

# A new cheirolepidiacean microsporangiate cone *Classostrobus archangelskyi* with in situ pollen from the Lower Cretaceous of Figueira da Foz Formation, central-western mainland Portugal<sup>☆</sup>

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## ABSTRACT

A new cheirolepidiacean conifer microsporangiate cone *Classostrobus archangelskyi* is described from the Carregueira opencast clay pit complex near the village of Juncal, in the Lusitanian Basin of central-western mainland Portugal. The plant-bearing horizon belongs to the Famalicão Member of the Figueira da Foz Formation, considered to be of Lower Cretaceous (upper Aptian–lower Albian) age. The new microsporangiate cone is characterised by the presence of distinctive and unusual pollen assigned to the genus *Classopollis*. The microsporangiate cone is ovoid and small, comprising only a few microsporophylls, each with a stalk and deltoid head bearing 4–5 pollen sacs. The new Portuguese species is compared to other microsporangiate cones attributed to the genus *Classostrobus*. The *Classopollis* pollen grains found in situ are characterised by a microechinate sculpture and typical ultrastructure. The pollen grains were studied using SEM, TEM and transmitted light microscopy. The studied pollen shares strong similarities with *Classopollis martinotii*, *Classopollis torosus*, but particularly with *Classopollis noelii*. The new microsporangiate cone *Classostrobus archangelskyi* co-occurs with frenalopsid leafy shoots of *Frenalopsis antunesii*, and their common association is suggested.

## 1. Introduction

Conifers of the Cheirolepidiaceae family were dominant in Mesozoic vegetation and have traditionally been characterised by the presence of distinctive pollen grains of *Classopollis* Pflug in their microsporangiate cones (Doludenko, 1978; Watson, 1988). The group was geographically widespread, and according to palynological evidence, first appeared in the latest Triassic (Vakhrameev, 1970; Srivastava, 1976; Alvin, 1982; Kürschner et al., 2013). However, even earlier in the fossil record there are conifers showing similarities to Cheirolepidiaceae. The most prominent among them is the genus *Patokaea* Pacyna, Barbacka et Zdebska with *Brachyphyllum-Pagiophyllum*-type leaves, reported from the Late Triassic of southern Poland, and assigned to the family Potokaeaceae Pacyna, Barbacka et Zdebska (Pacyna et al., 2017). The oldest macro remains of Cheirolepidiaceae were described from the basal-most

Jurassic (Clement-Westerhof and van Konijnenburg-van Cittert, 1991). The group attained its highest diversity and abundance during the Late Jurassic and Early Cretaceous (Vakhrameev, 1970, 1978; Barnard, 1973; Alvin, 1982; Escapa and Leslie, 2017), declined in the Late Cretaceous (Kvaček, 2000; van der Ham et al., 2003) and became extinct in perhaps the Early Tertiary (Alvin, 1982; Barreda et al., 2012). The Early Cretaceous was a time of diversification of the frenalopsids group, particularly in the area of Tethys (Romariz, 1946; Alvin and Pais, 1978; Mendes et al., 2010, 2014, 2018; Mendes and Friis, 2018; Mendes and Kvaček, 2022; Kvaček and Mendes, 2022; Mendes et al., 2023).

Several cheirolepidiacean microsporangiate cones with *Classopollis*-type pollen have been described attached to twigs of *Hirmeriella* Hörhammer (= *Cheirolepidium* Takhtajan) (Clement-Westerhof and van Konijnenburg-van Cittert, 1991), or associated with foliage of *Frenalopsis* Schenk (Hlušík and Konzalová, 1976; Hlušík and Kozlovas, 1976; Pons

<sup>☆</sup> This paper is dedicated to the memory of Dr. Sergio Archangelsky, the mentor of Palaeobotany in Argentina, who passed away on 10th of July 2022.

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and Broutin, 1978; Pons, 1979) and *Pseudofrenelopsis* Nathorst (Zhou, 1983; Axsmith et al., 2004).

The genus *Classostrobus* Alvin, R.A.Spicer et J.Watson was established to encompass microsporangiate cones containing in situ *Classopollis* grains (Alvin et al., 1978). The cones have a typically coniferous structure with a rounded to oval morphology, with microsporophylls bearing pollen sacs on hyposporangiate microsporangiophores (Alvin, 1982; Watson, 1988). The species *Classostrobus comptonensis* Alvin, R.A. Spicer et J.Watson was described from the Barremian of the Isle of Wight southern England, associated with the cheirolepidiaceous conifer *Pseudofrenelopsis parceramosa* (Fontaine) J.Watson (Alvin et al., 1978).

Remains of conifers assigned to the extinct family Cheirolepidiaceae have been reported from several Early Cretaceous floras of the Estremadura and Beira Litoral regions in western Portugal, but only few were actually described using careful examination of their cuticle microstructures under light and scanning electron microscopes (Alvin, 1977; Lauverjat and Pons, 1978; Alvin and Pais, 1978; Mendes et al., 2010, 2014, 2018; Mendes and Kvaček, 2022; Kvaček and Mendes, 2022; Mendes et al., 2023).

In the present paper, a new conifer microsporangiate cone *Classostrobus archangelskyi* with in situ *Classopollis* pollen grains is formally named and described in detail. It was recovered from the Lower Cretaceous of Figueira da Foz Formation, in the Carregueira clay pit complex, near the small village of Juncal, in the Lusitanian Basin, western Portugal. It provides additional details about the anatomy and histology of this extinct family's microsporangiate cones family contributing to our understanding of Mesozoic conifer diversity.

## 2. Material and methods

The fossil material described here is based on a single specimen extracted from a rock sample (Carregueira sample 414), collected in the Carregueira opencast clay pit complex, near the small village of Juncal, in the Lusitanian Basin of central-western mainland Portugal (39° 35' 24.9" N; 08° 55' 33.1" W) (Fig. 1).

The fossil specimen was isolated from dark-grey mudstone deposits previously assigned to the "Complexos Gresosos da Nazaré e Cós-Juncal" (Carta Geológica de Portugal, Folha 26-B Alcobaça, França and

Zbyszewski, 1963), and it was subsequently included in the Figueira da Foz Formation (Dinis, 1999, 2001; Rey, 2006). The plant-bearing sediments from the Carregueira site belong to the Famalicão Member of the Figueira da Foz Formation (Dinis, 1999, 2001; Rey, 2006). A late Aptian - early Albian age was suggested by Dinis et al. (2002) for the Figueira da Foz lower boundary, using mainly sedimentological and lithofacies correlations, as well as plant macrofossils and published palynological data (Teixeira, 1950; Friis et al., 1999). This suggestion was further supported by the stratigraphic studies of Rey (2006), who suggested a late Aptian to early Albian age for the Famalicão Member of the Figueira da Foz Formation (for a more detailed account of the geology and context, see Heimhofer et al., 2005 and Mendes et al., 2022).

The rock samples collected in Carregueira were dried in the laboratory, disaggregated in water, and sieved using a hand-shower though a 125 µm mesh net. The fossil cone documented here was cleaned in hydrofluoric (40% HF) and hydrochloric (10% HCl) acids, thoroughly rinsed in water and dried in the air following standard techniques previously described by Friis et al. (1988). The specimen was first observed under a Nikon SMZ 800 stereomicroscope, then mounted on an aluminium stub for scanning electron microscopy (SEM), coated with gold for 60 s in a sputter coater, and examined with a Hitachi S-3700 N Environmental Scanning Electron Microscope at 2 kV, at the National Museum Prague, Czech Republic.

A small part of one microsporophyll was detached from the holotype by scalpel knife. A two-step process was used to remove the opaque coal matter from the fossil material (following Kerp and Krings, 1999; Howell et al., 2022; Mendes et al., 2023). It was macerated for 10 min in Schulze solution, then washed in distilled water and treated with potassium hydroxide (20% KOH).

A microsporophyll of the microsporangiate cone and several small fragments were carefully removed and used for LM, SEM and TEM observations of the pollen. Glycerin slides of individual pollen grains were prepared, and these grains were photographed with a Carl Zeiss Axio-plan 2 light microscope equipped with a × 100 oil immersion objective and an AxioCam 105 digital camera. Individual pollen grains and pollen clumps were washed in ethanol and transferred to a piece of photographic film for SEM studies. The film was glued to an aluminium stub with nail polish and sputter-coated with gold for 8 min. The pollen grains were observed and photographed with a Tescan Vega3 XMU SEM with an accelerating voltage of 10 at the A. A. Borissiak Paleontological Institute, Russian Academy of Sciences (PIN RAS). For transmission electron microscopy (TEM) analyses, pollen mass and individual pollen grains were removed from the SEM stub and embedded in epoxy resin in the proportions described by Zaviyalova et al. (2018). The pollen grains were sectioned with a Leica EM UC6 ultramicrotome equipped with a diamond knife. The sections were examined with a Jeol 1011 TEM with an accelerating voltage of 80 kV at the Laboratory of Electronic Microscopy, Faculty of Biology, Lomonosov Moscow State University. The Jeol 1011 TEM was equipped with a side-mounted Orius SC1000W digital camera (11 megapixels, effective 8.5 megapixels); Digital-Micrograph version 2.0 (Gatan) software was used for image processing.

Remnants of polymerised resins with embedded fossil pollen grains, grids with ultrathin sections, and digital photos are kept at the Laboratory of Paleobotany, PIN RAS, in Moscow.

For X-ray microtomography, isolated cone was mounted on an aluminium pin stub and investigated with a Skyscan 1172 Bruker, using an aluminium filter (Al 0.5 mm), voltage 80 kV and current 123 µA. For reconstructions the program NRecon v.16.9.8 was used. Images were obtained, analysed and manipulated using Avizo v. 2020.3 software.

The new names of *Classostrobus* species are registered with unique PFN numbers in the Plant Fossil Names Registry, hosted and operated by the National Museum Prague, Czech Republic, for the International Organisation of Palaeobotany (IOP).

The specimen and preparations used in this work are housed in the palaeobotanical collections of the Geological Museum of Lisbon, Portugal (P numbers).



**Fig. 1.** (A) Geographical location of Lusitanian Basin in the westernmost sector of the Iberian Peninsula. (B) Detailed map showing approximate location of Carregueira opencast clay pit complex, near the small village of Juncal, where the fossil specimens were collected indicated by red star. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 3. Results

Systematic palaeontology

**Unranked clade:** CONIFERAE de Jussieu, 1789 (sensu Doyle et al. in de Queiroz et al., 2020).

**Family:** CHEIROLEPIDIACEAE Turutanova-Ketova, 1963

For detailed discussion on the nomenclature of the Cheirolepidiaceae family name see Doweld (2020) and Mendes et al. (2023).

**Genus:** *Classostrobus* Alvin, R.A.Spicer et J.Watson 1978.

**Type:** *Masculostrobus rishra* Barnard, 1968, p. 168.

The genus *Classostrobus* serves for accommodation of all microsporangiate cones possessing *Classopollis* pollen in situ. Some consider *Classostrobus* suitable only for detached material (van Konijnenburg-van Cittert, 1987); others tend to use the name even when the cones are borne on a sterile twig (Axsmith et al., 2004).

