

# Contribution to knowledge on ontogenetic developmental stages of *Lepidodendron mannebachense* Presl, 1838

STANISLAV OPLUŠTIL



A new reconstruction of *Lepidodendron mannebachense* is proposed here based on collection of well-preserved compressions from middle Moscovian volcanoclastics of the Radnice Basin, Czech Republic. These specimens that represent remains of juvenile and matured individuals make progress in our current knowledge on ontogeny of this species and help us to improve its whole plant reconstruction. The juvenile stage was characterised by an unbranched columnar stem. The mature stage of *L. mannebachense* had an umbrella-like canopy produced by combination of more or less isotomous apical dichotomies of the stem and main branches with anisotomous pseudomonopodial branching. Dichotomous branching built the frame of the crown and continued until the limit for meristem division was reached. However, most of thin terminal shoots were anisotomous lateral branches growing from the main dichotomies. Some of them as well as terminal branches bore cones on their tips. Only a narrow zone of leaves was maintained at any stage of tree development. In the mature stage, leaves were retained only at apical parts of terminal shoots. *L. mannebachense* was a monocarpic type of plant with a determinate growth. • Key words: *Lepidodendron mannebachense*, ontogeny, Pennsylvanian.

OPLUŠTIL, S. 2010. Contribution to knowledge on ontogenetic developmental stages of *Lepidodendron mannebachense* Presl, 1838. *Bulletin of Geosciences* 85(2), 303–316 (7 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received January 16, 2010; accepted in revised form April 26, 2010; published online June 3, 2010; issued June 30, 2010.

Stanislav Opluštil, Faculty of Sciences, Charles University, Albertov 6, 128 43 Prague 1, Czech Republic; oplustil@natur.cuni.cz

Lepidodendrid lycopsids dominated many early to middle Pennsylvanian tropical wetlands. During this period these spectacular plants contributed up to 60 to 80% to the biomass production in peat-forming habitats (Phillips et al. 1985). Therefore it is not surprising that most of the reconstructions depict the Pennsylvanian coal measure forests as dominated by the arborescent lycopsids (e.g. Walton in MacGregor & Walton 1948). However, most reconstructions, especially the earlier ones, show lepidodendrids only as mature trees with an umbrella-like canopy produced by dichotomous branching (e.g. Hirmer 1927). This interpretation was based on scarce findings of some large specimens (e.g. Lindley & Hutton 1835/37, Scott 1920) and on commonly found fragments of branch compressions showing more or less isotomous dichotomous patterns. This traditional and simplified view of these bizarre trees started to change with an onset of systematic study of anatomically preserved specimens and compressions of exceptionally complete lepidodendrid tree remains (e.g. Walton 1935, Andrews & Murdy 1958, Eggert 1961, Delevoryas 1964 and especially DiMichele 1979a, b, 1980; Wnuk 1985, 1989). These studies proved that whole plant morphology

of these plants is much more complex and that various growth strategies exist (for an overview see Phillips & DiMichele 1992 and DiMichele & Phillips 1994). Therefore it is not surprising that new findings that contribute to understanding of whole-plant reconstruction of particular species are of interest to paleobotanists. Recently, several specimens of *L. mannebachense* that can contribute to our knowledge on ontogenetic developmental stages of this common arborescent lycopsid have been found when revising fossil plant collections in the Museum of the Geological Survey of Austria in Vienna, the National Museum in Prague and the West Bohemian Museum in Pilsen. The whole plant reconstruction of juvenile and mature developmental stages of this species is therefore the main target of the paper.

## Ontogeny of lepidodendrid lycopsids

Our present-day knowledge on ontogeny of lepidodendrid lycopsids and their architecture is based on numerous observations of petrified and compression specimens

(e.g. Andrews & Murdy 1958; Eggert 1961; DiMichele 1979a, b; 1980, 1981; Wnuk 1985, 1989). Hypothetical reconstructions of very early ontogenetic stages of lepidodendrids depict these plants as leaf-bearing domed to cone-shaped poles stabilized by dichotomously branched anchoring and water absorbing rhizomorphs bearing helically arranged roots (Phillips & DiMichele 1992). It is supposed that when such a stage was once established it was capable of fast polar growth as well as of secondary thickening (e.g. Andrews & Murdy 1958, Eggert 1961, Phillips & DiMichele 1992). This resulted in development of an unbranched stem bearing long grass-like leaves thus resembling *Sigillaria* more than *Lepidodendron*. The anatomical studies have shown that the main stem underwent secondary thickening that decreased in extent up the stem as the apical meristem enlarged and produced more primary tissue. Consequently, much more secondary growth occurred in the lower parts of the stem (e.g. Eggert 1961). It is assumed that lepidodendrid leaf cushions once produced, did not change their size during the secondary growth and subsequent thickening of the stem (e.g. Walton 1935, Egger, 1961, Wnuk 1985, Phillips & DiMichele 1992). As a result, on a mature *Lepidodendron* stem we find largest leaf cushions on the main axis; they become progressively smaller in distal parts of branches and smallest on the ultimate branches as the meristem reduced in size after each branching. Since the size of leaf cushions (especially the length) remained the same once they appeared on the stem, the secondary growth and stem thickening could be accommodated by expansion of the inter-cushion areas (Thomas 1966, 1970; Thomas & Watson 1976; Wnuk 1985). However, potential for inter-cushion expansion varied among species. Those with high potential could retained leaf cushions (primary cortical tissues) over a large part of the stem (e.g. *Lepidodendron rimosum*, *L. aculeatum*) whereas species with low potential sloughed them off soon (e.g. *L. bretonense* which is probably *Synchysidenron*) and only a narrow zone of leaf cushion-bearing cortex remained below the stem apex at any stage of its development (Thomas 1970, Wnuk 1985). DiMichele (1983) mentioned extensive lateral expansion of cells in the base of the leaf cushions and in the outer parts of the periderm of *Lepidodendron hickii* (corresponds probably to compression species *L. aculeatum*) that allowed leaf cushions to be retained longer.

Observations of large specimens also revealed that unbranched stems had the longest leaves and that leaf length decreased as branch diameter decreased with each dichot-

omy (e.g. Hirmer 1927, Němejc 1947, Eggert 1961, Wnuk 1985). When a certain height and diameter was reached, the stem started branching. Depending whether main branches were produced by dichotomy or pseudomonopodially, the trees had either an umbrella-like crown or a main stem with lateral branches leaving a large ulodendroid scars on the stem after branch abscission (e.g. DiMichele & Phillips 1985, 1994). Cones were mostly produced at the tips of the branches.

