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REVISION OF *PROTOPTERIS* AND *ONCOPTERIS* TREE FERN STEM CASTS FROM THE LATE CRETACEOUS OF CENTRAL EUROPE

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Abstract. Stem casts of tree ferns from the genera *Protopteris* Sternberg and *Oncopteris* Dormitzer in Krejčí from the Czech Republic and Poland are revised. A new species, *Protopteris maletinensis* Greguš et J. Kvaček sp. nov. from the Peruc-Korycany Formation (Cenomanian) is described based on material from Starý Maletín. Its morphological similarity to other species of the genus is discussed. The genus *Protopteris* and two species *P. punctata* (Sternberg) C. Presl in Sternberg and *P. singeri* (Göppert) C. Presl in Sternberg 1838 are revised and emended based on biostatistical analysis (i.e, width/height ratio of leaf scars), as this character has proved to be quite stable and can be used in species recognition. Genera *Oncopteris* Dormizer in Krejčí and *Alsophilina* Dormizer in Krejčí with their types *O. netwallii* and *A. kauniciana* are revised. These two so far described genera and species are united and ascribed to the genus *Oncopteris* with the type *O. netwallii*.

■ *Protopteris*, *Oncopteris,* tree ferns, Cretaceous, Cenomanian, Czech Republic, Poland.

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Introduction

Tree ferns are regular accessory components of current tropical and paratropical forests of both hemispheres (e.g. Tryon and Tryon 1982, Marcus 2008). They are considered as good indicators of climate because they are not able to live in environments with prolonged hard frosts (e.g. Box 1981). Tree ferns prefer to grow in frost free humid microclimates, usually in shady places. Due to the importance of tree fern trunk finds in palaeoecology we have decided to revise those records which were found in several localities of the Czech Republic and Poland. In this contribution we leave aside all anatomically preserved silicified material of tree fern taxa (*Protopteris cottai* Corda 1845, *Protopteris fibrosa* Stenzel; Whiteside 1956) and the genus *Tempskya* Corda 1845 representing a specific type of fern pseudostem.

The first stem cast of a tree fern was originally described by Kašpar Sternberg (1820) as *Lepidodendron punctatum* from Kounice and interpreted as the stem of an arborescent lycopod. Later Sternberg recognized its real nature and assigned it correctly to tree ferns (Sternberg 1838). The specimen was than revised by J. Kvaček and Straková (1997). A complete revision of the Czech fossil tree ferns was published by Corda (1845) and O. Feistmantel (1872a). The last detailed report on the Cretaceous tree ferns from the Bohemian Cenomanian was published by Velenovský (1888). Later contributions are usually only summaries of already described material (Seward 1894, Posthumus 1931, Němejc 1963).

The main aim of this contribution is a revision of the already published data together with publishing newly documented facts which can improve our understanding of this important plant group. In this revision we try to identify major robustness and weaknesses of the so far used classification of stem casts of tree ferns as has already been carried out for Palaeozoic tree fern stems. This classification is based on the height / width ratio of leaf scars (Pfefferkorn 1976).

Geological setting

Czech Cretaceous

The Bohemian Cretaceous Basin (see text-fig. 1) as defined by Čech et al. (1980) consists of sediments ranging from the Cenomanian to Santonian. The Bohemian Cretaceous Basin is the largest sedimentary basin in the Czech Republic. It covers a considerable part of the Bohemian Massif across Bohemia, Moravia and Silesia. The basin is situated in the

Text-fig. 1. Geological setting and location of the fossil sites mentioned in this paper. Grey area indicates Cretaceous Basins.

northern part of the Czech Republic and extends in its marginal parts to Poland and Germany. The basin border is mostly erosional, a smaller part tectonical. The base of the basin is formed by Palaeozoic and pre-Palaeozoic bedrock (Herčík et al. 1999). The basin infill consists of 200–400 m of Cretaceous sediments. A maximum thickness of 1100 m in the basin was recorded in its eastern section near Děčín (Valečka 1979). The most-basal part of the basin infill is formed by the Cenomanian transgressional set of diachronic sedimentary bodies assigned to the Peruc Korycany Formation. The sedimentary succession of the Peruc – Korycany Formation is usually as follows: The lower units typically include fluvial pebbly sands, conglomerates and sandstones with interbeds of mudstones. The unit above consists of mudstones rich in pyrite concretions. This unit is a product of marginal marine and brackish sedimentation in back swamps and in supratidal marshes. Another unit above is represented by cross-bedded sandstones, mudstones and laminites, products of sedimentation on a tidal flat crossed by meandering tidal creeks. The final unit of the formation consists of sandstones containing marine fauna and occasionally preserved stems of tree ferns and poorly preserved leaf impressions (Uličný et al. 1997). Detailed biostratigraphical studies based on pollen spectra date the Peruc – Korycany Formation to the upper part of the middle Cenomanian (Pacltová 1977).

Polish Cretaceous

The described specimens occur in a single geological unit, the North Sudetic Basin (see text-fig. 1). The Cretaceous succession within this small syncline ranges from the middle Cenomanian to the middle Santonian (Walaszczyk in Voigt et al. 2008) and represents marine sediments deposited in a strait between the West Sudetic and the East Sudetic Islands (Milewicz 1997). The Late Cretaceous sediments (total thickness estimations vary between 565 and 1350 m, Śliwiński et al. 2003) are composed of marls, limestones, and sandstones: the predominantly marly Rakowice Wielkie Formation (Cenomanian to Coniacian) contains four major sandstone intercalations: the Wilków Member (upper Cenomanian), the Chmielno Member (lower Turonian), the Dobra Member (upper Turonian), and the Żerkowice Member (lower Coniacian). The overlying Czerna Formation (lower Santonian) also contains sandstone intercalations (all lithostratigraphic data after Milewicz 1997). Exact data for the stratigraphic position of tree fern stems preserved as sandstone casts, coming from old collections and labelled with village names, are not available and can be determined only hypothetically.

Material

The studied specimens are generally preserved as stem casts in sandstones. Typically nothing is known about the original sedimentological settings from where the specimens come from. They were collected in times when blocks of sandstone were excavated by hand in small quarries. The specimens are therefore all historical specimens accumulated over time in various museum collections. We have studied specimens housed in the National Museum Prague (NMP), Charles University, Faculty of Science, Prague (CUFS), Masaryk University, Faculty of Science (MUFS, UGV), Naturhistorisches Museum Wien (NHMW), Geologische Bundesanstalt Wien (GBA), (MUT), Muzeum Geologiczne Uniwersytetu Wrocławskiego (MGUWr), Museum für Mineralogie und Geologie in Dresden (MMG).

No more exact details are known about the original localities than those preserved on the labels which usually bear names of the closest villages only. Original names of quarries are generally unknown and we can only estimate where these historical quarries were situated from geological, geomorphological and geographical information.

Kounice

The quarries near Kounice were situated 1 km to the south-east and also north-west from the village of Kounice, 4 km north of Český Brod (Zelenka et al. 2000). The best known site in Kounice is the quarry "Na Skále" which is listed on the website of the Geological Survey – Geological localities (Čoupek et al. 2010).

