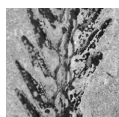


The epiphytic plants in the fossil record and its example from *in situ* tuff from Pennsylvanian of Radnice Basin (Czech Republic)

JOSEF PŠENIČKA & STANISLAV OPLUŠTIL



Recognizing true epiphytes in the fossil record is still a major problem for palaeobotanists. Many indirect examples of evidence of epiphytic plants were previously published in palaeobotanical papers, especially from Pennsylvanian and Cenozoic times. Due to the special life strategy of epiphytes, which depends on presence of other plants for growth (so-called phorophytes), their preservation in the fossil record depends on the taphonomy of these phorophytes. Generally, the main factors for preservation of epiphytes are the type of environment in which the phorophyte grew, the habit-type of the epiphyte, the position of the epiphytes on the phorophyte, and the rapidity of burial. The ideal facies for preservation of epiphytes are *in situ* volcanic ash-fall deposits where plants were very quickly buried in the original place of growth. Vegetation buried in such deposits represents a single T⁰ horizon that reveals the spatial distribution of plants including potential epiphytes. Examples of two such plants are described in this paper from middle Moscovian ash-fall deposits in the Radnice Basin (Czech Republic). Both are *Selaginella*-like plants, which are informally named *Selaginella* sp. 1 and *Selaginella* sp. 2. *Selaginella* sp. 1 is interpreted as an epiphyte that probably grew in the leafy distal parts of the tree-top branches of arborescent lycopsids. *Selaginella* sp. 2 probably represents an epiphyte that grew on the trunks of the arborescent gymnosperm *Cordaites borassifolius* or the lycopsid *Lepidodendron* (*Paralycopodites*) *simile*. The interpretation is based on a set of subjective and/or indirect evidence. Direct evidence of epiphytes in the fossil record is still lacking. This paper documents for the first time herbaceous fossil lycopsids as epiphytes, as well as epiphytes described from three-dimensional compression material. • Key words: *Selaginella*, Carboniferous, palaeoecology, tuff, taphonomy.

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What are epiphytes and their forms?

Epiphytic plants are an integral part of modern forests and were very likely equally important in Earth's first forests (Benzing 1990). The epiphytic plants are generally defined as non-parasitic plants that grow upon another plant (phorophyte) for support only (Chrtek *et al.* 1988). Extant epiphytes are mostly monocots, which occur mainly in tropical rain forests. Segregation of epiphytes has been made on many parameters. Based on their habit and size it is possible to distinguish two basic forms: 1) microphytic (non vascular) such as lichens, moss, fungi; and 2) macrophytic (vascular) forms such as ferns, orchids, cacti, bromeliads and others. Both habit-types have been also interpreted from the paleontological record (see below). Another classification of epiphytes arises from their tolerance to drought upon which vascular epiphytes are divided into three categories: 1) hygrophytes

which are drought intolerant, 2) mesophytes which grow in places where water is easily available and 3) xerophytes which are able endure drought (Benzing 1990). The first two types could be found in the palaeontological record but the xerophyte type (typical for arid or semiarid climates) could be difficult to find as fossils because of the unacceptable conditions of the surroundings for fossilization.

Adaptation of plants to epiphytic life strategy

Nutrients and moisture gain epiphytes from the surrounding air or from debris that accumulate around epiphyte on the phorophyte (Benzing 1990). One of the major reasons for this life strategy is to achieve more insolation, thereby improving photosynthesis. Epiphytic plants often use the

