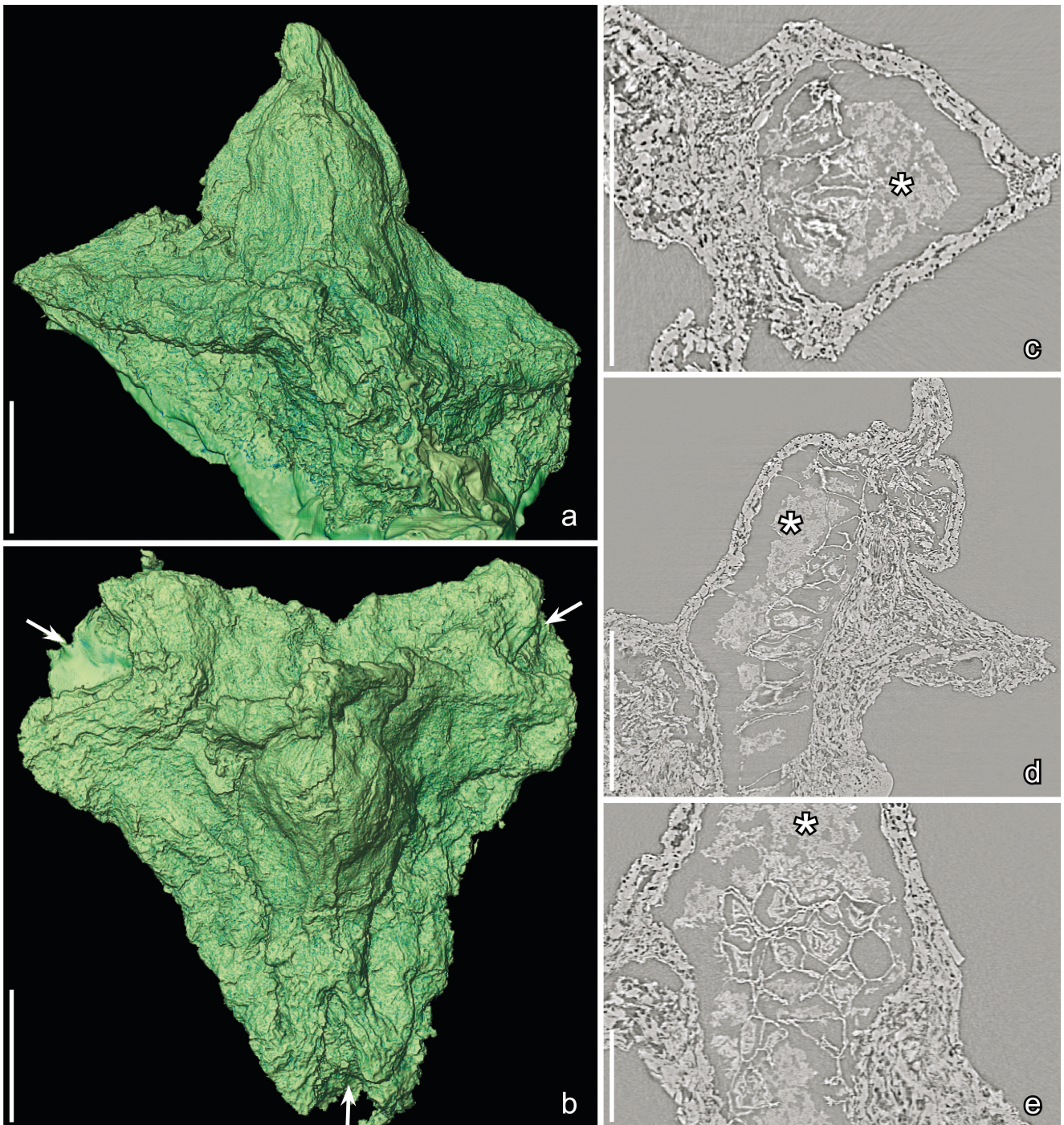
**Affinity and other occurrences.** These fossils are common in many of the mesofossil floras from Portugal including Buarcos, Famalicão and Vale de Água. The seeds have many features in common with seeds of extant Austrobaileyales and Nymphaeales and formal description and systematic analysis of the 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

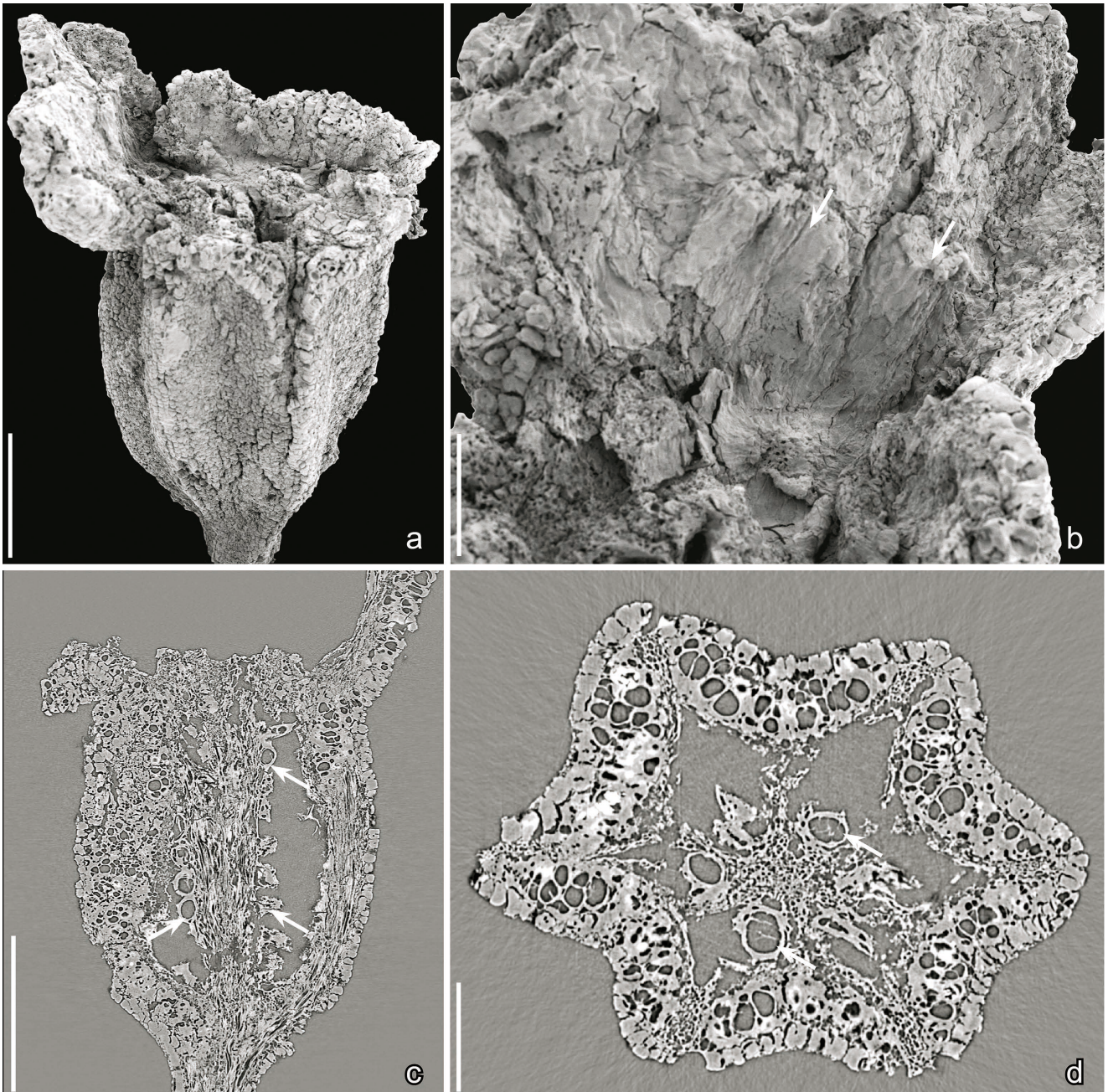


**Text-fig. 43.** Synchrotron radiation X-ray tomographic microscopy SRXTM images of “Tricarpellate flower sp. 2”; Catefica locality, Portugal. a) Lateral view of floral structure (volume rendering) showing the apical projection of the carpels and the semi-inferior organization; b) Apical view of floral structure (volume rendering) showing the triangular shape of the hypanthial rim, the tricarpellate ovary with a single apical style; note that one locule is fully developed while the other two are collapsed; note also slits of unknown nature in the corners of the triangular hypanthial rim (arrows); c) Transverse section (orthoslice xy0712) close to the floral apex showing the locule of the one fully developed carpel with ovules borne along ventral placentae; note amorphous substance (asterisk) associated with the developing ovules that fills part of the locule space; d) Longitudinal section (orthoslice xz0858) through the locule of the one fully developed carpel showing the semi-inferior organization and ovules arranged along the full length of the carpel; note amorphous substance (asterisk) associated with the developing ovules that fills part of the locule space; e) Tangential longitudinal section (orthoslice yz1019) through the one fully developed locule, showing the densely packed ovules and the amorphous substance (asterisk) with which they are associated. Specimen, Catefica 50-S174901 (a–e). Scale bars = 300  $\mu\text{m}$  (a–e).

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  $\mu\text{m}$  tall over most of the





**Text-fig. 44.** Scanning electron microscope (SEM, a, b) and synchrotron radiation X-ray tomographic microscopy (SRXTM, c, d) images of “Hexacarpellate flower”. a) Lateral view of flower showing epigynous organization with remains of tepals inserted at top of the hypanthium; b) Detail of apical part of flower showing laminar structures (arrows) that may be stamen bases, adhering to, or fused with, the tepals; c) Longitudinal section (orthoslice yz0540) of flower through the median plane showing the epigynous organization and central axis with ovules (arrows); d) Transverse section (orthoslice xy1250) through the ovary of the flower showing the hexagonal outline, the six locules and ovules (arrows) borne near the center of the gynoecium. Specimen, *Catefica* 153-S174313 (a–d). Scale bars = 300 µm (a, c), 100 µm (b, d).

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).

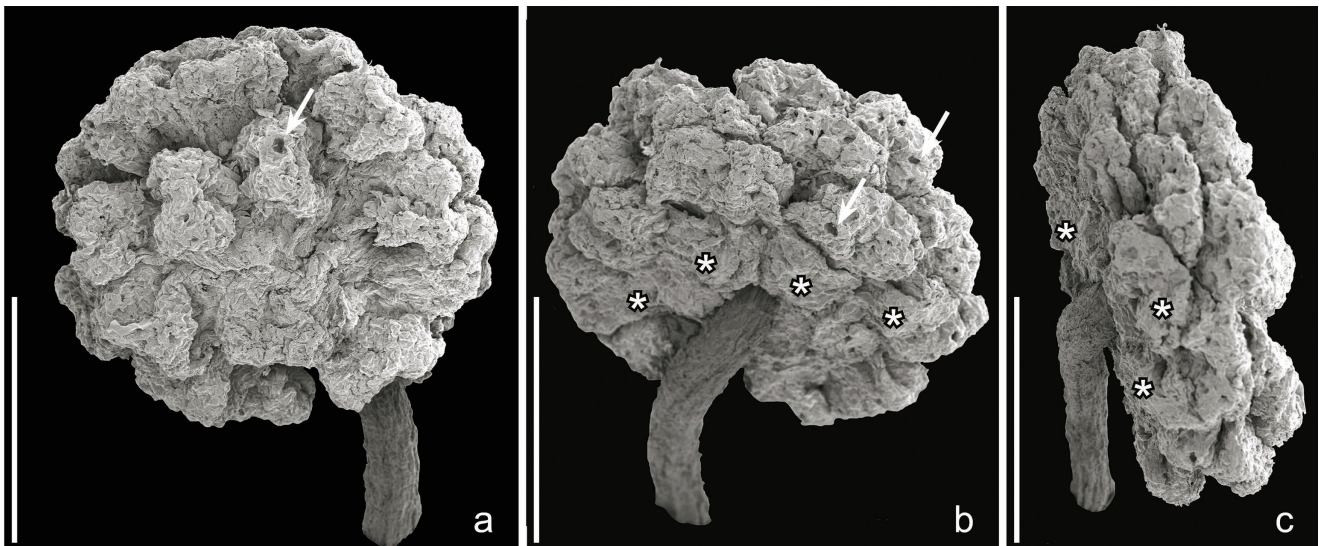
**Affinity and other occurrences.** Features of the seed coat, including the undulate anticlinal walls of the exotesta, indicate close relationship to other Early Cretaceous seeds that have been compared to seeds of extant Nymphaeales and Austrobaileyales (e.g., Friis et al. 2018c). The *Catefica* seeds 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



**Text-fig. 45.** Scanning electron microscope (SEM) images of “Staminate structure”; Catefica locality, Portugal. a–c) Staminate structure in oblique apical (a), oblique basal (b) and lateral (c) views showing distinct stalk and head with a cluster of about 20 stamens; note bracts at the base of the structure (asterisks) and probable secretory openings in the anther tissues (arrows). Specimen, Catefica 358-S135451 (a–c). Scale bars = 600  $\mu\text{m}$  (a–c).