Vyšehořovice

The locality of Vyšehořovice is situated 30 km east of Prague, and comprises several sandstone quarries that were a source of palaeobotanical material for nearly one century. All the quarries there are closed including the largest, Stupecký Quarry, which is listed as a Natural monument (e.g. Čoupek et al. 2010).

Vojice

Sandstone quarries in Vojice have been known since the 18th century. High quality sandstone known as Hořice Sandstone was used for sculptures and numerous historical buildings in the country. It was exploited particularly during the 19th and early 20th centuries (Rybařík 2007). The largest among them is Panský Quarry which took over smaller quarries in the area. It is the only one still mined, but in a modified state.

Starý Maletín

This locality is situated about 10 km north-east of Moravská Třebová (Šrámek 2003). There are three large and several smaller quarries in the western part of Starý Maletín. The mined sandstone, formerly termed as Maletín Sandstone, is one of the best sculptural and structural stones in the country. It was mined in the registered territory of four villages – Starý Maletín, Studená Loučka, Svojanov and Prklišov on the easternmost edge of the Bohemian Cretaceous Basin. The largest and best preserved is Kubíček Quarry. Regular mining took place there in the 16th century, reaching its peak in the 17th and 18th centuries. Regular mining ended there in the first half of the 20th century (Morávek 1994). The last profitable excavation was carried out at the end of the 20th century for construction of the Arion Fountain in Olomouc, which was completed in September 2002. Sandstone from this quarry is well known throughout the whole country, particularly in Moravia and Silesia. Many historical buildings have been built from this sandstone, for example, the famous Holy Trinity Column in Olomouc which is a UNESCO landmark.

Żeliszow

Żeliszów (Giersdorf) is a village situated in the valley of the Żeliszowski Potok River, an affluent of the Bóbr River. Santonian sandstones crop out in the village itself. Coniacian sandstones occur less than 1 km east of the village. Turonian sandstone was quarried 2.5 km east of Żeliszów, about midway between this village and Raciborowice (Baraniecki et al. 1955). A Santonian age is less probable for the strata containing *Protopteris* (P. Raczyński, pers. comm. 2013), so that the specimen labelled 'Giersdorf' probably comes from either Coniacian or Turonian strata. Cretaceous sediments from surroundings of Żeliszow were mined in the 19th and early 20th centuries as "Giersdorfer weisse Sandstein" (Scupin 1907).

Lwówek Śląski

Lwówek Śląski (Löwenberg in Schlesien) is a town situated on the Bóbr River. Turonian strata crop out in the immediate proximity of the town (Milewicz 1956). Cenomanian deposits crop out ca. 1 km south and ca. 2 km north from the town. However, organic remains are quite rare in those strata (Milewicz 1964). The most probable age of the specimen labelled 'Löwenberg' is therefore Turonian. Nonetheless, given that Lwówek Śląski is one of the oldest towns in Silesia, it cannot be excluded that the geographic reference is to be taken in a broader sense and in this case Coniacian deposits cropping out ca. 5 km NW from the town must also be taken into account.

Methods

Stem casts were observed and measured using a stereo microscope, Olympus SZX 12, and digital microscope, Keyence. Specimens were photographed using a Canon EOS-50D with macro-lens objective and Panasonic DMC-FS10. Images were adjusted in Adobe Photoshop CS5, version 12.0, software and plates were compiled in Adobe Illustrator CS5, version 15.0.0 and CorelDRAW X5, version 15.2.0.686.

Systematic palaeontology

Class: **Polypodiopdsida Cronquist, Takhtajan et Zimmerman 1966**

Order: **Cyatheales A.B. Frank in Leunis 1877**

Higher systematics used in this paper follows the classification system published in The Catalogue of Life (Roskov et al. 2013) and The Tree of Life (Pryer et al. 2009).

Genus ***Protopteris*** **Sternberg 1838**

Type: *Lepidodendron punctatum* Sternberg 1820, p. 20, 23, pl. 4, fig. 1 ≡ *Protopteris punctata* (Sternberg) C. Presl in Sternberg 1838, p. 170, pl. 65, figs 1-3.

Emended diagnosis. Stem casts with leaf scars helically arranged, each leaf scar bearing one horseshoe shaped continuous scar of vascular bundle.

Discussion. The genus *Protopteris* is defined from mostly Mesozoic tree fern taxa. It differs from the genus *Protocyathea* O. Feistmantel 1877 in having one continuous vascular bundle scar. Leaf scars of the genus *Protocyathea* bear vascular bundles forming several small irregular pits resembling leaf scars of the extant genus *Cyathea* J.E. Smith 1793.

The genus *Protopteris* differs from *Oncopteris* in having leaf scars helically arranged. The genus *Oncopteris* has leaf scars in longitudinal rows having two scars of vascular bundles. However, vascular bundles are not very reliable characters as already pointed out by Schenk (1871), because their shape and number can vary considerably (Pfefferkorn 1976). *Protopteris* differs from the Palaeozoic genus *Megaphyton* ARTIS 1825 in having more than two rows of leaf scars on the mature stem. Another Palaeozoic genus *Caulopteris* LINDLEY et HUTTON 1832 also has leaf scars helically arranged as in *Protopteris*, but the scars of *Caulopteris* also form rows, which is not the case in *Protopteris*. Additionally, both of the Palaeozoic genera have much larger leaf scars and vascular bundles than the genera *Oncopteris* and *Protopteris*.

Protopteris punctata (STERNBERG) C. PRESL in STERNBERG

Pl. 1, figs 1-8, Pl. 2, fig. 1

Synonymy:

1820 *Lepidodendron punctatum* STERNBERG 1820, p. 20, 23, pl. 4, fig. 1
1822 *Filicites punctatus* (STERNBERG) MARTIUS, p. 130
1828 *Sigillaria punctata* (STERNBERG) BRONGNIART, p. 64.
1836 *Caulopteris punctata* (STERNBERG) GÖPPERT, p. 449
1838 *Protopteris punctata* (STERNBERG) C. PRESL in STERNBERG, vol. II, 7/8: 170, pl. 65, figs 1-3
1880 *Protopteris punctata* (STERNBERG) C. PRESL in STERNBERG, Hosius et von der Marck, p. 205, pl. 43, fig. 185
1882 *Dicksonia punctata* (STERNBERG) HEER, p. 24, pl. 47
1888 *Dicksonia punctata* (STERNBERG) HEER, Velenovský, p. 20, pl. 5, figs 2-4
1963 *Protopteris punctata* (STERNBERG) C. PRESL in STERNBERG, Němejc, p. 448, pl. 55, figs 2-3
1871-75 *Protopteris punctata* (STERBERG) C. PRESL in STERNBERG, Geinitz, p. 304, pl. 67, fig. 1
1845 *Protopteris sternbergii* CORDA, p. 77, pl. 48, fig. 1, nom. illegit.
1872a *Protopteris sternbergii* CORDA, O. Feistmantel, p. 26, pl. 2, figs 5, nom. illegit.
1872b *Protopteris sternbergii* CORDA, O. Feistmantel, p. 214, nom. illegit.
1866 *Protopteris debeyi* SCHLÜTTER, p. 68
?1896 *Protopteris wohlgemuthii* FLICHE, p. 21, pl. 1, fig. 2

Holotype: NMP F1471, coll. National Museum, Prague (pl. 1, figs 1, 4).

