



NEW SPECIES OF *ZAMITES* FROM THE CENOMANIAN OF THE BOHEMIAN CRETACEOUS BASIN

I dedicate this article to the memory of my father Professor Zlatko Kvaček (1937–2020).

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Abstract: *Zamites pateri* J.KVAČEK is described as a new member of the Bennettitales from the Cenomanian of the Peruc-Korycany Formation, Bohemian Cretaceous Basin in the Czech Republic. It comes from fluvial sediments exposed in the Pecínov quarry. It is compared to *Zamites bayeri* J.KVAČEK from the Peruc-Korycany Formation, from which it differs in having pinnae attached to the dorsal part of the rachis and in cuticular details, particularly in having costal zones narrower than intercostal zones, stomata orientated always perpendicularly to the leaf margins and a thinner adaxial cuticle. Epidermal characters, particularly sunken stomata and numerous papillae underpin the mesophytic/xerophytic nature of the plant fossil.

Key words: Bennettitales, *Zamites*, Late Cretaceous, Cenomanian

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Introduction

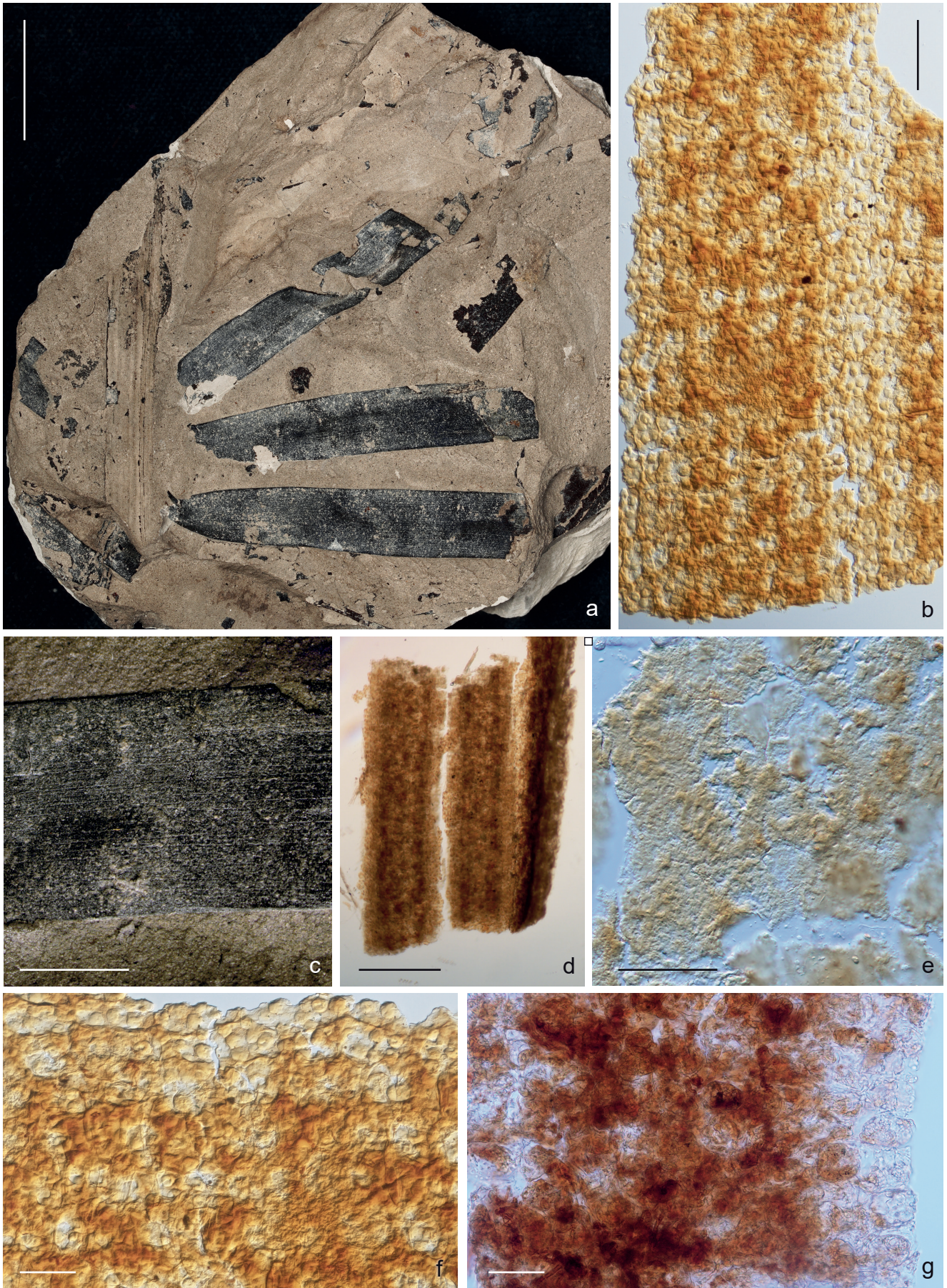
The Bennettitales represent a group of gymnosperms typical of the Mesozoic (e.g., Taylor et al. 2009, Cuneo et al. 2010). However, new discoveries have revealed an earlier origin, in the late Palaeozoic, based on finds from late Permian deposits in Jordan and China (Blomenkemper et al. 2018, 2021). Their slow start and sudden explosive diversity in the Late Triassic (e.g., Pott et al. 2016, Kustatscher et al. 2018) has not yet been satisfactorily explained. Bennettitales are typical for paratropical to warm temperate environments (Willis and Mc Elwain 2002). They are differentiated into two large groups: Cycadeoideaceae and Williamsoniaceae (Taylor et al. 2009). During the Jurassic and Early Cretaceous, the group reached its maximal diversity (Harris 1969, Barale 1981, Pott et al. 2014, McLoughlin et al. 2017, Lozano-Carmona and Velasco 2021).