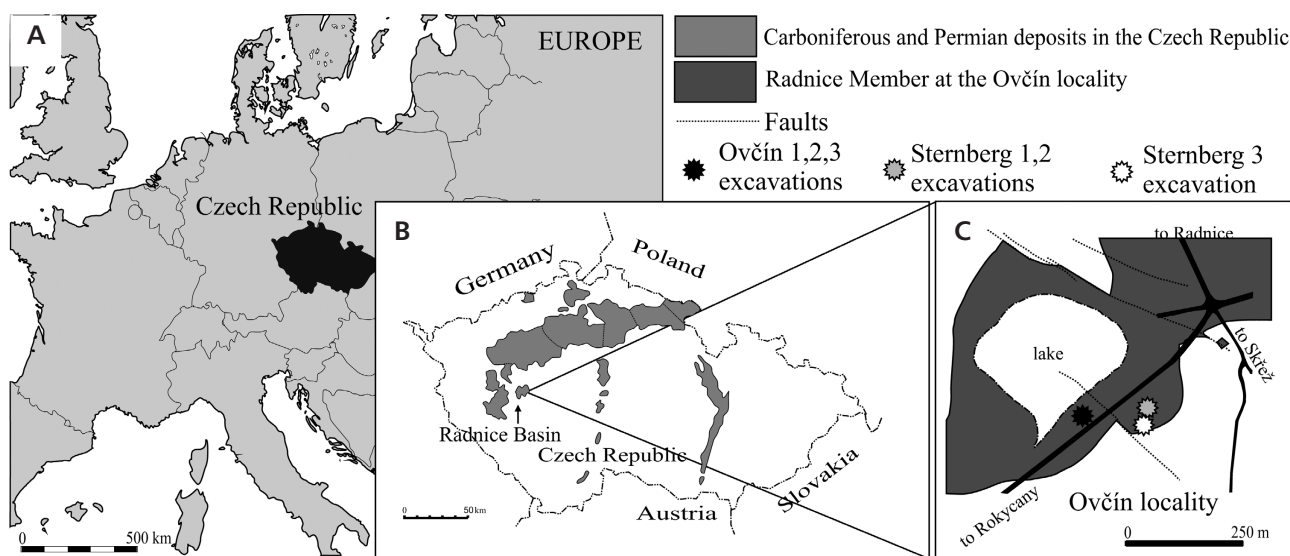


Figure 1. Schematic maps of the study area. • A – position of the Czech Republic in the Europe. • B – Late Paleozoic continental basins in Czech Republic and position of Radnice Basin. • C – position of the excavations at the Ovčín locality.

tallest plants of a forest to achieve this effect. Another reason for this life strategy is if the substrate conditions are poor, such as being waterlogged, providing unacceptable levels of nutrients.

For vascular plants epiphytic strategy requires special adaptations, including determinate tendrils produced by a variety of modified and/or special organs (often foliar) for retaining water or nutrients, and adventitious root adhesion. All these adaptations could be observed in fossilized plants (petrified as well as compression/impression) but this cannot lead to unequivocal affiliation to epiphytes because the same adaptations occur in climbing plants (Burnham 2009). Therefore, due to the fragmentary nature of fossil plant records, epiphytic plants cannot be clearly separated from climbing or scrambling plants based on morphology/anatomy evidence alone. However, the major problem seems to be non-parasitic clause in the definition, which makes identification of epiphytic plants in fossil record even more complicated. Identification of true epiphyte requires identification of parasite tissue grows into the host and forms a connection with the vascular system of the phorophyte (Khan *et al.* 2009, Těšitel *et al.* 2010). This is, however, possible only in case of permineralized plant fossils where is a chance to find structures that are typical for parasitic plants whereas for compression/impression type of preservation this task seems to be impossible to be solved.

Recognizing epiphytes in the fossil record (taphonomy, depositional)

The evidence for existence of epiphytic plants in geological history is still very poor, because the fossil plant remains are

usually found as a mixture of fragments of original plants, which resulted from a wide range of different taphonomic processes (Gastaldo 1988). Specific live strategy of epiphytes (they grew on another plant), rather than any particular morphological or anatomical features makes their identification difficult. True epiphytes can be clearly identified based on organic connection to phorophyte only.