Type Locality: Kounice.

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

Material studied: NMP F212, F213, F214, F1461, F1473, F1474, F1477, F1480, F1492, F2094, F2101, F2128, F3677, F3678, F3679, F3680, F3681, F3682, F3683, F3684, F3685, F3686, F3687, F3688, F3689, F3690, F3691, F3692, F3693, F3694, F3695, F3696, F3697, F3698, F3699, F3700, F3701, F3702, F3703, F3704, F3705, F3706, F3707, F3708, F3709, F3710, F3711, F3712, F3713, F3714, F3715, F3716, F3721, F3722, F3720; MGUWr 7398.p; MMG PB SaK 13.

Occurrence: Kounice, Vyšehořovice, Vojice, Paulsdorf in Dippoldiswalde, Germany (Cenomanian); Lwówek Śląski, Poland (Turonian-Coniacian).

Emended diagnosis. Stem covered by helically arranged leaf scars; each leaf scar flat, slightly sunken basally into the stem surface. Scar of vascular bundle leaving horseshoe shaped mark. Scars of aerial roots situated directly under each leaf scar leaving several small spherical pits, forming a U-shaped line. Height / width ratio of leaf scars 0.8-1.7; height / width ratio of vascular bundle scars (0.7) 1.0-1.3 (1.5). Stems rarely covered by aerial roots.

Description. The holotype (NMP F1471) described by Sternberg represents part of the stem preserved as a cast showing helically arranged leaf scars (pl. 1, fig. 1). This part of the stem is 130 mm wide, 180 mm tall. The flat or slightly sunken helically arranged leaf scars are oval to spherical in shape. The leaf scars are typically 15 mm wide and 18 mm high (pl. 1, fig. 4). Their density is 20 per 1 dm^2. Each leaf scar contains one scar of vascular bundle resembling a horseshoe. The vascular bundles are 8–11 mm wide and 11–12 mm high. Under the leaf scar there are 5–9 small root scars are seen under the leaf scar. A large tube-like cavity runs through the whole stem, it is 18×30 mm in cross section. Stem casts are usually flattened ranging from 30×55 mm to 103×165 mm in cross section. They are covered by leaf scars of various shapes and sizes showing traces of vascular bundles. The specimens NMP F2128 (pl. 1, fig. 2), F3720 from Vojice and Vyšehořovice (NMP F 3694, F3680) show extremely small leaf scars. In shape they are almost circular, up to 8 mm in diameter and a density of about 40 per 1 dm^2. The specimens NMP F1474 and F3688 show large leaf scars reaching 23×28 mm. The height / width ratio of leaf scars varies from 0.9 to 1.4 exceptionally 1.6. The height / width ratio of vascular bundle scars varies even more, from 1.0 to 1.3, exceptionally from 0.7 to 1.4. The mean height / width ratio of leaf scars of all studied specimens is 1.2 (text-fig. 2, tab. 1), the mean height / width ratio of vascular bundle scars is 1.2. The specimen NMP F3702 (pl. 1 fig. 8) shows two types of cortical tissue. The lower type shows rather elongate diamond shaped scars (size 10×40 mm) which are a product of decorticating of the cortex running above which shows a standard pattern of leaf scars (compare pl. 1, fig. 4). The specimen NMP F3692 shows a standard pattern of leaf scars, which is covered by a third type of cortical tissue forming bulging shapes (pl. 1, figs 5, 6). The specimens NMP F1477, F1480, F3677 and F3679 show the remains of aerial roots which originally overgrew the leaf scars and formed a several centimetres thick mantel (pl. 1, fig. 9). The specimen MGUWr 7398.p from the Wroclaw University Museum (pl. 2, fig. 1) is particularly illustrative this way. Some specimens from the Kounice locality (NMP F1471), Vojice (NMP F3720) and Vyšehořovice (NMP F3711) show the internal tube-like cavity running through the whole stem cast, as is documented in the holotype. The cavity is oval in cross-section; it is sometimes visible only from one side.

Discussion. In addition to the type species *Protopteris punctata,* three more species of the genus *Protopteris* were described from Central Europe. Göppert (1836) described *Protopteris singeri* (GÖPPERT) C. PRESL in STERNBERG from the Cretaceous of Poland and Engelhardt (1881) described *Protopteris laubei* (ENGELHARDT) STENZEL from the late Eocene of Staré Sedlo (Knobloch et al. 1996). Additionally *Protopteris witteana* SCHENK 1871 was described from the Lower Createaceous of Germany, from the vicinity of Hannover and *P. wohlgemuthii* FLICHE

1896 from the Lower Cretaceous of Argone. In the present paper, a newly described species *P. maletinensis* GREGUŠ et J. KVAČEK sp. nov. has been added.

P. laubei, *P. maletinensis* and *P. witteana* differ from *P. punctata* in having large bulgy leaf cushions. *P. laubei* and *P. maletinensis* also differ in the mean height / width ratio of leaf scars (see text-fig. 2 and tab. 1). *P. laubei, P. maletinensis* and *P. singeri* have a lower height / width ratio of leaf scars (0.4–1.0) than *P. punctata* (0.8–1.7). Stems of *P. singeri* show leaf scars less densely arranged, typically with a between scar distance as wide as the leaf scar. *P. wohlgemuthii* FLICHE shows leaf scars closely packed with a similar height / width ratio representing probably *P. punctata.*

The size of leaf scars in *P. punctata* is variable probably depending on the position on the stem and the diameter of the stem. Older stems show scars distributed less densely with broader inter-scar areas. However, the areas never exceed half the width of the leaf scar.

Protopteris singeri (GÖPPERT) C. PRESL in STERNBERG

Pl. 2, figs 2-5

Synonymy:

1836 *Caulopteris singeri* GÖPPERT, p. 449, pl. 41, figs 1, 2
1838 *Protopteris singeri* (GÖPPERT) C. PRESL in STERNBERG, vol. II, 7/8: p. 171, pl. 65, figs 7-10
1841 *Protopteris singeri* (GÖPPERT) C. PRESL in STERNBERG, Göppert, p. 119, pl. 53, figs 1, 2
1845 *Protopteris singeri* (GÖPPERT) C. PRESL in STERNBERG, Corda, p. 78, pl. 48, fig. 2
1872a *Protopteris singeri* (GÖPPERT) C. PRESL in STERNBERG, O. Feistmantel, p. 27, pl. 2, fig. 6
1872b *Protopteris singeri* (GÖPPERT) C. PRESL in STERNBERG, O. Feistmantel, p. 212

Holotype: MGUWr 2885b.p, coll. Muzeum Geologiczne Uniwersytetu Wrocławskiego, Wrocław (pl. 2, figs 2, 5).

Type locality: Żeliszów (Giersdorf), Poland.