**Remarks on nomenclature:** The protologue of *Classostrobus* Alvin, R.A. Spicer et J.Watson was published in 1978. Its type was not designed only indicated by indirect citation as “*Classostrobus rishra* (Barnard) comb. nov.”. The name itself was not validly published. However, there was clear intention of the authors to publish the type, although with an error. Art. 40.1 does not require designation of a type (Turland et al., 2018), but even indirect citation of the type (its epithet *rishra* and the author – Barnard) is considered satisfactory for its valid publication (Art. 10.2 of the Shenzhen Code, Turland et al., 2018).

*Classostrobus rishra* (P.D.W.Barnard) Alvin, R.A.Spicer et J.Watson was not validly published by Alvin et al. (1978), because the authors omitted citation of its basionym, and therefore failed to publish the new combination validly. This is corrected here in:

**Basionym:** *Masculostrobus rishra* P.D.W. Barnard, 1968 (in J. Lin. Soc. Bot., 61: 168); New combination – *Classostrobus rishra* (P.D.W.Barnard) Alvin, R.A.Spicer et J.Watson comb. nov. – designated herein. Plant Fossil Names Registry Number: PFN003140 (for new combination).

The same authors later published *Classostrobus comptonensis* as a type for *Classostrobus* (Alvin et al., 1994). This later designation is considered ineffective because it does not include the type. (Art. 10.3 and Art 10.3 of the Shenzhen Code Turland et al., 2018).

**Species:** *Classostrobus archangelskyi* J.Kvaček, M.M.Mendes et Tekleva sp. nov.

**Holotype:** P1124 (Juncal sample 414; illustrated here in Plates I–VII).

**Repository:** Geological Museum of Lisbon, Portugal.

**Plant Fossil Names Registry Number:** PFN003078.

**Etymology:** In honour of Sergio Archangelsky for his important contributions to our understanding of Mesozoic fossil floras.

**Type locality:** Carregueira opencast clay pit complex, close to the small village of Juncal, Lusitanian Basin, western-central mainland Portugal (39° 35' 24.9" N; 08° 55' 33.1" W).

**Type horizon:** Famalicão Member of the Figueira da Foz Formation.

**Age:** Early Cretaceous (late Aptian–early Albian).

**Diagnosis:** Microsporangiate cone ovoid in shape, consisting of about 12 peltate, imbricated microsporophylls of deltoid shape; each sporophyll consisting of stalk and microsporophyll head with obtuse apex, margin bearing long unicellular trichomes; each bearing abaxially 4–5 ovoid pollen sacs. Pollen sacs bearing *Classopollis* type pollen. Abaxial cuticle of microsporophyll bears rows of stomatal apparatus, surrounded by (3)–4 subsidiary cells, sometimes with small papillae. Pollen of *Classopollis* type spheroidal, with equatorial girdle, subequatorial rimula, proximal trilete scar, and distal cryptopore.

**Description:** The holotype is a microsporangiate cone 2.1 × 1.8 mm in size (Plate I, 1). It is ovoid in shape, consisting of about 12 deltoid microsporophylls helically arranged on slender main axis. Each microsporophyll consists of a stalk and deltoid head (Plate I, 2, 5). Each sporophyll shows a head 0.5–1.0 × 0.5–1.0 mm; it is quite smooth (Plate I, 7). Marginal parts of sporophylls bear long unicellular trichomes (Plate I, 3–6). Abaxial cuticle has stomatal apparatus arranged in short rows (Plate II, 3, 4). Ordinary cells are polygonal, rather elongated (5–20 × 20–55 µm), with straight anticlinal walls (3–5 µm). Stomatal

apparatus are formed by 3–4 subsidiary cells (15–20 × 20–35 µm), sometimes bearing internally small papillae (Plate II, 1).

Each head bears 4–5 ovoid pollen sacs, 100–150 × 180–200 µm in size (Plate III, 1). Their position and number are derived from SEM (Plate II, 1) and microCT images (Plate IV, 1, 2). Pollen is found in and near the pollen sacs (Plate III, 2–4), but also scattered over the microsporophylls (Plate I, 6, Plate II, 2).

Pollen grains are preserved as monads (Plate II, 2, Plate V, 1–8). They are spheroidal, with an equatorial girdle, subequatorial rimula, proximal trilete scar, and a distal cryptopore (Plate V, 1–11, Plate VI, 1–7). The pollen size is 26.1 (22.4–31.6) µm in LM and 25.7 (22–31) µm in SEM; the equatorial girdle is about 5.4 (3.1–6.9) µm wide, with six to ten striae. The proximal scar is opened, represented by a triangle with a side of 6.5 to 8.3 µm long (as measured in SEM, in LM it is often unclear) (Plate VI, 1, 5, 7). The rimula is narrow (Plate V, 1, 2, Plate VI, 2–4, 6). The distal cryptopore is rounded, about 5–9 µm in diameter (as measured in SEM, in LM it is not always clearly seen due to the pollen folding) (Plate V, 1, 4, Plate VI, 2–4, 6). The sculpture is microechinate, with microechini 0.3–0.6 µm high and 0.1–0.4 µm wide at the base, regularly and densely situated (Plate VI, 7–12). Orbicules of 2–2.9 µm in diameter with a hollow core occur on pollen grains (Plate VI, 1, 9, Plate II, 5, Plate VII, 4). In TEM, the exine consists of a tegillum, tectum, infratectum, and a poorly preserved endexine (Plate VII, 6–9). The tegillum is less electron dense than the underlying ectexine layers, about 0.23–0.44 µm thick. The elements constituting the tegillum appear as conical baculae and granules when observed in ultrathin sections under TEM, and as microechini of the exine surface under SEM. The tectum is homogeneous, roughly uniform in thickness, about 0.1–0.2 µm, except for the areas of the rimula, proximal scar, and a cryptopore (Plate III, 6), where it becomes slightly thinner and/or of non-uniform thickness. The infratectum is mostly 0.5–0.75 µm throughout the pollen, except for the equatorial area where it thickens up to 1.5 µm (Plate VII, 1–3, 9), and areas of the rimula, proximal scar, and a cryptopore, where it is lacking (Plate VII, 1–3, 8, 9). The infratectum is constituted of columella-like elements, about 0.4–0.6 µm high (up to 1.5 µm high in the equatorial area) and 0.2–0.4 µm wide. The infratectal elements are often branched in the equatorial area (Plate VII, 6, 8, 9). The foot layer is absent. The endexine is less electron dense than the ectexine in the majority of pollen studied with TEM, similar or less electron dense than the tegillum (Plate VII, 1, 5–9), although in two pollen grains the endexine is more electron dense (Plate VII, 2, 3). It is fragmentary and unstructured, about 0.1–0.2 µm thick, becoming up to 0.5 µm under the cryptopore and up to 0.4 µm under the proximal scar. At some sections, the endexine appears unclearly lamellated (Plate VII, 7).

### 4. Discussion

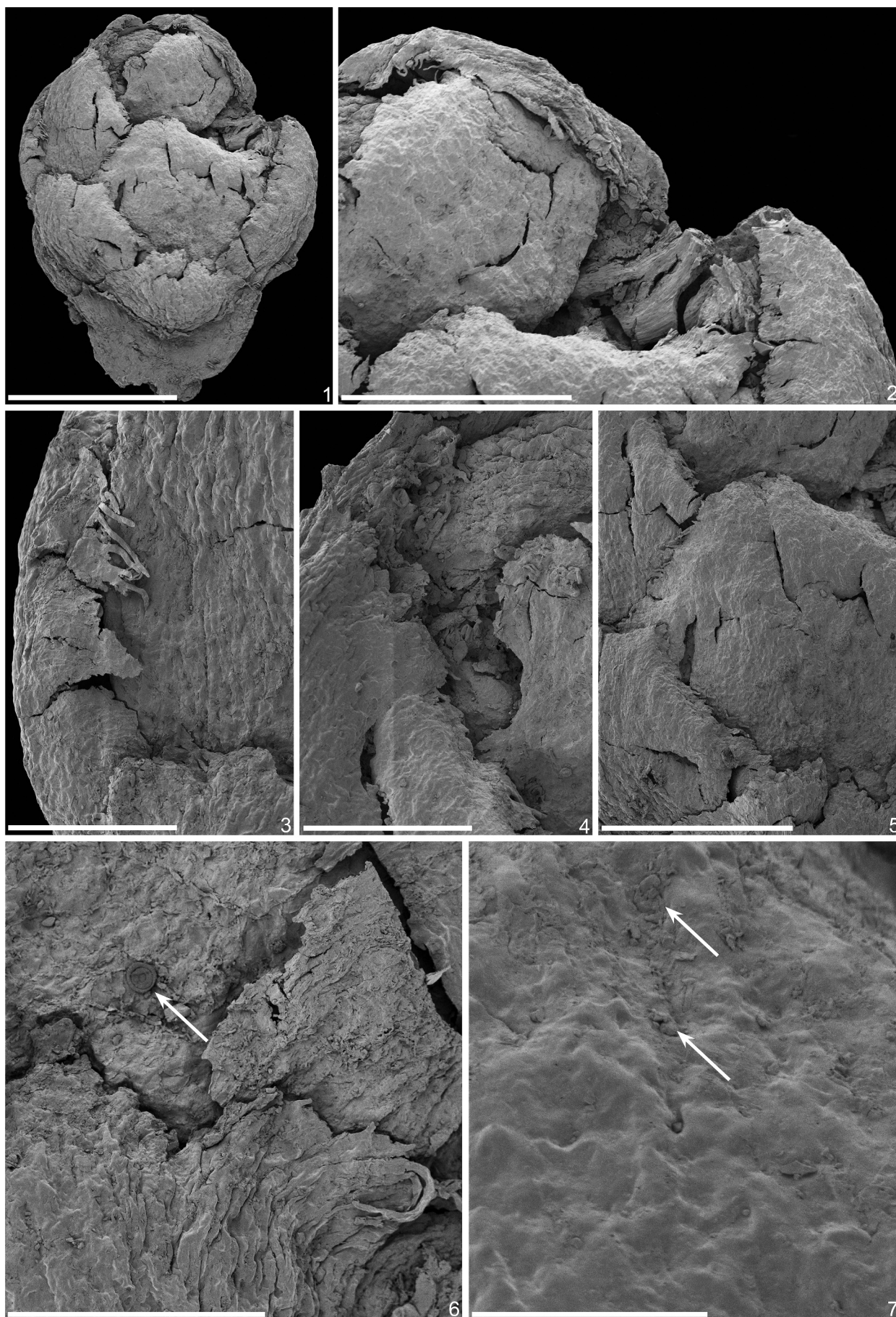
#### 4.1. Comparison with other microsporangiate cones

The new cheirolepidiacean microsporangiate cone *Classostrobus archangelskyi* differs from *C. rishra* (P.D.W.Barnard) Alvin, R.A.Spicer et J.Watson comb. nov. from the Middle Jurassic of Iran (Barnard, 1968) in having a microsporophyll margin fringed with unicellular hairs, instead of frilled margin and lower number of sporangia per microsporophyll. *C. rishra* has 6–8 sporangia per microsporophyll (Table 1). *C. archangelskyi* shows a quite obtuse apex of each sporophyll, as opposed to the acute microsporophyll apices of *C. rishra*.

