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The early angiosperm *Pseudoasterophyllites cretaceus* from Albian–Cenomanian of Czech Republic and France revisited

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The early halophytic angiosperm *Pseudoasterophyllites cretaceus* from the Cenomanian Peruc Korycany Formation of the Bohemian Cretaceous Basin and from the Late Albian of the Northern Aquitanian Basin is redescribed. The plant is characterized by semi-whorled linear, and heavily cutinized leaves with paracytic stomata. Stamens associated with *P. cretaceus* possess an apically emerging connective that possesses the same epidermal cell pattern as the leaves. The stamens are massive, tetrasporangiate, and contain *Tucanopollis* pollen, thus clearly indicating affinities of *P. cretaceus* to the basal angiosperms. The plants that co-occur with *P. cretaceus* in semi-autochthonous taphocoenoses include the conifer *Frenelopsis alata*, which was likely a halophyte or halo-tolerant glycophyte growing in habitats close to the sea.

Key words: Magnoliopsida, *Pseudoasterophyllites*, *Tucanopollis*, Cretaceous, Albian, Cenomanian, Bohemia, France.

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Introduction

The Cenomanian strata of the Czech Republic and France represent some of the classical sites of Cretaceous palaeobotany, and continue to date to provide new insights into the early evolution and diversification of angiosperms. The diversity of mid-Cenomanian angiosperms from the Bohemian Cretaceous Basin in the Czech Republic has been documented in numerous publications based on mega- and mesofossils. First fossil angiosperms were recorded as leaves (Velenovský 1882, 1883, 1884, 1885), but later also impressions and compressions of attached or detached reproductive organs were described (Velenovský 1889; Velenovský and Vinikláš 1927, 1929, 1931; Kvaček 1992). During the last decades scientific interest primarily focused on bulk macerated angiosperm mesofossils (Eklund and Kvaček 1998; Kvaček and Eklund 2003; Kvaček and Friis 2010). Angiosperm pollen has been described from dispersed assemblages (e.g., Pacltová 1977, 1978, 1981). Numerous megafossil remains of angiosperms leaves were reported from the late Albian–early Cenomanian of Charente-Maritime, western France (Gomez et al. 2004), but only a probable Lauraceae *Eucalyptolaurus deprei* was described in detail (Coiffard et al. 2009). This paper provides a re-interpretation of the systematic affinity and palaeoecology of *Pseudoasterophyllites*

cretaceus O. Feistmantel ex Velenovský, 1887, an enigmatic plant from the Cenomanian of the Czech Republic and Albian of France based on old collections and well-preserved, newly collected specimens.

The affinities of *Pseudoasterophyllites cretaceus* have remained a matter of debate since the plant was first discovered. *Pseudoasterophyllites cretaceus* was first collected by Otokar Feistmantel, and originally published as *Asterophyllites cretaceus* nomen nudum (O. Feistmantel 1874). Based on Feistmantel's experience with Carboniferous plants, this author interpreted the plant as a horsetail. Velenovský (1887), however, who validated the name, interpreted the plant as an aquatic pteridophyte. Later, Zeiller (1907), during his work on Montsec material of *Montsechia vidalii* (Zeiller, 1902) Teixeira, 1954 from the Barremian of Spain, studied and interpreted the original specimens of *P. cretaceus* as conifer remains. Conversely, Velenovský and Vinikláš (1926) interpreted the plant as a lycophyte based on reproductive structures believed to belong to *P. cretaceus*. This interpretation was also used by Němejč (1963). Finally, Kvaček and Eklund (1998) suggested that the plant may belong to the gnetophytes because of the phyllotaxis and the presence of paracytic stomata. In this paper we provide evidence that the plant represents an early angiosperm. Stamens associated with the vegetative parts of the plant contain *Tucanopollis*

pollen, which is an example of the oldest angiosperm pollen types recorded previously from the Barremian of Gabon (Doyle et al. 1977; Doyle 1999), Congo (Doyle and Hotton 1991) and Egypt (Schrank and Mahmoud 2002). As a result, *Pseudoasterophyllites cretaceus* provides yet another insight into the complex evolutionary history of early angiosperms.