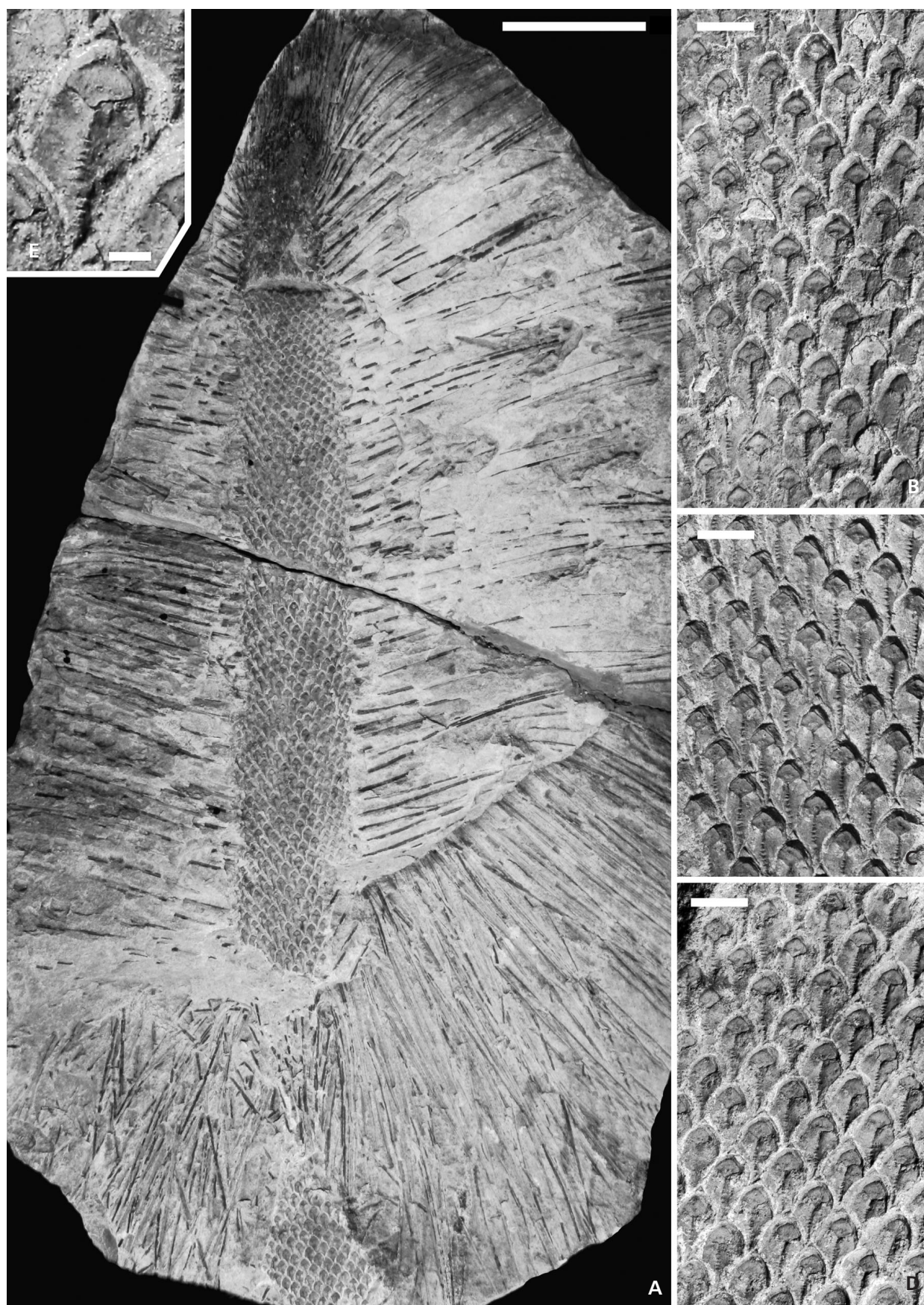
## Material

Specimens discussed and figured in this paper are stored in the collections of the Geologische Bundesanstalt Museum (Geological Survey Museum) in Vienna, Austria, in the National Museum in Prague, Czech Republic and in the West Bohemian Museum in Pilsen, Czech Republic. Although the total number of specimens in these collections belonging to this species is much higher, only five of them were selected for the purpose of this study. These specimens can significantly improve our understanding of whole plant morphology of this species in various stages of its ontogenic development whereas other specimens do not extend our current concept of the species.

In the Geological Survey Museum in Vienna, two specimens were selected. The larger one is the specimen No. 6857 preserved in about 900 mm long slab. It is a fragment of an apical part of vegetative stem described by Ettingshausen (1854, plate 27) as *Lepidodendron sternbergii* Lindley & Hutton. Re-examination of the specimen by the present author clearly proved that it is *Lepidodendron mannebachense*. The second one (No. 6886) is also an Ettingshausen (1854, plate 25) specimen of *Lepidodendron brevifolium* Ettingshausen. It preserves terminal leafy shoots. From the paleontological collection of the West Bohemian Museum in Pilsen, only one specimen (F 233) was selected. It shows terminal leafy shoots one of them with an attached cone. In the National Museum in Prague, among many specimens identified as *Lepidodendron mannebachense*, only two of them (E 5734, E 4745) have been selected for detailed description. The specimen E 5734 is a large fragment of branch system showing several orders of branching. Although it is identified as *L. dichotomum*, re-examination of the specimen revealed that it is also *L. mannebachense*. The second specimen (E 4745) is the Sternberg's syntype of *L. dichotomum*. The specimen preserves terminal and near-terminal leafy shoots and

**Figure 1.** A – the whole view of the Ettingshausen (1854) specimen No. 6857 representing an apical part of the stem of juvenile *Lepidodendron mannebachense*. Scale bar 100 mm. • B – detail of leaf cushions of the same specimen about 150 mm below the blunt apex. Scale bar 10 mm. • C – detail of leaf cushions about 400 mm below the apex. Scale bar 10 mm. • D – detail of leaf cushions of the isolated stem fragment in the lower part of the specimen. Scale bar 10 mm. • E – detail of a single leaf cushion from the Fig. 1D showing leaf scar and infrafoliar parichnos imprints. Scale bar 2.5 mm.





branches that clearly belong to *L. mannebachense*. This interpretation is fully in agreement with the opinion of Němejc (1946, 1947) who recognized that Sternberg mixed under the name of *L. dichotomum* two different species: *L. obovatum* and *L. longifolium*, the former having infrafoliar parichnos the latter without it. Both specimens from the National Museum have infrafoliar parichnos and there is no doubt they belong *L. obovatum*. Unfortunately, Sternberg (1820) involved under his *L. obovatum* (*Sagenaria obovata*) two evidently different species; *L. aculeatum* and Presl's *L. mannebachense* (1838) which resulted in more than a century-lasting taxonomical and nomenclature confusion in a literature. Němejc (1947) solved up only taxonomical part of the problem when he clearly stated differences between *L. aculeatum* and *L. obovatum* and provided their synonymy. Unfortunately he retained a confusing name *L. obovatum*. This nomenclature problem persisted until Thomas (1970) selected Presl's (1838) *L. mannebachense* as a suitable name to replace *L. obovatum*. Presl's species established only on a single specimen (figured on the plate 68, fig. 2) fully corresponds to Němejc's (1947) interpretation of *L. obovatum*, the name which Thomas (1970) placed into the synonymy of *L. aculeatum*.

All the specimens selected for description were collected in Svinná, in the northern part of the Radnice Basin, Czech Republic and are preserved in a volcanoclastic rock called Bělka. This about 500 mm thick tuff bed forms the roof of the Lower Radnice Coal of early Bolsovian (~ middle Moscovian) age. The Bělka preserves an *in situ* buried peat-forming flora and has provided many large and complete specimens (Opluštil *et al.* 2007, 2009a, b; Libertín *et al.* 2009a).