The genus *Zamites* was defined by Brongniart (1828). It is well known from Jurassic strata in Europe (e.g., Barale 1981, Harris 1969); ten species of *Zamites* are described from the English Wealden (Watson and Sincock 1992). Further well-documented Bennettitales are known from the Early Cretaceous of Germany (Pott et al. 2014). In the mid- and Late Cretaceous, we observe a gradual decline of Bennettitales (Kvaček 1995, Knobloch and Kvaček 1997, Yamada 2009, Sender 2018), particularly due to the expansion of quickly evolving and spreading angiosperms

(Friis et al. 2011, Kvaček et al. 2020). Foliage of the Bennettitales is characterised by simply pinnate leathery fronds similar to cycads, from which they differ in having syndetocheilic stomata and commonly typically sinuously formed anticlinal walls of the epidermal cells (Taylor et al. 2009). Together with the Erdmanithecales and Gnetales, they are considered one of the possible ancestral groups of angiosperms (Friis et al. 2011).

Bennetitales, particularly the Cycadeoideae, are considered good palaeoclimatic indicators of meso- to xerophytic environments (Willis and McElwain 2002). As stated by Rudall and Bateman (2019), certain epidermal traits in Bennettitales, including the characteristic guard-cell wall thickenings represent ecophysiological markers indicating the mesophytic to xerophytic nature of this group.

In the Peruc-Korycany Formation of the Bohemian Cretaceous Basin, Bennettitales are accessory components of various taphocoenoses. They were elements of wetland vegetation in the case of *Nilssoniopteris pecinovensis* J.KVAČEK (Kvaček 1995), and upland vegetation in the case of *Zamites bayeri* J.KVAČEK (Knobloch and Kvaček 1997). Additional findings, such as the silicified stems of *Cycadeoidea* sp. (Němejc 1968) and the newly collected specimen from Pecínov unit 5 indicate that the bennettites were probably substantial components of the upland meso-xerophytic flora in the Bohemian Massif.



Text-fig. 1. *Zamites pateri* J.KVAČEK sp. nov.; Pecínov locality, holotype, No. NM-F 5185. a: Holotype overview showing fragment of simply pinnate leaf, scale bar 20 mm. b: Abaxial cuticle showing costal and intercostal scale zones and stomata in ill-defined rows, LM micro-photograph, scale bar 100 µm. c: Pinnule detail showing venation pattern, scale bar 5 mm. d: Abaxial cuticle showing costal and intercostal zones, LM micro-photograph, scale bar 500 µm. e: Fragmentary preserved adaxial cuticle showing

Material and methods

The present unique specimen, No. NM-F 5185 was found together with the silicified stem of *Cycadeoidea* BUCKLAND in the Pecínov quarry. The fossil frond fragment was found in an allochthonous position in fluvial sediments, unit 2 (according to Uličný et al. 1997) in the Pecínov quarry. The stem of *Cycadeoidea* sp. comes from allochthonous coastal marine sandstone of unit 5 (according to Uličný et al. 1997). All the studied material is housed in the collection of the Department of Palaeontology, National Museum, Prague.