*Classostrobus comptonensis* Alvin, J.Watson et R.A.Spicer from the English Wealden (Alvin et al., 1994) differs from *C. archangelskyi* in a lower number of pollen sacs (probably three) and higher number of microsporophylls (about 50) per cone.

*Classostrobus ugnensis* B.Gomez from the Barremian of Spain and *C. turolensis* B.Gomez from the Albian of Spain (Gomez et al., 2002) show similar morphology to *C. archangelskyi*. They differ in having the abaxial side of the microsporophylls covered by numerous papillae, while *C. archangelskyi* shows a quite smooth abaxial surface. The number of

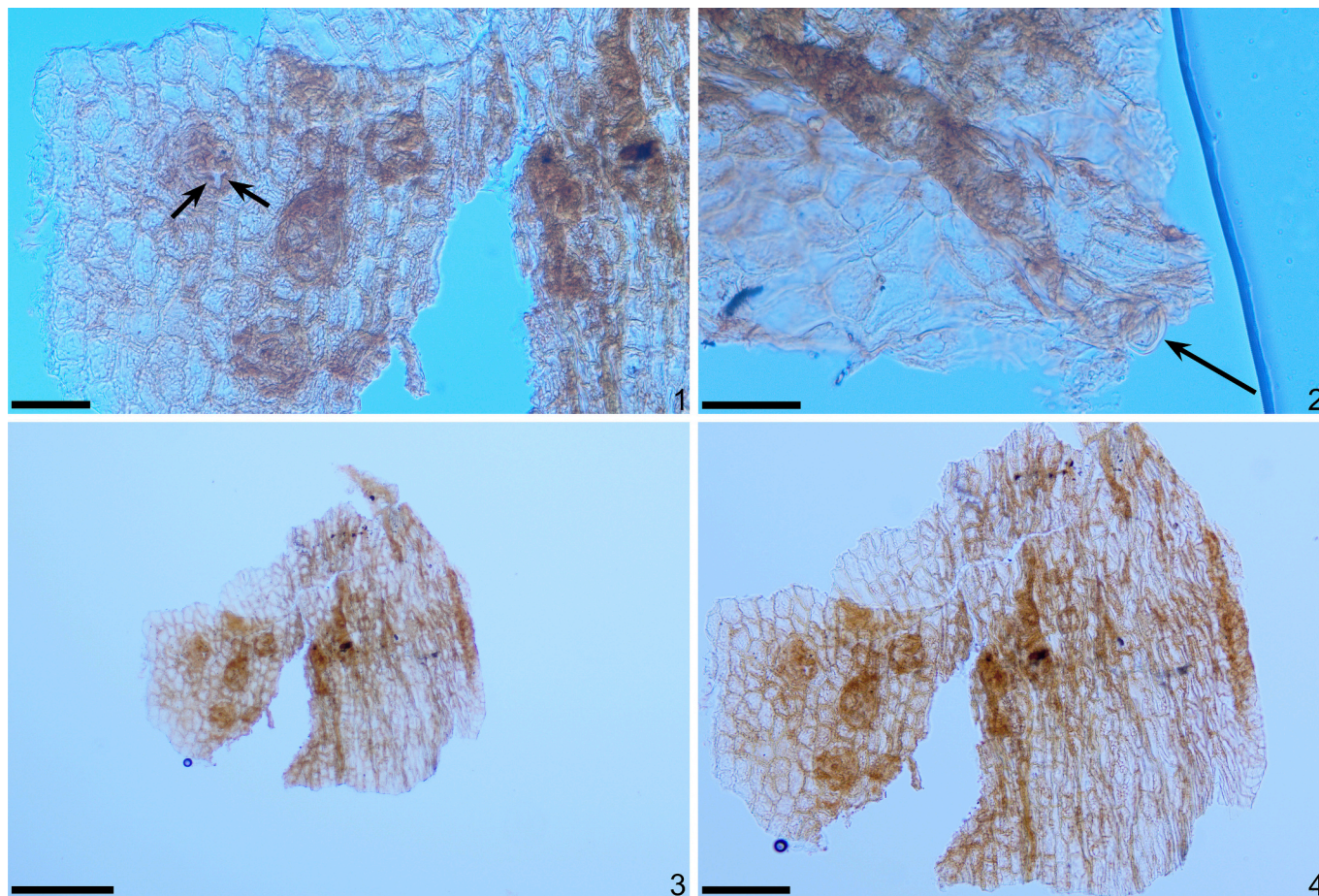




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**Plate I.** SEM images of *Classostrobus archangelskyi* sp. nov. (Holotype No. P1124, sample Carregueira 414) from Lower Cretaceous of Figueira da Foz Formation, Lusitanian Basin, central-western Portugal. 1. Complete microsporangiote cone 2. Detail of microsporophylls helically arranged on slender main axis. 3. Detail of long unicellular trichomes in marginal parts of sporophyll. 4, 5. Detail of microsporophyll margin. 6. Detail of long unicellular trichomes in marginal parts of sporophyll and *Classopollis* pollen (arrow). 7. Surface of microsporophyll showing stomatal apparatus apertures (arrow). Scale bars: 1 mm (1), 500  $\mu$ m (2, 5), 200  $\mu$ m (3, 4, 6), 50  $\mu$ m (7).



**Plate II.** Transmitted light photomicrographs of *Classostrobus archangelskyi* sp. nov. (Holotype No. P1124, sample Carregueira 414) from Lower Cretaceous of Figueira da Foz Formation, Lusitanian Basin, central-western Portugal. 1. Microsporophyll abaxial cuticle showing stomatal apparatus surrounded by 4 subsidiary cells, arrows indicating small papillae. 2. *Classopollis* pollen grain sticking on cuticle (arrow). 3, 4. Abaxial cuticle showing short rows of stomatal apparatus. Scale bars: 200  $\mu$ m (3), 100  $\mu$ m (4), 50  $\mu$ m (1, 2).

pollen sacs of both *C. ugnensis* and *C. turolensis* is not known. Both species are similar in having *Classopollis* in situ, but compared to the pollen under study, these pollen grains have a wider equatorial girdle and poorly marked infratectal striae. The exine sculpture on illustrations appears similar to that of our pollen but described as having smaller sculpture elements. Gomez et al. (2002) compared the observed pollen with *Classopollis noelii* Reyre, *C. mirabilis* Reyre, *C. obidosensis* J.J.Groot et C.R.Groot, and in situ *Classopollis* described by Taylor and Alvin (1984).

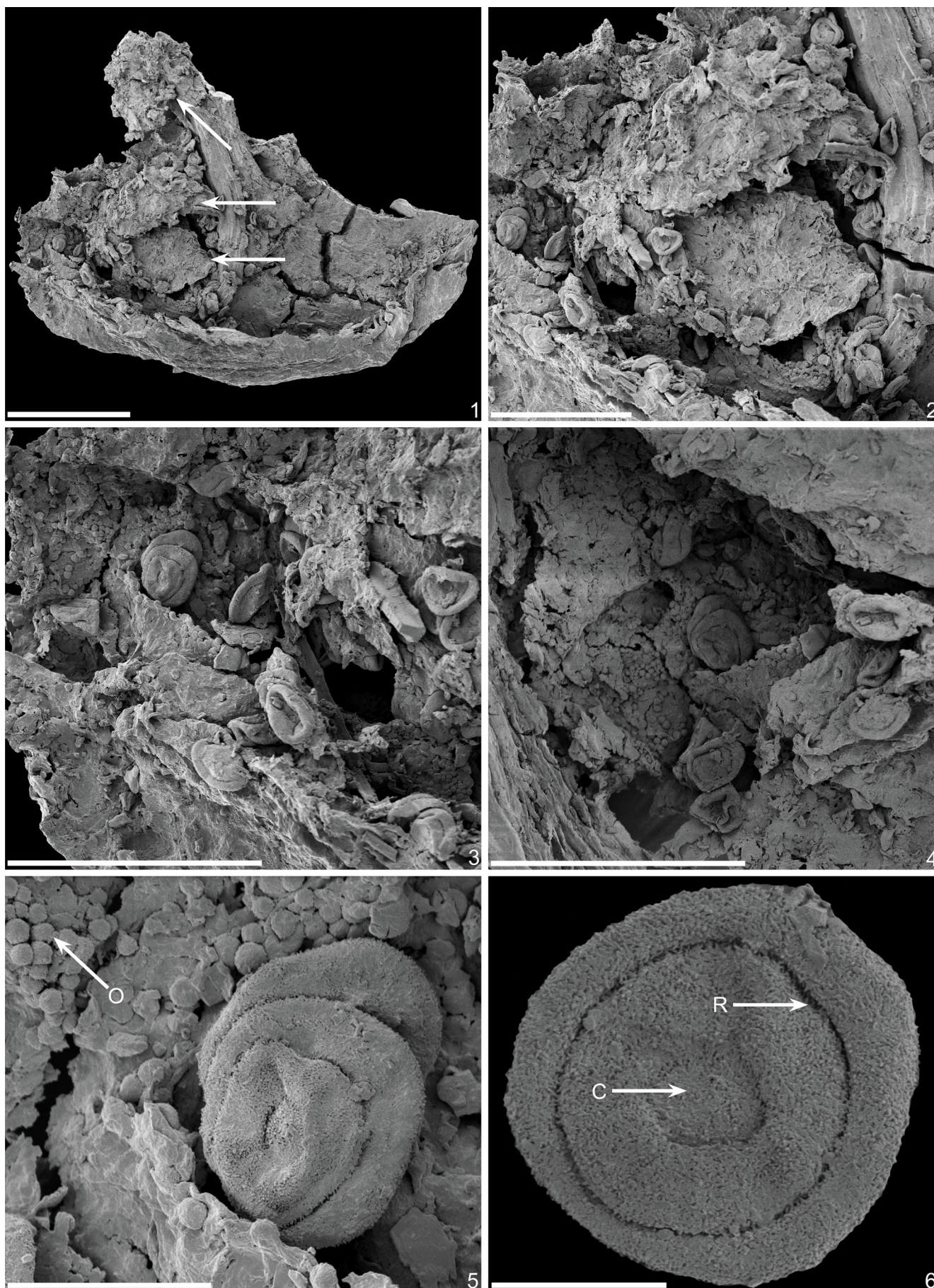
The microsporangiote cone *Classostrobus arkansensis* Axsmith, M. Krings et Waselkov described from the Lower Cretaceous (Aptian-Albian) of the Holly Creek Formation in Arkansas (Axsmith et al., 2004) is associated (or in connection) with twigs described as *Pseudofrenelopsis parceramosa*. However, the microsporangiote cone differs remarkably from *C. comptonensis* associated with *P. parceramosa* in the English Wealden (Axsmith et al., 2004). Microsporangiote cones of *C. arkansensis* differ from *C. archangelskyi* in having a much higher number of microsporophylls per cone (about 70), and probably only two pollen sacs per microsporophyll. Pollen grains from *C. arkansensis* have a narrower equatorial girdle, smaller cryptopore and proximal scar in

comparison with our pollen; the pollen size on average is smaller, while showing a wider range (12.5–37.5  $\mu$ m); the microechini are also smaller.