### Description of the specimens of *Lepidodendron mannebachense*

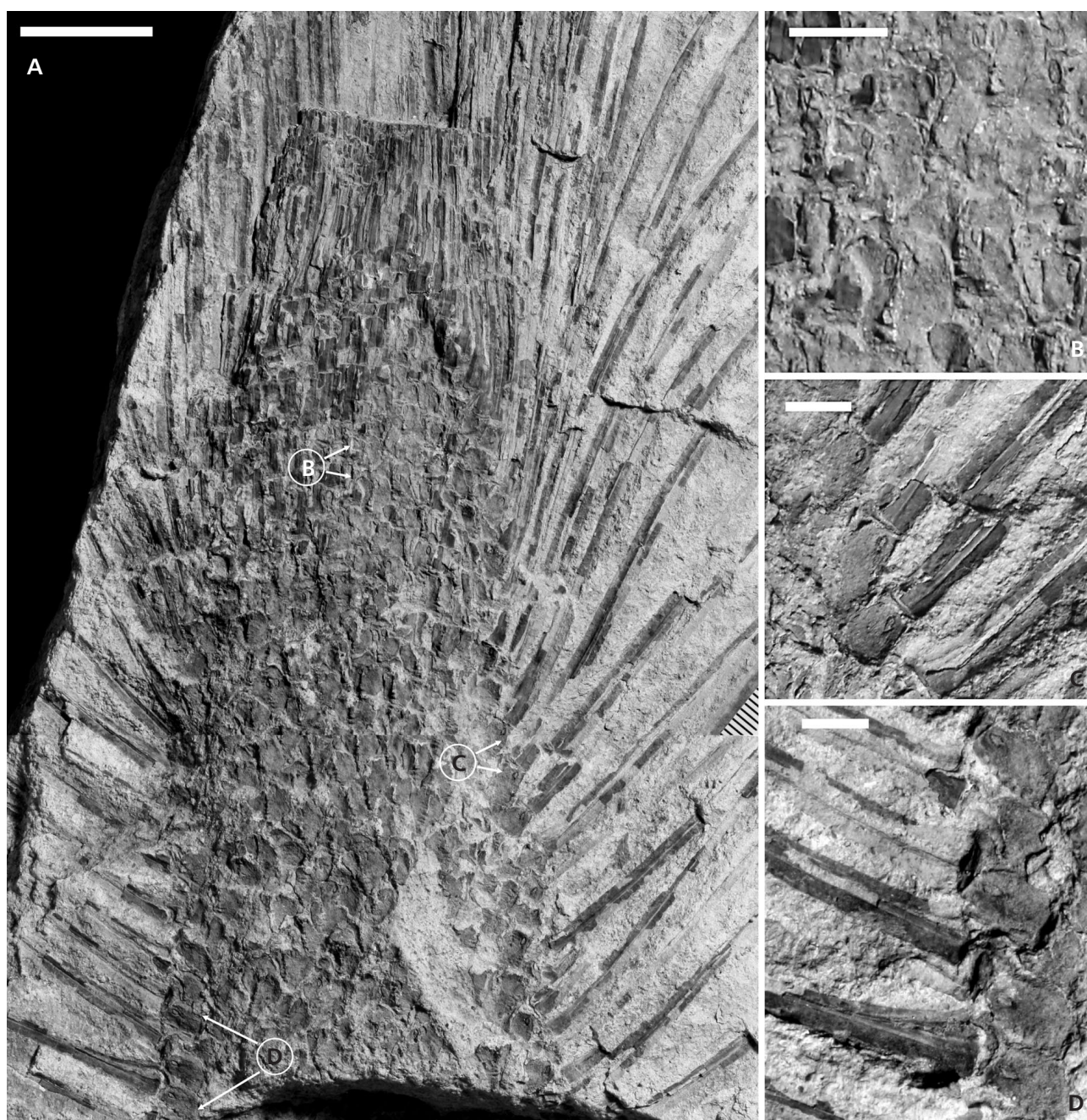
The specimen No. 6857 consists of two pieces of vegetative stem both with the same type of leaf cushions (Fig. 1A). The smaller fragment in the lower part of the slab represents an about 130 mm long and 65 mm wide impression of the stem with leaf cushions pointing up to the second stem fragment. The original width of the stem had to be larger because no stem margins are preserved. The second fragment is a much larger piece of straight leafy axis terminated by a blunt apex (Figs 1A, 2A), which evidently represents a natural/biological termination of this vegetative axis. This stem fragment is about 570 mm long but including leaves at the stem apex its length increases to about 680 mm. The width of the stem tapers to the apex very gradually; in the lower part, about 500 mm below the apex, it is 82 mm wide, 300 mm below the apex it is 70 mm wide but only 62 mm and 42 mm wide about 140 mm and 40 mm below the apex respectively. The stem is preserved mostly

as an impression in the tuff matrix but apical part about 120 mm long is preserved as a compression, the pith of which is filled by the same volcanoclastic rock embedding the stem. Leaf cushions are preserved along the whole length although at the apex they are partly hidden by long grass-like leaves. Leaves are attached to leaf cushions along both sides of the stem throughout its whole length (Fig. 1A). Both stem fragments possess leaf cushions of the same type pointing in the same direction. No indications of branching or branch scars were observed.

Leaf cushions are raised, rhomboidal, vertically and horizontally asymmetrical, approximately twice as long as wide, and arranged into a helix. One of lateral angles is rounded whereas the opposite one is more angular as a result of asymmetry of leaf cushions (Fig. 1B–E). The lower end is more acute than the upper one. Both ends are very slightly inflected in opposite directions. The cushions have distinct lateral lines extending from the lateral corners of the leaf scar to the outer edge of the cushions. The lateral lines divide the cushion into an upper and lower field. The upper field of the leaf cushion is very small with a short, indistinct keel. Striations typical of the upper field of this species as described by Thomas (1970) were observed only exceptionally probably due to a coarse nature of the tuff matrix. The lower field is large and with a distinct keel that bears several prominent but short transverse folds or notches (Fig. 1B–E). The leaf scar is located in upper half of the leaf cushion. It is rhomboidal with a rounded upper margin. Its lower margin is in a form of wide 'V'. Leaf scars are fairly large compared to the whole leaf cushion. They are between 3.5 and 5.0 mm wide and 2.6 and 3.5 mm high depending either on preservation or on the position on the stem. The width of leaf scar reaches about one-third to one-half of the width of leaf cushion. Leaf scars bear two characteristic parichnos scars with one vascular bundle imprint between them. Below the leaf scar there are two distinct infrafoliar parichnos (Figs 1B–D, 2B–D). The size of leaf cushions changes throughout the length of the specimen only slightly. They are largest in the lower part, about 500 mm below the apex, where they are about 17 mm long and 7.5 mm wide on average. Acropetally, about 250 mm below the apex, they are 14.5 mm long and 6.5 mm wide. A few centimetres below the apex they are about 10–11 mm long and 6–7 mm wide. Leaf cushions are densely spaced without inter-cushion areas between them (Fig. 1). There is only slight distortion of leaf cushion shape or size toward the sides of the stem.