Pseudoasterophyllites cretaceus comes from taphocoenoses dominated by the cheirolepidiaceae conifer *Frenelopsis alata* (K. Feistmantel, 1885) Knobloch, 1971. These taphocoenoses are interpreted as sea-influenced deposits, and hence represent environments affected by high salinity (Uličný and Špičáková 1996; Uličný et al. 1997; Néraudeau et al. 2005). The *P. cretaceus*-bearing taphocoenoses from the Czech Republic are characterised by low plant diversity; apart from *F. alata*, the ginkgophyte *Nehvizdyella bipartita* Kvaček Falcon-Lang, and Dašková, 2005 (Kvaček et al. 2005), the enigmatic conifer *Dammarites albens* Presl in Sternberg, 1838 (Hlušík 1976, 1977), and an angiosperm named "*Diospyros*" *cretacea* Velenovský and Viniklář, 1927 have been described from these deposits. Similarly, poorly diversified assemblage co-occurs with *P. cretaceus* from Les Renardières (Néraudeau et al. 2005).

Institutional abbreviations.—NMP, National Museum, Prague, Czech Republic; UL, University Lyon 1 (Claude Bernard), Villeurbanne, France.

Other abbreviations.—LM, light microscope; SEM, scanning electron microscope.

Geographic and geological setting

The plant material described in this paper was collected from localities in the Czech Republic and France. The Czech material comes from the Peruc-Korycany Formation, the basal-most lithostratigraphic unit of the Bohemian Cretaceous Basin (sensu Čech et al. 1980). Palynological data indicate a late middle Cenomanian age for these beds (Pačtová 1977, 1978). The main localities of *Pseudoasterophyllites* include the Pecínov Quarry near Rynholec (50°08'00"N, 13°54'34"E), the Hloubětín Brickpit (50°06'45"N, 14°32'02"E), an abandoned brick pit in the eastern part of Prague (material collected by Antonín Hlušík, 1973–1974), and the type locality Lipenec.

Geological and sequence stratigraphical analyses indicate that the Peruc-Korycany Formation represents a series of palaeovalley infills (Uličný and Špičáková 1996). These palaeovalley-fill successions (Uličný and Nichols 1997; Uličný et al. 1997) comprise the deposits of a variety of continental (braided rivers, meandering streams and floodplains, and anastomosed fluvial systems) and coastal environments (tidally influenced braided rivers, supratidal marshes, tidal flats, ebb-tidal deltas, estuaries, and lower shoreface). The studied plant fossils come from mudstone units interpreted as supratidal marsh/mangrove facies (Nguyen Tu et al. 2002). The dominant fossils in these deposits are *Frenelopsis alata*

(K. Feistmantel, 1885) Knobloch, 1971 and *Eretmophyllum obtusum* (Velenovský, 1885) Kvaček, 1998 (Uličný et al. 1997).

The French material was collected from the subunit A1s1A in the former sand quarry Les Renardières, Tonnay-Charente, western France, which unconformably overlaid Kimmeridgian substratum (Néraudeau et al. 2005). The clay beds of the subunit A1 are dated by a palynological study as uppermost Albian (Néraudeau et al. 2002). They are covered by estuarine sands of A1s1-S and A2sm and above change progressively to marine Cenomanian carbonates without the sand/clay alternation typical of margino-littoral series. Thus these Albian–Cenomanian sediments were deposited in coastal environments.

Material and methods

Samples of mudstone containing plant material were treated in a solution of sodium carbonate and samples of clays were bulk macerated in hydrogen peroxide. These extractions were followed by maceration in HF. Some specimens (particularly detached leaves and isolated stamens) were macerated for 1 hour in Schulze's solution and then stored in glycerine. Leaf cuticles were prepared using standard Schulze's techniques (Kvaček 1999, 2000). Pollen grains were obtained from the macerated stamens and separated using a dissecting needle with a human hair glued to its tip (Zetter 1989; Zetter et al. 2002). The material was sorted and examined under an Olympus SZX 12 stereomicroscope, an Olympus BX 50 light microscope, a Phillips 515, and a Jeol JSM-6400 SEM.

Systematic palaeontology

Class Magnoliopsida Brongniart, 1843

Family unknown

Genus *Pseudoasterophyllites* O. Feistmantel ex Velenovský, 1887

Type species: Pseudoasterophyllites cretaceus, Lipenec, Cenomanian, Late Cretaceous.