*Classostrobus cathayanus* Z.-Y.Zhou associated with *Pseudofrenelopsis intermedia* (T.-Y.Chow et C.-Y.Tsao) J.Watson from the Lower Cretaceous of Zhoujiawan, Qiya town, in the eastern outskirts of Nanjing (Nanking) city, Jiangsu Province, China (Zhou, 1983) differs from *C. archangelskyi* in much higher number of microsporophylls per cone and in their shape, having the microsporophylls lanceolate in shape with acute apex. It shows pollen of *Classopollis* type with a similar or somewhat larger pollen size, slightly wider equatorial girdle, smaller number or striae, and “grumous-verrucose or occasionally echinulate” exine sculpture; Zhou (1983) did not indicate the size of the sculpture elements and illustrations do not help much, but on the whole the sculpture pattern appears different from that of the pollen under study.

*Classostrobus dalatzensis* X.-J.Yang recovered in close association with *Pseudofrenelopsis dalatzensis* (T.-Y.Chow et C.-Y.Tsao) Z.-Y.Cao ex Z.-Y.Zhou from the Lower Cretaceous (Aptian–Albian), Dalazi Formation of Yanji Basin, eastern Jilin, China (Yang, 2008) differs from *C. archangelskyi* in having each cell of abaxial cuticle of microsporophylls by a large papilla. Number and position of its pollen sacs is not

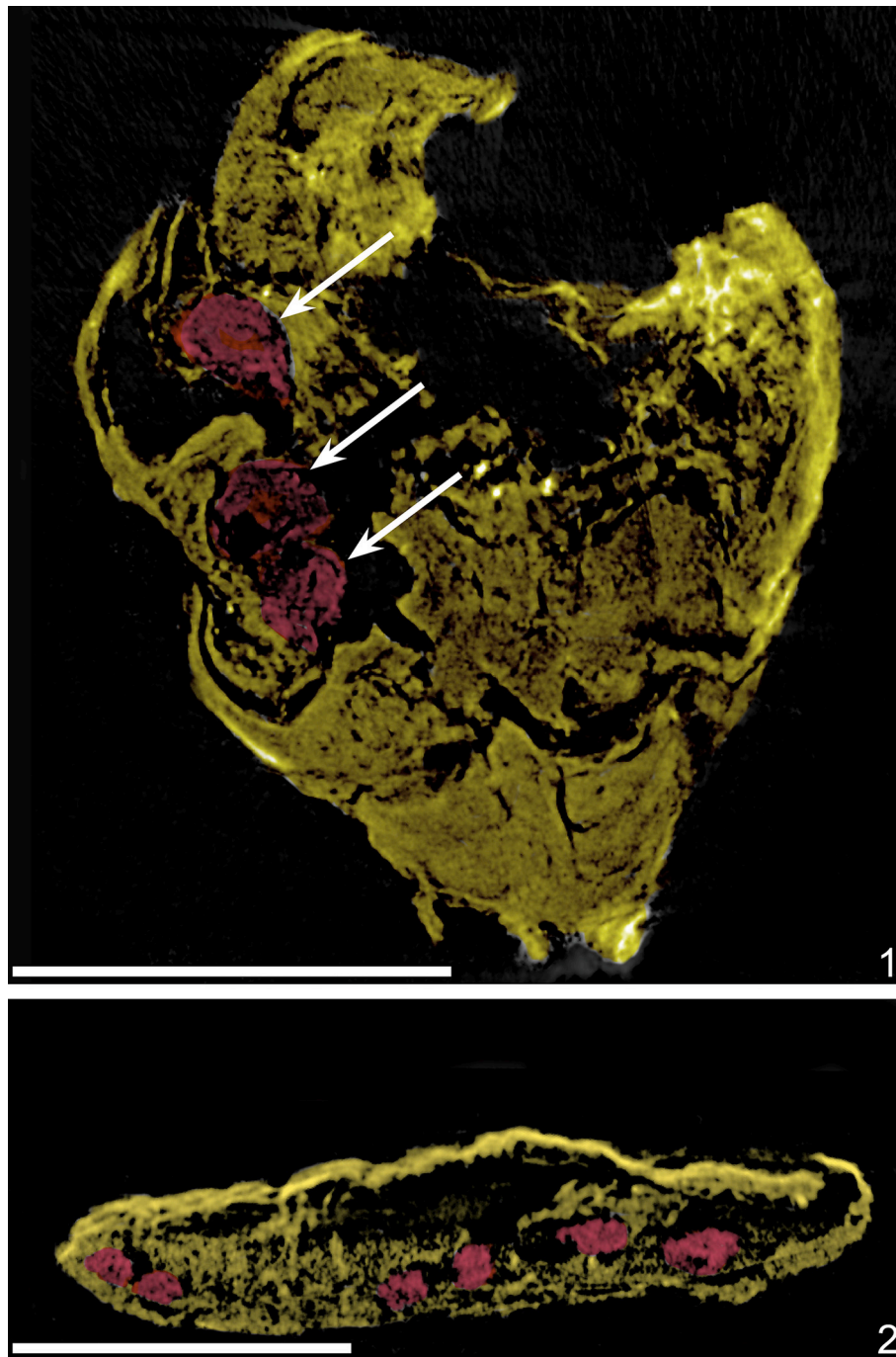




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**Plate III.** SEM images of *Classostrobus archangelskyi* sp. nov. (Holotype No. P1124, sample Carregueira 414) from Lower Cretaceous of Figueira da Foz Formation, Lusitanian Basin, central-western Portugal. **1.** Detached microsporophyll showing its proximal site, stalk and three pollen sacs (arrows). **2.** Detail of ovoid drop-shaped pollen sacs. **3, 4.** *Classopollis* grains on the surface of the pollen sac. **5.** Detail of in situ *Classopollis* pollen grain and orbicules (O) attached to tapetal membrane. **6.** Detail of in situ *Classopollis* pollen grain in distal polar view showing cryptopore (C) and rimula (R). Scale bars: 200  $\mu$ m (1), 100  $\mu$ m (2, 3, 4), 20  $\mu$ m (5), 10  $\mu$ m (6).



**Plate IV.** MicroCT images of *Classostrobus archangelskyi* sp. nov. (Holotype No. P1124, sample Carregueira 414) from Lower Cretaceous of Figueira da Foz Formation, Lusitanian Basin, central-western Portugal. **1, 2.** Vertical (yz) and horizontal (xy) sections of 3D microCT of the microsporangiata cone showing stalk and three pollen sacs (arrows). Scale bars: 1 mm (1), 0.8 mm (2).

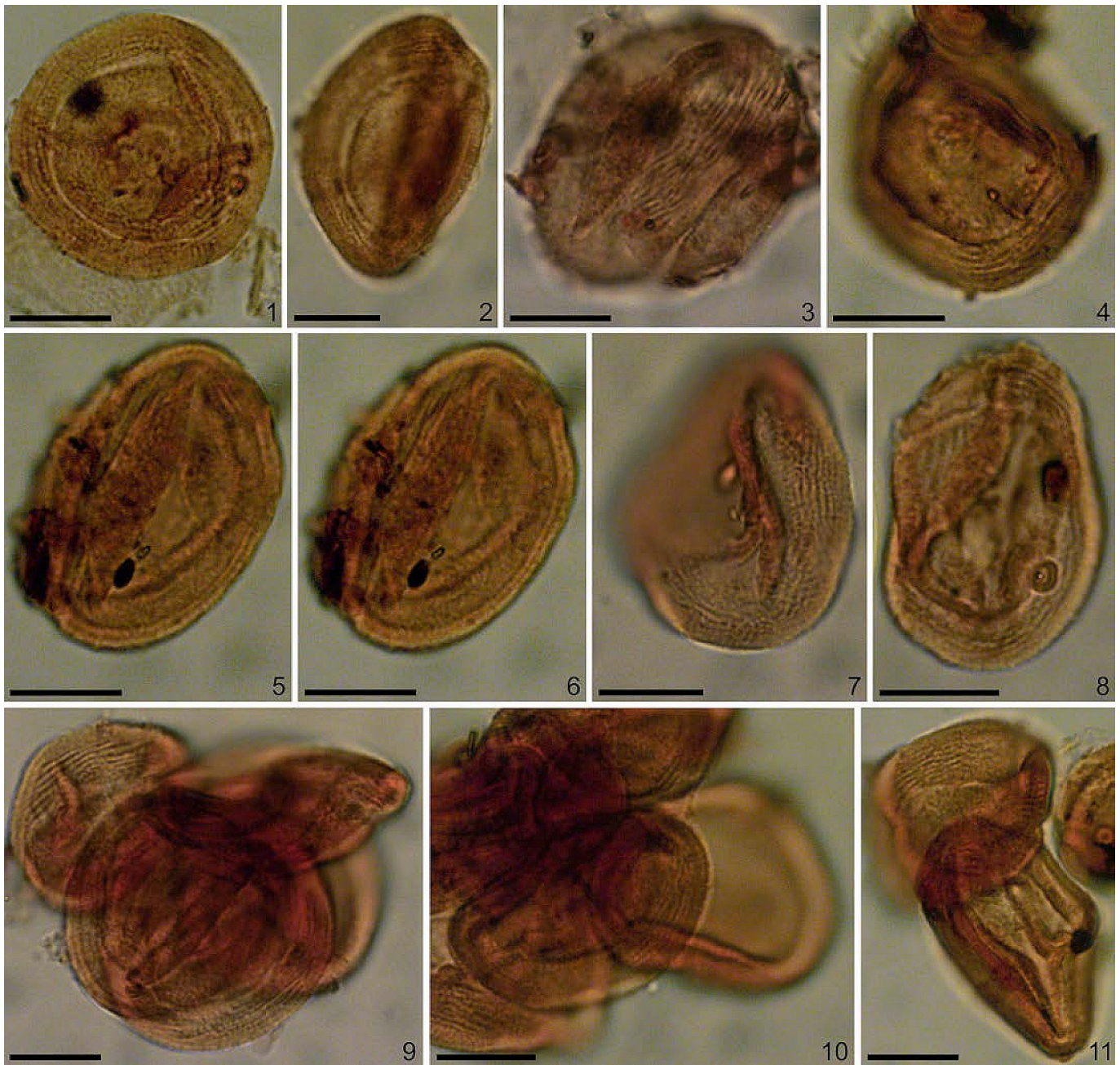
known.

The microsporangiata cone *Classostrobus crossii* Rothwell, Mapes, J. Hilton et Hollingworth from the upper Middle Jurassic (Callovian) of Freeth Wood Gravel pit in Ashton Keynes, near Cirencester, Gloucestershire, United Kingdom (Rothwell et al., 2007) differs from

*C. archangelskyi* in having a higher number of pollen sacs per microsporophyll and a higher number of microsporophylls per cone. It also differs in having an elongate shape of microsporophylls.