Single-veined, grass-like leaves are incompletely preserved. The longest but still incomplete leaves are about 250 mm long and about 3.5–4.5 mm wide at the base where they are connected to the leaf cushion (Fig. 2). However, they decrease rapidly in width to be about 2.8–3.2 mm wide throughout most of their length. The leaves are mostly straight or only slightly bent downward. Leaves of





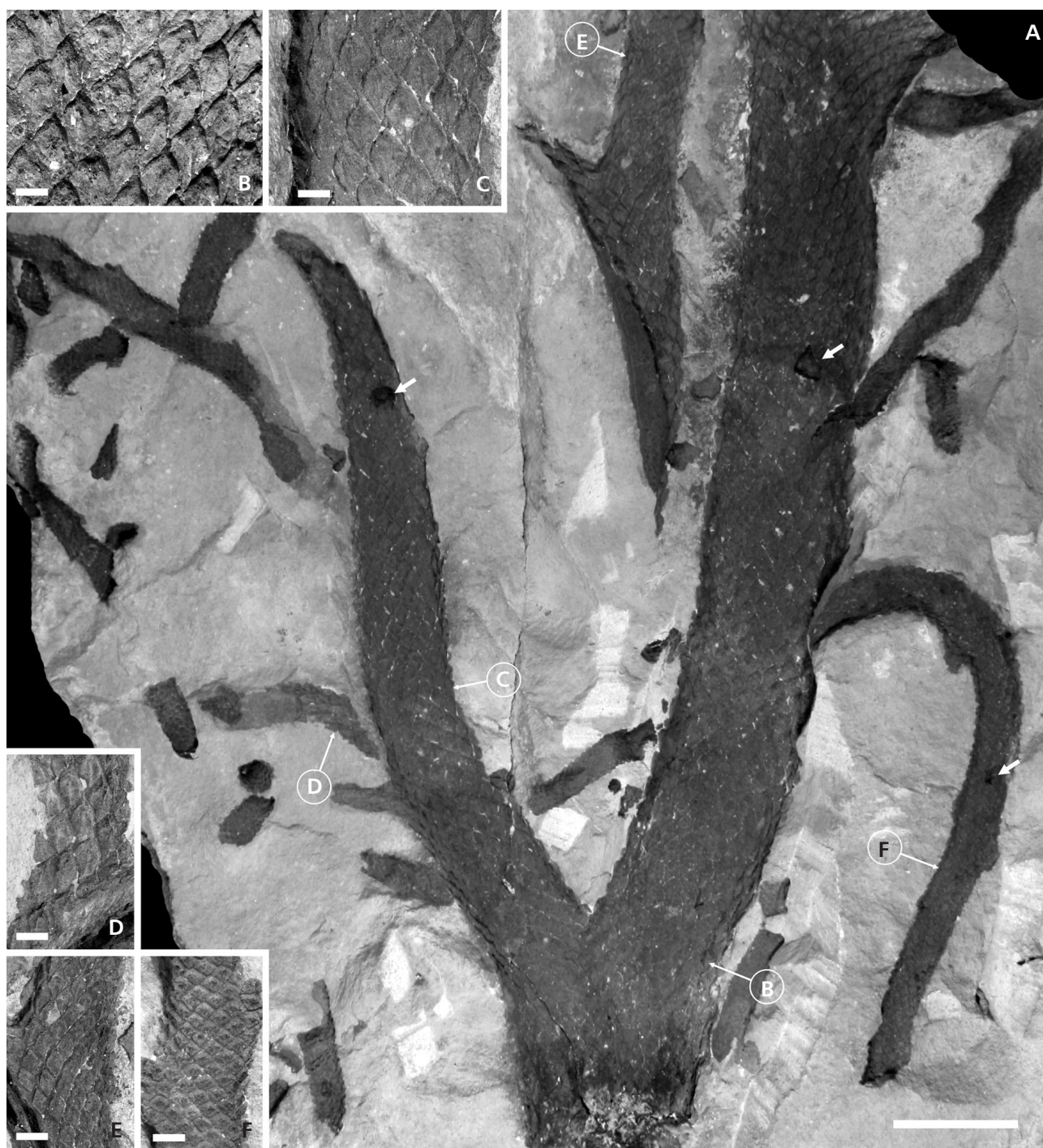
**Figure 2.** A – detail of the apex of the Specimen No. 6857. Scale bar 20 mm. • B – detail of leaf cushion near the apex. For precise position see the Fig. 2A. Scale bar 5 mm. • C – detail of lateral view of leaf cushions with leaves from the Fig. 2A. Note the infrafoliar parichnos imprints and character of connection of leaves to the cushions. For position see the indication in Fig. 2A. Scale bar 5 mm. • D – lateral view of leaf cushions with attached leaves. For location see Fig. 2A. Scale bar 5 mm.

laterally positioned leaf cushions are inserted at an angle of about  $70\text{--}75^\circ$  to the stem axis, however, near the apex this angle starts to rapidly decrease so the leaves at the apex are parallel to the stem axis. This change in leaf orientation is indicated also by direction of leaf cushions located along the margins of compressed stem (Fig. 2A) and leaf bases, which follow the same pattern of orientation. The leaf

bases are clearly separated from the leaf cushions by a straight narrow line (Fig. 2B, C). Leaves on the opposite side of the stem were folded during burial. Therefore they are directed downward and are preserved and partly exposed in a plane few millimetres beneath the stem.

The remaining four specimens represent mature ontogenetic stages of the same species. Specimen E 5734 is