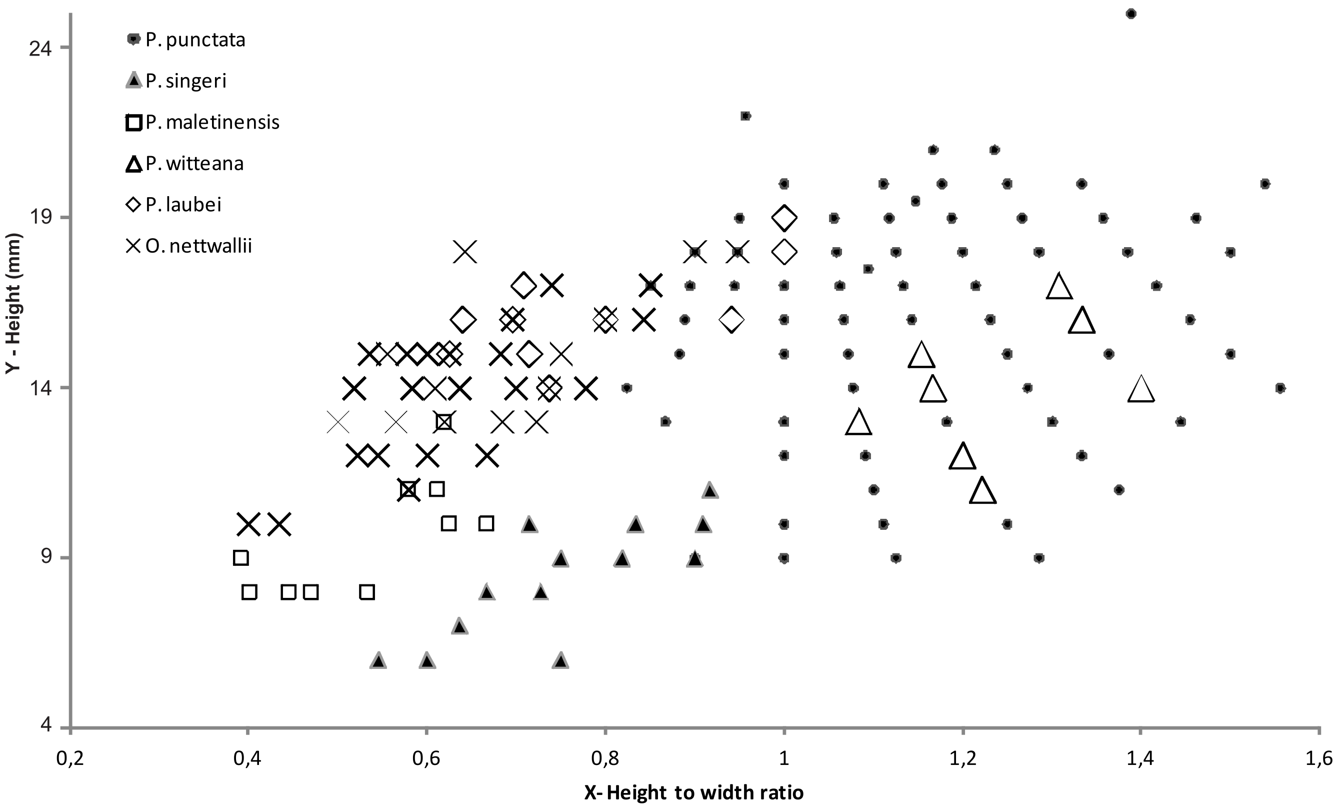
Type horizon: Turonian-Coniacian, Late Cretaceous.

Material studied: MGUWr 2885a.p.

Occurrence: only the type locality.

Emended diagnosis. Stem covered by helically arranged leaf scars. Each leaf scar includes one vascular bundle leaving a horseshoe shaped scar. Leaf scars occurring at some considerable distance from each other. Height / width ratio of leaf scars 0.6–0.9; height / width ratio of vascular bundle scars 0.5–0.8.

Description. The holotype (MGUWr 2885b.p) is a fragment of a stem cast consisting of two parts glued together (pl. 2, fig. 2). The fragment of the stem is 56 mm wide, and 128 mm high, showing helically arranged leaf scars. The flat leaf scars are oval to spherical in shape. The leaf scars are typically 12 mm wide and 10 mm high (pl. 2, fig. 5). Leaf scars are arranged at a distance equal to the width of a leaf scar; their density is about 30 per 1 dm^2. Each leaf scar contains one scar of the vascular bundle resembling a horseshoe. Leaf scars are usually slightly sunken into the stem in the apical part and protruding in the basal part, forming a bulging structure but never as



Text-fig. 2. Plot of height versus height to width ratio of leaf scars of the studied species of *Protopteris* and *Oncopteris*.

developed as in *P. maletinensis*. The vascular bundles are 5–9 mm wide and 4–5 mm high. The second specimen from the collection (MGUWr 2885a.p) shows a fragment of a stem, 49×97 mm (pl. 2, fig. 3). Its leaf scars are on average smaller than in the holotype (11 mm wide and 8 mm high, pl. 2, fig. 4). The vascular bundles are 6–8 mm wide and 3–4 mm high. Under the leaf scar there are up to 15 small scars, the remains of aerial roots.

D i s c u s s i o n . *Protopteris singeri* is similar to *P. punctata* in having similar shaped scars of leaf vascular bundles. However, it differs from *P. punctata* in two major characters: in the height / width ratio and larger distances between leaf scars. *P. singeri* has a height /width ratio usually under 0.9 while *P. punctata* has a higher value ratio (0.8) 0.9–1.7. *P. singeri* differs in having leaf scars sparsely distributed. Stems of *P. singeri* are generally smaller than stems of *P. punctata*. *Protopteris maletinensis*, *P. laubei* and *P. witteana* differ from *P. singeri* in the presence of large bulgy leaf cushions. The occurrence of *P. singeri* in Kounice as reported by Corda (1845) was not confirmed. The specimen mentioned in the text by Corda (1845) was not available for the present study.

***Protopteris maletinensis* Greguš et J. Kvaček sp. nov.**

Pl. 3, figs 1-4

H o l o t y p e d e s i g n a t e d h e r e : NHMW 1878B/0006/7141, coll. Naturhistorisches Museum, Wien (pl. 3, fig. 1-3).

T y p e l o c a l i t y : Starý Maletín.

T y p e h o r i z o n : Cenomanian, Late Cretaceous.

E t y m o l o g y : Derived from the name of the type locality – Starý Maletín.

M a t e r i a l s t u d i e d : UGV S17/2, GBA 2013/019/0001, GBA 2013/019/0002, NMP F3717.

O c c u r r e n c e : Starý Maletín, Vyšehořovice.

D i a g n o s i s . Stem cast covered by helically arranged leaf cushions bearing leaf scars. Each leaf scar includes one vascular bundle leaving a horseshoe shaped scar. Leaf scars with enlarged appendages forming pouch-like structure. Height / width ratio of leaf scars 0.4–0.7.