*Classostrobus elliotii* Hieger, Serbet, C.L.Harper, T.N.Taylor, Ed.L. Taylor et Gulbranson from the Lower Jurassic of Antarctica (Hieger





**Plate V.** *Classostrobus archangelskyi* sp. nov. (Holotype No. P1124, sample Carregueira 414) from Lower Cretaceous of Figueira da Foz Formation, Lusitanian Basin, central-western Portugal. In situ *Classopollis* pollen grains in transmitted light microscopy (LM). **1, 2.** Distal view, cryptopore and rimula are seen. Pollen mass figured in 1 is also figured in pollen [Plate VI](#), 1. **3.** Equatorial view, equatorial girdle with striation is seen. **4.** Distal view, cryptopore and striate equatorial girdle are visible. **5, 6.** Same pollen, different focus, proximal view. Scar and layered pollen wall are seen. **7, 8.** Folded pollen, equatorial girdle is seen. Pollen figured in 7 is also figured in pollen [plate VI](#), 7. Pollen figured in 8 is also figured in Pollen [Plate VI](#), 3. **9–11.** Pollen mass. One of the pollen grains figured in 9 is also figured in pollen [Plate VI](#), 6. Scale bars: 10  $\mu$ m for all specimens.

[et al., 2015](#)) differs from the studied microsporangiote cone in having higher number of pollen sacs and higher number of microsporophylls per cone.

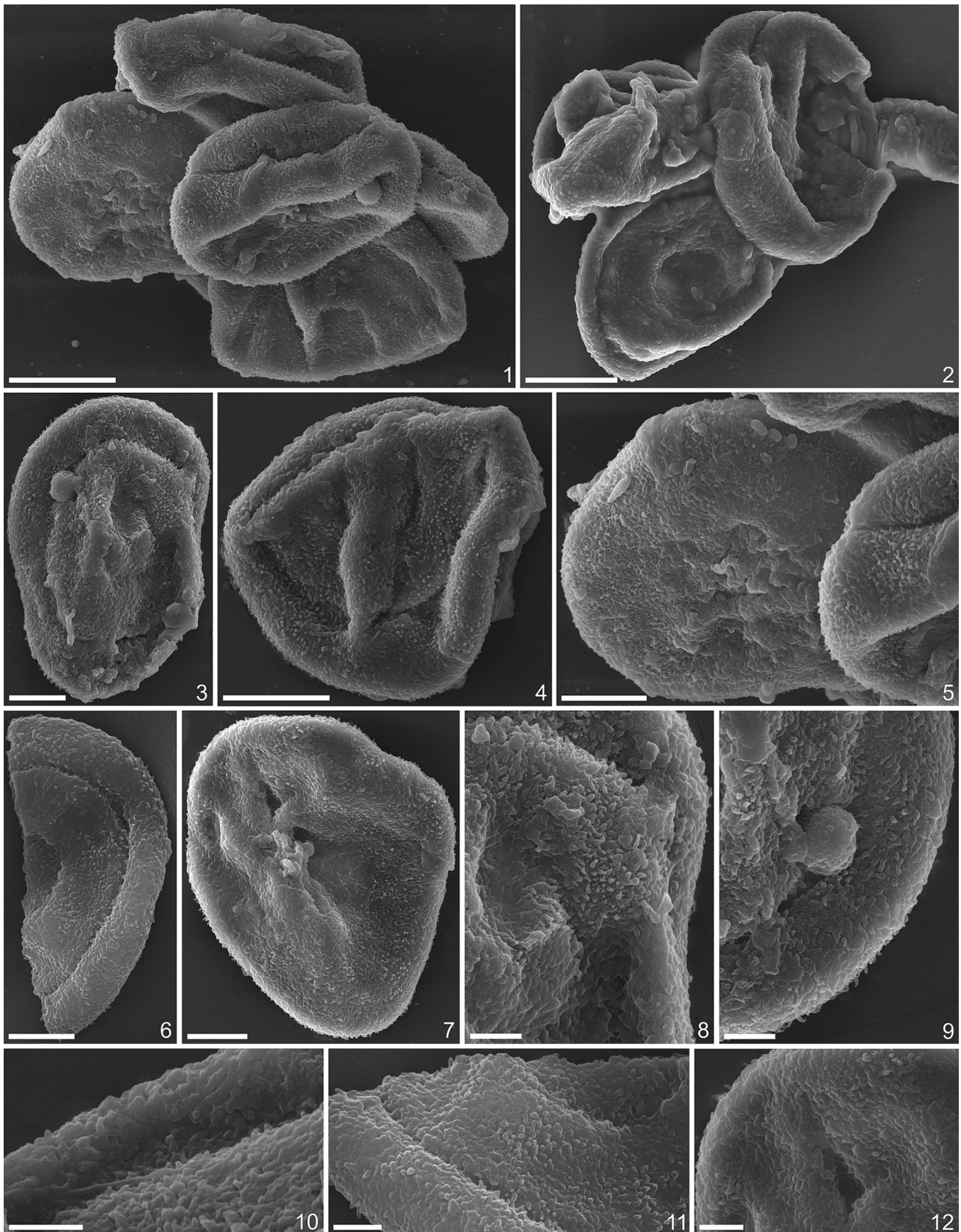
*Classostrobus cloughtonensis* van Konijnenb. from the Jurassic of Yorkshire ([van Konijnenburg-van Cittert, 1987](#)) differs from *C. archangelskyi* in having a lower number of pollen sacs (probably 3) and higher number of microsporophylls per cone. The abaxial cuticle of microsporophylls of *C. cloughtonensis* differs from abaxial cuticle of *C. archangelskyi* in possessing Florin rings surrounding stomatal pits. Comparison of all the species of *Classosotrobus* is summarised in [Table 1](#).

[Barale et al. \(1988\)](#) studied isolated microsporangiote cones that

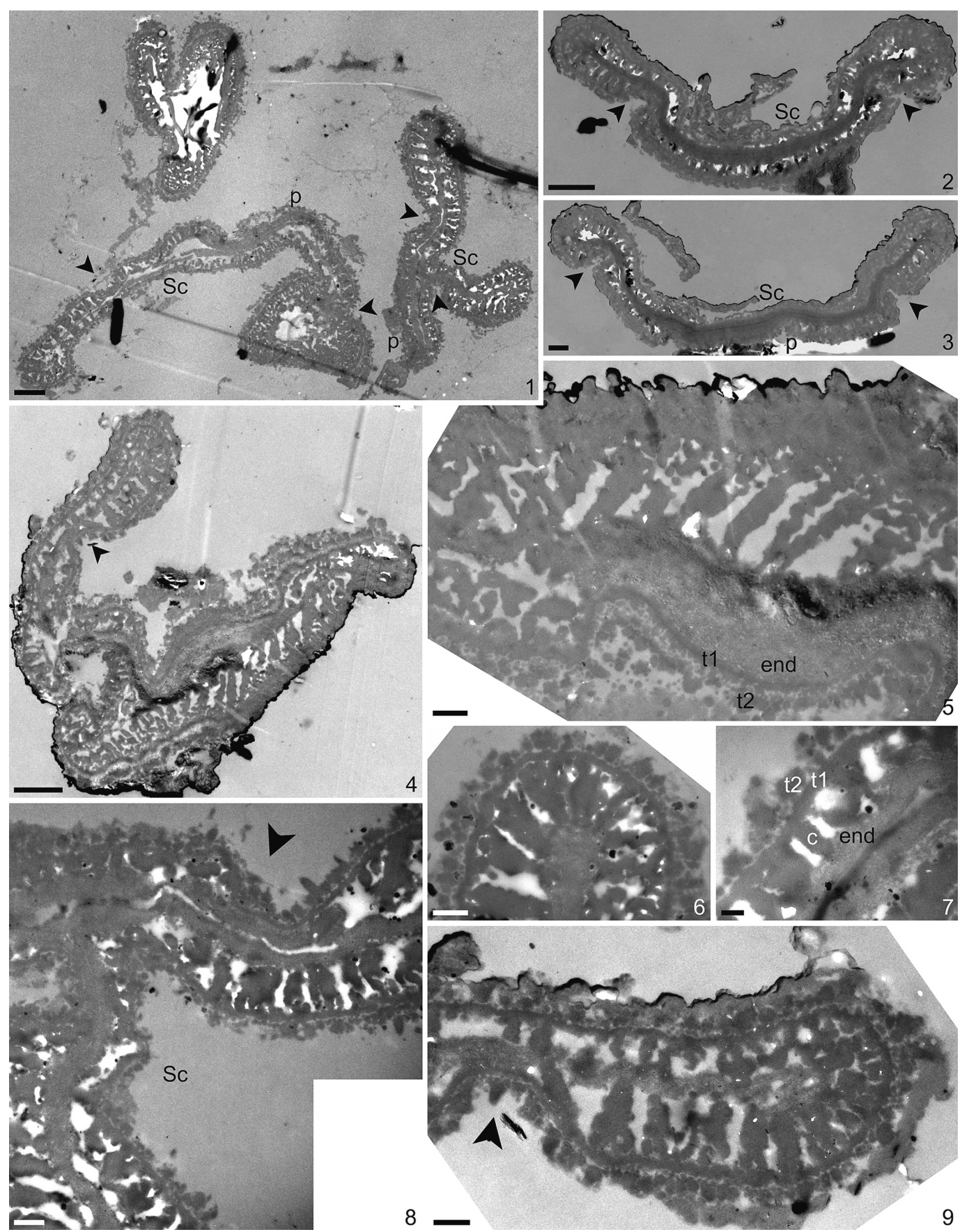
were associated with *Frenelopsis* sp. from the Upper Cenomanian of Torrelaguna (Madrid, Spain). These cones consist of 11–20 microsporophylls. Size of the *Classopollis* pollen from the cone is on average smaller (20–30  $\mu$ m), cryptopore size larger, scar smaller. The sculpture is verrucate-echinulate, and the sizes of the sculpture elements were not described; they compared their pollen with *Classopollis classoides* Fensome.

Microsporangiote cones associated with or attached to *Frenelopsis alata* (K. Feistm.) Erw. Knobloch from the Cenomanian of the Czech Republic ([Hlušík and Konzalová, 1976](#); [Hlušík and Kozlovas, 1976](#); [Kvaček, 2000](#)) consist of 13–22 microsporophylls. The number of pollen





**Plate VI.** *Classostrobus archangelskyi* sp. nov. (Holotype No. P1124, sample Carregueira 414) from Lower Cretaceous of Figueira da Foz Formation, Lusitanian Basin, central-western Portugal. In situ *Classopollis* pollen in scanning electron microscopy (SEM). **1, 2.** Pollen mass, scar, cryptopore and striae of the broken equatorial girdle are seen. **3, 4.** Distal view, cryptopore, rimula, and equatorial girdle are seen. **5, 7.** Proximal view, scar is visible. **6.** Distal view of the folded in half pollen, cryptopore, rimula, and equatorial girdle are seen. **7, 8.** Close-ups of the pollen figured in 3. **10.** Close-up of a distal surface, rimula is seen. **11.** Close-up of the pollen figured in 6. **12.** Close-up of the pollen figured in 7. Scale bars: 10  $\mu$ m (1, 2), 5  $\mu$ m (3–7), 2  $\mu$ m (8–12).