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  $\mu\text{m}$  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 mesofossil 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

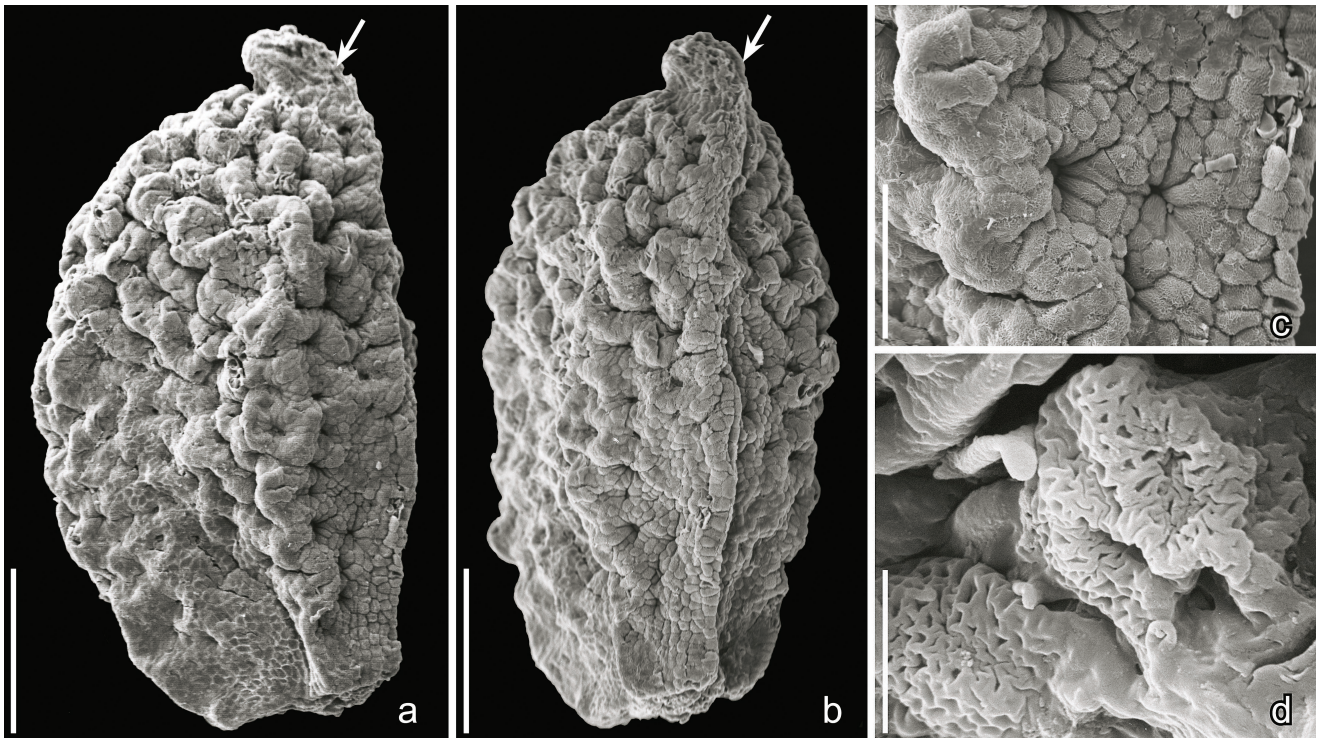
**Description and remarks.** In addition to the various exotestal seeds described separately above the Catefica mesofossil flora includes a few other kinds of exotestal seeds (not illustrated), each of which is represented by only a single specimen. The seeds are about 1 mm long, circular in lateral 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 mesofossil 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 mesofossil flora

In addition to the angiosperm remains described here, the Catefica mesofossil 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



**Text-fig. 46.** Scanning electron microscope (SEM) images of “Rugulate fruit”; Catefica locality, Portugal. **a, b**) Lateral (**a**) and ventral (**b**) views of a rugulate fruit showing the short extension of the sessile stigma at the apex (arrows); **c**) Irregular surface of fruit that probably reflects an irregular endocarp; note the isodiametric outlines of the epidermal cells; **d**) Semi-tectate reticulate pollen grains embedded in the remains of a secretion on the stigmatic surface. Specimen, Catefica 154-S101291 (a–d). Scale bars = 300  $\mu\text{m}$  (a, b), 100  $\mu\text{m}$  (c), 6  $\mu\text{m}$  (d).

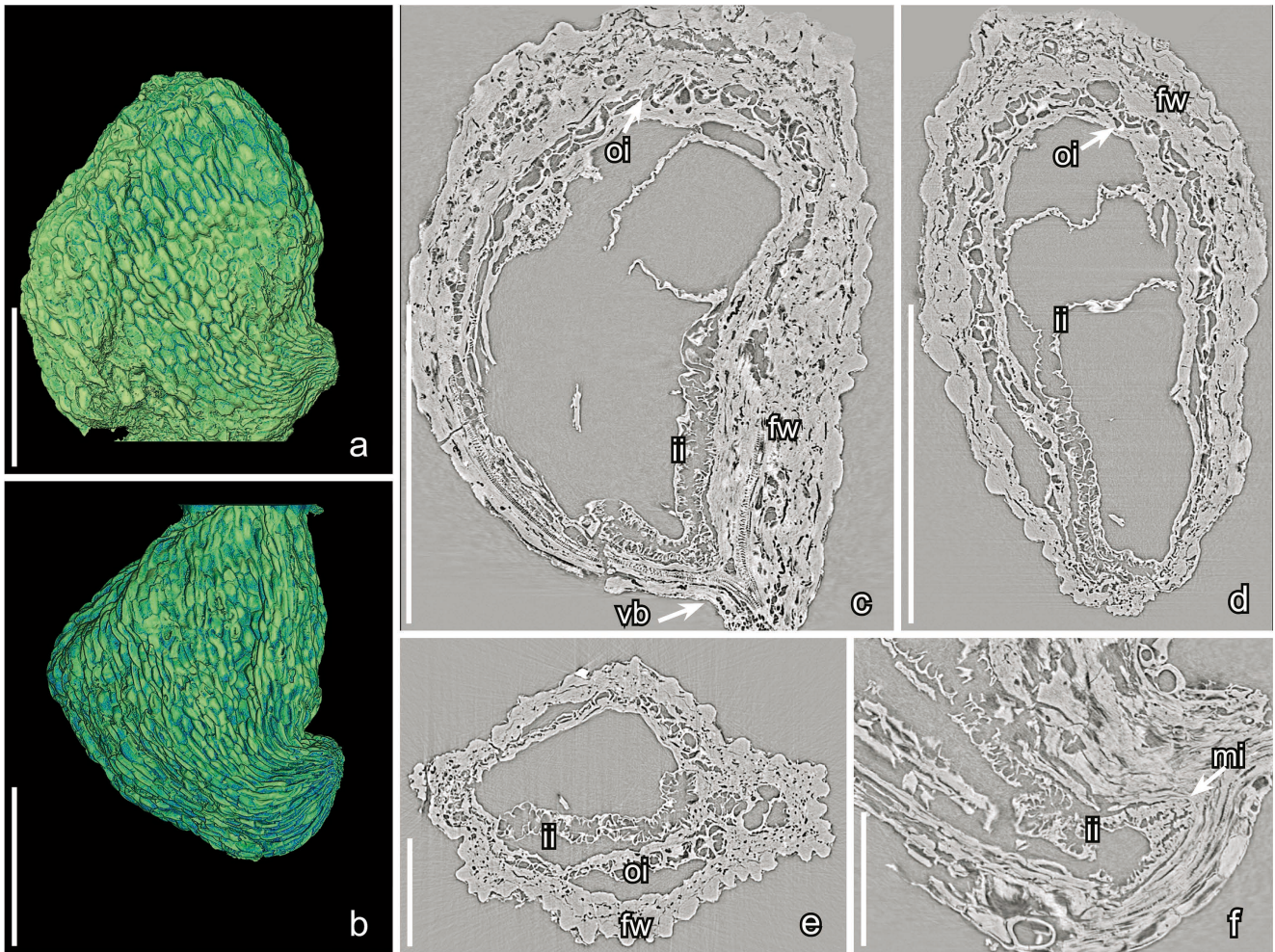
structures are also present. In addition to angiosperm flowers, fruits, inflorescences, infructescences, seeds and stamens, there are lycopsid and salvinialean megaspores, sporangia and sori of ferns, and cones, cone scales, seeds and pollen sacs of several kinds of conifers, as well as seeds assigned to the BEG group. Some of these fossils have already been formally described, such as most of the BEG seeds including *Battenispermum hirsutum* M.M.MENDES, K.R.PEDERSEN et E.M.FRIIS, *Buarcospermum tetragonium* E.M.FRIIS, K.R.PEDERSEN et P.R.CRANE, *Lignierispermum 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 sousai* J.KVAČEK et M.M.MENDES (Kvaček and Mendes 2020), the podocarpacean conifer *Friisia lusitanica* M.M.MENDES et J.KVAČEK (Mendes and Kvaček 2020), and the cheirolepidiacean 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



**Text-fig. 47.** Synchrotron radiation X-ray tomographic microscopy (SRXTM) images of “One-seeded fruit sp. 1”; Catefica locality, Portugal. a, b) Lateral view of fruits showing slightly sinuous ventral margin and the curved stalk; c, d) Longitudinal sections perpendicular to each other through the median part of fruit and its single seed (c, orthoslice yz0652, d, xz0739) showing the bitegmic seed closely adhering to the fruit wall (fw); the several cell layer thick outer integument (oi) and the membranous inner integument (ii); note the vascular bundle (vb) branching into a dorsal and lateral bundle near the base of the fruit; e) Transverse section (orthoslice xy0600) showing fruit wall (fw) and outer (oi) and inner (ii) integuments of the seed; f) Longitudinal section (orthoslice yz0871) through the micropylar region showing micropyle (mi) formed from membranous inner integument (ii). Specimens, Catefica 49-S174927 (a), Catefica 49-S174923 (b, f), Catefica 49-S174769 (c–e). Scale bars = 300  $\mu$ m (a–d), 100  $\mu$ m (e, f).