Fragments of coalified material were carefully picked from the pinnae with a preparation needle and treated for cuticle analysis. Coaly material obtained by needle sampling was cleaned from silicates by treatment in 40% hydrofluoric acid. After this procedure, it was soaked and macerated in Schulzes reagent: HNO₃ + KClO₃, and neutralised in water. Finally, it was treated in 10% solution of KOH in water. The time for oxidation was about 15 minutes. After all the chemical treatments, fragments of cuticle were washed in water in Petri dishes. The fragments were soaked in glycerine and prepared with needles to separate the thin adaxial cuticle and the thick abaxial cuticle with remains of mesophyll. When separated from mesophyll cuticle fragments, they were embedded in glycerine for light microscopy and framed by Noyer framing cement. For SEM observations, cuticle fragments were also soaked in distilled water and placed on celluloid film in a position showing the inner and outer sites of adaxial and abaxial cuticles.

The new name is registered with a unique PFN number in the Plant Fossil Names Registry, hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany (IOP).

Systematic palaeobotany

Order Bennettitales ENGL., 1892

Genus *Zamites* BRONGN., 1828

Type. *Zamia gigas* LINDL. et HUTTON, 1835 in Foss. Fl. Gr. Brit. 3: 45 ≡ *Zamites gigas* (LINDL. et HUTTON) MORRIS, 1841 in Ann. Mag. Nat. Hist. 7: 116.

The genus *Zamites* was proposed for conservation with the conserved type *Z. gigas* by Zijlstra and Van Konijnenburg-van Cittert (2020), and accepted by the nomenclatural committee of fossil plants (Herendeen 2022).

Remarks. The genus differs from other similar genera of the Bennettitales in having a symmetrical basal part of the pinnae, commonly slightly contracted on both sides, although occasionally a slightly dissimilar base occurs (Watson and Sincock 1992).

Its generic diagnosis was most recently emended by Watson and Sincock (1992).

Zamites pateri J.KVAČEK sp. nov.

Text-figs 1, 2

Holotype. NM-F 5185, Text-figs 1, 2.

Plant Fossil Names Registry Number. PFN003021.

Etymology. The species name is derived from pater, meaning father in Latin. It is devoted to my father and teacher Professor Zlatko Kvaček.

Type locality. Pecínov quarry, 50 km west of Prague, the Czech Republic.

Type horizon. Peruc-Korycany Formation.