According to the definition of epiphytic plants, identifying this growth habit in the fossil record remains a major problem, especially for vascular types. The condition that they must be non-parasitic arises the question whether we are able to recognize the parasitism in the fossil record? Living parasitic plants have tissue that grows into the host and forms a connection with the vascular system (Khan *et al.* 2009, Těšitel *et al.* 2010). This could possibly be identified only when we have anatomically preserved plants. Anatomically preserved potential epiphytic plants were described by Mamay (1952), Rothwell (1991), Rößler (2000) and Schneider & Kenrick (2001), since they did not note any connection between the vascular systems of the small plants and the arborescent host.

From previously paragraph results that the type of fossil preservation is an important factor, which affects the type of information that can be gained from fossils (*e.g.* Walton 1936 or Rex & Chaloner 1983). Galtier (1986) distinguished two major types: 1) compressions and 2) permineralizations and summarized type of information which can be obtained from them. Compressions bring information about morphology or external anatomy (like epidermis, hairs, spines or cushions) but very little information about internal anatomy (Galtier 1986). In contrast, permineralized material clearly shows information about internal anatomy but only very poor information about

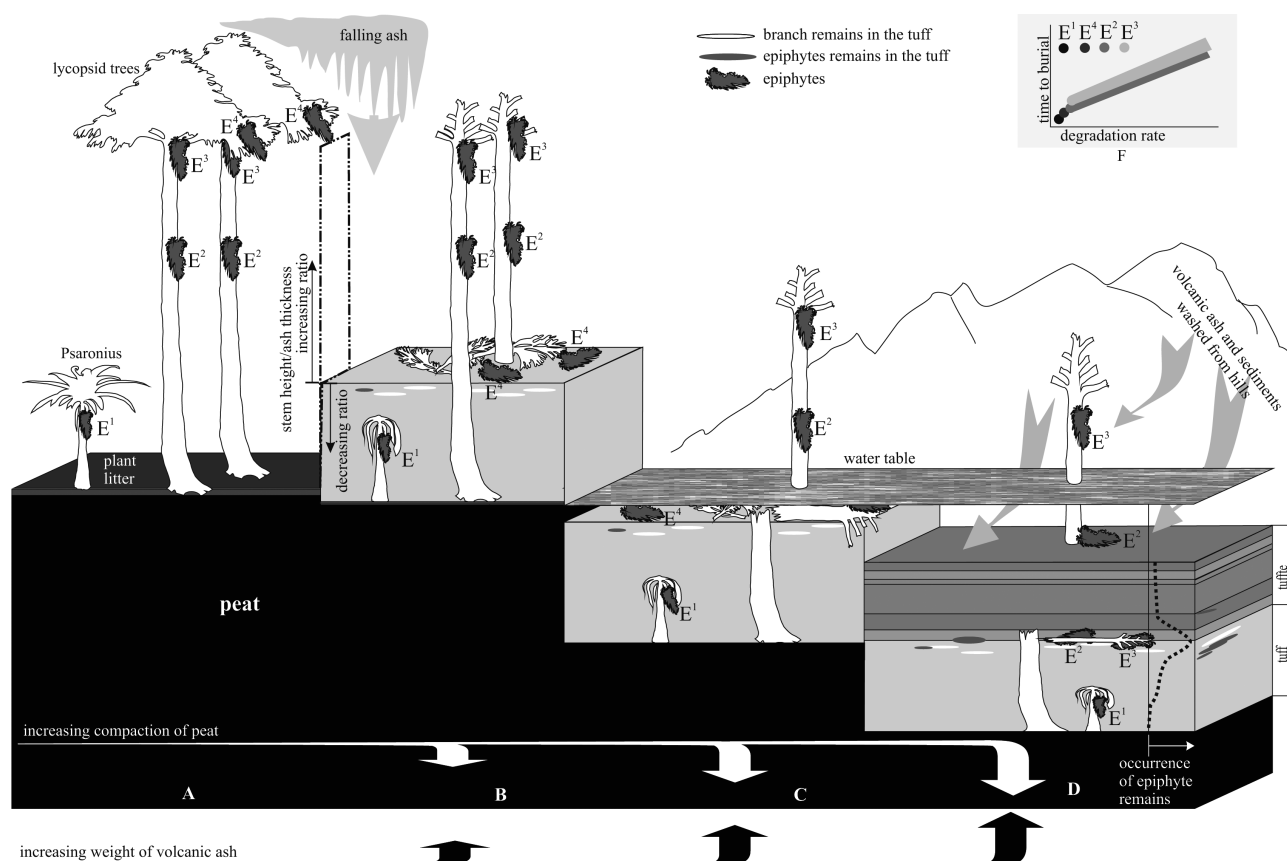


Figure 2. Taphonomic process during the volcanic ash-fall. • A – original forest with two representative tree plants – small *Psaronius* and high lycopsid tree. • B – the plants are heavily damaged by volcanic ash load. Ground cover plants are completely buried while trees protruded from tuff unit. The branches of trees have been broken off. • C – the groundwater level raised up due to a peat compaction. Some protruding trees fell to the ground, *i.e.* at the top of tuff bed, and some trees stay in upright position protruding from water. • D – the *in situ* tuff is in a short time overlain by several meters of redeposited volcaniclastics with siliciclastic admixture. The remaining upright tree trunks exhibit a high level of decomposition. They tend to fall in the water very soon. The dash line curve of a graph on right side of unit represents hypothetical occurrence of