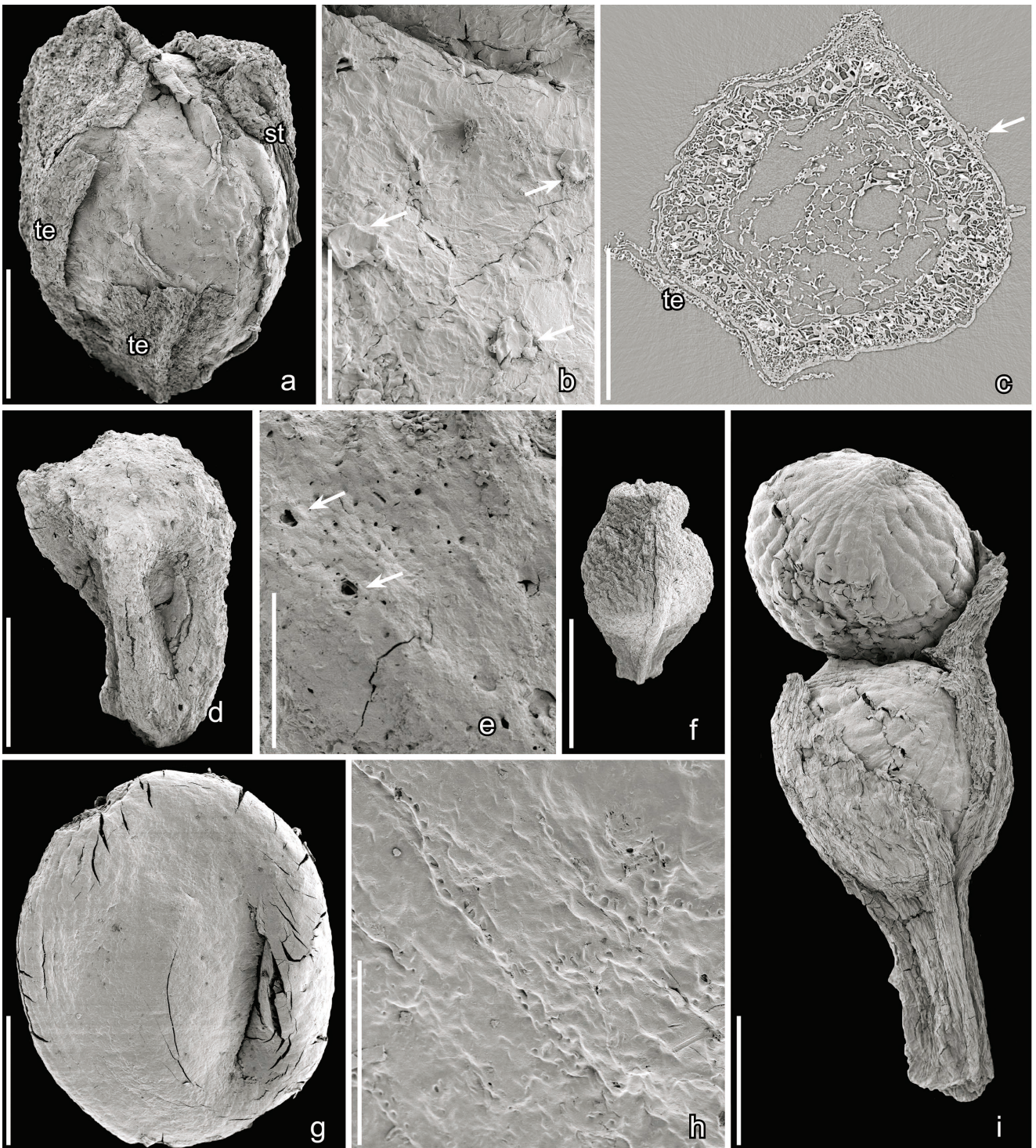
angiosperm count. Similarly, they account for 41 % of the specimens and 27 % of all angiosperm species in sample 49 (Text-fig. 51). Most abundant among the chloranthoid fossils are fruits and seeds of *Canrightia* (45 % of the chloranthoid specimens in the total count, 44 % of the chloranthoid specimens 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 Magnoliales (species of *Serialis*), Canellales (*Catanthus*), Laurales (*Saportanthus parvus*) and Piperales (*Aristospermum*, *Appomattoxia*,

*Goczania*). In sample 49 magnoliid 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 (*Elasmotemon*, *Endressianthus*, cf. *Endressistemon*, “Laminar stamen with monocolpate reticulate pollen”, *Valvidistemon*), 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.

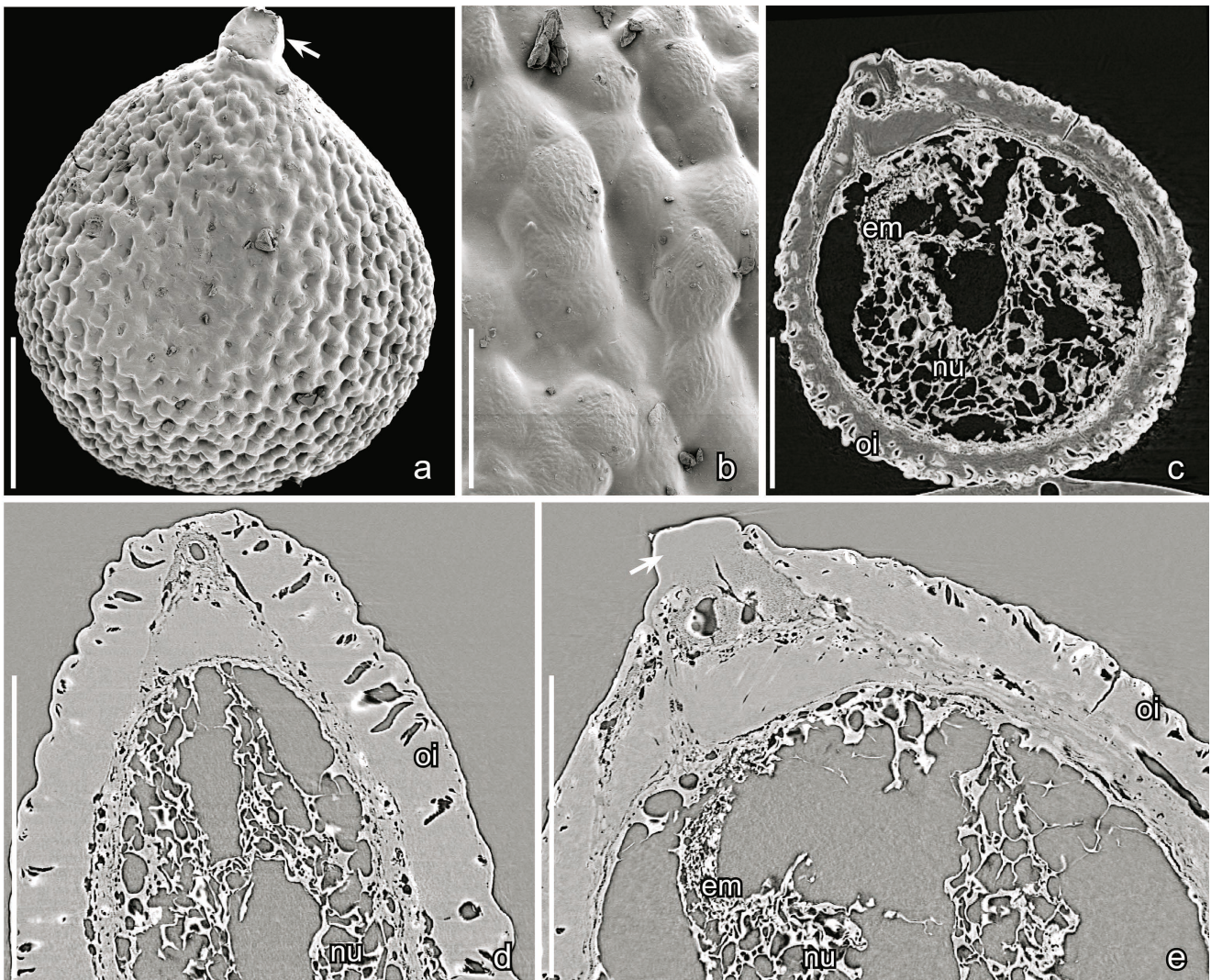
One species, *Paisia pantoporata*, is assigned unequivocally to eudicot angiosperms based on its pentamerous flowers and pantoporate pollen and a further five species are assigned to the eudicots based on their tricolpate



**Text-fig. 48.** Scanning electron microscope (SEM, a, b, d–i) and synchrotron radiation X-ray tomographic microscopy (SRXTM, c) images of “One-seeded fruit sp. 2” (a–c), “Unassigned, unnamed fruits” (d–f), *Pazliopsis* sp. (g, h) and “Follicular fruit with exotestal seeds” (i); Catefica locality, Portugal. a) Lateral view of fruit showing remains of tepals (te) and a single stamen (st); b) Detail of fruit surface showing short, scale-like, peltate trichomes (arrows); c) Transverse section (orthoslice xy0475) of fruit containing a single seed showing tepals (te) and fruit surface with peltate trichomes (arrow); note partial preservation of internal nutritive tissue; d) Fruit in lateral view showing the almost smooth epidermis with scattered openings; e) Detail of fruit surface from (d) showing the scattered openings in the epidermis interpreted as burst secretory cells (arrows); f) Dorsi-ventral view of tiny fruit with an irregular surface; g) Lateral view of exotestal seed assigned to cf. *Pazliopsis* sp.; h) Detail of fruit surface of seed in (g) showing faint facets of outer palisade layer with fine jigsaw-puzzle outlines of the anticlinal walls; i) Lateral view of fragmentary follicular fruit showing two exposed exotestal seeds. Specimens, Catefica 153-S174314 (a–c), Catefica 50-S170420 (d, e), Catefica 152-S174300 (f), Catefica 49-S172319 (g, h), Catefica MM158-P0272 (i). Scale bars = 300  $\mu$ m (a, c, d, f, g, i), 100  $\mu$ m (e), 50  $\mu$ m (b, h).

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



**Text-fig. 49.** Scanning electron microscope (SEM, a, b) and synchrotron radiation X-ray tomographic microscopy (SRXTM, c–e) images of “Foveolate seed sp. 1”; Catefica locality, Portugal. a) Lateral view of seed showing foveolate surface; note the slightly pointed hilar-micropylar region with the preservation of a presumed secretion (arrow) from the micropyle; b) Detail of seed surface showing shallow pitting and very faint outlines of the undulate anticlinal walls of the exotestal cells; c) Longitudinal section (volume rendering cut between orthoslices yz0450 and yz0460) through the middle of the seed showing the slightly pointed hilar-micropylar region and the rounded chalazal region; note the thick exotesta of the outer integument composed of thick-walled palisade-like cells (oi); note partial preservation of large cells of the nutritive tissue (nu) and the smaller cells of the embryo (em) at the micropylar end of the seed; d, e) Longitudinal sections (d, orthoslice xz0750, e, orthoslice yz0485) through middle of the seed perpendicular to each other showing the hilar-micropylar region with the preservation of a presumed secretion from micropyle (e, arrow), thick palisade-like cells of outer integument (oi), larger cells of the nutritive tissue (nu) and remains of the smaller cells of the embryo (em). Specimen, Catefica 49-S172316 (a–e). Scale bars = 300  $\mu\text{m}$  (a, c–e), 50  $\mu\text{m}$  (b).

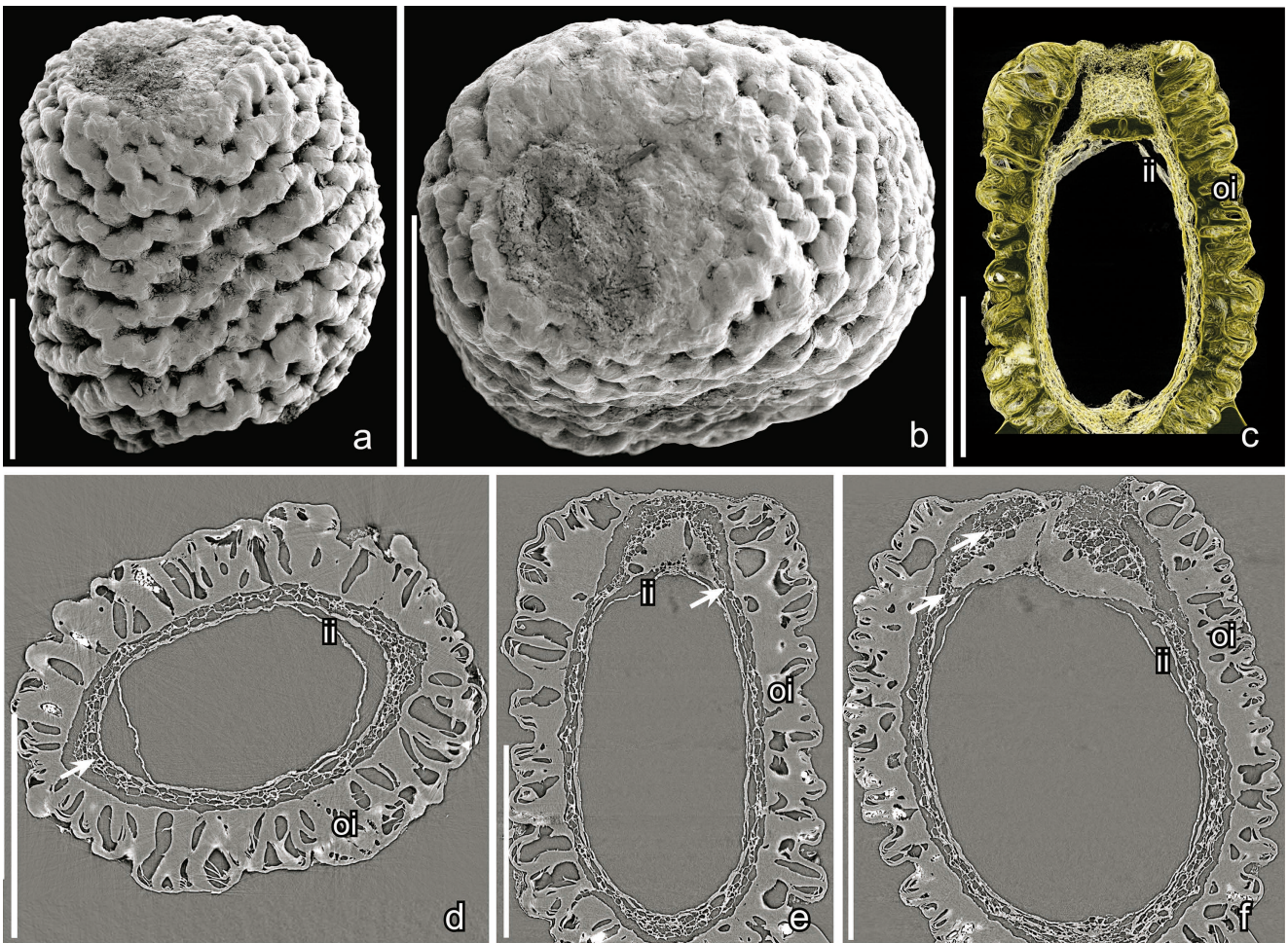
sp. 2”) and the small one-seeded fruits (“One-seeded fruit sp. 1”) may be monocotyledons. Others that we include as “Angiosperms of uncertain affinity”, such as *Pazliopsis* sp., the “Follicular fruit with exotestal seeds”, “Foveolate seed sp. 1”, “Foveolate seed sp. 2”, and other exotestal seeds, are probably related to ANA-grade or magnoliid angiosperms. Notably, in addition to the possible monocot representatives mentioned above, the only other taxon from Catefica assigned to the monocots is *Pennicarpus* sp.