D e s c r i p t i o n . The holotype shows a fragmentary stem cast 80 mm wide, 180 mm, with large bulging leaf cushions arranged helically (pl. 3, fig. 1). They are 18–27 mm wide and 32–43 mm high. Each leaf cushion is topped by a leaf scar. The leaf scars are generally poorly preserved; two of them (8–13 mm high, 18–20 mm wide) showing remains of undivided vascular bundles resembling a horseshoe (pl. 3, fig. 2, 3). Scars of aerial roots are preserved as small pits. Width to height ratio of leaf scars is 0.4–0.7. The density of scars is about 10 per 1 dm^2. Leaf cushions on the holotype show longitudinal grooves below each leaf scar, these structures may be the remains of aerial roots. Other specimens are generally poorly preserved showing helically arranged leaf cushions with leaf scars similar to those in the holotype. Their stems range from 55 mm to 85 mm in diameter. The specimen (UGV S17/2) shows large leaf cushions 14–26 mm wide and 23–45 mm high. The height / width ratio of leaf scars reaches 0.4. Remains of aerial roots are preserved in this specimen as small pits (pl. 3, fig. 4). The specimen from Vyšehořovice (NMP F3717) displays leaf cushions 21–25 mm wide and 36–43 mm high. The height / width ratio of leaf scars is up to 0.6. Remains of aerial roots are also preserved in this specimen as small pits.

D i s c u s s i o n . *Protopteris maletinensis* differs from *P. punctata* and *P. singeri* in having pouch like leaf cushions. *Protopteris laubei* (Engelhardt) Stenzel from the Late Eocene of Staré Sedlo (Engelhardt 1881, Knobloch et al. 1996) is very similar to *P. maletinensis*, particularly in having pouch-like cushions arranged helically on the stem. The size of leaf cushions in both species is similar even regarding the width of leaf scars. They differ only in the height of the leaf scars which is 8–13 mm for *P. maletinensis* and 14–19 mm for *P. laubei.* This height difference affects their average height / width ratio, which is 0.5 for *P. maletinensis* and 0.8 for *P. laubei* (tab. 1). *P. laubei* differs from *P. maletinensis* also in having leaf scars protruding from the stem and with wider gaps between them. However, more distant leaf scars may reflect only greater physiological age, so it is not a conclusive feature. The basal parts of each leaf scar in *P. laubei* show a sharply undulating vascular bundle scar, which is lacking in *P. maletinensis*. Additionally, they differ remarkably in geological age; *P. laubei* comes from the Late Eocene whereas *P. maletinensis* is known from the Cenomanian.

Another similar species is represented by *Protopteris witteana* Schenk from the Lower Cretaceous of Germany (Schenk 1871). It consists of a fragment of a stem cast (50 mm wide, 190 mm tall) also with bulging leaf cushions arranged helically (pl. 3, figs 5, 6). The leaf cushions are much smaller than in *P. maletinensis*; their size being 12–15 ×17–24 mm. Between leaf cushions there are 5–7 mm wide gaps. Each leaf cushion is topped by the leaf scar with a relatively well preserved vascular bundle resembling a horseshoe (pl. 3, fig. 6). Leaf scars of *P. witteana* in comparison to *P. maletinensis* are higher than they are wide, their mean height / width ratio (1.2) is the same as in *P. punctata*. The density of scars is about 24 per 1 dm^2. These scars are arranged in the same plane as the surface of the stem cast while *P. maletinensis* exhibits leaf scars orientated almost perpendicular to the surface of the stem. *P. witteana,* in comparison to *P. maletinensis*, does not show longitudinal grooves below each leaf scar.

Genus ***Oncopteris* Dormitzer in Krejčí 1853**

Synonymy:
Alsophilina Dormitzer in Krejčí 1853, p. 28, pl. 1

T y p e : *Oncopteris nettwallii* Dormitzer in Krejčí 1853, p. 28, pl. 2

E m e n d e d d i a g n o s i s . Stem casts with leaf cushions arranged in longitudinal rows; each leaf cushion bearing one leaf scar of vascular bundle divided into two parts.

D i s c u s s i o n . The genus *Oncopteris* is defined from fossil stem casts which show leaf cushions in longitudinal rows. The genus *Alsophilina* was established by Dormitzer in Krejčí (1853) at the same time as

Oncopteris. Both genera show the same key diagnostic character – leaf scars in lines. They differ in the shape of the leaf cushions; *Alsophilina* having hexagonal leaf cushions, while *Oncopteris* has circular. As already pointed out by Velenovský (1888), the shape of leaf cushions is a secondary character, particularly because the shape of leaf cushions in the genus *Oncopteris* varies considerably, while the shape of the leaf scars is stable.

Regarding the key character – having leaf scars in lines, the genus *Oncopteris* differs from the genus *Protopteris.* The in-line arrangement of leaf scars is typical for Palaeozoic stems of the genus *Megaphyton* (compare Pfefferkorn 1976). *Megaphyton* differs from *Oncopteris* in having much larger leaf scars. They are arranged in two longitudinal rows, one on each side of the stem.

Oncopteris nettwallii Dormitzer in Krejčí

Pl. 4, figs 1-7.

Synonymy:
1853 *Oncopteris nettwallii* Dormitzer in Krejčí, p. 28, pl. 2
1872a *Oncopteris nettwallii* Dormitzer in Krejčí, O. Feistmantel, p. 28, pl. 2, figs 3
1872b *Oncopteris nettwallii* Dormitzer in Krejčí, O. Feistmantel, p. 212
1888 *Oncopteris nettwallii* Dormitzer in Krejčí, Velenovský, p. 23, pl. 5, figs 6
1853 *Alsophilina kauniciana* Dormitzer in Krejčí, p. 28, pl. 1
1872a *Alsophilina kauniciana* Dormitzer in Krejčí, O. Feistmantel, p. 28, pl. 2, figs 4
1872b *Alsophilina kauniciana* Dormitzer in Krejčí, O. Feistmantel, p. 212 ("*Alsophilina vouniciana*")
1874 *Alsophilina kauniciana* Dormitzer in Krejčí, O. Feistmantel, p. 270
1888 *Oncopteris kauniciana* (Dormitzer in Krejčí) Velenovský, p. 22, pl. 5, figs 1
1873 *Alsophilina westphalenii* Stur, p. 242

Holotype: NMP F1514, coll. National Museum, Prague (pl. 4, figs 1, 4).

Material studied: NMP F1476, F1479, F1483; two unnumbered specimens from Charles University, Faculty of Science (CUFS).

Type Locality: Kounice.

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

Occurrence: Only the type locality Kounice.

Emended diagnosis. Stems covered by leaf cushions arranged in longitudinal rows. Leaf cushions oval to elongate hexagonal. Each leaf cushion bearing an oval leaf scar with vascular bundle divided into two parts accompanied by scars of aerial roots arranged in a semicircle.