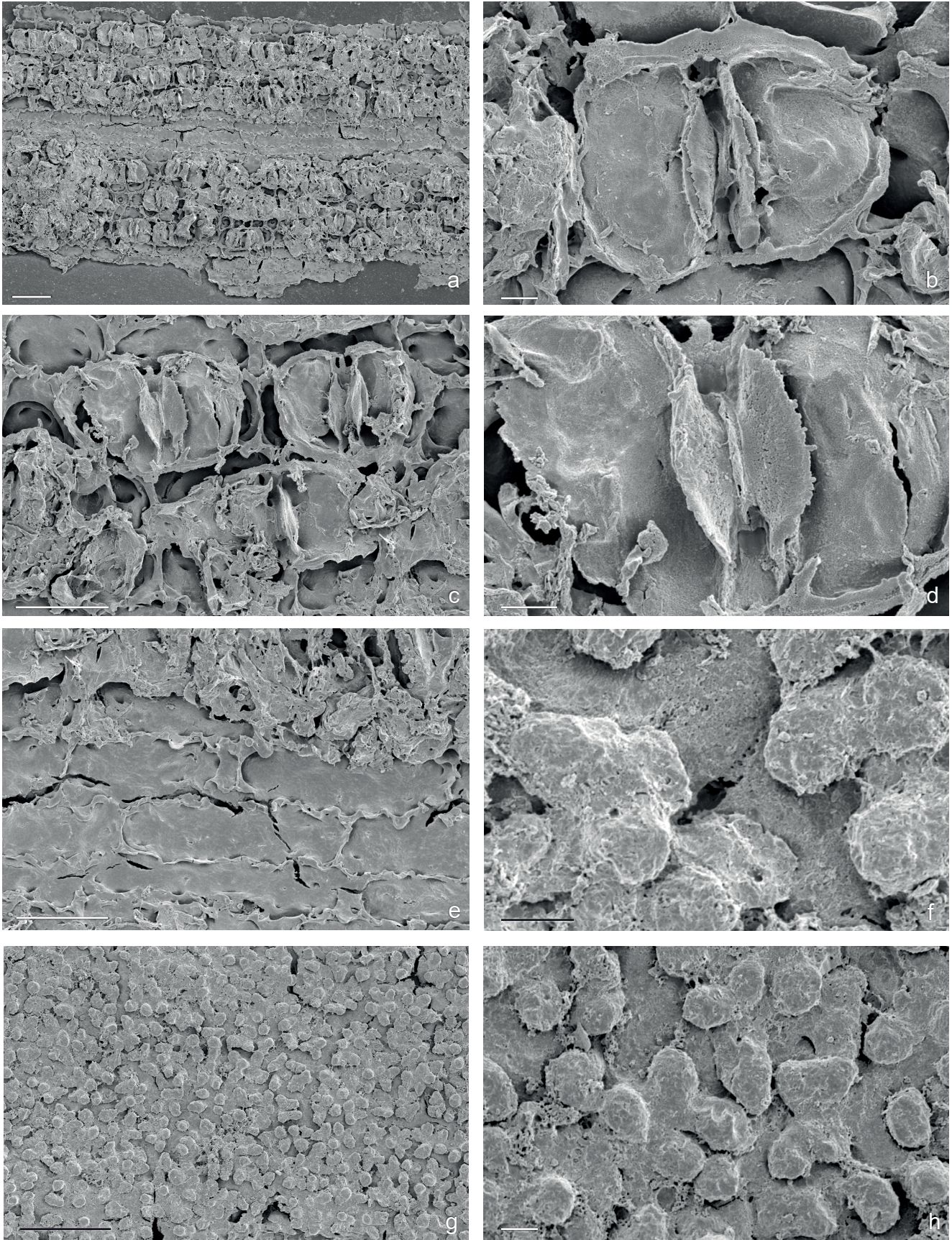
Age. Cenomanian, Late Cretaceous.

Diagnosis. Leaf simply pinnate, pinnae linear to narrowly lanceolate, entire-margined. Base of pinna slightly contracted, apex unknown. Veins 2–3 per mm, simple or rarely dichotomising. Leaf hypostomatic. Adaxial cuticle very thin, bearing polygonal cells with tightly sinuous anticlinal walls. Mesophyll present, consisting of isodiametric cells. Abaxial cuticle thick, showing distinct marginal band bearing tetragonal ordinary cells. Inner part of leaf consists of costal ordinary cells forming zones typically narrower than intercostal zones, formed by 4–5 rows of syndetocheilic stomata (sometimes ill-defined). Subsidiary cells large, ellipsoidal, thickly cutinised, bearing one or several papillae. Ordinary cells of intercostal zone polygonal in shape with roughly straight anticlinal walls. Ordinary cells of costal zones quadrangular in shape with sinuous anticlinal walls. Epidermal cells of both costal and intercostal zones bearing 3–5 papillae.

Description. The holotype corresponds to a fragment of a simply pinnate leaf (Text-fig. 1a). Leaves are attached to the upper part of the robust, longitudinally striated rachis, 7–9 mm broad. The holotype shows 5 incomplete pinnae arising from a common rachis. The pinnae are attached to the dorsal part of the rachis, where they seem to touch each other. Each pinna is linear to narrowly lanceolate, gradually widening from a contracted base to about 10 mm wide in the parallel-sided middle region (Text-fig. 1a). From the base, parallel, rarely dichotomising veins arise in density 2–3 per 1 mm (Text-fig. 1c).