#### Angiosperm pollen in the Catefica 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 Catefica mesofossil flora. The pollen grains are minute to small with the smallest ranging between 8–11  $\mu\text{m}$  in diameter (*Saportanthus parvus*, *Endressistemon portugallicus*, cf. *Endressistemon* sp. 1 and sp. 2) and the largest ranging between 24–26  $\mu\text{m}$  in diameter (*Clavatipollenites* sp. 2, *Tricolpate* sp. 2). Chloranthoid pollen ranges in diameter from 12–26  $\mu\text{m}$ , while the tricolpate pollen grains range between 19–25  $\mu\text{m}$ .

Of the different aperture configurations among the pollen types identified in the mesofossil flora, most (25, 75 %) are monoaperturate-reticulate (monocolpate, trichotomo-, 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



**Text-fig. 50.** Scanning electron microscope (SEM, a, b) and synchrotron radiation X-ray tomographic microscopy (SRXTM, c–f) images of “Foveolate seed sp. 2”; Catefica locality, Portugal. a, b) Lateral (a) and apical (b) views of seed showing the coarsely foveolate surface; note the truncate apex and the slightly depressed hilar-micropylar region; c) Longitudinal section (volume rendering cut between orthoslices xz0740 and xz0840) through the middle of seed showing the truncate apex with slightly depressed hilar-micropylar region and basal rounded chalazal region; note thick outer integument (oi) composed of an exotesta of thick-walled palisade-like cells and a thin inner integument (ii); d, e, f) Transverse (d, orthoslice xy0800) and longitudinal sections (e, orthoslice xz1100, f, orthoslice yz0800) through seed hilar-micropylar region, showing the exotesta comprised of the thick-walled palisade-like cells of the outer integument (oi), small, thin-walled meso- endotestal cells of the outer integument (arrows) and thin inner integument (ii). Specimen, Catefica 153-S172332 (a–f). Scale bars = 300  $\mu\text{m}$  (a–f).

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*, *Mugideiriflora portugallica*, *Paisia pantoporata* and the two tricarpeolate 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 assemblage. Interestingly, the stamen assemblage differs from that encountered in most other Early Cretaceous mesofossil floras in having a high proportion of stamens with a massive connective, as seen for example, in *Elasmotemon*

**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
<i>Mugideiriflora portugallica</i>		3	1															4
<i>Canrightia resinifera</i>	148		4	3		5	8	17	23	14	2	6			11	3		244
<i>Canrightia foveolata</i>	11						1	1										13
<i>Canrightia</i> sp.																		
<i>Canrightiopsis crassitesta</i>	6	1				2	1		1	1								12
<i>Canrightiopsis intermedia</i>		1																1
<i>Canrightiopsis</i> sp.	80	1	3		8	7	4	12	1	1			11	21	7	1	1	158
<i>Hedyflora crystallifera</i>	111	2		1	1		2			1			1			2		121
<i>Proencistemon portugallicus</i>	2	2	1						1									6
<i>Proencistemon</i> sp.	1																	1
<i>Clavatipollenites</i> type sp. 1		1																1
<i>Clavatipollenites</i> type sp. 2		1																1
<i>Clavatipollenites</i> type sp. 3		1																1
<i>Clavatipollenites</i> type sp. 4	1																	1
<i>Asteropollis</i> type sp. 1	3																	3
<i>Asteropollis</i> type sp. 2	1																	1
<i>Asteropollis/Clavatipollenites</i> type sp. 1		1																1
<i>Asteropollis/Clavatipollenites</i> type sp. 2	1																	1
<i>Asteropollis/Clavatipollenites</i> type sp. 3		1																1
<i>Serialis communis</i>	25																	25
<i>Serialis crassitesta</i>	36																	36
<i>Serialis</i> spp.	74	50	11	3			8		10					100				256
<i>Catanthus dolichostemon</i>	8	3	2				1						2					16
<i>Saportanthus parvus</i>	25	3			3		2	2	1			1	4					41
<i>Aristospermum huberi</i>	19	6	1	1	1		3		2		1		2	4			2	42
<i>Appomattoxia</i> sp.	3	1																4
<i>Goczania rugosa</i>	3	2																5
<i>Anacostia portugallica</i>														1	1		1	3
<i>Choffaticarpus compactus</i>	62	7						2	1									72
<i>Ibericarpus cuneiformis</i>	59	12																71
Stamen with zona-aperturate pollen	1																	1
<i>Elasmotemon paisii</i>	2	1		1														4
Laminar stamen/monocolpate reticulate pollen		1																1
<i>Valvidistemon globiferus</i>	1																	1
<i>Endressistemon cateficensis</i>	5																	5
cf. <i>Endressistemon</i> sp. 1	1																	1
cf. <i>Endressistemon</i> sp. 2	1																	1
cf. <i>Endressistemon</i> sp. 3	1																	1
<i>Pennicarpus tenuis</i>		2																2
<i>Kempia longicarpites</i>	1																	1
<i>Piercipollis</i> sp.	1	1																2
<i>Teebacia</i> sp.														1				1
Stamen with monocolpate reticulate pollen	1																	1
<i>Paisia pantoporata</i>	27	17		1				2	2	3				2			1	55
? <i>Paisia</i> sp.																		
<i>Paisia</i> -like	45									1								46
Tricolpate pollen sp. 1		1																1

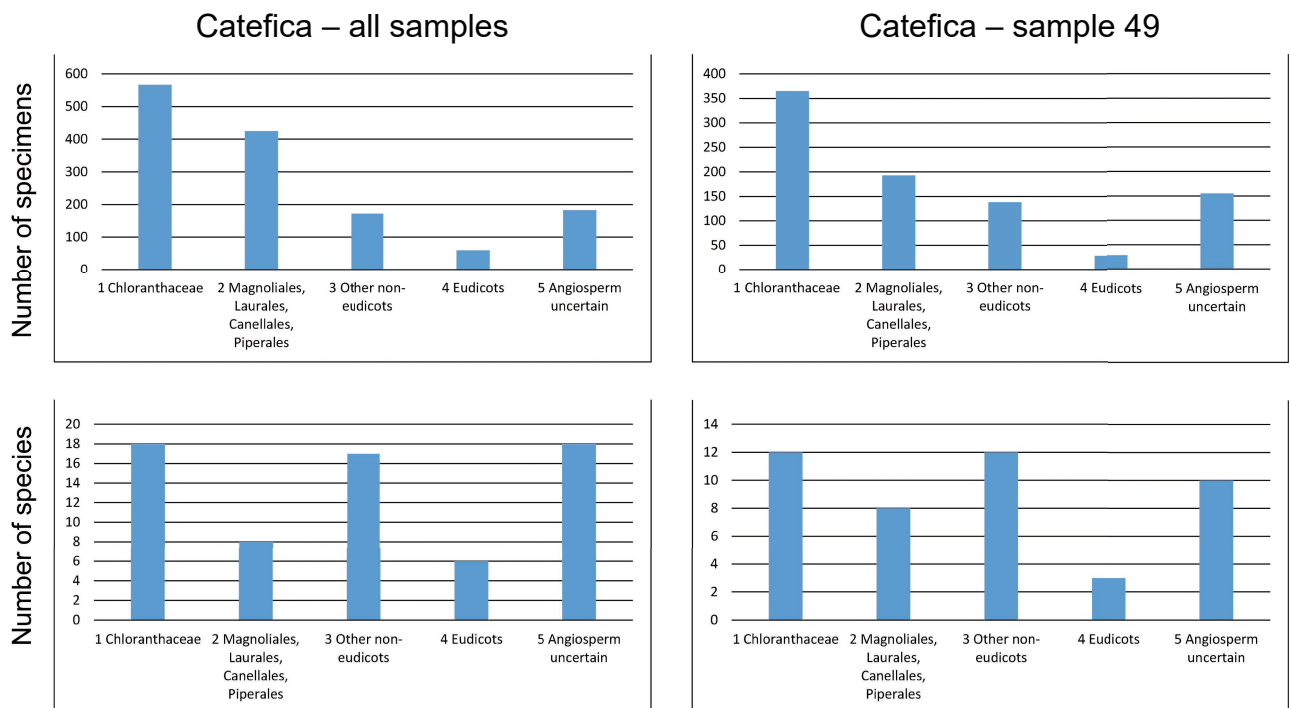


Table 2. continued

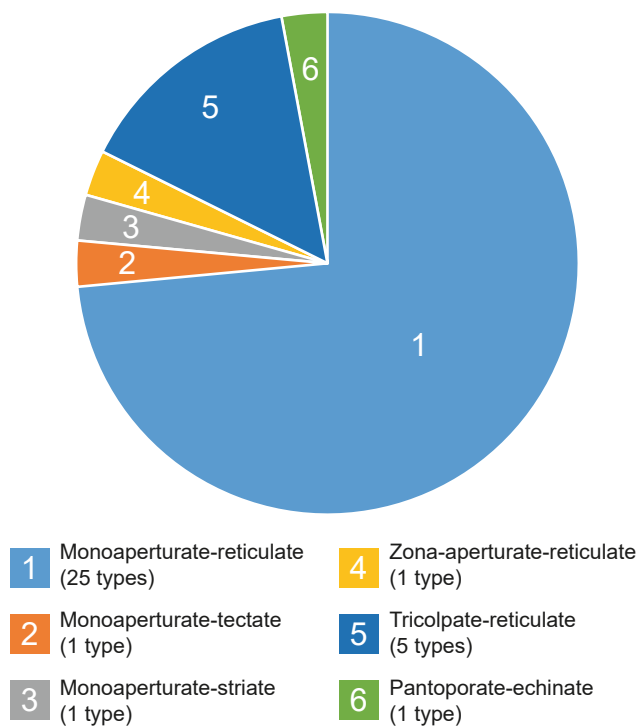
Taxon/Sample	49	50	150	151	152	153	154	242	342	343	358	359	360	361	362	381	382	all
Tricolpate pollen sp. 2						1												1
Tricolpate pollen sp. 3	1																	1
Tricolpate pollen sp. 4		1																1
Tricolpate pollen sp. 5	1																	1
Tricarpellate flower sp. 1	2	3							2									7
Tricarpellate flower sp. 2		1																1
Hexacarpellate flower						1												1
Staminate structure	1										1							2
Rugulate fruit							1											1
One-seeded fruit sp. 1	37					1			2					2				42
One-seeded fruit sp. 2						1								1	1			3
Fruit spp.	5	1				1								1				8
<i>Pazliopsis</i> sp.	16			1											1	2		20
Follicular fruit with exotestal seeds	36																	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
<b>TOTAL</b>	<b>880</b>	<b>128</b>	<b>23</b>	<b>11</b>	<b>13</b>	<b>20</b>	<b>31</b>	<b>36</b>	<b>46</b>	<b>21</b>	<b>4</b>	<b>7</b>	<b>12</b>	<b>137</b>	<b>25</b>	<b>8</b>	<b>5</b>	<b>1,407</b>

*paisii*, *Endressistemon cateficensis*, the three species of cf. *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.