Description. The holotype described by Dormitzer (NMP F1514) shows a fragmentary stem cast covered with longitudinal rows of leaf cushions (pl. 4, fig. 1). The stem cast is flattened, 100 mm wide, 250 mm tall. The leaf cushions are pouch like, almost spherical with leaf scars in the upper part. Leaf cushions are 26–36 mm wide and 32–36 mm high. The leaf scars are oval to elliptical, 18–28 mm wide and 12–18 mm high. Height / width ratio for leaf scars is 0.5–0.9 and their density is 8 per 1 dm^2. The vascular bundle scar is divided into two parts which are heart-shaped (pl. 4, fig. 4), the distance between them is 4 mm on average. The external parts of both vascular bundle scars are 15 mm apart and their height is 5 mm. Scars of aerial roots are situated on the upper part of the leaf scars, near to the vascular bundle, forming a semicircle. Aerial roots on the stem were not observed. The specimen (holotype of *Alsophilina kauniciana,* No. NMP F1515) shows part of a stem with longitudinal rows of leaf cushions (pl. 4, fig. 2). This part of the stem is 300 mm tall, flattened – 100×60 mm. The leaf cushions are in physical contact and they are preserved only on one half of the trunk. In shape they are rounded to elongate hexagonal, narrow at the top and bottom. The leaf cushions are 17–26 mm wide and 21–31 mm high. Leaf scars are elliptical in shape, 18–20 mm wide and 11–18 mm high (pl. 4, fig. 5). The height / width ratio of leaf scars varies from 0.6 to 1.0 and the density is about 18 per 1 dm^2. Leaf scars of vascular bundles are divided into two parts which are U shaped (7×10 mm). Aerial root scars are situated in the middle part of the leaf scars and create a semicircular formation. Oblong grooves run through the leaf scars, these could be the remains of aerial roots. Aerial roots on the stem were not observed. The specimens (NMP F1476, F1479, and two specimens from CUFS) (pl. 4, figs 3, 7) display leaf cushions clearly arranged in longitudinal rows separated by gaps of about 14 mm. The distance between leaf cushions within a row is 8–10 mm. The leaf cushions are oval elongated (22–31 mm wide, 32–43 mm high) with oval leaf scars in the upper part (21–26 mm wide, 13–16 mm high). The leaf scar height / width ratio is 0.6 – 0.7 and the density on the stem is 7 per 1 dm^2. Vascular bundle scars are the same as those from the holotype.

Discussion. The available specimens of *O. nettwallii* show a remarkable arrangement of their leaf cushions. The differences among the described specimens are in size, shape and distance between the leaf cushions. These differences can be caused by different ontogenetic stages. The specimen (NMP F1515) originally described as *A. kauniciana* with elongated hexagonal leaf cushions probably represents physiologically the youngest specimen (pl. 4, fig. 2). The holotype, specimen NMP F1483 and the specimen from Vojice (pl. 4, fig. 7) may represent medium ontogenetic stages. The specimens (NMP F1476, F1479) probably represent the oldest ontogenetic stage (pl. 4, fig. 3).

Oncopteris nettwallii and *Alsophilina kauniciana* show a number of similarities, including leaf cushions arranged in longitudinal rows, a similar leaf scar shape and the height / width ratio. They differ only in size, shape and distance between leaf cushions. These features support the idea of joining those two taxa into one as suggested already by Velenovský (1888). *Alsophilina wesphalenii* described by Stur (1873) also shows the same characters. This fact was already confirmed by Feistmantel (1874). *Oncopteris nettwallii* differs from *Protopteris punctata*, *P. singeri* and *P. maletinensis* in having leaf cushions longitudinally arranged and in having typically divided vascular bundles.

Table 1. Height to width ratios of leaf scars, vascular bundle scars and leaf cushions for the considered species.

		LEAF SCARS			VASCULAR BUNDLE SCARS			LEAF CUSHIONS		
		Width	Height	Ratio H/W	Width	Height	Ratio H/W	Width	Height	Ratio H/W
P. punctata	average	1.37	1.60	1.19	0.81	0.94	1.18			
	minimum	0.70	0.90	0.82	0.50	0.50	0.73			
	maximum	2.30	2.80	1.67	1.20	1.70	1.50			
P. singeri	average	1.13	0.87	0.78	0.71	0.42	0.59			
	minimum	0.80	0.60	0.55	0.50	0.30	0.50			
	maximum	1.40	1.10	0.92	0.90	0.50	0.83			
P. maletinensis	average	1.82	0.96	0.53				2.20	3.56	1.63
	minimum	1.50	0.80	0.39				1.40	2.30	1.24
	maximum	2.30	1.30	0.67				2.70	4.50	1.95
P. witteana	average	1.14	1.40	1.23	0.93	0.94	1.01	1.34	2.05	1.54
	minimum	0.90	1.10	1.08	0.70	0.60	0.86	1.20	1.70	1.29
	maximum	1.30	1.70	1.40	1.00	1.10	1.25	1.50	2.40	1.92
P. laubei	average	2.10	1.62	0.79	1.77	1.40	0.80	2.58	4.03	1.57
	minimum	1.70	1.40	0.63	1.50	1.30	0.65	2.40	3.90	1.44
	maximum	2.50	1.90	1.00	2.00	1.60	1.00	2.90	4.40	1.67
O. nettwallii	average	2.23	1.43	0.65	1.35	0.58	0.44	2.68	3.23	1.21
	minimum	1.80	1.00	0.40	1.00	0.40	0.27	1.70	2.10	0.88
	maximum	2.80	1.80	0.95	1.70	0.70	0.70	3.60	4.30	1.50

Conclusions

As a result of the present investigation of tree fern stem casts from Czech and Polish localities we can state that in the Central European Cretaceous there are three clearly defined species of the genus *Protopteris* – *P. punctata*, *P. singeri* and *P. maletinensis* and one species of the genus *Oncopteris* – *O. netwallii*.

Genera and subsequently species can be distinguished by the distribution of leaf scars on the trunk and their height to width ratio. Genera *Protopteris* and *Oncopteris* differ in the generally different arrangement of leaf scars reflecting the inner structure of their trunks. The genus *Protopteris* has leaf scars arranged helically, while the genus *Oncopteris* has leaf scars in rows.

The described species of *Protopteris* are recognized based on the height / width ratio of leaf scars. This character was suggested by Pfefferkorn (1976) to be fairly stable and suitable for differentiation of tree ferns. *P. punctata* is characterised by having a height / width ratio of 1.2 while *P. singeri* shows a height / width ratio of 0.8. The new species, *Protopteris maletinensis* Greguš et J. Kvaček sp. nov. has a height / width ratio of 0.5. It differs from *Protopteris punctata, P. singeri* and *P. witt*eana in having pouch like leaf cushions. It shares a number of similar characters with *P. laubei* but it differs in height / width ratio.

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Explanation of the plates

All scale bars – 20 mm.

PLATE 1

Protopteris punctata **(Sternberg) C. Presl in Sternberg**

All scale bars – 20 mm.

1. Holotype showing stem casts with helically arranged leaf scars, Sternberg 1820, pl. 4, fig. 1., Kounice, NMP F1471.
2. Stem cast with small leaf scars, Vojice, NMP F2128.
3. Large stem cast showing regular pattern of leaf scars, Kounice, NMP F1474.
4. Holotype, detail of the leaf scar also showing scar of vascular bundle, Kounice, NMP F1471.
5. Detail of leaf scar covered with cortical tissue forming bulging shapes, Kounice, NMP F3692.
6. Detail of leaf scar covered with cortical tissue forming bulging shapes, Kounice, NMP F 3692.
7. Stem cast with leaf scars rather distantly spaced, Corda 1845, pl. 48, fig. 1, Kounice, NMP F1492.
8. Stem cast showing two types of cortical tissue; lower type shows rather elongate diamond shaped scars, upper running cortex is covered by standard pattern of leaf scars. Kounice, NMP F3702.
9. Stem cast showing remains of aerial roots overgrowing leaf scars. Kounice, NMP F3677.