Pseudoasterophyllites cretaceus O. Feistmantel ex Velenovský 1887

Figs. 1–3.

1874 *Asterophyllites cretaceus*; O. Feistmantel 1874: 267 nomen nudum.

1887 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský, 1887; Velenovský 1887: 643, figs. 19–25.

1889 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský, 1887; Velenovský 1889: 44, 48, 52.

1901 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský 1887; Frič and Bayer 1901: 87, fig. 37.

1926 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský 1887; Velenovský and Viniklář 1926: 24, 53, pl. 2: 11, pl. 3: 6, 7, 9, 10.

1902 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský 1887; Zeiller 1902: 11.



Fig. 1. Early angiosperm *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský, 1887 from the Late Cretaceous (Cenomanian) of Czech Republic. **A.** Lectotype, branched leafy axis, Lipenec, NMP F 654. **B.** Detail of lectotype, showing semi-whorled arrangement of leaves, Lipenec, NMP F 654. **C.** Leaf cuticle with stomata arranged perpendicularly, longitudinally, and obliquely to the leaf axis, Pecínov (unit 3), NMP F 2880a. **D.** External surface of paracytic stoma, Pecínov (unit 3), NMP F 2880a. **E.** Papillae in marginal part of the leaf, Pecínov (unit 3), NMP F 2880b. **F.** Axillary branches on a leafy twig, Pecínov (unit 3), NMP F 2880. Scale bars A, B 5 mm; C 100 μ m; D, E 50 μ m; F 10 mm.

1954 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský 1887; Teixeira 1954: 144, figs. 1, 2.

1963 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský 1887; Němejc 1963: 318, text-fig. 167.

1997 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský 1887; Uličný et al. 1997: 193.

2003 *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský 1887; Kvaček and Eklund 2003: 1033, fig. 12.