Text-fig. 51. Number of specimens and number of species for the five categories of angiosperms distinguished from the Catefica mesofossil flora.



**Text-fig. 52. The distribution of aperture and tectum types among the 34 different kinds of angiosperm pollen encountered in 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 Almagem Formation. However, while the Torres Vedras mesofossil floras is in the Lower Almagem Formation, the Catefica mesofossil flora is probably slightly younger and is most likely from the basal part of Upper Almagem 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*, *Goczanina*, *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 *Aristospermum 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 *Catanthus dolichostemon*, *Canrightia resinifera*, *Canrightiopsis intermedia*, “Foveolate seed sp. 2”, *Hedyflora crystallifera*, *Serialis communis* and *Serialis crassitesta*, 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 Arazede 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 than 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 of basal eudicots, probably close to extant Ranunculales. The other eudicot fossils in the Catefica mesofossil flora are represented only by stamens and pollen. For these, characters are insufficient for a precise systematic assessment, but there are no fossils in the Catefica mesofossil flora that indicate the presence of 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.

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## References

- von Balthazar, M., Pedersen, K. R., Crane, P. R., Stamparoni, M., Friis, E. M. (2007): *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of eastern North America. – *American Journal of Botany*, 94: 2041–2053.  
<https://doi.org/10.3732/ajb.94.12.2041>
- von Balthazar, M., Pedersen, K. R., Crane, P. R., Friis, E. M. (2008): *Carpestella lacunata* gen. et sp. nov., a new basal angiosperm flower from the Early Cretaceous (Early to Middle Albian) of eastern North America. – *International Journal of Plant Sciences*, 169: 890–898.  
<https://doi.org/10.1086/589692>
- von Balthazar, M., Crane, P. R., Pedersen, K. R., Friis, E. M. (2011): New flowers of Laurales from the Early Cretaceous (Early to Middle Albian) of eastern North America. – In: Wanntorp, L., Ronse De Craene, L. P. (eds), *Flowers on the tree of life*. Cambridge University Press, Cambridge, pp. 49–87.  
<https://doi.org/10.1017/CBO9781139013321.003>

- Brenner, G. J. (1963): The spores and pollen of the Potomac Group of Maryland. – *Bulletin, Maryland Department of Geology, Mines and Water Resources*, 27: 1–215.
- Buchner, R., Halbritter, H., Pfundner, G., Hesse, M. (1990): Pollen of *Limnanthes douglasii*: a reinvestigation. – *Grana*, 29: 207–211.  
<https://doi.org/10.1080/00173139009427753>
- Canright, J. (1952): The comparative morphology and relationships of the Magnoliaceae. I. Trends of specialization in the stamens. – *American Journal of Botany*, 39: 484–497.  
<https://doi.org/10.1002/j.1537-2197.1952.tb13058.x>
- Carlquist, S. (1961): Pollen morphology of Rapateaceae. – *Aliso*, 5: 39–66.  
<https://doi.org/10.5642/aliso.19610501.07>
- Corner, E. J. H. (1976): *The Seeds of Dicotyledons*. – Cambridge University Press, Cambridge, 312 pp.
- Crane, P. R. (1987): Vegetational consequences of the angiosperm diversification. – In: Friis, E. M., Chaloner, W. G., Crane, P. R. (eds), *The Origins of Angiosperms and their Biological Consequences*. Cambridge University Press, Cambridge, pp. 107–144.
- Crane, P. R., Friis, E. M., Pedersen, K. R. (1989): Reproductive structure and function in Cretaceous Chloranthaceae. – *Plant Systematics and Evolution*, 165: 211–226.  
<https://doi.org/10.1007/BF00936003>
- Crane, P. R., Friis, E. M., Pedersen, K. R. (1994): Paleobotanical evidence on the early radiation of magnoliid angiosperms. – In: Endress, P. K., Friis, E. M. (eds), *Early Evolution of Flower*. *Plant Systematics and Evolution*, Supplement 8: 51–72.  
[https://doi.org/10.1007/978-3-7091-6910-0\\_4](https://doi.org/10.1007/978-3-7091-6910-0_4)
- Crane, P. R., Lidgard, S. H. (1989): Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. – *Science*, 246: 675–678.  
<https://doi.org/10.1126/science.246.4930.675>
- Dilcher, D. L. (1979): Early angiosperm reproduction: an introductory report. – *Review of Palaeobotany and Palynology*, 27: 291–328.  
[https://doi.org/10.1016/0034-6667\(79\)90015-0](https://doi.org/10.1016/0034-6667(79)90015-0)
- Dinis, J. L., Oliveira, F. P., Rey, J., Duarte, I. L. (2010): Finding geological heritage: Legal issues on private property and fieldwork. The case of outstanding early angiosperms (Barremian to Albian, Portugal). – *Geoheritage*, 2: 77–90.  
<https://doi.org/10.1007/s12371-010-0013-x>
- Dinis, J. L., Rey, J., Cunha, P. P., Callapez, P., Pena Dos Reis, R. (2008): Stratigraphy and allogenic controls of the western Portugal Cretaceous: an updated synthesis. – *Cretaceous Research*, 29: 772–780.  
<https://doi.org/10.1016/j.cretres.2008.05.027>
- Doyle, J. A. (1969): Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. – *Journal of the Arnold Arboretum*, 50: 1–35.  
<https://doi.org/10.5962/bhl.part.24686>
- Doyle, J. A., Endress, P. K. (2014): Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: ANITA lines and relatives of Chloranthaceae. – *International Journal of Plant Sciences*, 175: 555–600.  
<https://doi.org/10.1086/675935>
- Doyle, J. A., Endress, P. K. (2018): Phylogenetic analyses of Cretaceous fossils related to Chloranthaceae and their evolutionary implications. – *The Botanical Review*, 84: 156–202.  
<https://doi.org/10.1007/s12229-018-9197-6>
- Doyle, J. A., Hickey, L. J. (1976): Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. – In: Beck, C. B. (eds), *Origin and early evolution of angiosperms*. Columbia University Press, New York, pp. 139–206.
- Doyle, J. A., Hotton, C. L., Ward, J. V. (1990): Early Cretaceous tetrads, zonaulculate pollen, and Winteraceae. I. Taxonomy, morphology and ultrastructure. – *American Journal of Botany*, 77: 1544–1557.  
<https://doi.org/10.1002/j.1537-2197.1990.tb11395.x>
- Doyle, J. A., Jardiné, S., Doerenkamp, A. (1982): *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy of paleoenvironments of northern Gondwana. – *Bulletin Centres de Recherches Exploration-Production Elf-Aquitaine*, 6: 39–117.
- Doyle, J. A., Robbins, E. I. (1977): Angiosperm pollen zonation of the continental Cretaceous of the Atlantic coastal plain and its application to deep wells in the Salisbury embayment. – *Palynology*, 1: 41–78.  
<https://doi.org/10.1080/01916122.1977.9989150>
- Doyle, J. A., Le Thomas, A. (2012): Evolution and phylogenetic significance of pollen in Annonaceae. – *Botanical Journal of the Linnean Society*, 169: 190–221.  
<https://doi.org/10.1111/j.1095-8339.2012.01241.x>
- Drinnan, A. N., Crane, P. R., Pedersen, K. R., Friis, E. M. (1991): Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. – *American Journal of Botany*, 78: 153–176.  
<https://doi.org/10.1002/j.1537-2197.1991.tb15743.x>
- Eklund, H., Friis, E. M., Pedersen, K. R. (1997): Chloranthaceous floral structures from the Late Cretaceous of Sweden. – *Plant Systematics and Evolution*, 207: 13–42.  
<https://doi.org/10.1007/BF00985207>
- Endress, P. K. (1987): The Chloranthaceae: reproductive structures and phylogenetic position. – *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 109: 153–226.
- Endress, P. K., Doyle, J. A. (2015): Ancestral traits and specializations in the flowers of the basal grade of living angiosperms. – *Taxon*, 65: 1093–1116.  
<https://doi.org/10.1002/646.1>
- Endress, P. K., Hufford, L. D. (1989): The diversity of stamen structures and dehiscence patterns among Magnoliidae. – *Botanical Journal of the Linnean Society*, 100: 45–85.  
<https://doi.org/10.1111/j.1095-8339.1989.tb01709.x>
- Fontaine, W. M. (1889): *The Potomac or younger Mesozoic flora*. – *Monographs of the United States Geological Survey*, 15: 1–377, pls 1–180.  
<https://doi.org/10.5962/bhl.title.36034>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (1988): Reproductive structure of Cretaceous Platanaceae. – *Biologiske Skrifter, det Kongelige Danske Videnskabernes Selskab*, 31: 1–56.

- Friis, E. M., Crane, P. R., Pedersen, K. R. (1997): *Anacostia*, a new basal angiosperm from the Early Cretaceous of North America and Portugal with trichotomocolpate/monocolpate pollen. – *Grana*, 36: 225–244.  
<https://doi.org/10.1080/00173139709362611>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2011): Early flowers and angiosperm evolution. – Cambridge University Press, Cambridge, 585 pp.  
<https://doi.org/10.1017/CBO9780511980206>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2017): *Sporanthus*, an extinct genus of Laurales from the Early Cretaceous of Portugal. – *International Journal of Plant Sciences*, 178: 650–672.  
<https://doi.org/10.1086/693108>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2018b): *Rightcarnia* and *Kvacekispermum*: Early Cretaceous seeds from eastern North America and Portugal provide further evidence of the early chloranthoid diversification. – *Fossil Imprint*, 74: 65–76.  
<https://doi.org/10.2478/if-2018-0006>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2018c): Extinct taxa of exotestal seeds close to Austrobaileyales and Nymphaeales from the Early Cretaceous of Portugal. – *Fossil Imprint*, 74: 135–158.  
<https://doi.org/10.2478/if-2018-0010>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2018d): *Tanispermum*, a new genus of distinctive hemi-orthotropous to hemi-anatropous angiosperm seeds from the Early Cretaceous of eastern North America. – *American Journal of Botany*, 105: 1369–1388.  
<https://doi.org/10.1002/ajb2.1124>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2018e): Fossil seeds with affinities to Austrobaileyales and Nymphaeales from the Early Cretaceous (early-middle Albian) of Virginia and Maryland, U.S.A.: new evidence for extensive extinction near the base of the angiosperm tree. – In: Krings, M., Harper, C. J., Cúneo, N. R., Rothwell, G. W. (eds), *Transformative Paleobotany: Papers to Commemorate the Life and Legacy of Thomas N. Taylor*. Academic Press, London, pp. 417–435.  
<https://doi.org/10.1016/B978-0-12-813012-4.00017-6>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2019a): The Early Cretaceous mesofossil flora of Torres Vedras (NE of Forte da Forca), Portugal: a palaeofloristic analysis of an early angiosperm community. – *Fossil Imprint*, 75: 153–257.  
<https://doi.org/10.2478/if-2019-0013>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2019b): *Hedyosmum*-like fossils in the Early Cretaceous diversification of angiosperms. – *International Journal of Plant Sciences*, 180: 232–239.  
<https://doi.org/10.1086/701819>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2019c): Extinct diversity among Early Cretaceous angiosperms: mesofossil evidence of early Magnoliales from Portugal. – *International Journal of Plant Sciences*, 180: 93–127.  
<https://doi.org/10.1086/701319>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2019d): The endothelium in seeds of early angiosperms. – *New Phytologist*, 224: 1419–1424.  
<https://doi.org/10.1111/nph.16024>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2019e): Chlamydospermous seeds document the diversity and abundance of extinct gnetalean relatives in Early Cretaceous vegetation. – *International Journal of Plant Sciences*, 180: 643–666.  
<https://doi.org/10.1086/704356>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2020a): Multiparted, apocarpous flowers from the Early Cretaceous of eastern North America and Portugal. – *Fossil Imprint*, 76: 279–296.  
<https://doi.org/10.37520/fi.2020.023>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2020b): *Mello-niflora*, a new extinct multiparted flower from the Early Cretaceous of Virginia. – *International Journal of Plant Sciences*, 181: 887–897.  
<https://doi.org/10.1086/710490>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2020c): *Catanthus*, an extinct magnoliid flower from the Early Cretaceous of Portugal. – *International Journal of Plant Sciences*, 182(online): 18 pp. [online version of Friis et al. (2021), which meets the requirements of ICN for effectively published publication]  
<https://doi.org/10.1086/711081>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2021): *Catanthus*, an extinct magnoliid flower from the Early Cretaceous of Portugal. – *International Journal of Plant Sciences*, 182: 28–45.  
<https://doi.org/10.1086/711081>
- Friis, E. M., Crane, P. R., Pedersen, K. R. (2022): Early and mid-Cretaceous Aristolochiaceae seeds from Portugal and North America. – *International Journal of Plant Sciences*, 183: 587–603.  
<https://doi.org/10.1086/721259>
- Friis, E. M., Crane, P. R., Pedersen, K. R., Stampanoni, M., Marone, F. (2015b): Exceptional preservation of tiny embryos documents seed dormancy in early angiosperms. – *Nature* 528, 551–554.  
<https://doi.org/10.1038/nature16441>
- Friis, E. M., Crane, P. R., Pedersen, K. R., Bengtson, S., Donoghue, P. C. J., Grimm, G. W., Stampanoni, M. (2007): Phase-contrast X-ray microtomography links Cretaceous seeds with Gnetales and Bennettitales. – *Nature*, 450: 549–552.  
<https://doi.org/10.1038/nature06278>
- Friis, E. M., Eklund, H., Pedersen, K. R., Crane, P. R. (1994): *Virginianthus calycanthoides* gen. et sp. nov. – a calycanthaceous flower from the Potomac Group (Early Cretaceous) of Eastern North America. – *International Journal of Plant Sciences*, 155: 772–785.  
<https://doi.org/10.1086/297217>
- Friis, E. M., Grimm, G. W., Mendes, M. M., Pedersen, K. R. (2015a): *Canrightiopsis*, a new Early Cretaceous fossil with *Clavatipollenites*-type pollen bridge the gap between extinct *Canrightia* and extant Chloranthaceae. – *Grana*, 54: 184–212.  
<https://doi.org/10.1080/00173134.2015.1060750>
- Friis, E. M., Marone, F., Pedersen, K. R., Crane, P. R., Stampanoni, M. (2014): Three-dimensional visualization of fossil flowers, fruits, seeds and other plant remains using synchrotron radiation X-ray tomographic microscopy (SRXTM): New insights into Cretaceous plant diversity. – *Journal of Paleontology*, 88: 684–701.  
<https://doi.org/10.1666/13-099>