PLATE 2

Protopteris punctata **(Sternberg) C. Presl in Sternberg**

All scale bars – 20 mm.

1. Stem cast showing remains of aerial roots overgrowing leaf scars. Lwówek Śląski, MGUWr 7398.p.

Protopteris singeri **(Göppert) C. Presl in Sternberg**

All scale bars – 20 mm.

2. Holotype showing distantly spaced leaf scars, Żeliszów (Giersdorf), MGUWr 2885a.p.
3. Stem cast showing distantly spaced leaf scars, Żeliszów (Giersdorf), MGUWr 2885b.p.
4. Detail of leaf scar showing horseshoe shape, Żeliszów (Giersdorf), MGUWr 2885b.p.
5. Detail of holotype showing horseshoe shape, Żeliszów (Giersdorf), MGUWr 2885a.p.

PLATE 3

Protopteris maletinensis **Greguš et J. Kvaček sp. nov.**

All scale bars – 20 mm.

1. Holotype showing helically arranged leaf cushions bearing leaf scars, Starý Maletín, NHMW 1878B/0006/7141.
2. Detail of holotype showing leaf scar with horseshoe shape indicated by arrow, Starý Maletín, NHMW 1878B/0006/7141.
3. Detail of holotype showing leaf scar, Starý Maletín, NHMW 1878B/0006/7141.
4. Stem cast showing helically arranged leaf cushions, Starý Maletín, UGV S17/2.

Protopteris witteana **Schenk**

5–6. Illustrations from the publication by Schenk 1871, pl. 30, figs 6, 6a.

PLATE 4

Oncopteris nettwallii **Dormitzer in Krejčí**

All scale bars – 20 mm.

1. Holotype showing leaf cushions and scars in rows, Dormitzer in Krejčí, pl. 2, Kounice, NMP F1514.
2. Holotype of *Alsophilina kauniciana* Dormitzer in Krejčí, p. 28, pl. 1, Kounice, NMP F1515.
3. Stem cast showing rows of leaf cushions with clearly defined gaps, Kounice, NMP F1479.
4. Detail of holotype leaf scars showing leaf scar with bipartite scar of vascular bundle, Kounice, NMP F1514.
5. Detail of leaf cushions and leaf scars of the specimen NMP F1515, Kounice.
6. Detail of leaf cushions and leaf scars of an unnumbered specimen (CUFS), Vojice.
7. Stem cast showing leaf cushions and scars in rows. Vojice, unnumbered specimen (CUFS).