(caption on next page)



**Plate VII.** *Classostrobus archangelskyi* sp. nov. (Holotype No. P1124, sample Carregueira 414) from Lower Cretaceous of Figueira da Foz Formation, Lusitanian Basin, central-western Portugal. In situ *Classopollis* pollen in transmission electron microscopy (TEM). 1. Section through a pollen mass. 2, 3. Sections of the same pollen at different levels, reduced ectexine in cryptopore, rimula, and scar regions is seen in 3, the section in 2 is closer to the periphery and shows reduced ectexine in rimula and scar only. 4. Oblique section of the whole pollen showing thicker ectexine in the equatorial region and striae of merged infratectal elements. 5. Close-up of 4, showing in detail striae of the equatorial girdle. 6–8. Close-ups of the pollen grains figured in 1, cut at different levels. 6. Equatorial region showing thickened ectexine and branched infratectal elements. 7. Exine in the distal region of the pollen grain. 8. Part of the pollen, showing reduced ectexine in scar (right), rimula (upper part), and cryptopore (upper left). 9. Part of the pollen in the equatorial region. Arrowheads indicate rimula regions, t1 – tegillum, t2 – tectum, c – infratectal columella-like elements, end – endexine, p – cryptopore region, Sc – trilete scar region. Scale bars: 2 µm (1, 2, 4), 1 µm (3), 0.5 µm (5, 6, 8, 9), 0.2 µm (7).

**Table 1**  
Morphological characters among described species assigned to the genus *Classostrobus*.

Species	Number of pollen sacs	Number of microsporophylls	Microsporophyll margin	Shape of apex	Abaxial papillae	Age	Reference
<i>Classostrobus rishra</i>	6–8	More than 60	Frilled	Acute	Absent	Middle Jurassic	Barnard, 1968
<i>Classostrobus cloughtonensis</i>	Probably 3	Unknown	Unknown	Broadly acute	Absent	Middle Jurassic	van Konijnenburg-van Cittert, 1987
<i>Classostrobus crossii</i>	More than 6	More than 50	Unknown	Attenuate	Unknown	Callovian–Middle Jurassic	Rothwell et al., 2007
<i>Classostrobus elliotii</i>	4–7	About 30	Unknown	Unknown	Obtuse	Lower Jurassic	Hiegar et al., 2015
<i>Classostrobus comptonensis</i>	About 3	About 50	With unicellular trichomes	Acute	Present	Barremian	Alvin et al., 1978
<i>Classostrobusugnaensis</i>	Unknown	About 30	With unicellular trichomes	Obtuse	Present	Barremian	Gomez et al., 2002
<i>Classostrobussturoloensis</i>	Unknown	About 40	With small papillae	Rounded	Present	Albian	Gomez et al., 2002
<i>Classostrobus arkansensis</i>	Probably 2	About 60	Entire, scarious, often with patches of prominent unicellular tri-chomes	Acute to slightly rounded	Present	Aptian/Albian	Axsmith et al., 2004
<i>Classostrobus cathayanus</i>	Unknown	About 50	Unknown	Acuminate	Present	Lower Cretaceous	Zhou, 1983
<i>Classostrobus dalatzensis</i>	Unknown	About 50	Unknown	Acute to acuminate	Present	Aptian/Albian	Yang, 2008
<i>Classostrobus archangelskyi</i>	4–5	About 12	With long unicellular trichomes	Obtuse	Absent	Aptian/Albian	Present paper

sacs is not known, therefore it hampers comparison with presently described material. Their pollen grains differ from the studied material in the microgranulate sculpture, having proximal pole with tenuitas, larger pollen size, cryptopore diameter, and equatorial girdle.

Microsporangiate cones of *Frenelopsis oligostomata* Romariz from the Maastrichtian of Esgueira, Portugal (Pons and Broutin, 1978) show about 20–22 microsporophylls per cone. Their number of pollen sacs is not known, so it is difficult to compare it closely with *C. archangelskyi*.

The microsporangiate cones of *Classostrobus archangelskyi* resemble *Potokaea* Pacyna, Barbacka et Zdebska from the Triassic of Poland (Pacyna et al., 2017) in shape and morphology. However, they differ in having different in situ pollen and arrangement of the pollen sacs on the abaxial side, while *Potokaea* has a whorl of microsporangia on the microsporophyll corresponding more closely with early diverging conifers of Permian and Triassic Voltziales.

#### 4.2. Comparison of in situ pollen

Pollen grains of *Classopollis* are among most popular fossil palynological objects studied with LM, SEM, and TEM. Their unique morphology and ultrastructure (distal cryptopore, proximal scar often with filaments, striate equatorial girdle, subequatorial rimula, tegillum (outer tectum of a lesser electron density), and columella-like infratectal elements), along with wide distribution made them an attractive object for any palynologist. Numerous studies included descriptions of the pollen characters of mature grains, pollen ontogeny, and even pollen germination (Kürschner et al., 2013). Differences between *Classopollis* species include pollen size, prominence of the equatorial girdle and rimula, girdle width and number of the inner striae, size of the cryptopore and scar area, and differences in tegillum and infratectal ultrastructure.

Reviews of pollen studies of the Circumpolles group (where *Classopollis* belongs along with several more genera) show a rather uniform

morphology and ultrastructure of *Classopollis* species, but a trend of transformation of the infratectal structure from granular in earlier members to columella-like and branched columella-like infratectal elements in older members of the genus (Srivastava, 1976; Pocock et al., 1990; Zavialova et al., 2010 and papers cited there). These authors also discussed in detail each pollen character, characterising the unique *Classopollis* pollen, their functional load, possible pollination biology of their parent plants, palaeoecology, and different opinions on their taxonomy.

In pollen micromorphology, Cheirolepidiaceae are superficially similar to Araucariaceae and Gnetales (Srivastava, 1976). Pollen grains of those two quite distinct groups of gymnosperms share some peculiar characters. Some gnetophytalean pollen grains (e.g., Tekleva and Krasilov, 2009) share with *Classopollis* pollen columellate-like infratectal, but without any thickening throughout the pollen. Araucariaceae pollen show similarity in possessing characters unusual for gymnosperm pollen: microechinate sculpture and outer part of the ectexine (*Araucariacites*, *Callialasporites*; e.g., Tekleva et al., 2022), and equatorial thickenings and pore or polar exine thinnings (*Balmeiopsis*, *Cyclusphaera*, *Callialasporites*, e.g., Archangelsky, 1994; Del Fueyo et al., 2012). However, each of these plant groups (gnetales, araucarians, and cheirolepidiales) shows its own unique combination of pollen characters of general morphology and sporoderm ultrastructure.

#### 4.3. Comparison with *Classopollis* pollen studied with TEM

Three Cretaceous members of Circumpolles were studied using TEM: two in situ *Classopollis* sp., (Raetic-Liassic, England, Pettitt and Chaloner, 1964 and Barremian, England; Taylor and Alvin, 1984) and two dispersed species, *Classopollis martinotii* Reyre (Albian–Cenomanian, Lebanon, Zavialova et al., 2010), *Classoidites glandis* Amerom (Turonian, France; Médus, 1977; Upper Cretaceous, Portugal; Kedves, 1994).

Pettitt and Chaloner (1964) studied pollen grains extracted from the

pollen sacs of *Cheirolepidium muensteri* (Schenk) Takht. (Raetic-Liassic, England) with LM, SEM and TEM. They identified those grains as *Classopollis torosus* type, occurring in monads and tetrads. Judging from their description of the tegillum, the exine sculpture is microechinate, similarly to the pollen under study, and is also characterised by a similar exine ultrastructure and thickness of the ectexine layers, although Pettitt and Chaloner (1964) reported a possible thin foot layer, which is absent in our material.

In situ *Classopollis* sp. was described from the microsporangiate cone *Classostrobus comptonensis* from the Barremian of England (Taylor and Alvin, 1984). The authors did not specify to what species it belongs. In general, pollen grains from *Classostrobus comptonensis* show much similarity to the studied pollen, having infratectal elements, tectum, tegillum of comparable thickness/width, and orbicules that are similar in size and structure. The differences are in the larger size of the pollen grains of *Classostrobus comptonensis* (31–35 µm as measured from illustrations, the authors did not specify the sizes in their paper), in a better preserved lamellate endexine, larger number of the girdle striae (11–13), although they counted them on TEM sections and did not indicate the width of the girdle. The tectum is reported to be discontinuous in the areas of the rimula, cryptopore, and scar; in our material the tectum appears to be thinner, but continuous.

Dispersed pollen grains referred to as *Classopollis martinotii* (Albian–Cenomanian, Lebanon, Zavialova et al., 2010, but probably of an older, Barremian–Aptian, age, see Zavialova, 2015, p. 54) were studied by LM, SEM, and TEM, and showed close similarity to the pollen under study, especially considering the exine sculpture and ultrastructure. The pollen size of *C. martinotii* (Zavialova et al., 2010) appears to be slightly larger, as well as the cryptopore diameter, the trilete scar area and the thickness of the equatorial girdle. The number of equatorial striae is higher in the pollen under study. Another possible difference is that the Lebanon material contained dyads and tetrads, rarely tryads along with monads, while we observed monads only.

Dispersed pollen *Classoidites glandis* was studied with TEM by Médus (1977; Turonian, France) and Kedves (1994; Upper Cretaceous, Portugal). Unfortunately, their descriptions are quite short and concern mostly the ultrastructure, impeding an adequate comparison with our material. The main difference from other Circumpolles members they indicated is branched infratectal elements, which were not observed in older members of the group. Médus (1977) described those branched columella-like elements in the distal region, although judging from his illustration, they might be equatorial, and they appear somewhat similar to what we observed in our pollen (Plate VI, 6, 8, 9).

Another in situ *Classopollis* from the microsporangiate cone *Classostrobus dalatzensis* was not studied with TEM, but numerous broken pollen grains viewed in SEM allowed Yang (2008) to describe the sporoderm ultrastructure. The pollen grains were considered immature, and they are smaller than any known *Classopollis* pollen, including our material; the cryptopore, trilete scar, and equatorial girdle also show smaller sizes. The ultrastructural details fit a normal *Classopollis* pattern, being similar with our pollen as well. The exine sculpture differs from the studied pollen in having smaller baculae. Numerous illustrations of the striae of the equatorial girdle are what make this species specific.

Hieger et al. (2015) described microsporangiate cones *Classostrobus elliotii* with in situ *Classopollis* pollen from the Lower Jurassic of Antarctica. The pollen grains were studied only with SEM, and the exine ultrastructure was observed as well. In general morphology and exine sculpture, the pollen grains of *Classostrobus elliotii* are similar to the pollen grains under study, but differ in larger pollen size, smaller cryptopore, similar or larger trilete scar, and smaller orbicules. Additionally, inner striations are vaguely seen under LM in pollen grains of *Classostrobus elliotii*. The exine ultrastructure of pollen from *Classostrobus elliotii* also appears similar to pollen from our *C. archangelskyi* cones, although the figures for *C. elliotii* tectum, infratectum, and nexine are slightly larger than those for our pollen.

Two detailed and important studies on *Classopollis* pollen with SEM

should be mentioned to make a comparison of the pollen under study with a particular *Classopollis* species.