- Friis, E. M., Mendes, M. M., Pedersen, K. R. (2018a): *Paisia*, an Early Cretaceous eudicot angiosperm flower with pantoporate pollen from Portugal. – *Grana*, 57: 1–15. <https://doi.org/10.1080/00173134.2017.1310292>
- Friis, E. M., Pedersen, K. R. (2011): *Canrightia resinifera* gen. et sp. nov., a new extinct angiosperm with *Retimonocolpites*-type pollen from the Early Cretaceous of Portugal: missing link in the eumagnoliid tree? – *Grana*, 50: 3–29. <https://doi.org/10.1080/00173134.2011.559728>
- Friis, E. M., Pedersen, K. R., von Balthazar, M., Grimm, G. W., Crane, P. R. (2009a): *Monetianthus mirus* gen. et sp. nov., a nymphaealean flower from the Early Cretaceous of Portugal. – *International Journal of Plant Sciences*, 170: 1086–1101. <https://doi.org/10.1086/605120>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (1995): *Appomattoxia ancistrophora* gen. et sp. nov., a new Early Cretaceous plant with similarities to *Circaeaster* and extant Magnoliidae. – *American Journal of Botany*, 82: 933–943. <https://doi.org/10.1002/j.1537-2197.1995.tb15710.x>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (1999): Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras. – *Annals of the Missouri Botanical Garden*, 86: 259–296. <https://doi.org/10.2307/2666179>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (2000): Fossil floral structures of a basal angiosperm with monocolpate, reticulate-acolumellate pollen from the Early Cretaceous of Portugal. – *Grana*, 39: 226–245. <https://doi.org/10.1080/00173130052017262>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (2006): Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232: 251–293. <https://doi.org/10.1016/j.palaeo.2005.07.006>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (2009b): Early Cretaceous mesofossils from Portugal and eastern North America related to the Bennettitales-Erdtmanithecales-Gnetales group. – *American Journal of Botany*, 96: 252–283. <https://doi.org/10.3732/ajb.0800113>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (2010a): Diversity in obscurity: Fossil flowers and the early history of angiosperms. – *Philosophical Transactions of the Royal Society, B*, 365: 369–382. <https://doi.org/10.1098/rstb.2009.0227>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (2010b): Cretaceous diversification of angiosperms in the western part of the Iberian Peninsula. – *Review of Palaeobotany and Palynology*, 162: 341–361. <https://doi.org/10.1016/j.revpalbo.2009.11.009>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (2013): New diversity among chlamydospermous seeds from the Early Cretaceous of Portugal and North America. – *International Journal of Plant Sciences*, 173: 530–558. <https://doi.org/10.1086/668250>
- Friis, E. M., Pedersen, K. R., Crane, P. R. (2016): *Kenilanthus*, a new eudicot flower with tricolpate pollen from the Early Cretaceous (early-middle Albian) of eastern North America. – *Grana*, 56: 161–173. <https://doi.org/10.1080/00173134.2016.1158863>
- Goldblatt, P., Le Thomas, A. (1997): Palynology, phylogenetic reconstruction, and classification of the Afro-Madagascan genus *Aristea* (Iridaceae). – *Annals of the Missouri Botanical Garden*, 84: 263–284. <https://doi.org/10.2307/2400004>
- González, F., Rudall, P. J. (2003): Structure and development of the ovule and seed in Aristolochiaceae, with particular reference to *Saruma*. – *Plant Systematics and Evolution*, 241: 223–244. <https://doi.org/10.1007/s00606-003-0050-x>
- Grayum, M. H. (1992): Comparative external pollen ultrastructure of the Araceae and putatively related taxa. – *Monographs on Systematic Botany of the Missouri Botanical Garden*, 43: 1–167.
- Groot, J. J., Groot, C. R. (1962): Plant microfossils from Aptian, Albian and Cenomanian deposits of Portugal. – *Comunicações dos Serviços Geológicos de Portugal*, 46: 133–176.
- Halbritter, H. (2016): *Austrobaileya scandens*. – PalDat – A palynological database. [accessed May 23, 2021] [https://www.paldat.org/pub/Austrobaileya\\_scandens/300275](https://www.paldat.org/pub/Austrobaileya_scandens/300275)
- Harley, M. M., Baker, W. J. (2001): Pollen aperture morphology in Arecaceae: application within phylogenetic analyses, and a summary of the fossil record of palm-like pollen. – *Grana*, 40: 45–77. <https://doi.org/10.1080/00173130152591877>
- Hasenboehler, B. (1981): Étude paléobotanique et palynologique de l’Albien et du Cenomanien du “Bassin occidental Portugais” au sud de l’accident de Nazaré (Province d’Estremadura, Portugal). – Université Pierre et Marie Curie, Paris, 319 pp.
- Hedlund, R. W., Norris, G. (1968): Spores and pollen grains from Fredericksburgian (Albian) strata, Marshall County, Oklahoma. – *Pollen et Spores*, 10: 129–159.
- Heer, O. (1881): Contributions a la flore fossile du Portugal. – Section des Travaux Géologiques du Portugal, Lisbonne, 51 pp. <https://doi.org/10.5962/bhl.title.78053>
- Heimhofer, U., Hochuli, P. A., Burla, S., Dinis, J. M. L., Weissert, H. (2005): Timing of Early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change. – *Geology*, 33: 141–144. <https://doi.org/10.1130/G21053.1>
- Heimhofer, U., Hochuli, P. A., Burla, S., Weissert, H. (2007): New records of Early Cretaceous angiosperm pollen from Portuguese coastal deposits: Implications for the timing of the early angiosperm radiation. – *Review of Palaeobotany and Palynology*, 144: 39–76. <https://doi.org/10.1016/j.revpalbo.2005.09.006>
- Henderson, R. J. F. (1982): *Romnalda grallata*, a new species of the Xanthorrhoeaceae from Queensland. – *Kew Bulletin*, 37: 229–235. <https://doi.org/10.2307/4109965>
- Hesse, M., Bogner, J., Halbritter, H., Weber, M. (2001): Palynology of the perigoniata Aroideae: *Zamioculcas*, *Gonatopus* and *Stylochaeton* (Araceae). – *Grana*, 40: 26–34. <https://doi.org/10.1080/00173130152591859>