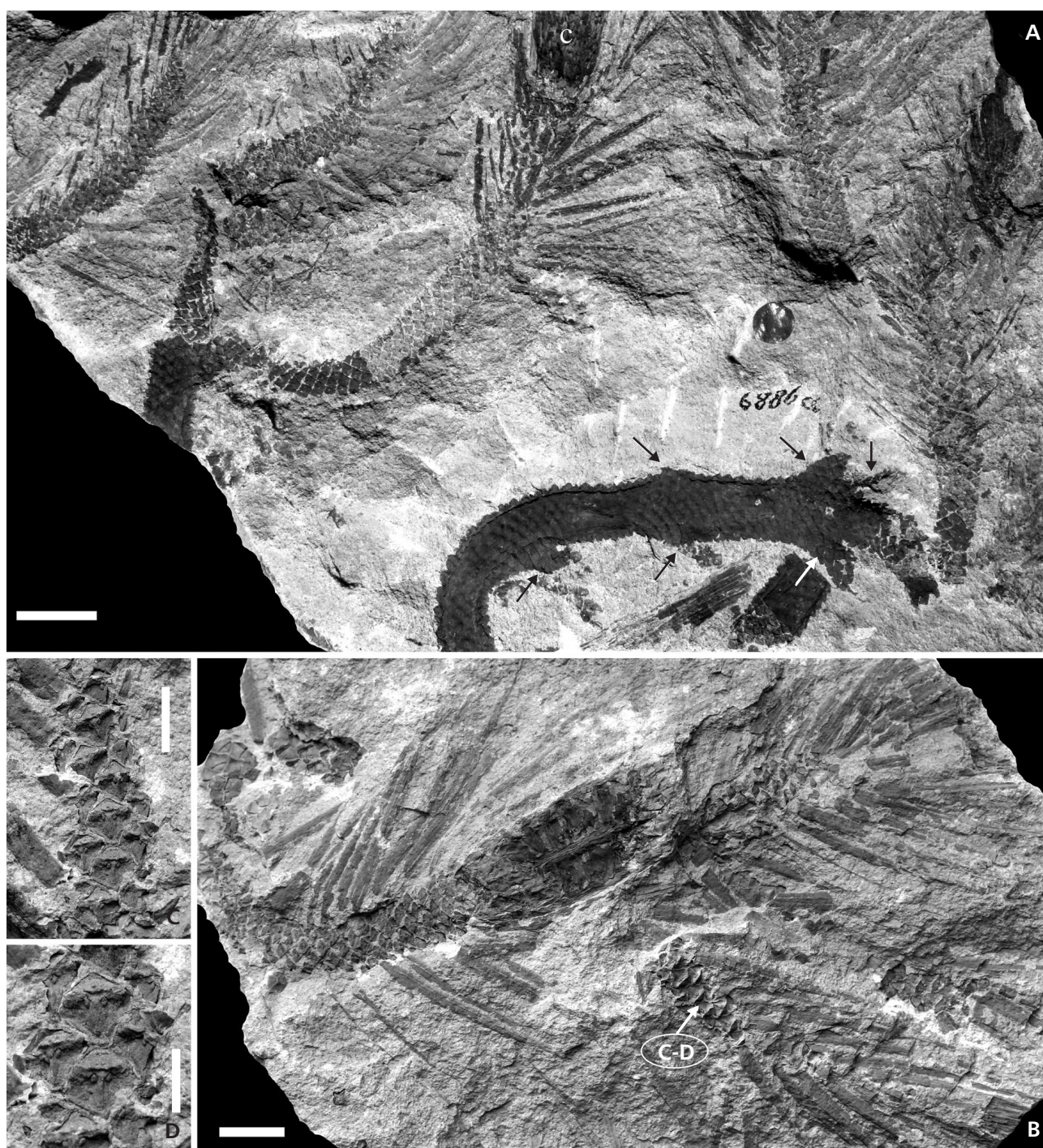


**Figure 3.** A – the specimen E 5734 (National Museum in Prague). Short thicker arrows without an encircled letter point to hollow left by branch protruding into the rock. Scale bar 50 mm. • B–F – details of leaf cushions from various parts of the specimen. For location see the letters with arrows pointing to the position of detailed pictures on a Fig. 3A. All scale bars are 5 mm.

a rectangular slab about 500 mm long that preserves the impression of part of a branch system (Fig. 3A) of about middle crown. It exhibits two types of branching, dichotomous and pseudomonopodial. In the lower part of the slab, a branch about 72 mm wide is divided by slightly

anisotomous dichotomy into branches of 56 and 40 mm in diameter. These two forks diverge at an angle of  $55^\circ$ . The thicker of them probably bifurcates again about 420 mm above the previous dichotomy as indicated by an apparent increase in diameter of the branch at the slab margin and by



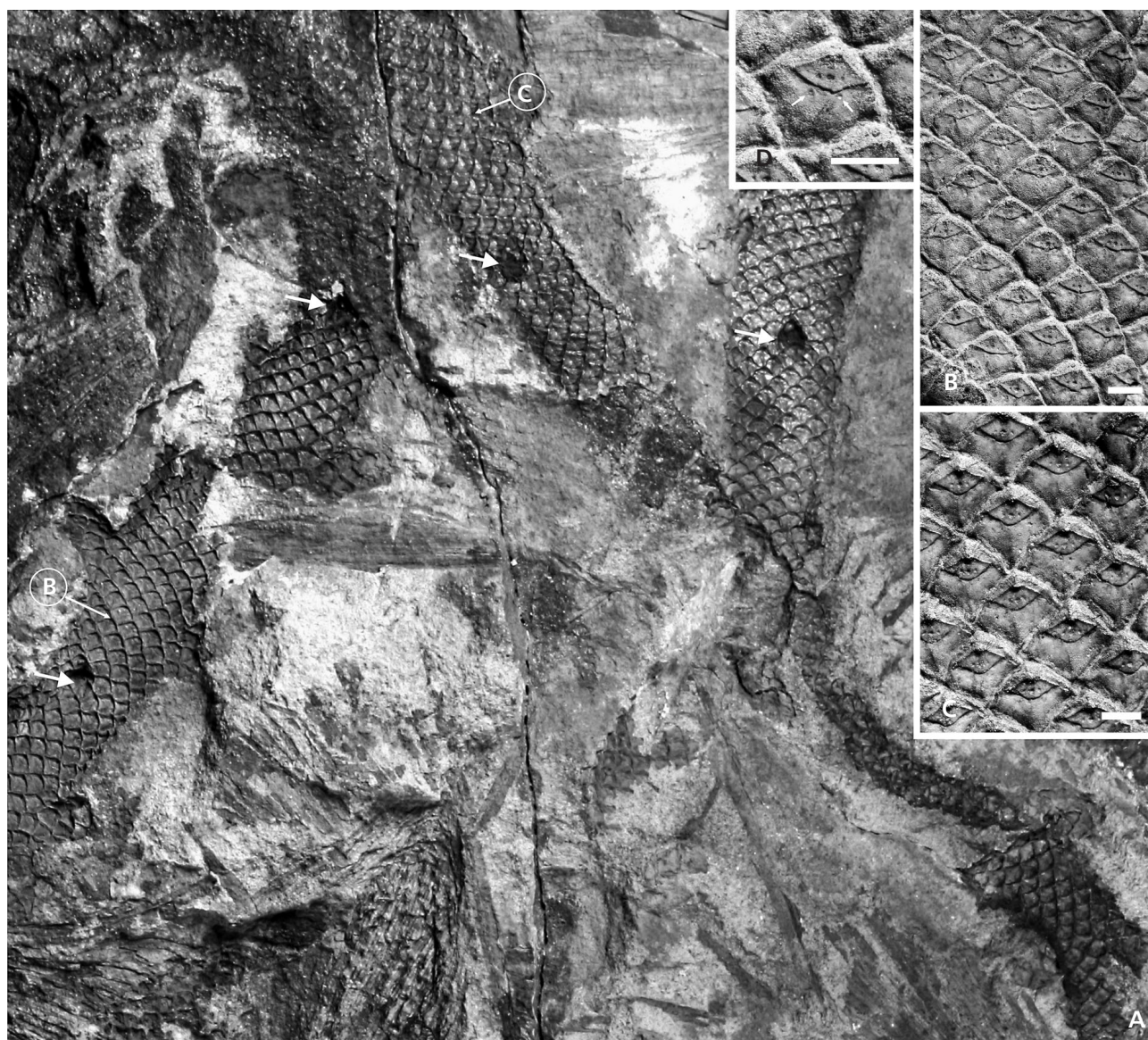


**Figure 4.** A – the specimen No. 6886 (Geologische Bundesanstalt Museum, Vienna) showing leafy shoots one of them terminated with cone (c). Note the leaves are only preserved near the apex. Arrows indicate position of branching. Scale bar 20 mm. • B – leafy shoot terminated with cone. The specimen F 233 (West Bohemian Museum in Pilsen). Scale bar 10 mm. • C – detail of leafy shoot from the specimen in the Fig. 4B. Scale bar 5 mm. • D – detail of leaf cushions from shoot in Fig. 4C. Scale bar 3 mm.

the change in direction of the leaf cushions. Both these, which were part of the dichotomizing “crown” branches, bear several smaller isotomous lateral branches (Fig. 3A). These lateral branches attain only about 25–40% of the thickness of the main branch, which they depart at angles

as high as 60° and 65°. However, with increasing distance from their point of forking they bend downward (Fig. 3A). Neighbouring branches are about 30–70 mm apart and they seem to be randomly arranged. Hollows in the both main dichotomies (Fig. 3A) indicate branches protruding into





**Figure 5.** A – the specimen E 4745 (National Museum in Prague). Impression of terminal and near-terminal shoots and branches. Arrows without encircled letters point to hollows left by pseudomonopodial branch bases pointing to the rock. Scale bar 10 mm. • B, C – detail of leaf cushions from the specimen E 4745. Infrafoliar parichnos imprints are absent probably as a result of preservation. For location see Fig. 5A. Scale bar 5 mm. • D – detail of leaf cushion from Fig. 3B showing infrafoliar parichnos (indicated by arrows). Scale bar 5 mm.