epiphytes in fossil record in the tuff bed. • E¹ – epiphyte growing on stem or base of the frond rachis of lower trees, E² – epiphyte growing on stems, E³ – epiphyte growing on branching part of trees, E⁴ – epiphyte growing on the end parts of branches. • F – the schema of individual types of epiphytes and their degradation during the time (based on data presented in this paper).

morphology or external anatomy (Galtier 1986). The type of preservation depends on conditions how and where the plants were entombed. Sometimes it is possible to observe transitions between the two types of preservation as in the case of plant remains preserved in volcanoclastics. Burial in volcanic ash enhances three-dimensional preservation of plant remains with morphology and some internal anatomy (especially xylem band) being preserved (Rößler & Barthel 1998, Pšenička *et al.* 2005, Pšenička & Schultka 2009, Pšenička & Bek 2009).

Another potential type of preservation where true epiphytes can be found is in fossil resin such as amber, however, because of the small size of most amber specimens, only fragments have been documented (Gomez 1982).

Plant versus Phorophyte Context: The important fact is that epiphytes have dependence on phorophytes. The epiphytes could be placed on different parts of the phorophyte such as the branches (Fig. 2, epiphyte E³), the base of

a frond rachis (Fig. 2, epiphyte E¹), or sometimes the terminal part of branches (Fig. 2, epiphyte E⁴) and stems (Fig. 2, epiphyte E²). This dependence plays an important role in the taphonomical processes. True epiphytic plants start to become fossilized when the phorophyte necrotizes and falls down. So long as the phorophyte stays in an upright position, the epiphytes could continue to grow on the phorophyte even though it is dead. Generally, the function of the phorophyte is support only, which means that the epiphyte will continue growing so long as the phorophyte remains functional, *i.e.* it is still standing.

Another factor for preservation of epiphytes is the tissue-type of phorophyte, in particular its solidity. In recent nature, angiosperms with solid wood form the most common phorophytes for epiphytes. Angiosperms are very stable phorophytes providing epiphytes with sound support. In geological history other plant groups have also been phorophytes, such as tree ferns, arborescent lycosids,