The adaxial cuticle is very thin and thus difficult to prepare. It consists of polygonal ordinary cells (25–30 × 30–55 μm). Their anticlinal walls are thin and tightly sinuous (Text-fig. 1e). It is devoid of papillae. The tissue between the adaxial and abaxial cuticle is probably mesophyll, consisting of isodiametric cells (30–40 × 40–50 μm; Text-fig. 1f). The abaxial cuticle shows costal and intercostal zones. The costal zones are narrower than the intercostal ones, typically 75–90 μm wide (Text-fig. 1b, d). They consist of basically quadrangular ordinary epidermal cells (25–38 × 50–125 μm) with sinuous anticlinal walls (Text-fig. 2a, e). Intercostal zones

two better-preserved ordinary cells, LM micro-photograph, scale bar 50 μm. f: Abaxial cuticle showing perpendicularly arranged stomata and papillae per ordinary cell, LM micrograph, scale bar 50 μm. g: Detail of mesophyll tissue consisting of isodiametric cells, LM micrograph, scale bar 50 μm.



Text-fig. 2. *Zamites pateri* J.KVAČEK sp. nov.; Pecínov locality, holotype, No. NM-F 5185. a: Abaxial cuticle showing costal and intercostal zones, SEM micro-photograph, scale bar 100 μm . b: Abaxial cuticle, detail of syndetocheilic stoma, SEM micro-photograph, scale bar 10 μm . c: Abaxial cuticle showing transversely oriented stomata, SEM micro-photograph, scale bar 50 μm . d: Abaxial cuticle, detail of syndetocheilic stoma showing ledges of guard cells, SEM micro-photograph, scale bar 10 μm . e: Abaxial cuticle showing costal ordinary cells seen from inside, SEM micro-photograph, scale bar 50 μm . f: External side of abaxial cuticle showing stoma sunken in a stomatal pit surrounded by papillae, SEM micro-photograph, scale bar 10 μm . g: External side of abaxial cuticle showing papillae, SEM micro-photograph, scale bar 100 μm . h: External side of abaxial cuticle showing detail of fused papillae, SEM micro-photograph, scale bar 10 μm .

Table 1. Comparison of *Zamites pateri* with related species.

species	shape of pinnae	orientation of stomata	anticlinal walls of abaxial cuticle	number of papillae per ordinary cell on abaxial cuticle	cells of adaxial cuticle	hypodermis	source
<i>Zamites pateri</i>	linear to narrowly lanceolate	perpendicular in all cases	sinuous in all cases	3–5	weakly defined, nearly invisible	present	this paper
<i>Zamites bayeri</i>	linear to narrowly lanceolate	in inner part perpendicular, in marginal parts longitudinal	straight in intercostal areas	one to several	ordinary cells well-discernible	absent	Knobloch and Kvaček 1997
<i>Zamites carruthersii</i>	broadly oval to oblong	perpendicular in all cases	sinuous, in some cases straight in intercostal areas	one to several	ordinary cells well-discernible	present	Watson and Sincock 1992
<i>Zamites manoniae</i>	broadly oval to oblong	perpendicular in all cases	slightly and unevenly sinuous	0	unknown	absent	Watson and Sincock 1992
<i>Zamites dowellii</i>	narrowly lanceolate	perpendicular in all cases	usually sinuous, occasionally straight	1–2	ordinary cells well-discernible	absent	Watson and Sincock 1992
<i>Zamites wendyellisae</i>	triangular, narrowly lanceolate	perpendicular or slightly oblique	strongly sinuous in all cases	0	ordinary cells well-discernible	present	Watson and Sincock 1992
<i>Zamites coderi</i>	linear to narrowly lanceolate	perpendicular or slightly oblique	sinuous in all cases	0	ordinary cells well-discernible	absent	Watson and Sincock 1992
<i>Zamites nicolae</i>	narrowly lanceolate	perpendicular in all cases	moderately sinuous in all cases	1	weakly defined	absent	Watson and Sincock 1992
<i>Zamites tatianae</i>	linear to narrowly lanceolate	perpendicular in all cases	sinuous in all cases	0	ordinary cells well-discernible	absent	Watson and Sincock 1992
<i>Zamites notokenensis</i>	oblong	orientation unknown	strongly sinuous in all cases	0	weakly defined, but discernible	absent	Watson and Sincock 1992
<i>Zamites decurrens</i>	oblanceolate	perpendicular in all cases	straight in all cases	1	ordinary cells well-discernible	absent	Menéndez 1966

are 220–300 µm wide with syndetocheilic stomata (Text-fig. 2b–d). Stomata are oriented perpendicularly to the leaf margin, typically arranged in 3–4 ill-defined rows (Text-figs 1b, 2a). Externally, they are sunken in pits, surrounded by 2–5 papillae (Text-fig. 2f). Their subsidiary cells are 27–35 × 55–66 µm. Ordinary epidermal cells are isodiametric to elongate (15–25 × 28–40 µm), with straight anticlinal walls (Text-fig. 2c). The external side of the cuticle shows numerous papillae, typically 4–5 per ordinary epidermal cell (Text-fig. 2i, h). They are so dense that they are sometimes fused, forming united groups (Text-fig. 2h).