the rock since this specimen is an impression, whereas on compression it would be slightly raised thus resembling tubercles of *Halongia* branches. Although these pseudomonopodially borne branches are only between 14 and 19 mm thick they display another order of branching. However, these second order pseudomonopodial branches are all broken and only bases, not longer than 1 cm, are preserved (Fig. 3A, F). However, remains of these second order branches are not present with the rest of the remains, as might be expected if they were broken off during burial of the branch. These bases, about 10 to 12 mm thick, may be located at any point on the circumference of the branches;

those along the margins are in a slightly alternating position perhaps indicating a helical arrangement. Neighbouring branches within a helix are about 50–70 mm apart. Although only branch bases are preserved, the angles at which these branches depart are comparable with angles between larger branches. All branches in this slab are leafless but they display leaf cushions. The size of the leaf cushions is approximately the same between branches but decreases as stem diameter shrinks acropetally (Fig. 3B–F). The apparent absence of leaves, even isolated in the rock, may indicate that this branch system represents the rather older part of the canopy, from which leaves had

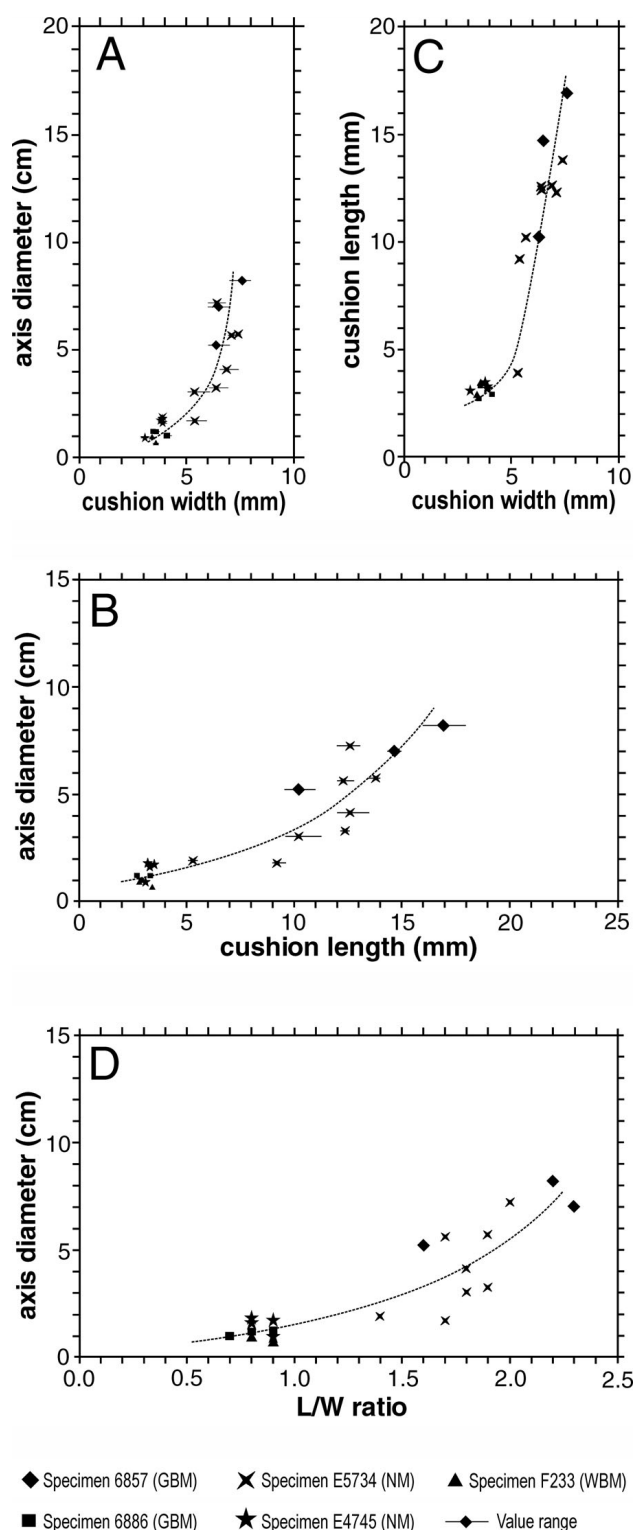


abscised already before volcanic ash fall. There is no sudden change in size and shape of leaf cushions below and above dichotomies. Instead it is more gradual over distance of several tens of centimetres. However, this contrast exists between thick branches and much thinner pseudomonopodial branches they bear. Leaf cushions of the pseudomonopodial branches are apparently smaller and shorter (Figs 3, 6).

Specimens No. 6886, F 233 and E 4745 preserve terminal leafy shoots, some showing isotomous and/or anisotomous branching. Specimen No. 6886 displays anisotomously branched shoots (Fig. 4A), which are 14 to 16 mm wide, one of them curved arch-like. This axis branches pseudomonopodially, the lateral shoots borne about 35 mm apart. Both branch and shoot bases are leafless. Another of the shoot fragments is about 6 cm long and 13 mm wide and bears arch-like bent lateral shoot that terminates with a cone at the tip. This terminal shoot is 10–12 mm wide and about 130 mm long (without cone) bearing leaves for about 40 mm below the cone. There are at least five more or less complete isolated remains of terminal shoots partly clothed in leaves, of similar diameter to the one in organic connection to the parent branch. Some of these shoots have preserved apices with leaves. The part of shoot with leaves can be up to 65 mm long. Grass-like leaves of the terminal shoots are more than 55 mm long (estimated length is about 75 to 80 mm) and about 2.5 mm wide near the base from which they gradually taper to the apex. Leaf cushions of terminal shoots are wider than long; their length varies from 2.7 to 3.3 mm whereas width is between 3.5 and 4.1 mm (Fig. 4C).

Specimen F 233 preserves remains of about 6 terminal shoots (Fig. 4B). The largest one is a fragment, about 6 cm long, of an arch-like bent terminal shoot with a male cone at the tip and leaves near the apex. One of the other remains represents an apical part of terminal leafy shoot only 6 mm in diameter. Leaf cushions of these terminal branches are between 2.7 and 3.5 mm long and from 3.1 to 3.7 mm wide (Fig. 4C, D). The male cone of *L. mannebachense* is *Lepidostrobus obovatus*, which produced *Lycospora loganii* microspores (Bek & Opluštil 2004). These cones are often found in organic connection with the leafy shoot of the parent plant, *L. mannebachense* whereas female cones are unknown.

Specimen E 4745 bears fragments of several shoots of two different diameters (Fig. 5). The thicker shoots are leafless, about 16–18 mm in diameter. They bear bases of thinner pseudomonopodial branches. These branch bases correspond in diameter to thinner leafy terminal shoots scattered on the slab surface. Leaf cushions are of diamond shape between 3.2 and 3.5 mm long and from 3.8 to 3.9 mm wide (Fig. 5B, C). Most of them have poorly preserved infrafoliar parichnos markings, although these can be identified on some cushions (Fig. 5D).



**Figure 6.** Relationship between axis diameter and various leaf cushion parameters as measured at the specimens described herein. For thorough explanation see the text. • A – relationship between axis diameter and leaf cushion width. • B – relationship between axis diameter and leaf cushions length. • C – relationship between leaf cushions width and length. • D – relationship between axis diameter and leaf cushion L/W (length/width) ratio.



All of the specimens in the studied collections and identified as *L. mannebachense* do not display ulodendroid branch scars.