calamitaleans, pteridosperms and gymnosperms. Some of them (*e.g.* gymnosperms) have created a solid support for epiphytes. However, there is only a slim chance for epiphytes growing on these plants to get into the fossil record because such solid phorophytes could stay upright for a very long time after death. This fact also resulted in situations where epiphytes could continue to grow on a phorophyte even when the phorophyte was dead. Epiphytes fall on the ground when the protruding part of phorophyte falls down due to decay or/and physical (*e.g.* wind, falling-down other trees) destruction. Unfortunately, the organic connection between the phorophyte stem and epiphyte is fragile and could be often destroyed when falling down. In some case the epiphytes could necrotize and decay directly on this type of phorophyte. Contrariwise, those types of plant with more or less fragile stems (*e.g.* tree ferns or calamitaleans) would cause any epiphytes growing on them to become much easily a part of the litter. The solidity of individual plants depends on tissue-composition. According to Phillips & DiMichele (1992) the stems of some types of arborescent lycopods and calamitaleans have a resistant ring of woody or sclerenchymatous tissue surrounding a hollow central area formed by decay of parenchymatous tissue shortly after death. In this case a stem become fragile. It means that trees very probably broken with still living epiphytes growing on this type of phorophyte and could get into the sediment relatively fast. Tree-ferns and pteridosperms have stems composed of a complex mixture of tissue types, which led to rapid decay and consecutive destruction of the stem (Baker & DiMichele 1997, DiMichele & Falcon-Lang 2011). The plant remains could be conserved very quickly by sediment or permineralized by minerals. In this case the epiphytes would be destroyed together with their phorophyte and so there is a chance to find them together in the fossil record. An example of this could be the petrified aerial roots of *Psaronius*-plant found associated with potential epiphytes (Mamay 1952, Rothwell 1991, Rößler 2000).

Depositional environment context: Generally, preservation is strongly influenced by sedimentary conditions in which plant remains are transported and buried, *i.e.* by sedimentary context. The most important aspects affecting the preservation include (1) sedimentary environment; (2) the rapidity of deposition; and (3) the chemistry of the accumulated material (covering material must not be chemically or thermally aggressive).

Many environments, especially alluvial, aeolian or glacial ones, are not generally suitable for the preservation of any fossils, let alone fossil of epiphytes. Lacustrine facies are also not usually suitable for the good preservation of plants due to very slow sedimentation rate resulting in decay of plant remains by microbial activity and/or wave action. On the opposite, environments with fast accumulation of sediments are potential sites where vegetation can be

buried *in situ* fast enough to preserve not only morphology but also life forms including the epiphytic one. This is especially the case of so-called T⁰ horizons, which preserve T⁰ plant assemblages (Gastaldo *et al.* 1995, 2004, 2006; Jonson 2007; DiMichele & Gastaldo 2008; Opluštil *et al.* 2009a, 2009b) buried in a geological instant, *i.e.* virtually frozen in time. DiMichele & Falcon-Lang (2011) summarised the following typical environments and processes which generate T⁰ horizons: 1) some fluvial processes such as within-channel sedimentation, riparian crevasse splays, progradation of distributary lobes, and general sediment aggradation in low-lying areas of floodplains; 2) coastal flooding (associated with rapid eustatic sea-level rise or regional subsidence); and 3) volcanic ash-falls (sometimes associated with lava or pyroclastic flows).

Fluvial settings include variety of sedimentary processes, which generally result in transportation, fragmentation and mixing of plant remains of various habits and life forms. Nevertheless fluvial settings still represent potential places where it is possible to expect findings of true epiphytes although they have not been documented so far.

According to DiMichele & Falcon-Lang (2011) coastal flooding can result in rapid burial of vegetation. Although it is much slower comparing to volcanic ash-fall it often preserves upright *in situ* buried stems of various plants especially of lycopods, cordaitalean or calamitalean. As an example, Gastaldo *et al.* (2004) described Pennsylvanian standing stems buried in tidal rhythmites. Epiphytes that could stay on standing stems may get into litter after the physical destruction of their phorophyte. However, because the epiphytes would fall down together with the phorophyte, they are exposed to the effects of sea water and their organic connection could be broken. Therefore, this facie has variable potential for the preservation of epiphytes.