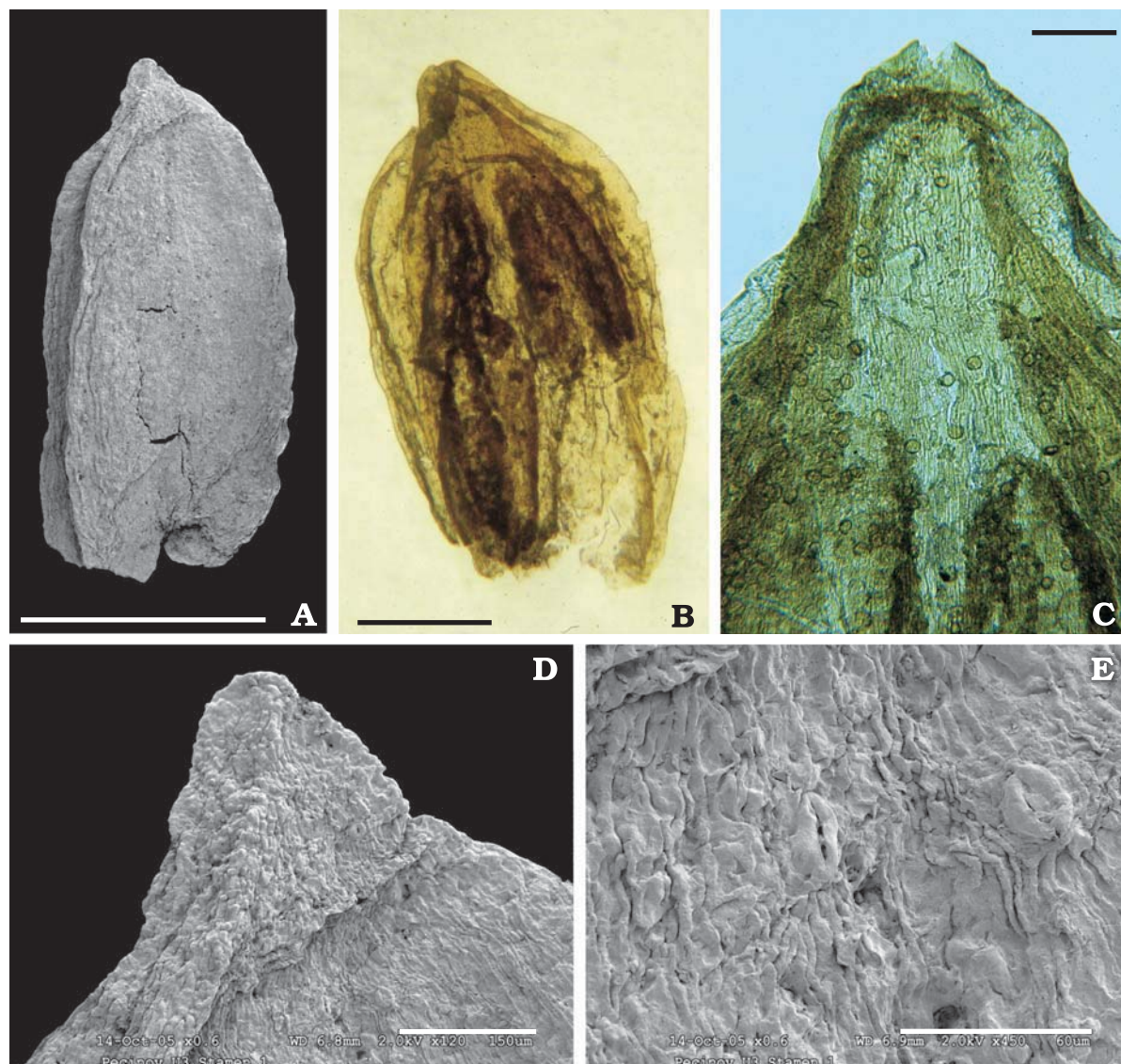


Fig. 2. Early angiosperm *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský, 1887 from the Late Cretaceous of Pecinov (unit 3), Czech Republic (A, D, E; SEM photographs) and Les Renardières, France (B, C). **A.** Isolated stamen showing apical extension of connective, NMP F 2880c. **B.** Macerated stamen showing two pairs of pollen sacs, UL REN 001. **C.** Detail of macerated stamen showing pollen in situ, UL REN 002. **D.** Detail of the apical extension of connective, NMP F 2880c. **E.** Epidermis surface of the apical extension of connective showing paracytic stomata and papillae, NMP F 2880c. Scale bars: A 1 mm, B 0.5 mm, C 100 µm, D 150 µm, E 60 µm.

Lectotype: designated here, NMP F 654, Velenovský 1887: fig. 22 (refigured in Fig. 1A of this paper).

Type locality: Lipenec, Czech Republic.

Type horizon: Peruc Korycany Formation, Cenomanian, Late Cretaceous.

Other material.—NMP F 654, NMP F 655, NMP F 656, NMP F 657, NMP F 1423, NMP F 2280, NMP F 2285, NMP F 2899, UL REN002.

Emended diagnosis.—Twigs branch 3–4 times. Axes consisting of nodes and internodes. Nodes consisting of two pairs of decussately arranged leaves very closely spaced forming semi-whorls. Lateral branches borne in leaf axils; branches either well developed or represented only by axilar bud. Leaves coriaceous, linear to cylindrical with rounded tip

and broad, shortly decussate base. Leaves amphistomatic, bearing stomata in two distinct bands on adaxial and abaxial sides of leaf. Ordinary epidermal cells rectangular to isodiametric, with thick anticlinal walls, stomata paracytic with two narrow subsidiary cells and two exposed guard cells.

Dimensions.—Length of the axis: more than 110 mm; width of the axis: 0.5–3 mm; length of the leaves: 1–10 mm; width of leaves: 0.6–1 mm; length of guard cells: 20–24 µm; width of guard cells: 5–8 µm; length of epidermal cells: 20–35 µm; width of epidermal cells: 15–20 µm.