## Discussion

Specimen No. 6857 most likely represents the apical part of the stem of *Lepidodendron mannebachense* before it reached the first branching otherwise the specimen would be slightly curved and/or dichotomously divided or shows densely spaced pseudomonopodially-born branches, as seen in other specimens described herein. This interpretation is also indicated by the straight leafy axis, blunt apical termination, and insertion of leaves at the apex. In addition, leaf length in this specimen is much larger than that in specimens with smaller leaf cushions. Leaves of terminal leafy shoots are not longer than 100 mm (e.g. Němejc 1947; Bek & Opluštil 1998, 2004). Inter-cushion areas have never been observed on any specimen in the studied collections. This may indicate that *L. mannebachense* had probably a limited potential to accommodate stem thickening due to secondary growth by expansion of inter-cushion areas. As a result, these outer cortical tissues were probably soon sloughed off and only a narrow zone of primary cortex remained on the stem below the apex as in the case of this specimen. On the contrary, bark fragments of similar species *L. aculeatum* often display inter-cushion areas well developed, although Thomas & Watson (1976) observed closely spaced (!) leaf-cushion outlines 18 m above the base of 34.5 m long trunk of this species. Leary and Thomas (1989) described about 6 m long stem of *L. aculeatum*, which still bear leaves along whole length. This suggests existence of other mechanisms of leaf-cushion retention as in the case of *L. hickii* (a possible anatomically preserved equivalent of *L. aculeatum*) where there was extensive lateral expansion of cells in basal cushion parenchyma and periderm resulting in “stretching” not only of inter-areas but partly also of leaf cushions (DiMichele 1983).

The size of leaf cushions of *L. mannebachense* changed from the base to the top of tree. Observations of the specimens and their morphometric analysis proved that leaf cushions reduce in size, both length and width, as the thickness of the axis decreases. This is in agreement with Eggert (1961) who suggested that cushion dimensions reflect the size of meristem, which is reduced with each branching, especially with apical dichotomy. However, whereas the length of leaf cushions significantly decreases with reduced axis diameter, changes in width are much less ap-

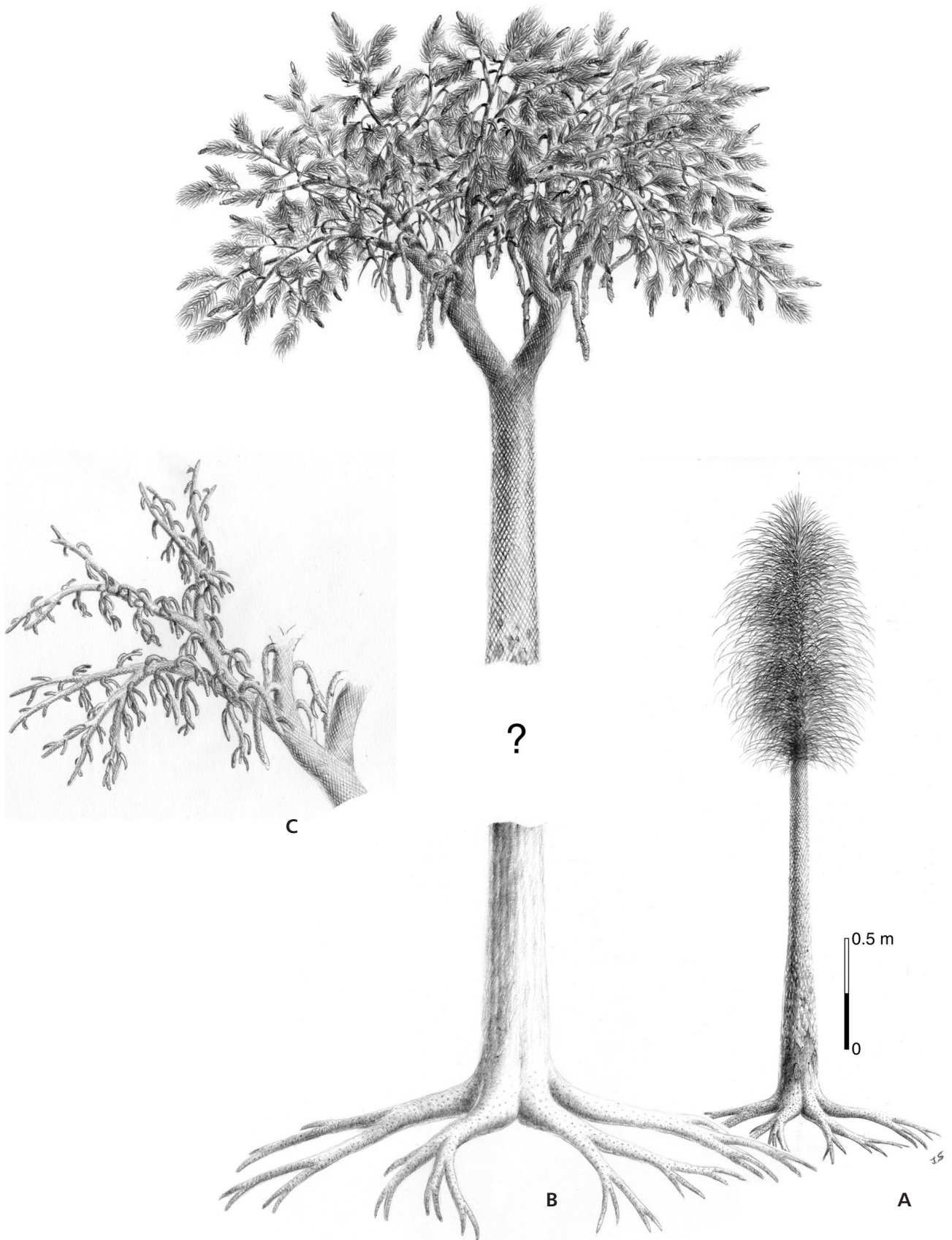
parent (Fig. 6A, B). The length of the leaf cushions of the described specimens varies from 2.7 to 18 mm (Fig. 6B). The largest leaf cushions known to the author has one of Thomas (1970) specimens (plate 32, fig. 2) the length of which is about 22 mm. Since primary cortical tissues form the leaf cushions their length is permanently fixed once the primary tissues matured (Eggert 1961, Wnuk 1986). The length of leaf cushions therefore reflects the size of the cushions at the time of their formation (Wnuk 1986). Reduction of length also was observed just below the dichotomy preserved on specimen E 5734. This reduction is explained as a response to decrease in growth rate of the apical meristem prior to dichotomy (Wnuk 1986). The width of the cushions decreases from maximum values of about 9 mm to minimum width on terminal shoots of about 3.1 mm (Fig. 6C). The consequence of more rapid decrease of cushion length than of width is that leaf cushions of terminal shoots, i.e. usually those less than 15 mm in diameter, are wider than long (Fig. 6D).

Branching observed on the study specimens clearly show two types of patterns. The basic pattern concerns main branches produced by isotomous to slightly anisotomous dichotomies that built the base of determinate crown. These “main” branches bear smaller pseudomonopodial and strongly anisotomous lateral branches densely located at any point on the circumference only several centimeters apart. These branches, in turn, bear even smaller second order pseudomonopodial branches some of them terminated by cones. Unfortunately, the material is too fragmentary to estimate the rate between leafy and cone-bearing branches.