Volcanic ash-beds appear to have the best potential for preservation of identifiable remains of epiphytic plants (Fig. 2). This is because the simple burial history and extremely rapid deposition which usually make possible to distinguish the individual storeys (litter, understory, bush storey, tree storey, lianas, *etc.*). In addition plants are often less fragmented due to absence of transport and more or less three-dimensionally preserved (Opluštil *et al.* 2009a, b). The ratio between the thickness of ash-bed and the height of the plant is also an important factor for the condition of conservation of plant-habit as well as for ability to identify the forest storeys (Fig. 2). A lower ratio means that the whole plant body is entombed in volcanic ash (Fig. 2, *Psaronius* together with epiphyte E¹) and leads to a reliable reconstruction of the original plant-habit and storeys. This produces a great possibility to find epiphytic plants still organically attached to the phorophyte (Fig. 2, epiphyte E¹) even in original growth position. When the ratio is high,

then the upper part of trees remains exposed above the ash-fall (Fig. 2B). Although some plants may still survive and continue in growth, resulting in the development of a post-eruption vegetation (Scott 1990), most plants are more or less damaged by volcanic ash load. Moreover, weight of ash increases compaction of the peat, which could raise groundwater level to open water table conditions (Fig. 2C). This, in turn can result in the total collapse of vegetation if the water depth is too high.

Preservation of epiphytes depends on their position on the phorophyte (Fig. 2). The greatest chance for epiphytes to be well preserved in the fossil record (in ash-falling facies) is where they were growing either on a relatively small phorophyte which both can be completely buried (even in organic connection) by volcanic ash (Fig. 2B, E¹). Similarly epiphytes attached to thin terminal branches (Fig. 2B, E⁴) can be buried during the volcanic ash fall, if the branches bearing epiphytes are broken due to a volcanic ash load. The epiphyte E² growing on stems has also a relatively high potential to be preserved in the fossil record being still attached to phorophyte (Fig. 2B, E²). It can be taken down either due to volcanic ash load or later during decortication of decaying tree torso. On the contrary, epiphyte E³ attached to thicker branches and partly E² have a relatively smaller chance for preservation in the fossil record (Fig. 2C, E³, Fig. 2C E²), due to their long subaerial exposure (Fig. 2C E², Fig. 2C, E³) or, when they are detached and fall down (Fig. 2C E^{2*}, Fig. 2C, E^{3*}), due to mechanical and chemical processes once they are involved into sedimentary environment. Epiphytes E² and E³ (Fig. 2D) could be found in sediments (usually a mixture of redeposited volcanoclastics and siliciclastics) above the tuff generated by ash fall. Their preservation depends on many factors: whether epiphyte was still alive or not on the rest of phorophyte, weather conditions, environmental chemistry and more.

An important factor in the preservation of plants in tuff is also the chemistry and temperature of former volcanic ash. High temperature can lead to all the vegetation being destroyed by burning and/or charred. Volcanic ash with an aggressive chemistry (for example too acid) can lead to the etching or destruction of some of the plant tissues.

The two examples published in this paper show the E² and E⁴ (see Fig. 2) types of epiphyte, whose reconstructions are based on many indirect lines of evidence.

Previous record of fossil epiphytes

Kress (1989) stated that epiphytes arose from the Pliocene-Pleistocene boundary while Schuettpelz (2007) presumed that a great expansion of epiphytic fern occurred at the K-T boundary, when angiosperm (potential good phorophytes) underwent rapid evolution. By contrast,

some authors (Rothwell 1991, Rößler 2000, Dubuisson *et al.* 2009) placed the origin of epiphytes at latest in the Carboniferous and pointed to the relatively considerable diversity (ferns epiphytes) in Pennsylvanian times.

Up to the present day supposedly fossil vascular and microphytic epiphytes have been described from permineralized material, notably from coal-balls (Mamay 1952, Rothwell 1991, Schneider & Kenrick 2001, Krings *et al.* 2010a) but also from petrified material in volcanoclastic deposits (Rößler 2000). On the contrary, vascular fossil epiphytes from compression/impression material have not to be described yet. Potential epiphytes from the transitional type of preservation (three-dimensional remains in tuffs) are described later in this paper, although possible parasitism cannot be excluded because internal anatomy is lacking or very poorly preserved.