- Hesse, M., Zetter, R. (2005): Ultrastructure and diversity of recent and fossil zona-aperturate pollen grains. – *Plant Systematics and Evolution*, 255: 145–176.  
<https://doi.org/10.1007/s00606-005-0358-9>
- Hickey, L. J., Doyle, J. A. (1977): Early Cretaceous fossil evidence for angiosperm evolution. – *The Botanical Review*, 43: 3–104.  
<https://doi.org/10.1007/BF02860849>
- Horikx, M., Hochuli, P. A., Feist-Burkhardt, S., Heimhofer, U. (2016): Albian angiosperm pollen from shallow marine strata in the Lusitanian Basin, Portugal. – *Review of Palaeobotany and Palynology*, 228: 67–92.  
<https://doi.org/10.1016/j.revpalbo.2015.12.008>
- Hughes, N. F. (1976): *Palaeobiology of Angiosperm Origins*. – Cambridge University Press, Cambridge, 242 pp.
- Ibrahim, M. I. A., Zobia, M. K., El-Noamani, Z. M., Tahoun, S. S. (2015): A review of the angiosperm pollen genus *Cretacaeiporites* Herngreen, with one new species from the Upper Cretaceous of Egypt. – *Palynology*, 41: 101–116.  
<https://doi.org/10.1080/01916122.2015.1093561>
- Igersheim, A., Buzgo, M., Endress, P. K. (2001): Gynoecium diversity and systematics in basal monocots. – *Botanical Journal of the Linnean Society*, 136: 1–65.  
<https://doi.org/10.1111/j.1095-8339.2001.tb00555.x>
- Juhász, M., Góczán, F. (1985): Comparative study of Albian monosulcate angiosperm pollen grains. – *Acta Biologica Szegediensis*, 31: 147–172.
- Kvaček, J., Mendes, M. M. (2020): *Callialastrobus sousai* gen. et sp. nov., a new araucariaceous pollen cone from the Early Cretaceous of Catefica (Lusitanian Basin, western Portugal) bearing *Callialasporites* and *Araucariacites* pollen. – *Review of Palaeobotany and Palynology*, 283: 104313 (9 pp.).  
<https://doi.org/10.1016/j.revpalbo.2020.104313>
- Kvaček, J., Mendes, M. M. (2021): A new Cheirolepidiaceae conifer *Watsoniocladius cunhae* sp. nov. from the Early Cretaceous (late Aptian–early Albian) of western Portugal. – *Review of Palaeobotany and Palynology*, 295: 104519 (11 pp.).  
<https://doi.org/10.1016/j.revpalbo.2021.104519>
- Lidgard, S., Crane, P. R. (1990): Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. – *Paleobiology*, 16: 77–93.  
<https://doi.org/10.1017/S009483730000974X>
- Llorens, M., Perez Loinaze, V. S. (2015): Late Aptian angiosperm pollen grains from Patagonia: Earliest steps in flowering plant evolution at middle latitudes in southern South America. – *Cretaceous Research*, 57: 66–78.  
<https://doi.org/10.1016/j.cretres.2015.07.019>
- Lupia, R., Crane, P. R., Lidgard, S. (2000): Angiosperm diversification and Cretaceous environmental change. – In: Culver, S. J., Rawson, R. F. (eds), *Biotic Response to Global Change: The Last 145 Million Years*. Cambridge University Press, Cambridge, pp. 307–222.  
<https://doi.org/10.1017/CBO9780511535505.016>
- May, F. (1975): *Dichastopollenites reticulatus*, gen. et sp. nov. – potential Cenomanian guide fossil from southern Utah and northeastern Arizona. – *Journal of Paleontology*, 49: 528–533.
- Médus, J., Berthou, P. Y. (1980): Palynoflores dans la coupe de l’Albien de Foz do Folcão (Portugal). – *Geobios*, 13: 263–269.  
[https://doi.org/10.1016/S0016-6995\(80\)80034-9](https://doi.org/10.1016/S0016-6995(80)80034-9)
- Mendes, M. M., Barrón, E., Batten, D. J., Pais, J. (2017): A new species of the spore genus *Costatoperforosporites* from Early Cretaceous deposits in Portugal and its taxonomic and palaeoenvironmental significance. – *Grana*, 56: 401–409.  
<https://doi.org/10.1080/00173134.2016.1269189>
- Mendes, M. M., Barrón, E., Dinis, P., Rey, J., Batten, D. J. (2018a): A new palynoflora from upper Barremian-lower Aptian rocks at Casal do Borracho, Torres Vedras, western Portugal, and its palaeoecological significance. – *Cretaceous Research*, 90: 363–374.  
<https://doi.org/10.1016/j.cretres.2018.06.012>
- Mendes, M. M., Dinis, P., Kvaček, J. (2018b): Some conifers from the Early Cretaceous (late Aptian–early Albian) of Catefica, Lusitanian Basin, western Portugal. – *Fossil Imprint*, 74: 317–326.  
<https://doi.org/10.2478/if-2018-0019>
- Mendes, M. M., Dinis, J., Pais, J., Friis, E. M. (2011): Early Cretaceous flora from Vale Painho (Lusitanian Basin, western Portugal): an integrated palynological and mesofossil study. – *Review of Palaeobotany and Palynology*, 166: 152–162.  
<https://doi.org/10.1016/j.revpalbo.2011.04.003>
- Mendes, M. M., Dinis, J., Pais, J., Friis, E. M. (2014): Vegetational composition of the Early Cretaceous Chicalhão flora (Lusitanian Basin, western Portugal) based on palynological and mesofossil assemblages. – *Review of Palaeobotany and Palynology*, 200: 65–81.  
<https://doi.org/10.1016/j.revpalbo.2013.08.003>
- Mendes, M. M., Friis, E. M. (2018): The Nossa Senhora da Luz flora from the Early Cretaceous (early Aptian–late Albian) of Juncal in the western Portuguese Basin. – *Acta Palaeobotanica*, 58: 159–174.  
<https://doi.org/10.2478/acpa-2018-0015>
- Mendes, M. M., Kvaček, J. (2020): *Friisia lusitanica* gen. et sp. nov., a new podocarpaceous ovuliferous cone from the Lower Cretaceous of Lusitanian Basin, western Portugal. – *Review of Palaeobotany and Palynology*, 108: 154352 (10 pp.).  
<https://doi.org/10.1016/j.cretres.2019.104352>
- Mendes, M. M., Pedersen, K. R., Friis, E. M. (2020): *Battenisperrum hirsutum* gen. et sp. nov., a new Early Cretaceous seed from Portugal with chlamydospermous organisation. – *Cretaceous Research*, 109: 104376 (8 pp.).  
<https://doi.org/10.1016/j.cretres.2020.104376>
- Mendes, M. M., Polette, F., Cunha, P. P., Dinis, P., Batten, D. J. (2019): A new Hauterivian palynoflora from the Vale Cortiço site (central Portugal) and its palaeoecological implications for western Iberia. – *Acta Palaeobotanica*, 59: 215–228.  
<https://doi.org/10.2478/acpa-2019-0010>
- Mendes, M. M., Vajda, V., Cunha, P. P., Dinis, P., Svobodová, M., Doyle, J. A. (2022): A Lower Cretaceous palynoflora from Carregueira (Lusitanian Basin, westernmost Iberia): taxonomic, stratigraphic and palaeoenvironmental implications. – *Cretaceous Research*, 130: 105036 (14 pp.).  
<https://doi.org/10.1016/j.cretres.2021.105036>

- Pais, J., Reyre, Y. (1981): Problèmes posés par la population sporo-pollinique d'un niveau à plantes de la série de Buarcos (Portugal). – *Boletim da Sociedade Geológica de Portugal*, 22: 35–40.
- Paudel, N. Heo, K. (2020): Comparative pollen morphology of Calycanthaceae for their taxonomic implication. – *European Journal of Biological Research*, 10: 74–80.
- Penny, J. H. J. (1991): Early Cretaceous angiosperm pollen from the borehole Mersa Matruh 1, North West Desert, Egypt. – *Palaeontographica, Abt. B*, 222: 31–88.
- Pedersen, K. R., von Balthazar, M., Crane, P. R., Friis, E. M. (2007): Early Cretaceous floral structures and in situ tricolpate-striate pollen: New early eudicots from Portugal. – *Grana*, 46: 176–196.  
<https://doi.org/10.1080/00173130701526507>
- Pierce, R. L. (1961): Lower Upper Cretaceous plant microfossils from Minnesota. – *Minnesota Geological Survey Bulletin*, 42: 1–86.
- Rey, J. (1992): Les unités lithostratigraphiques du Crétacé inférieur de la région de Lisbonne. – *Comunicações dos Serviços Geológicos de Portugal*, 78: 103–124.
- Rey, J. (1993): Les unités lithostratigraphiques du groupe de Torres Vedras (Estremadura, Portugal). – *Comunicações Instituto Geológico e Mineiro*, 79: 75–85.
- Sajo, M. G., Rudall, P. J., Prychid, C. J. (2004): Floral anatomy of Bromeliaceae, with particular reference to the evolution of epigyny and septal nectaries in commelinid monocots. – *Plant Systematics and Evolution*, 247: 215–231.  
<https://doi.org/10.1007/s00606-002-0143-0>
- Sampson, F. B. (1975): Aperture orientation in *Laurelia* pollen (Atherospermataceae syn. subfamily Atherospermatoidae). – *Grana*, 15: 153–157.  
<https://doi.org/10.1080/00173134.1975.11864631>
- Sampson, F. B. (1996): Pollen morphology and ultrastructure of *Laurelia*, *Laureliopsis* and *Dryadodaphne* (Atherospermataceae [Monimiaceae]). – *Grana*, 35: 257–265.  
<https://doi.org/10.1080/00173139609429081>
- Sampson, F. B. (2000): Pollen diversity in some modern magnoliids. – *International Journal of Plant Sciences*, 161: S193–S210.  
<https://doi.org/10.1086/317573>
- Saporta, G. de (1894): Flore fossile du Portugal. Nouvelles contributions à la flore Mésozoïque. Accompagnées d'une notice stratigraphique par Paul Choffat. – Imprimerie de l'Académie royale des Sciences, Lisbonne, 288 pp., 39 pls.  
<https://doi.org/10.5962/bhl.title.149948>
- Sauquet, H., Le Thomas, A. (2003): Pollen diversity and evolution in Myristicaceae (Magnoliales). – *International Journal of Plant Sciences*, 164: 613–628.  
<https://doi.org/10.1086/375424>
- Stampanoni, M., Groso, A., Isenegger, A., Mikuljan, G., Chen, Q., Bertrand, A., Henein, S., Betemps, R., Frommherz, U., Bohler, P., Meister, D., Lange, M., Abela, R. (2006): Trends in synchrotron-based tomographic imaging: the SLS experience. – In: Bonse, U. (ed.), *Developments in X-Ray Tomography V. Proceedings of SPIE – The International Society for Optical Engineering*, San Diego, 6318: 63180M (14 pp).  
<https://doi.org/10.1117/12.679497>
- Sun, G., Dilcher, D. L., Zheng, S., Zhou, Z. (1998): In search of the first flower: a Jurassic angiosperm, *Archaeofructus* from N. E. China. – *Science*, 282: 1692–1695.  
<https://doi.org/10.1126/science.282.5394.1692>
- Taylor, M. L., Cooper, R. L., Schneider, E. L., Osborn, J. M. (2015): Pollen structure and development in Nymphaeales: Insights into character evolution in an ancient angiosperm lineage. – *American Journal of Botany*, 102: 1685–1702.  
<https://doi.org/10.3732/ajb.1500249>
- Teixeira, C. (1945): *Nymphéacées Fossiles du Portugal*. – *Serviços Geológicos de Portugal, Lisbonne*, 13 pp.
- Teixeira, C. (1946): *Flora cretácica de Esgueira (Aveiro)*. – *Portugaliae Acta Biologica, Sér. B*, 1: 235–242.
- Teixeira, C. (1947): *Nouvelles recherches et revision de la flore de Cercal (Portugal)*. – *Brotéria, Série de Ciências Naturais*, 16(1): 5–14.
- Teixeira, C. (1948): *Flora mesozóica portuguesa. Part I [The Mesozoic flora of Portugal. Part I]*. – *Serviços Geológicos de Portugal, Lisboa*, 118 pp., 45 pls. (in Portuguese)
- Teixeira, C. (1950): *Flora mesozóica portuguesa. Part II [The Mesozoic flora of Portugal. Part II]*. – *Serviços Geológicos de Portugal, Lisboa*, 33 pp., 13 pls. (in Portuguese)
- Teixeira, C. (1952): *Notes sur quelques gisements de végétaux fossiles du Crétacé des environs de Leiria*. – *Revista da Faculdade de Ciências de Lisboa*, 2. Série, C, 2(1): 133–154.
- Tekleva, M., Mendes, M. M., Kvaček, J., Endress, P. K., Doyle, J. A. (2021): Morphology, ultrastructure, and evolutionary significance of pollen in a chloranthaceous staminate structure from the Early Cretaceous of Portugal. – *International Journal of Plant Sciences*, 182: 817–832.  
<https://doi.org/10.1086/716778>
- Trincão, P. (1985): *Estudo palinostratigráfico do Cretácico inferior Português ante-Albiano [Palynological study of the Portuguese Early Cretaceous, pre-Albian]*; Master thesis. – MS, Edição do Centro de Geociências da Universidade de Coimbra (INIC), Coimbra, Portugal, 103 pp. (in Portuguese) (copy in private library of EMF)
- Trincão, P. R. P. (1990): *Esporos e pólenes do Cretácico inferior (Berriasiano-Aptiano) de Portugal: paleontologia e biostratigrafia [Pollen and spores from the Early Cretaceous (Berriasian-Aptian) of Portugal: palaeontology and biostratigraphy]*; Ph.D. Thesis. – MS, Universidade Nova de Lisboa, Lisbon, Portugal, 312 pp., 47 pls. (in Portuguese) (copy in private library of EMF)
- Van Heusden, E. C. H. (1992): *Flowers of Annonaceae: morphology, classification, and evolution*. – *Blumea, Supplement*, 7: 1–218.
- Venturelli, M. (1988): *Development of ovule and seed in Rapateaceae*. – *Botanical Journal of the Linnean Society*, 97: 267–294.  
<https://doi.org/10.1111/j.1095-8339.1988.tb01584.x>
- Walker, J. W. (1971): *Pollen morphology, phytogeography, and phylogeny of the Annonaceae*. – *Contributions from the Gray Herbarium of Harvard University*, 202: 3–130.  
<https://doi.org/10.5962/p.272704>
- Walker, J. W. (1974): *Aperture evolution in the pollen of primitive angiosperms*. – *American Journal of Botany*, 61: 1112–1137.  
<https://doi.org/10.1002/j.1537-2197.1974.tb12329.x>



Walker, J. W., Walker, A. G. (1984): Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. – *Annals of the Missouri Botanical Garden*, 71: 464–521.  
<https://doi.org/10.2307/2399035>

Woodland, P. S., Garlick, P. R. (1982): The fine structure of the pollen of Eupomatiaceae. – *Australian Journal of Botany*, 30: 297–301.  
<https://doi.org/10.1071/BT9820297>

Zbyszewski, G., Torre De Assunção, C. (1965): Carta geológica de Portugal na escala de 1/50 000. Notícia explicativa da folha 30-D Alenquer [Geological map of Portugal in scale 1/50 000. Explanatory notes to the map 30-D Alenquer]. – *Serviços Geológicos de Portugal*, Lisbon. (in Portuguese)