Villar de Seoane (2014) observed a number of dispersed *Classopollis* species from the Cretaceous of Argentina using a SEM, and published three new species from those observations. The illustrations of the exine sculpture show that our *Classopollis* is similar to *C. chateaunovi* Reyre, *C. rarus* Reyre, and *C. noelii* Reyre; the comparison with these species based on their descriptions shows that *C. rarus* differs from our pollen by a smaller scar, *C. noelii* by a verrucate sculpture with smaller sculpture elements, and *C. chateaunovi* by smaller verrucae (not microechini). Reyre (1970) provided the most details for both his species, which made the differences between them and our pollen clearest. In particular, *C. rarus* has a larger girdle, a wider size range of sculpture elements (0.3–1 µm compared to 0.5 (0.3–0.6) µm in our pollen), and SEM shows the cryptopore is not well-shaped. *C. chateaunovi* is characterised by vague “pseudostriations” and a larger girdle; the exine sculpture is also different from that of the pollen under study. *C. noelii* has a slightly larger girdle and smaller sculpture elements (verrucae) compared with higher microechini in our pollen. *C. martinotii* (as described by Reyre, 1970) shows similarity to the pollen under study in terms of the exine sculpture, but the diagnosis states that the rimula is often hard to discern, the cryptopore outline is unclear, and striae are usually less numerous.

Among older Circumpolles members, studied with TEM, there are *Duplicisporites granulatus* (Leschik) Scheuring, *D. verrucosus* (Leschik) Scheuring (Carnian, Italy, Zavialova and Roghi, 2005), *Circulina* sp. forms 1–3 (Upper Triassic, France; Médus, 1977), *Classopollis meyeriana* (Klaus) Venkatachala et Góczán, *Geopollis zwolinskae* (J.J.Lund) Brenner, *C. torosus* (Reissinger) Couper (Rhaetian, England; Zavialova et al., 2010), *C. torosus* (Rhaetian–Liassic, England; Pettitt and Chaloner, 1964), *C. harrissii* Muir et van Konijnenburg-van Cittert (Rhaetian–Liassic, France; Médus, 1977), *C. classoides* Pflug, *C. minor* Pocock et Jansonius (Liassic, Hungary, Egypt; Kedves, 1994), *Classopollis* sp. (Callovian, western Siberia; Zavialova, 2003), *C. classoides* (Oxfordian, England; Rowley and Srivastava, 1986), and *Classopollis* sp. (Upper Jurassic, Kazakhstan; Krassilov et al., 1997; Zavialova and Tekleva, 2005; Tekleva and Krassilov, 2009). Most of these species differ from our pollen both in exine sculpture and ultrastructure; only *Classopollis* sp. (Zavialova, 2003), *C. torosus* and *C. classoides* show some similarity to our pollen. However, *C. classoides* is characterised by a somewhat smaller pollen size, larger cryptopore and girdle (Rowley and Srivastava, 1986; Kedves, 1994). *Classopollis* sp. (Zavialova, 2003) shows some similarity in the exine, but the general morphology and exine sculpture were not described, so it is impossible to make an adequate comparison with our material.

#### 4.4. Remarks on palaeoecology

The microsporangiate cone *Classostrobus archangelskyi* is found in the same taphocoenose as sterile axes of *Frenelopsis attunesii* M.M.Mendes et J.Kvaček. It is the only cheirolepidiaceae conifer in sample 414. Therefore, we propose the microsporangiate cones could be associated with the latter sterile foliage. It shows further similarities - similar number of subsidiary cells (4), and quite similar stomatal apparatus that externally do not show any large papillae (Mendes and Kvaček, 2022). However, besides sample 414, other members of Cheirolepidiaceae occur in the locality, namely *Pseudofrenelopsis zlatkoi* J.Kvaček et M.M. Mendes (Kvaček and Mendes, 2022) and *Watsoniocladius cunhae* J.Kvaček et M.M.Mendes (Kvaček and Mendes, 2021). Further studies focused on this problem are planned for future research.

Pollination of Cheirolepidiaceae is one of the intriguing questions. The high amount of pollen produced by all taxa of the family, including the newly studied taxon would argue for wind pollination, however, finds of *Classopollis* pollen in and around bodies of fossil insects (Zavialova and Tekleva, 2005; Labandeira et al., 2007), in their guts (Krassilov et al., 1997), the pollen characters and the complicatedly

elaborated surfaces of Cheirolepidiaceae ovuliferous structures with trichomes and papillae (Kvaček, 2000) argue for entomophily (Labandeira et al., 2007).

## 5. Conclusions

The new cheirolepidiacean microsporangiate cone *Classostrobus archangelskyi* described here shows an ovoid shape, consisting of about twelve spirally arranged microsporophylls, and each microsporophyll possessing a stalk and deltoid head, bearing 4–5 pollen sacs. The microsporangiate cone *C. archangelskyi* was found associated in taphocoenose with *Frenelopsis antunesii* shoots. This suggests that the microsporangiate cone *C. archangelskyi* may have been produced by *F. antunesii*.

The in situ pollen grains display a distinctive morphology and ultrastructure characteristic for the genus *Classopollis*. The *Classopollis* pollen documented here shares strong similarities with other species previously described, namely *C. martinoti*, and *C. torosus*, but particularly with *C. noelii*.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

No data was used for the research described in the article.

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## References

- Alvin, K.L., 1977. The conifers *Frenelopsis* and *Manica* in the Cretaceous of Portugal. *Palaeontology* 2, 387–404.
- Alvin, K.L., 1982. Cheirolepidiaceae: biology, structure and paleoecology. *Rev. Palaeobot. Palynol.* 37, 71–98.
- Alvin, K., Pais, J., 1978. A *Frenelopsis* with opposite decussate leaves from the Lower Cretaceous of Portugal. *Palaeontology* 21, 873–880.
- Alvin, K.L., Spicer, R.A., Watson, J., 1978. A *Classopollis*-containing male cone associated with *Pseudofrenelopsis*. *Palaeontology* 21, 847–856.
- Alvin, K.L., Watson, J., Spicer, R.A., 1994. A new coniferous male cone from the English Wealden and a discussion of pollination in the Cheirolepidiaceae. *Palaeontology* 37, 173–180.
- Archangelsky, S., 1994. Comparative ultrastructure of three early cretaceous gymnosperm pollen grains: *Araucariacites*, *Balmeiopsis* and *Callialasporites*. *Rev. Palaeobot. Palynol.* 83, 185–198.
- Axsmith, B.J., Krings, M., Waselkov, K., 2004. Conifer pollen cones from the Cretaceous of Arkansas: implications for diversity and reproduction in the Cheirolepidiaceae. *J. Paleontol.* 78 (2), 402–409.
- Barale, G., Fernandez Marron, T., Alvarez Ramis, C., 1988. Étude de cones males de *Frenelopsis* Schenk emend. Reymanówna et Watson, 1976 (Cheirolepidiaceae) du Crétacé Supérieur de Torrelaguna (Province de Madrid – Espagne). *Geobios* 21 (2), 187–193.
- Barnard, P.D.W., 1968. A new species of *Masculostrobus* Seward producing *Classopollis* pollen from the Jurassic of Iran. *Bot. J. Linn. Soc.* 61, 167–176.
- Barnard, P.D.W., 1973. Mesozoic floras. In: Hughes, N.F. (Ed.), *Organisms and Continents Through Time*, Spec. Pap. Palaeontol., 12, pp. 175–187.
- Barreda, V.D., Cúneo, N.R., Wilf, P., Currano, E.D., Scasso, R.A., Brinkhuis, H., 2012. Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low extinction, and a *Classopollis* spike. *PLoS One* 7, e25455.
- Clement-Westerhof, J.A., Van Konijnenburg-van Cittert, J.H.A., 1991. *Hirmeriella muensteri*: new data on the fertile organs leading to a revised concept of the Cheirolepidiaceae. *Rev. Palaeobot. Palynol.* 68, 147–179.
- de Jussieu, A.L., 1789. *Genera plantarum secundum ordines naturales disposita, juxta methodum in Horto regio parisiensi exarata*. Herissant et Theophilum Barrois, Paris, p. 498.
- De Queiroz, K., Cantino, P.D., Gauthier, J.A., 2020. *Phylogeny: A Companion to the PhyloCode*. CRC Press, Boca Raton, FL.
- Del Fueyo, G.M., Archangelsky, S., Archangelsky, A., 2012. An ultrastructural study of the araucarian pollen grain *Cyclisphaera radiata* Archangelsky from the Albian of Patagonia. *Rev. Palaeobot. Palynol.* 173, 57–67.
- Dinis, J.L., 1999. Estratigrafia e sedimentologia da Formação de Figueira da Foz. Aptiano a Cenomaniano do sector norte da Bacia Lusitânica. Ph.D. Thesis, University of Coimbra, Portugal.
- Dinis, J.L., 2001. Definição da Formação da Figueira da Foz – Aptiano a Cenomaniano do sector central da margem oeste ibérica. *Comun. Inst. Geol. Min.* 88, 127–160.
- Dinis, J.L., Rey, J., de Graciansky, P.C., 2002. Le Bassin Lusitanien (Portugal) à l'Aptien supérieur-Albien: organisation séquentielle, proposition de corrélations, evolution. *Compt. Rend. Geosci.* 334, 757–764.
- Doludenko, M.N., 1978. Rod *Frenelopsis* (Coniferales) i ego nakhodki v melu SSSR. [Genus *Frenelopsis* (Coniferales) and its occurrence in the Cretaceous of USSR]. *Paleontol. Zh.* 1978 (3), 107–121 (in Russian).
- Doweld, A., 2020. The controversial nomenclature of the fossil plant names *Cheirolepis*, *Cheirolepidium* and *Hirmeriella* (Cheirolepidiaceae/Cheirolepidiaceae/Hirmeriaceae). *Taxon* 69 (5), 1092–1098.
- Escapa, I.H., Leslie, A., 2017. A new Cheirolepidiaceae (Coniferales) from the Early Jurassic of Patagonia (Argentina): reconciling the records of impression and permineralized fossils. *Am. J. Bot.* 104, 322–334.
- França, J.C., Zbyszewski, G., 1963. Carta Geológica de Portugal na escala 1:50 000. Notícia explicativa da folha 26-B (Alcobaça). Serviços Geológicos de Portugal, Lisboa.
- Friis, E.M., Crane, P.R., Pedersen, K.R., 1988. Reproductive structure of Cretaceous Platanaceae. *Kong. Danske Vidensk. Selskab, Biol. Skrift.* 31, 1–55.
- 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 from Portugal. *Ann. Miss. Bot. Gard.* 86, 259–296.
- Gomez, B., Martín-Closas, C., Barale, G., Solé de Porta, N., Thévenard, F., Guignard, G., 2002. *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ genera from the Lower Cretaceous of Spain. *Palaeontology* 45 (5), 997–1036.
- Heimhofer, U., Hochuli, P.A., Burla, S., Dinis, J., Weissert, H., 2005. Timing of Early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change. *Geology* 33, 141–144.
- Hiegar, T.J., Serbet, R., Harper, C.J., Taylor, T.N., Taylor, E.L., Gulbranson, E.L., 2015. Cheirolepidiacean diversity: an anatomically preserved pollen cone from the Lower Jurassic of southern Victoria Land, Antarctica. *Rev. Palaeobot. Palynol.* 220, 78–87.
- Hlušík, A., Konzalová, M., 1976. *Frenelopsis alata* (K. Feistm.) Knobloch (Cupressaceae) from the Cenomanian of Bohemia, a new plant producing *Classopollis* pollen. *Evol. Biol. Proceedings*, 125–131.
- Hlušík, A., Kozlovsk, M., 1976. Polliniferous cones of *Frenelopsis alata* (K. Feistm.) Knobloch from the Cenomanian of Czechoslovakia. *Věst. Úst. Geol.* 51, 37–45.
- Howell, M.M., Gossmann, R., Gee, C.T., 2022. A modified, step-by-step procedure for the gentle bleaching of delicate fossil leaf cuticles. *Foss. Impr.* 78, 445–450.
- Kedves, M., 1994. Transmission electron microscopy of the Fossil Gymnosperm Exines. *Attila Josef Univ. Szeged*.
- Kerp, H., Krings, M., 1999. Light microscopy of fossil cuticles. In: Jones, T.P., Rowe, N.P. (Eds.), *Fossil Plants and Spores: Modern Techniques*. Geological Society, London, pp. 52–56.
- Krassilov, V.A., Zherikhin, V.V., Rasnitsyn, A.P., 1997. *Classopollis* in the guts of Jurassic insects. *Paleontology* 40, 1095–1101.
- Kürschner, W.M., Batenburg, S.J., Mander, L., 2013. Aberrant *Classopollis* pollen reveals evidence for unreduced (2n) pollen in the conifer family Cheirolepidiaceae during the Triassic–Jurassic transition. *Proc. R. Soc. B* 280, 20131708.
- Kvaček, J., 2000. *Frenelopsis alata* and its microsporangiate and ovuliferous reproductive structures from the Cenomanian of Bohemia (Czech Republic, Central Europe). *Rev. Palaeobot. Palynol.* 112, 51–78.
- 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. *Rev. Palaeobot. Palynol.* 295 (384) (article number 104519).
- Kvaček, J., Mendes, M.M., 2022. A new species of the cheirolepidiacean conifer *Pseudofrenelopsis* from the Lower Cretaceous of Figueira da Foz Formation, Portugal. *Rev. Palaeobot. Palynol.* 309 (article number 104821).
- Labandeira, C., Kvaček, J., Mostovski, M.B., 2007. Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms. *Taxon* 56, 663–695.
- Lauverjat, J., Pons, D., 1978. Le gisement Sémonien d'Esgueira (Portugal): stratigraphie et flore fossile. *C. R. Congr. Nat. Soc. Savantes, (Nancy) fasc. 2*, 119–137.
- Médus, J., 1977. The ultrastructure of some Circumpollis. *Grana* 16, 23–29.
- 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 Palaeobot.* 58, 159–174.