We can be sure that fossil epiphyte remains will be generally mixed with fragments of plants with a variety of growth forms, making the recognition of plants with an epiphytic habit difficult to distinguish. According to Burnham (2009) it is nearly impossible to separate climbers from epiphytes in the palaeontological record and as a result, evidence of potential epiphytes is probably hidden among fossil remains that have been interpreted as climbers.

Extinct epiphytes are known from several groups such as fungi (Krings *et al.* 2010a, 2010b, 2011), lichens or mosses, as well as vascular plants such as ferns (Mamay 1952, Rothwell 1991, Schneider & Kenrick 2001, Gómez 1982), magnoliophytes (Benzing 1990), cycads and rarely from gnetophytes (Benzing 1990). Late Paleozoic epiphytes are known also among some extinct pteridosperm groups (Krings *et al.* 2003, DiMichele *et al.* 2006).

Fungal epiphytes of Pennsylvanian age growing on *Cordaites* leaves or tree fern pinnules were described by Krings *et al.* (2010a, 2010b, 2011). Epiphytic fungi are also described from Early Cretaceous cycad leaves (Shao-lin & Wu 1986). Nevertheless, Krings *et al.* (2010a) objectively stated that the interpretation of epiphytic microbial plants is difficult because some of the structures may represent entire organisms or stage of the life history of organisms, while others have been produced by the pinnules themselves or are the results of diagenesis and fossilization.

Mamay (1952) published a presumed vascular epiphyte *Tubicaulis scandens* Mamay, which belongs to the coenopterid ferns based on Upper Pennsylvanian petrified material (coal-balls) from the Illinois Basin. Mamay (1952) stated that the species represents an epiphytic fern that grew on *Psaronius* trunks. His opinion resulted from the observation that root remains of *Tubicaulis scandens* penetrated the tissue of *Psaronius* trunks. Rößler (2000) followed Mamay's (1952) opinion that many species of the

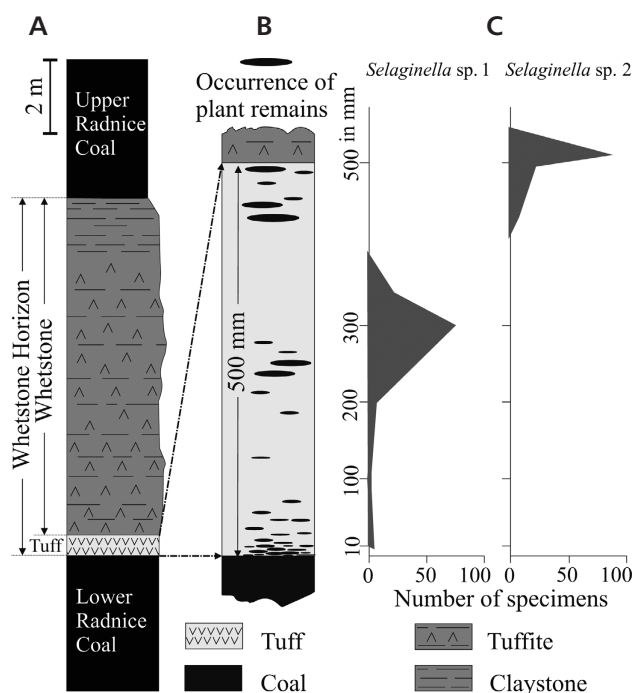


Figure 3. A – position of the Whetstone Horizon between Lower and Upper Radnice Coals. • B – distribution of plant remains in *in situ* volcanic ash. • C – vertical occurrence of *Selaginella* sp. 1 and *S. sp. 2* in *in situ* volcanic ash.

genus *Tubicaulis* represent epiphytic plants and mentioned more than 40 *Tubicaulis* shoots penetrating the free root zone of *Psaronius*. Rößler's (2000) silicified specimens come from Lower Permian volcanoclastic deposits in Chemnitz (Germany). Rothwell (1991) described stems and adventitious roots of *Botryopteris forensis* intertwined with *Psaronius* roots from Upper Pennsylvanian coal-balls (Ohio, USA) and he concluded that the *Botryopteris* represents stems of epiphytic plants rather than rhizomes of climbing plants. Schneider & Kenrick (2001) published a similar interaction between the Early Cretaceous anatomically preserved lindsaeoid fern and a trunk of the tree fern *Tempskya* Corda. All cases are described from fragmentary petrified material and so their interpretation as epiphytes is made on indirect evidence of their anatomy and close association with other plants.