Description.—The lectotype specimen consists of 3 axes, each constructed of 4–6 nodes and internodes. Each axis is 10–15 mm long, and gives off leaves that are 7–9 mm long

(Fig. 1A, B). Another specimen is 32 mm long (Fig. 1F). It shows axillary branching. Each branch possesses at least 5 nodes and internodes. The axis is longitudinally striate and 0.5–3 mm in diameter. The nodes consist of whorls of simple coriaceous linear leaves, which are wrinkled, suggesting that they were 3D cylindrical in vivo. Leaves are heavily cutinized and variable in size, i.e., 1–10 × 0.3–1 mm; they extend from the nodes in semi-whorls each consisting of two pairs very closely spaced of decussately arranged leaves. Lateral branches are given off in axillary position of each leaf. Branches may be well developed (i.e., real branches), or present only as axilar buds. The buds, together with the leaves, form rich semi-whorls. Due to their shape, the leaves do not possess clearly defined abaxial and adaxial sides. Stomata are arranged in two bands, probably one on the adaxial and one on the abaxial side. The stomata are oriented perpendicularly, longitudinally or obliquely to the leaf margin. The stomatal apparatus consists of two partly exposed guard cells (8–10 × 22–27.5 μm) and two narrow subsidiary cells (2–3 × 25–32.5 μm). Ordinary epidermal cells are isodiametric quadrangular or polygonal; their size is (8)–15–(20) × (8)–20–(25) μm (Fig. 1C, D). Anticlinal cell walls are straight (up to 3 μm in thickness). The periclinal walls are covered by small wrinkles and papillae, especially in parts close to the leaf margin (Fig. 1E).

Associated with the vegetative remains are stamens that are very similar in appearance to sterile leaves. Moreover, they possess the same epidermal cell pattern and idiocuticular features as the sterile leaves (compare Fig. 1D, E with Fig. 2E). Stamens are ovoid-elongate, 3–3.5 mm long and 1–1.5 mm wide, massive, and not divided into an anther and filament showing a considerable amount of sterile tissues (Fig. 2A). They possess an apically expanded connective forming acute apical extensions (Fig. 2D), with a blunt apex bearing paracytic stomata. The stamens are tetrasporangiate and consist of two indistinct lobes. If macerated, each lobe shows two narrow pollen sacs (Fig. 2B) embedded in the tissue of the abaxial side of the stamen. Dehiscence is by longitudinal slits.

In situ pollen grains of the *Tucanopollis* type are sulcate, oblate to spheroidal, in polar view elliptic to circular, 18–24 μm in diameter (Fig. 3A, C, D). The aperture is broad and short, the membrane thin and often covered by echinate Ubisch bodies (Fig. 3D). The sculpture is psilate in LM, microechinate, perforate in SEM (Fig. 2B); exine thick (1.5–2 μm), nexine 0.8–1 μm, short columellae, tectum 1–1.2 μm.

Stratigraphic and geographic range.—Early to Late Cretaceous, Albian to Cenomanian. Czech Republic (Cenomanian): Pecínov, Praha-Hloubětín, Lipenec, Touchovice; France (Albian): Les Renardières, Tonnyay-Charente, Charente-Maritime.

Discussion

We were unsuccessful to trace the suite of original specimens of *Pseudoasterophyllites cretaceus* collected by Feistmantel