## 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	<i>Paisia</i> sp.	10	×10	
P0292_10xb	Catefica MMM	<i>Paisia</i> sp.	10	×10	
P0338_20x	Catefica MMM	<i>Paisia pantoporata</i>	10	×20	
P0355_10x	Catefica MMM	<i>Battenispermum hirsutum</i>	10	×10	Lateral stacking 2 blocks
P0357_10x	Catefica MMM324	Axis – uncertain	10	×10	Stacked 2 blocks
S100754new	Catefica 49	<i>Tomcatia taylorii</i>	10	×20	S100254new incorrect number; 3 blocks
S100757new	Catefica 49	<i>Tomcatia taylorii</i>	10	×10	
S101214a	Catefica 49	<i>Paisia pantoporata</i>	10	×10	
S118680a	Catefica 49	<i>Paisia pantoporata</i>	10	×20	
S118688phase	Catefica 49	<i>Catanthus dolichostemon</i>	20	×10	
S154526new	Catefica 151	<i>Tomcatia taylorii</i>	10	×20	Stacked 2 blocks
S156219-01a	Catefica 49	<i>Lignierispermum maroneae</i>	10	×10	
S156369_20x	Catefica 381	<i>Buarcospermum tetragonium</i>	10	×20	
S156369a	Catefica 382	<i>Buarcospermum tetragonium</i>	10	×10	Stacked 2 blocks
S156370_20x	Catefica 358	<i>Lobospermum rugosum</i>	10	×20	Stacked 3 blocks
S156370a	Catefica 358	<i>Lobospermum rugosum</i>	10	×10	Stacked 3 blocks
S156529a	Catefica 49	Axis – uncertain	10	×4	Stacked 2 blocks
S156530a	Catefica 49	Axis – uncertain	10	×10	Stacked 2 blocks
S156531a	Catefica 49	Axis – uncertain	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 343	<i>Battenispermum hirsutum</i>	10	×4	
S156540a	Catefica 342	<i>Lignierisperma maroneae</i>	10	×4	
S156541a	Catefica 342	Coniferales	10	×10	Stacked 2 blocks
S171508b	Catefica 50	<i>Canrightia resinifera</i>	10	×10	
S171506a	Catefica 50	<i>Canrightia resinifera</i>	10	×20	Stacked 2 blocks
S171507a	Catefica 50	<i>Canrightia resinifera</i>	10	×20	
S171509a	Catefica 50	<i>Canrightia resinifera</i>	10	×10	
S171514a	Catefica 343	<i>Paisia pantoporata</i>	10	×20	
S171514b	Catefica 343	<i>Paisia pantoporata</i>	10	×20	
S171514c	Catefica 343	<i>Paisia pantoporata</i>	10	×20	Stacked 2 blocks
S171515a	Catefica 343	<i>Paisia</i> -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	<i>Paisia pantoporata</i>	10	×10	
S171520a	Catefica 50	Tricarpellate flower sp. 1	10	×10	
S171521a	Catefica 50	Tricarpellate flower sp. 1	10	×10	
S171522a	Catefica 50	Bryophyta	10	×20	Stacked 2 blocks
S171523a	Catefica 50	<i>Paisia</i> -like follicle	10	×20	Stacked 3 blocks
S171524a	Catefica 50	<i>Paisia</i> -like follicle	10	×20	Stacked 3 blocks
S171525a	Catefica 50	<i>Paisia</i> -like follicle	10	×20	Stacked 2 blocks
S171526-01a	Catefica 49	<i>Paisia pantoporata</i>	10	×20	Stacked 2 blocks
S171526-02a	Catefica 49	<i>Paisia pantoporata</i>	10	×20	
S171526a	Catefica 49	<i>Paisia pantoporata</i>	10	×20	
S171527a	Catefica 49	Stamen with zonaperturate pollen	10	×10	
S171528a	Catefica 49	Axis – uncertain	10	×10	Stacked 4 blocks
S171529a	Catefica 49	<i>Paisia pantoporata</i>	10	×20	Stacked 2 blocks
S171530a	Catefica 151	<i>Paisia pantoporata</i>	10	×20	
S172313a	Catefica 49	<i>Hedyflora crystallifera</i>	10	×10	

S172314a	Catefica 49	Tricarpellate flower sp. 1	10	×10	
S172315a	Catefica 49	Uncertain	10	×10	
S172316a	Catefica 49	Foveolate seed sp. 1	10	×10	
S172317a	Catefica 49	Exotestal seed	10	×10	
S172318a	Catefica 49	Coprolite	10	×10	
S172319a	Catefica 49	<i>Pazliopsis</i> sp.	10	×10	
S172320a	Catefica 49	<i>Choffaticarpus compactus</i>	10	×10	
S172321a	Catefica 49	<i>Choffaticarpus compactus</i>	10	×10	
S172322a	Catefica 49	<i>Choffaticarpus compactus</i>	10	×10	
S172323a	Catefica 49	<i>Choffaticarpus compactus</i>	10	×10	
S172324a	Catefica 49	<i>Hedyflora crystallifera</i>	10	×20	Stacked 2 blocks
S172325a	Catefica 49	<i>Hedyflora crystallifera</i>	10	×20	Stacked 2 blocks; rec only B1
S172326a	Catefica 49	Axis – uncertain	10	×20	
S172327a	Catefica 49	<i>Paisia</i> -like follicle	10	×20	Stacked 3 blocks
S172329a	Catefica 153	<i>Quadrispermum parvum</i>	10	×20	Scan interrupted!
S172329b	Catefica 153	<i>Quadrispermum parvum</i>	10	×20	Stacked 2 blocks
S172330a	Catefica 153	One-seeded fruit sp. 2	10	×10	
S172331a	Catefica 153	<i>Canrightiopsis crassitesta</i>	10	×20	
S172332a	Catefica 153	Foveolate seed sp. 2	10	×20	Stacked 2 blocks; rec only B1
S172333a	Catefica 153	<i>Canrightiopsis crassitesta</i>	10	×10	
S172554a	Catefica 49	<i>Catanthus dolichostemon</i>	10	×10	Stacked 2 blocks
S172555a	Catefica 49	<i>Catanthus dolichostemon</i>	10	×10	Stacked 2 blocks
S172556a	Catefica 49	<i>Catanthus dolichostemon</i>	10	×10	Stacked 2 blocks
S172592a	Catefica 49	<i>Quadrispermum parvum</i>	10	×20	Stacked 2 blocks
S174008a	Catefica 50	<i>Canrightia</i> sp.	10	×20	
S174038a_B1_B2_B3	Catefica 49	Lycopsid axis	10	×10	Stacked 3 blocks
S174039a	Catefica 49	<i>Canrightiopsis crassitesta</i>	10	×10	
S174040a	Catefica 49	<i>Canrightiopsis crassitesta</i>	10	×10	
S174093a	Catefica 49	Axis – uncertain	10	×10	Moved during scan
S174114b	Catefica 49	<i>Saportanthus parvus</i>	10	×10	
S174159a	Catefica 49	<i>Canrightiopsis crassitesta</i>	10	×10	
S174160a	Catefica 49	Lycopsid axis	10	×10	
S174161a	Catefica 49	One-seeded fruit sp. 1	10	×10	Stacked 2 blocks
S174162a	Catefica 342	<i>Choffaticarpus compactus</i>	10	×10	
S174248_10x_	Catefica 49	<i>Canrightiopsis crassitesta</i>	10	×10	
S174249a	Catefica 49	<i>Canrightia foveolata</i>	10	×10	Stacked 2 blocks
S174249a_B1a_	Catefica 49	<i>Canrightia foveolata</i>	10	×10	Rescanned top
S174249Re_B1_B2	Catefica 49	<i>Canrightia foveolata</i>	17	×10	Stacked 2 blocks
S174250a	Catefica 359	Axis – uncertain	10	×10	
S174251a	Catefica 49	Bryophyta	10	×20	
S174254L	Catefica 150	<i>Mugideiriflora portugallica</i>	10	×10	Lateral stacking
S174254La	Catefica 150	<i>Mugideiriflora portugallica</i>	10	×10	Lateral stacking
S174255L_B1_B2_B3	Catefica 150	<i>Catanthus dolichostemon</i>	10	×10	Lateral stacking 3 blocks
S174299a_B1_B2	Catefica 152	Axis – uncertain	10	×10	Lateral stacking 2 blocks
S174301_10x	Catefica 242	<i>Saportanthus parvus</i>	10	×10	
S174301_20x	Catefica 242	<i>Saportanthus parvus</i>	10	×20	Stacked 2 blocks
S174309a	Catefica 154	<i>Canrightiopsis crassitesta</i>	10	×10	
S174310a	Catefica 154	<i>Canrightiopsis crassitesta</i>	10	×10	
S174311_10x	Catefica 343	<i>Canrightiopsis crassitesta</i>	10	×10	
S174312_10x	Catefica 153	<i>Canrightia resinifera</i>	10	×10	
S174313_B1_B2	Catefica 153	Hexamerous flower/fruit	10	×10	Stacked 2 blocks
S174314_10x	Catefica 153	One-seeded fruit sp. 2	10	×10	
S174356a	Catefica 360	<i>Saportanthus parvus</i>	10	×10	
S174739_10x	Catefica 50	<i>Paisia pantoporata</i>	10	×10	
S174743_10x	Catefica 361	<i>Paisia pantoporata</i>	10	×10	
S174766_10x	Catefica 49	Axis – uncertain	10	×10	
S174767_10x	Catefica 49	<i>Serialis communis</i>	10	×10	
S174768_20x	Catefica 49	<i>Serialis communis</i>	10	×20	Stacked 2 blocks
S174769_20x	Catefica 49	One-seeded fruit sp. 1	10	×20	

S174899_10x	Catefica 50	<i>Catanthus dolichostemon</i>	10	×10	Stacked 2 blocks
S174900_10x	Catefica 50	<i>Mugideiriflora portugallica</i>	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	<i>Canrightiopsis crassitesta</i>	10	×10	
S174905_10x	Catefica 50	<i>Canrightiopsis crassitesta</i>	10	×10	
S174906_10x	Catefica 50	<i>Canrightia resinifera</i>	10	×10	
S174907_10x	Catefica 50	<i>Ibericarpus cuneiformis</i>	10	×10	
S174908_10x	Catefica 50	<i>Choffaticarpus compactus</i>	10	×10	
S174910_20x	Catefica 50	<i>Paisia</i> -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	<i>Appomattoxia</i> sp.	10	×20	
S174914_20x	Catefica 49	<i>Paisia</i> -like follicle	10	×20	Stacked 2 blocks
S174915_10x	Catefica 49	<i>Paisia</i> -like follicle	15	×10	Stacked 2 blocks
S174916_20x	Catefica 49	<i>Paisia</i> -like follicle	10	×20	Stacked 2 blocks
S174917_20x	Catefica 49	<i>Paisia</i> -like follicle	10	×20	Stacked 2 blocks
S174919_20x	Catefica 49	Leaf-uncertain	10	×20	Stacked 2 blocks
S174920_20x	Catefica 49	<i>Paisia</i> -like follicle	10	×20	Stacked 2 blocks
S174921_20x	Catefica 49	<i>Serialis</i> 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	
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	<i>Canrightia resinifera</i>	10	×20	
S174929_20x	Catefica 49	<i>Paisia</i> -like follicle	10	×20	
S174930_20x	Catefica 49	Coprolite	10	×20	
S175178_10x	Catefica 242	<i>Canrightia</i> -like	10	×10	Stacked 2 blocks
S175179_10x	Catefica 49	<i>Canrightia foveolata</i>	10	×10	
S175180_10x	Catefica 49	<i>Serialis</i> sp.	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	<i>Canrightiopsis crassitesta</i>	10	×10	
S266038_10x	Catefica 50	<i>Mugideiriflora portugallica</i>	10	×10	
S266039_10x	Catefica 50	Axis – uncertain	10	×10	
S266045_10x	Catefica 49	<i>Aristospermum huberi</i>	10	×10	Stacked 2 blocks
S266046_10x	Catefica 49	Seed reticulate	10	×10	Stacked 2 blocks
S266047_10x	Catefica 49	<i>Catanthus dolichostemon</i>	10	×10	Stacked 2 blocks
S266048_10x	Catefica 49	Seed reticulate	10	×10	Stacked 2 blocks
S266049_10x	Catefica 49	<i>Aristospermum huberi</i>	10	×10	Stacked 2 blocks
S266050_10x	Catefica 49	<i>Serialis</i> 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	