PLATE 1

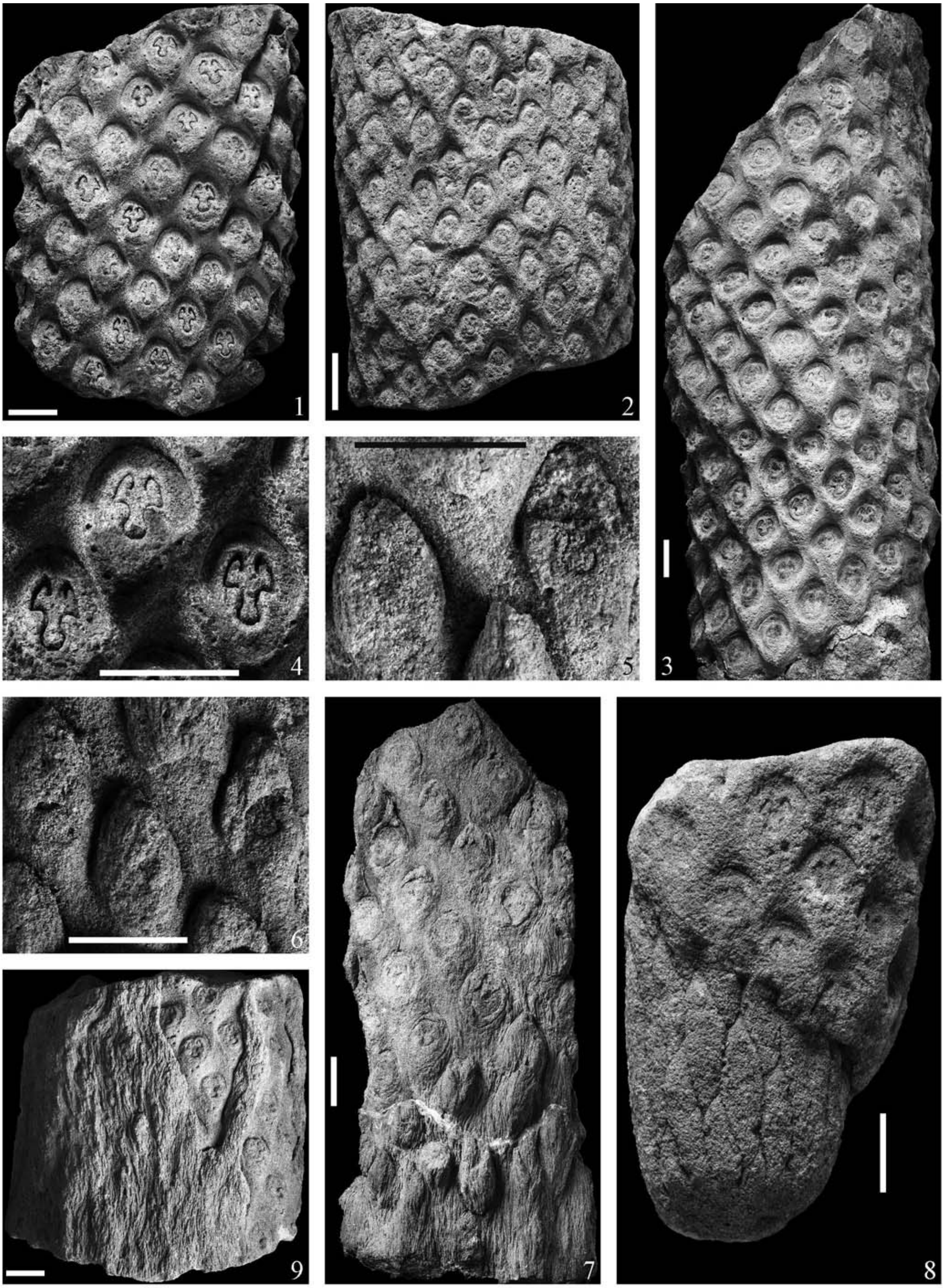

PLATE 2

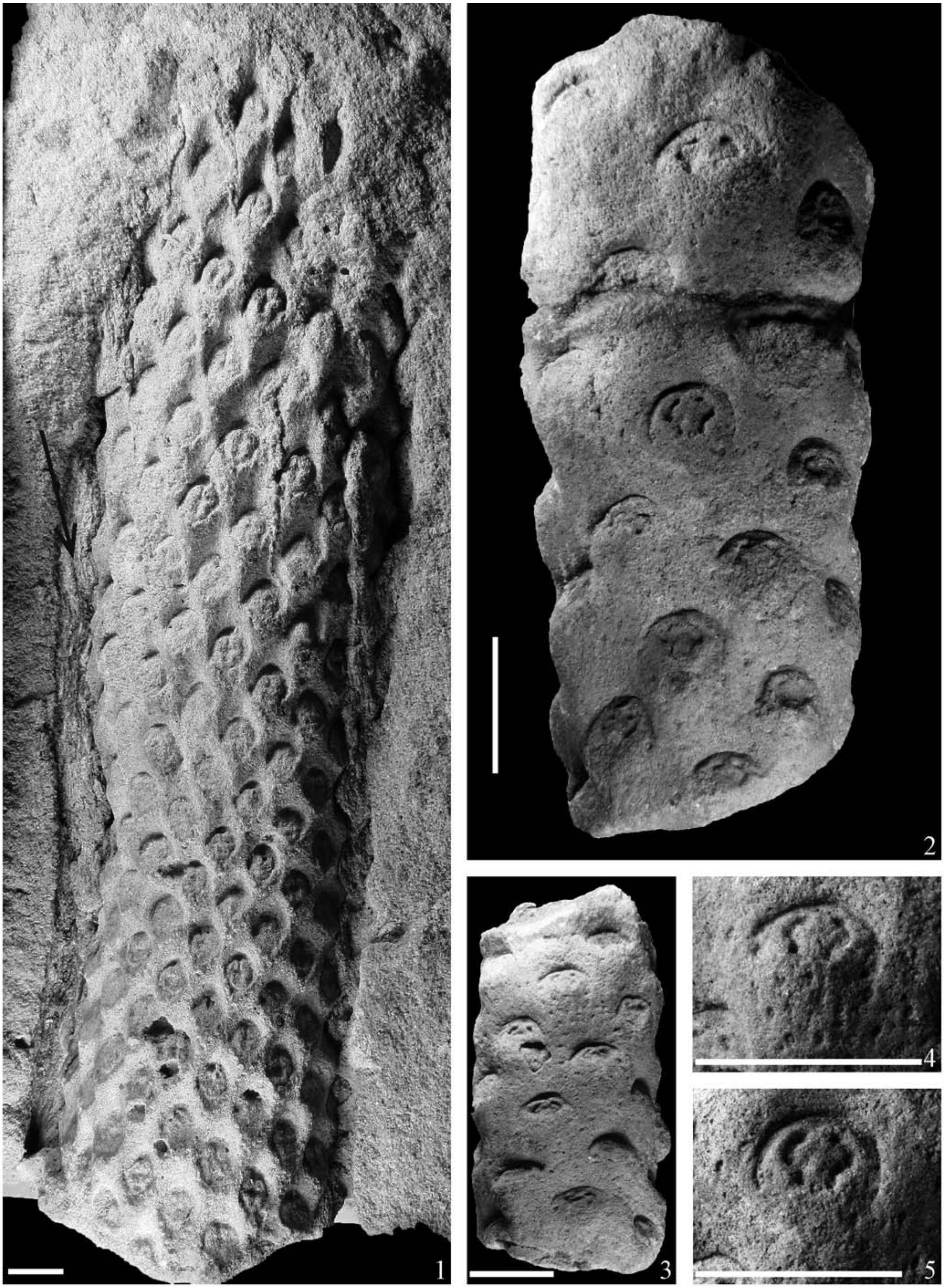

PLATE 3

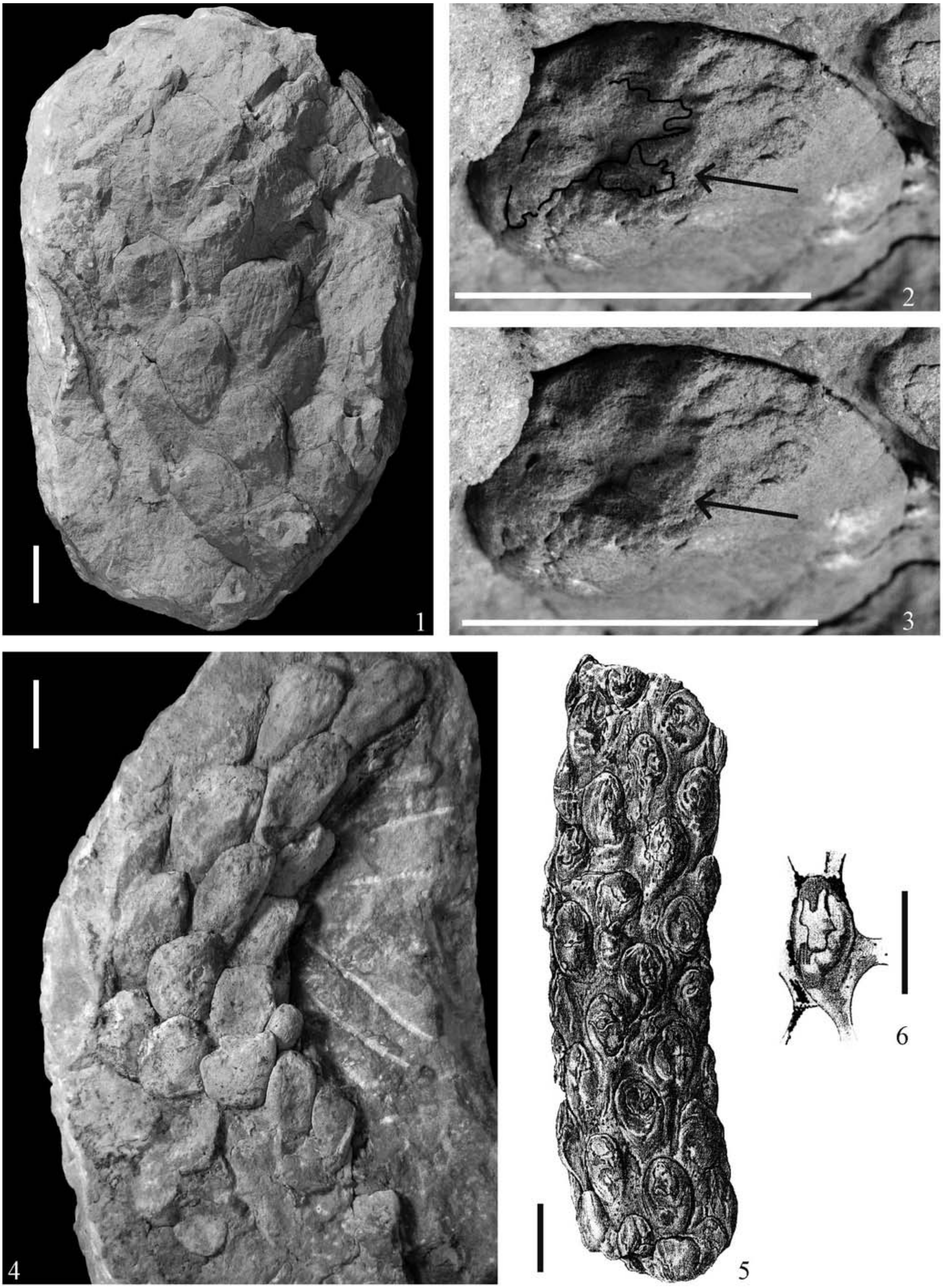

PLATE 4