Combination of these two branching patterns suggests that the stem started to split by apical dichotomy and this branching pattern continued throughout the whole canopy until a determinate growth limit was reached. The average number of dichotomies is difficult to estimate because material is fragmentary; nevertheless, specimen E 5734 (Fig. 3) shows that dichotomies could be quite frequent about half a meter apart or even less. This branching pattern is in agreement with absence of ulodendroid scars typical for arborescent lycopsids where canopy is formed by pseudomonopodial branching (e.g. DiMichele & Phillips 1994). It is therefore suggested that *L. mannebachense* had an umbrella-like character as proposed already by Hirmer (1927, fig. 200). Apart from Hirmer’s reconstruction, however, branches resulting from these dichotomies bear anisotomous lateral branches, which, subsequently produce another order of thinner lateral branches representing terminal shoots, some of them bearing cones at least. These second-order lateral branches are very often

**Figure 7.** The whole plant reconstruction of *Lepidodendron mannebachense*. • A – juvenile unbranched stem with leafy upper part of stem. • B – matured stage showing crown built of combination of dichotomous and pseudomonopodial branching. • C – detail of a branch of matured tree. Leaves are omitted. Drawn by J. Svoboda.







preserved only as branch bases resembling tubercles of *Halonia* which also represent bases of small lateral branches on major *Lepidophloios* branches (e.g. Weiss 1903). Common presence of leaf bases suggests that they were shed during the life of the tree when they lost their leaves and were themselves shed, probably as the cones, they bore, matured. We can speculate that most of the photosynthate sugars supplied local tissues growth and development since lepidodendrid lycopsids had a very limited phloem system to transport photosynthates around (e.g. DiMichele 1983, Phillips & DiMichele 1992). Once local tissues matured, the leaves were no longer needed. These small cone-bearing lateral branch systems of *Lepidodendron mannebachense* are similar in function to lateral branches of continuously reproducing arborescent lycopsids like *Diaphorodendron* and *Paralycopodites* which Bateman & DiMichele (1991) and Bateman (1994) considered as to be the homologues of cone peduncles in those lycopsids with short pedunculate attachments bearing a single cones (e.g. *Lepidophloios* and *Sigillaria*). The lateral cone-bearing branch system of *L. mannebachense* is in architecture closer to those of *Diaphorodendron* and *Paralycopodites* whereas *Lepidophloios* and *Sigillaria* represent the most reduced state.

Shortening of leaves with each subsequent branching is also evident from the specimens described here. This is consistent with reduction of leaf cushions in a similar way throughout the crown of the plant and in different taxa due to reduction of meristem size after each branching (Eggert 1961; DiMichele 1979a, b, 1981). Absence of leaves at most branches except for the terminal shoots indicates that leaves had a short functional life span and were abscised early. This is in agreement with the author's observations of many specimens of this species, which are mostly preserved as leafless bark compressions/impressions.

Unfortunately, the specimens described herein are insufficient for estimation of the height of the mature tree. Although Niklas (1984) derived formulae for estimation of the height of plants of various growth forms, the basic parameter, the diameter at breast height is not known. Moreover, except specimen No. 6857 preserving apical part of the juvenile stem, there is no other specimen known to the present author, which preserves clearly both sides of the stem to calculate the height of the plant. Surprisingly, the widest but still incomplete stem fragment ever observed in the collection is only about 100 mm wide, which is much less than the similar species, *Lepidodendron aculeatum*, where stem fragments are commonly more than 200 mm wide (max. more than 500 mm, Libertín *et al.* 2009b). This disproportion suggests that either *L. mannebachense* was smaller tree than *L. aculeatum* (probably about 15–20 m tall if the diameter was about 15–20 cm) thus producing smaller bark fragments or that its stem decorticated in smaller pieces than that of *L. aculeatum*. We can speculate

that *L. mannebachense* could decorticate more easily comparing to *L. aculeatum* as indicated by absence of evidence of inter-cushion area development in former species.

## Restoration of ontogenetic development of *L. mannebachense*

The development of aerial part of *L. mannebachense* most probably followed the pattern of other lepidodendrid lycopsids (Andrews & Murdy 1958, Eggert 1961, Phillips & DiMichele 1992). It started as unbranched tall columnar stem before branching occurred.

This unbranched stage of development was probably a period of rapid growth (e.g. Wnuk 1986, Phillips & DiMichele 1992). It is suggested here that the canopy was established and then elaborated by means of apical dichotomies. These dichotomies continued till the determinate limit was reached. For *L. mannebachense* the width of the apical part of terminal shoots is about 6 to 10 mm. It is assumed that this species had an umbrella-like canopy as suggested by Hirmer (1927). However, most of the terminal shoots were thin cone-bearing lateral branches produced by anisotomous pseudomonopodial branching of two orders (Fig. 7). Although these lateral branch systems occur throughout the tree crown, this final (apoxogenic) phase of tree development represents relatively short period of time when reproduction occurred. *L. mannebachense* thus can be considered as a monocarpic plant with reproduction at the end of its life cycle comparing to lycopsids with deciduous lateral branch systems produced up the stem with much more extended period of reproduction, lasting much of the life of the aerial part of the plant.

Leaves of *L. mannebachense* were longest on the main unbranched stem, and their length decreased as branch diameter and leaf-cushion size reduced with each dichotomy. This mode of development is characteristic not only of this species but also for other lepidodendrid species (Lindley & Hutton 1833, 1835; Hirmer 1927; Andrews 1961; Eggert 1961; Wnuk 1985). Leaf functional life span was probably quite short after which leaves were shed from stems or branches leaving a characteristic scar. Consequently, only zone with leaves was maintained on the plant in any developmental stage. However, it is currently impossible to specify the width of this zone from specimens available. Leary & Thomas (1989) observed attached leaves along about 6 m long remain of the main stem of similar but probably a larger species *L. aculeatum*. At the final stage of its life cycle, leaves were retained only on terminal branches or even their apical parts. Primary cortical tissues have no potential to compensate stem/branch thickening produced by secondary growth. Leaf cushions therefore, were probably sloughed off quite soon and persisted on a stem only in a zone near the current apex. A similar growth pattern,

with determinate umbrella-like canopy, as proposed here for *L. mannebachense* is characteristic of all monocarpic forms of lepidodendrid lycopsids (see Phillips & DiMichele 1992 or DiMichele & Phillips 1994 for an overview). *L. mannebachense* is a representative of the genus *Lepidodendron* in the sense of DiMichele (1979b, 1981, 1983) who segregated *Lepidodendron* “sensu stricto” based on stem anatomy linked to certain leaf cushion attributes (especially infrafoliar parichnos), from the original concept of Sternberg relying only on leaf cushion shape.

## Acknowledgement

This contribution to Carboniferous palaeobotany was supported by the project MSM 0021620855 of the Faculty of Science, Charles University in Prague, which allowed the author to visit and study the specimen in the collection of the Geologische Bundesanstalt Museum in Vienna, Austria. The author is also very grateful to B. Meller, a curator of the palaeobotanical collection in this institution for providing access to specimens No. 6857 and No. 6886. M. Libertín (National Museum in Prague) and J. Pšenička (West Bohemian Museum in Pilsen) are thanked for making accessible the specimens E 5734, E 4745 and F 233, respectively, for detailed study. The paper benefited significantly from thorough and constructive review of B.A. Thomas (Aberystwyth University, UK) and W.A. DiMichele (Smithsonian Institution, Washington, USA) who also provided a language correction of the manuscript. J. Svoboda is thanked for drawing of the Figure 7.

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