- Mendes, M.M., Kvaček, J., 2022. *Frenelopsis antunesii* sp. nov., a new cheirolepidiacean conifer from the Lower Cretaceous of Figueira da Foz Formation in West Portugal. Rev. Palaeobot. Palynol. 300 (article number 10464).
- Mendes, M.M., Dinis, J.L., Gomez, B., Pais, J., 2010. Reassessment of the cheirolepidiacean conifer *Frenelopsis teixeirae* Alvin et Pais from the Early Cretaceous (Hauterivian) of Portugal and palaeoenvironmental considerations. Rev. Palaeobot. Palynol. 161, 30–42.
- Mendes, M.M., Dinis, J.L., Gomez, B., Pais, J., 2014. *Frenelopsis teixeirae* Alvin et Pais from the lower Hauterivian of Santa Susana Formation (Torres Vedras, Portugal): emended diagnosis and palaeoenvironmental setting. Comun. Geol. 101 (Especial I), 505–507.
- Mendes, M.M., Dinis, P., Kvaček, J., 2018. Some conifers from the Early Cretaceous (late Aptian–early Albian) of Catefica, Lusitanian Basin, western Portugal. Foss. Impr. 74, 317–326.
- 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. Cretac. Res. 130 (article number 105036).
- Mendes, M.M., Kvaček, J., Doyle, J.A., 2023. *Pseudofrenelopsis dinisii*, a new species of the extinct conifer family Cheirolepidiaceae from the lower Hauterivian (Cretaceous) of western Portugal. Rev. Palaeobot. Palynol. 315 (article number 04905).
- Pacyna, G., Barbacka, M., Zdebska, D., Ziaja, J., Fijałkowska-Mader, A., Bóka, K., Sulej, T., 2017. A new conifer from the Upper Triassic of southern Poland linking the advanced voltzialean type of ovuliferous scale with *Brachyphyllum*-*Pagiophyllum*-like leaves. Rev. Palaeobot. Palynol. 245, 28–54.
- Pettitt, J.M., Chaloner, W.G., 1964. The ultrastructure of the Mesozoic pollen *Classopollis*. Pollen Spores 6, 611–620.
- Pocock, S.A.J., Vasanthy, G., Venkatachala, B.S., 1990. Pollen of Circumpolles – an enigma or morphotrends showing evolutionary adaptations. Rev. Palaeobot. Palynol. 65, 179–193.
- Pons, D., 1979. Les organes reproducteurs de *Frenelopsis alata* (K. Feistm.) Knobloch, Cheirolepidiaceae du Cénomanién de l'Anjou, France. C. R. 104<sup>e</sup> Congr. Natl. Soc. Savantes (Bordeaux) 1, 209–231.
- Pons, D., Broutin, J., 1978. Les organes reproducteurs de *Frenelopsis oligostomata* a (Crétacé, Portugal). 103<sup>e</sup> Congr. Nat. Soc. Sav. Nancy, Sci. 2, 139–159.
- Rey, J., 2006. Stratigraphie séquentielle et séquences de dépôt dans le Crétacé inférieur du Bassin Lusitanien. Ciências Terra, Volume Especial 6, 1–120.
- Reyre, Y., 1970. Stereoscan observations on the pollen genus *Classopollis* Pflug, 1953. Palaeontology 13, 303–322.
- Romário, C., 1946. Estudo e revisão das formas portuguesas de *Frenelopsis*. Bol. Mus. Miner. Geol. Univ. Lisboa 14, 135–149.
- Rothwell, G.W., Mapes, G., Hilton, J., Hollingworth, N.T., 2007. Pollen cone anatomy of *Classtrobus crossii* sp. nov. (Cheirolepidiaceae). Int. J. Coal Geol. 69, 55–67.
- Rowley, J.R., Srivastava, S.K., 1986. Fine structure of *Classopollis* exines. Can. J. Bot. 64, 3059–3074.
- Srivastava, S.K., 1976. The fossil genus *Classopollis*. Lethaia 9, 437–457.
- Taylor, T.N., Alvin, K.L., 1984. Ultrastructure and development of Mesozoic pollen: *Classopollis*. Am. J. Bot. 71, 575–587.
- Teixeira, C., 1950. Flora mesozóica portuguesa, parte II. Serviços Geológicos de Portugal, Lisboa, p. 33.
- Tekleva, M.V., Krassilov, V.A., 2009. Modern Gnetales and fossil gnetophytes: comparative pollen morphology and ultrastructure. Rev. Palaeobot. Palynol. 156, 130–138.
- Tekleva, M.V., Mendes, M.M., Kvaček, J., 2022. The ultrastructure of in situ araucarian pollen from the male cone *Callialastrobus sousai*, Lower Cretaceous of Catefica, Lusitanian Basin, western Portugal. Rev. Palaeobot. Palynol. 307, 104782.
- Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J., Smith, G.F. (Eds.), 2018. International Code of Nomenclature for Algae, fungi, and Plants (Shenzhen Code) Adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten.
- Turutanova-Ketova, A.I., 1963. Semejstvo Cheirolepidiaceae (=Cheirolepidaceae) Hirmer und Hörhammer, 1934. In: Orlov, Yu.A. (Ed.), Osnovy Paleontologii. Akademia Nauk SSSR, pp. 249–250.
- Vakhrameev, V.A., 1970. Zakonomernosti rasprostraneniya i paleoekologiya mezozojskikh khvoynykh Cheirolepidiaceae [Relationships of occurrence and palaeoecology of Mesozoic conifers Cheirolepidiaceae]. Paleontol. Zh. 1970, 19–34 (in Russian).
- Vakhrameev, V.A., 1978. Klimaty severnogo polushariya v melovom periode i dannye paleobotaniki [Climate of the northern hemisphere during the Cretaceous period and paleobotanical data]. Palaeontol. Zh. 1978, 143–154 (in Russian).
- van der Ham, R.W.M., van Konijnenburg-van Cittert, J.H.A., Dortangs, R.W., Herengreen, G.F.W., van der Burgh, J., 2003. *Brachyphyllum patens* (Miquel) comb. nov. (Cheirolepidiaceae?): remarkable conifer foliage from the Maastrichtian type area (Late Cretaceous, NE Belgium, SE Netherlands). Rev. Palaeobot. Palynol. 127, 77–97.
- van Konijnenburg-van Cittert, J.H.A., 1987. New data on *Pagiophyllum maculosum* Kendall and its male cone from the Jurassic of North Yorkshire. Rev. Palaeobot. Palynol. 51, 95–105.
- Villar de Seoane, L., 2014. Estudio morfológico del género *Classopollis* (Pflug) Pocock et Jansonius (Crétácico, Argentina). Rev. Bras. Paleobot. 17, 91–104.
- Watson, J., 1988. The Cheirolepidiaceae. In: Beck, C.B. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 382–447.
- Yang, X.-J., 2008. A male cone of *Pseudofrenelopsis dalatzensis* with in situ pollen grains from the Lower Cretaceous of Northeast China. Geobios 41, 689–698.
- Zavialova, N.E., 2003. On the ultrastructure of *Classopollis* exine: a tetrad from the Jurassic of Siberia. Acta Palaeont. Sin. 42, 1–7.
- Zavialova, N.E., 2015. Evolutionary transformations of sporoderm ultrastructure in certain monophyletic lineages of higher plants. Bot. Pac. 4 (2), 49–57.
- Zavialova, N., Roghi, G., 2005. Exine morphology and ultrastructure of *Duplicisporites* from the Triassic of Italy. Grana 44, 337–342.
- Zavialova, N.E., Tekleva, M.V., 2005. Ul'trastruktura jekziny pyl'cevykh zeren roda *Classopollis*, izvlechennykh iz zheludkov nasekomykh jurskogo vozrasta [Exina ultrastructure of pollen grains of the genus *Classopollis* from stomachs of Jurassic insects]. In: Proceedings of the 11th All Russia Palynological Conference "Palynology: Theory and Practice", Tipografiya ARES, Moscow, pp. 86–87 (in Russian).
- Zavialova, N.E., Tekleva, M.V., Smirnova, S.B., Mroueh, M., 2010. Exine ultrastructure in pollen grains of *Classopollis* Pflug from the Cretaceous of Lebanon. Paleontol. J. 44 (10), 1353–1367.
- Zavialova, N.E., Tekleva, M.V., Polevova, S.V., Bogdanov, A.G., 2018. Electron Microscopy for Morphology of Pollen and Spores. RIPOL Classic Press, Moscow.
- Zhou, Z., 1983. A heterophyllous cheirolepidiacean conifer from the Cretaceous of East China. Paleontology 26 (4), 789–811.