Discussion. *Zamites pateri* is reminiscent of *Zamites bayeri* J.KVAČEK, from the same Peruc-Korycany Formation in Praha Malá Chuchle (Knobloch and Kvaček 1997). They are similar in morphology of the pinnae. *Zamites pateri* differs from *Z. bayeri* in having pinnae attached to the dorsal part of the rachis. Further differences are in epidermal structures. Abaxial ordinary epidermal cells in the intercostal zones of the newly described species are nearly straight, bearing 3–5 papillae, whereas *Z. bayeri* shows ordinary cells more sinuously waved, bearing typically one, rarely several papillae per ordinary epidermal cell. Stomata of *Z. bayeri* in the marginal parts are occasionally oriented longitudinally to the leaf margin, whereas in *Z. pateri* they

are always perpendicularly oriented (Tab. 1). Furthermore, *Z. bayeri* does not have preserved any mesophyll tissues. Additionally, *Z. bayeri* comes from calcareous substrates of Barrandian limestones, whereas *Z. pateri* comes from silicate substrates of Carboniferous clastic.

Discussion about other similar impression material, including *Zamites bohemicus* VELEN. described from the Peruc-Korycany Formation by earlier authors was published in detail by Knobloch and Kvaček (1997), and therefore not discussed here.

Z. pateri resembles some *Zamites* species described from the English Wealden by Watson and Sincock (1992). It particularly shares characters with *Z. dowellii* J.WATSON et SINCOCK, *Z. coderi* J.WATSON et SINCOCK and *Z. nicolae* J.WATSON et SINCOCK in having long and narrow pinnae. *Zaimets dowellii* is similar in possessing papillae on the abaxial cuticle, but differs from the present material in having stomata on the adaxial cuticle, thus being amphistomatic. Additionally, its abaxial cuticle shows stomata with clearly sinuous anticlinal walls. *Zamites coderi* differs from *Z. pateri* in lacking papillae on the abaxial side, while its cuticle shows ordinary epidermal cells with conical trichome bases and well-developed sinuous anticlinal walls. *Zamites nicolae* differs from *Z. pateri* in having abaxial ordinary cells

with sinuous anticlinal walls, and with only one papilla per ordinary cell. *Zamites decurrens* C.A.MENÉNDEZ from the Early Cretaceous of Argentina (Menéndez 1966) resembles *Z. pateri* in cuticle, having stomata perpendicularly oriented, forming rows and belts. It differs from *Z. pateri* in having spatulate pinnae. Its adaxial cuticle is thicker, consisting of uniform elongated cells. Its abaxial cuticle shows less dense stomata, forming regular rows (Tab. 1).

Other Early Cretaceous species of *Zamites* from the English Wealden show more profound differences from *Z. pateri*: *Z. carruthersii* SEWARD and *Z. manoniae* J.WATSON et SINCOCK differ in having narrowly to broadly oval pinnae with rounded bases and bluntly rounded apex; *Z. wendyellisiae* J.WATSON et SINCOCK differs in having pinnae triangular in outline; *Z. notokenensis* J.WATSON et SINCOCK and *Z. tatianae* J.WATSON et SINCOCK differ in having smooth or tuberculate but not papillate external side of abaxial cuticle (Watson and Sincock 1992). Further differential characters in epidermal micromorphology of the discussed species are shown in Table 1.

Remarks on palaeoecology

The Bennettitales are good indicators of palaeoenvironment. *Zamites pateri* is preserved as a leaf fragment mirroring its allochthonous nature, probably having been delivered to the sedimentary basin from upland. Its mesophytic to xerophytic physiognomy is underpinned by its thick coriaceous pinnae with additional micromorphological characters, such as numerous papillae and thickly cutinised stomata. We consider the studied compression specimen to be an uncommon example of upland vegetation that was found in an allochthonous position in fluvial sediments. The same can be stated about *Cycadeoidea* sp., recovered from unit 5 of the Pecínov quarry. Its detailed description will be published elsewhere.

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