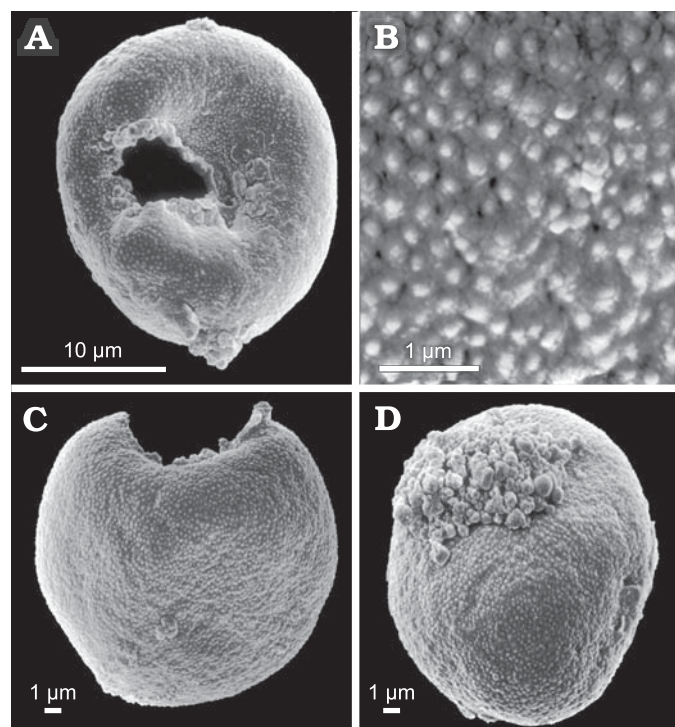


Fig. 3. Pollen *Tucanopollis* sp. from the stamen on Fig. 2C, which is associated with the vegetative parts of angiosperm *Pseudoasterophyllites cretaceus* O. Feistmantel ex Velenovský, 1887 from the Late Cretaceous of Les Renardières, France, specimens UL REN 002. **A.** Monosulcate pollen grain in situ showing irregular sulcus area. **B.** Microechinate, perforate exine sculpturing, detail of pollen exina. **C.** Monosulcate pollen grain in situ showing sulcus area. **D.** Pollen grain in situ showing Ubisch bodies. Scale bars: A 10 μm, B–D 1 μm.

(1874) from the locality Touchovice in the old museum collection. However, one important specimen, which was used by Velenovský (1887) in his validation of the genus and species, could be located. It comes from the locality of Lipenec. Consequently, this specimen is here designated as the lectotype.

The only other fossil plant similar in overall morphology to *Pseudoasterophyllites cretaceus* is *Montsechia vidalii* (Zeiller, 1902) Teixeira, 1954 from the Barremian limestone of Las Hoyas (La Huérguina Formation, South-western Iberian Ranges) and of El Montsec (Plant and Vertebrate limestone Formation, Western Pyrenees, Spain) (Zeiller 1902; Teixeira 1954; Blanc-Louvel and Barale 1983; Gomez et al. 2006). *Montsechia*, which was originally included in *Pseudoasterophyllites* by Zeiller (1902), shows a branching pattern very similar to that seen in *P. cretaceus*. Moreover, *M. vidalii* displays paracytic stomata that are similar to *P. cretaceus*. *Pseudoasterophyllites* differs from *Montsechia* in having leaves arranged in semi-whorls and narrow subsidiary cells in the paracytic stomata. Both plants probably represent members of an extinct lineage of basal angiosperms. The presence of *Tucanopollis*-type pollen grains suggests a relationship of *Pseudoasterophyllites* with the Piperales; it is possible, however, that this correspondence in pollen morphology is only

superficial. Whorled leaves are typical for certain species of the genus *Peperomia*, a member of the Piperaceae. James Doyle (personal communication 2006) regards certain features of *Tucanopollis* similar to pollen of the family Austrobaileyaceae. *Pseudoasterophyllites cretaceus* is also remotely similar to the gnetophyte *Drewria potomacensis* from the Aptian of the Potomac Formation (Crane and Upchurch 1987). However, *P. cretaceus* differs from *D. potomacensis* in having single-veined leaves (instead of two- to three-veined leaves in *Drewria*) that are arranged in whorls.

Isolated stamens were found in the same layer as leafy axes of *P. cretaceus* at the localities Pecínov and Les Renardières. Because of their close co-occurrence with the sterile remains of *P. cretaceus* and because the stamens display the same epidermal cell pattern and idiocuticular features as the foliage, we believe that both structures were produced by the same plant. The pollen grains contained in the stamens are monosulcate, which adds support to the hypothesis that *P. cretaceus* was an angiosperm.

Superficially similar to *Pseudoasterophyllites cretaceus* in overall morphology are several species in the extant genera *Myriophyllum* Linnaeus, 1753 and especially *Hippuris* Linnaeus, 1753. These taxa remind *Pseudoasterophyllites* in the general appearance of the axes, in which simple linear leaves are arranged in whorls. Moreover, certain species in *Hippuris* (e.g., *H. tetraphylla* Linnaeus, 1782 and *H. lanceolata* Retzius, 1783) are halophytes. However, both families, the Hippuridaceae and Haloragaceae (Orchard 1979; Couch and Nelson 1988; Husák 1997), belong to the eudicots and produce triaperturate pollen grains, which argues against a closer biological relationship with *P. cretaceus*.

Further studies on additional specimens from historical collections and newly collected material are needed to fully decipher the affinities and palaeoecology of this interesting early angiosperm.

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