Gomez (1982) described supposedly epiphytic ferns *Grammitis succinea* Gómez from Late Oligocene ambers.

During palaeobotanical research between 2002 and 2009, a Middle Pennsylvanian forest preserved *in situ* in volcanic ash was uncovered and studied at the Ovčín locality, near Radnice, Czech Republic (Fig. 1). During this research interesting “herbaceous” lycopsid remains referred to *Selaginella* sp. and associated with branches of arborescent plants were observed. Evidence of potential epiphytes described from ash-fall deposits is presented for the first time in palaeobotanical history.

Two examples of potential epiphytes from a Pennsylvanian volcanic ash bed from the Radnice Basin (Czech Republic)

The specimens described in this paper come from the Radnice Basin, which is a small basin in western Bohemia (Fig. 1B). Stratigraphically, the basin is filled with the Lower Moscovian (Bolsovian) Radnice Member (Kladno Formation) dominated by fluvial sediments, which fill the palaeovalleys on top of the basement (Opluštil 2005). This member contains several tuff horizons (Pešek 2004). One of them, the Whetstone Horizon, situated between the Lower and Upper Radnice coals (Fig. 3A) covers vast areas in the western and central Bohemia. The Whetstone Horizon consists of 0.4 to 0.6 m of massive, pale yellow to whitish tuff representing *in situ* volcanic ash, overlain by a laminated tuffite to tuffaceous mudstone up to 10 m thick (Opluštil *et al.* 2009a). The plant fossils come from the *in situ* tuff bed at the base of the Whetstone Horizon (Mašek 1973, Pešek 2004) (Fig. 3B). The fossils presented in this paper were obtained from six paleontological excavations situated near the abandoned opencast Ovčín Mine (Fig. 1D). The first set of excavations is known as the “Ovčín Excavations 1, 2 and 3” (O1, O2 in July and October 2002, O3 in 2003) (Opluštil *et al.* 2009b). The second group of excavations was located about 150 meters to the east, and were known as “Sternberg Excavation 1” (S1 in 2005), “Sternberg Excavation 2” (S2 in 2006) (Opluštil *et al.* 2009a) and a previously unreported “Sternberg Excavation 3” (S3 in 2009). A total surface area of 185 m² of the tuff was exposed in these six excavations.

The methodology was described by Opluštil *et al.* (2009a). Shortly, the excavation was divided into one-meter-square units allowing for precise location of the fossils. The tuff was carefully removed with x, y and z coordinates recorded for each specimen. All recovered fossil material is housed in the Palaeontology Department of the West Bohemia Museum in Pilsen.

The basal tuff unit contains *in situ* plant fragments representing nearly all components of original taphocenose except alga, mosses, lichens and fungi. Nevertheless, the current maceration of cordaitalean leaves shows the presence of some probable epiphytic fungi (still unpublished data of the first author). The fragments of plant fossils are of variable sizes, including large axial fragments and nearly complete aerial plant parts.

An important factor when looking for epiphytes is the vertical distribution of plant fragments in the tuff unit. Plant remains representing understorey or original litter are situated in the lowermost centimetres of the unit. The middle part of the tuff unit contains many trunks, branches and fertile organs of short trees, and aerial parts of a climbing plant (Opluštil *et al.* 2009a, b). The uppermost part of the unit contains mostly large lycopsid branches, and rarely climbing plant such as *Sphenophyllum*, *Corynepteris angustissima*

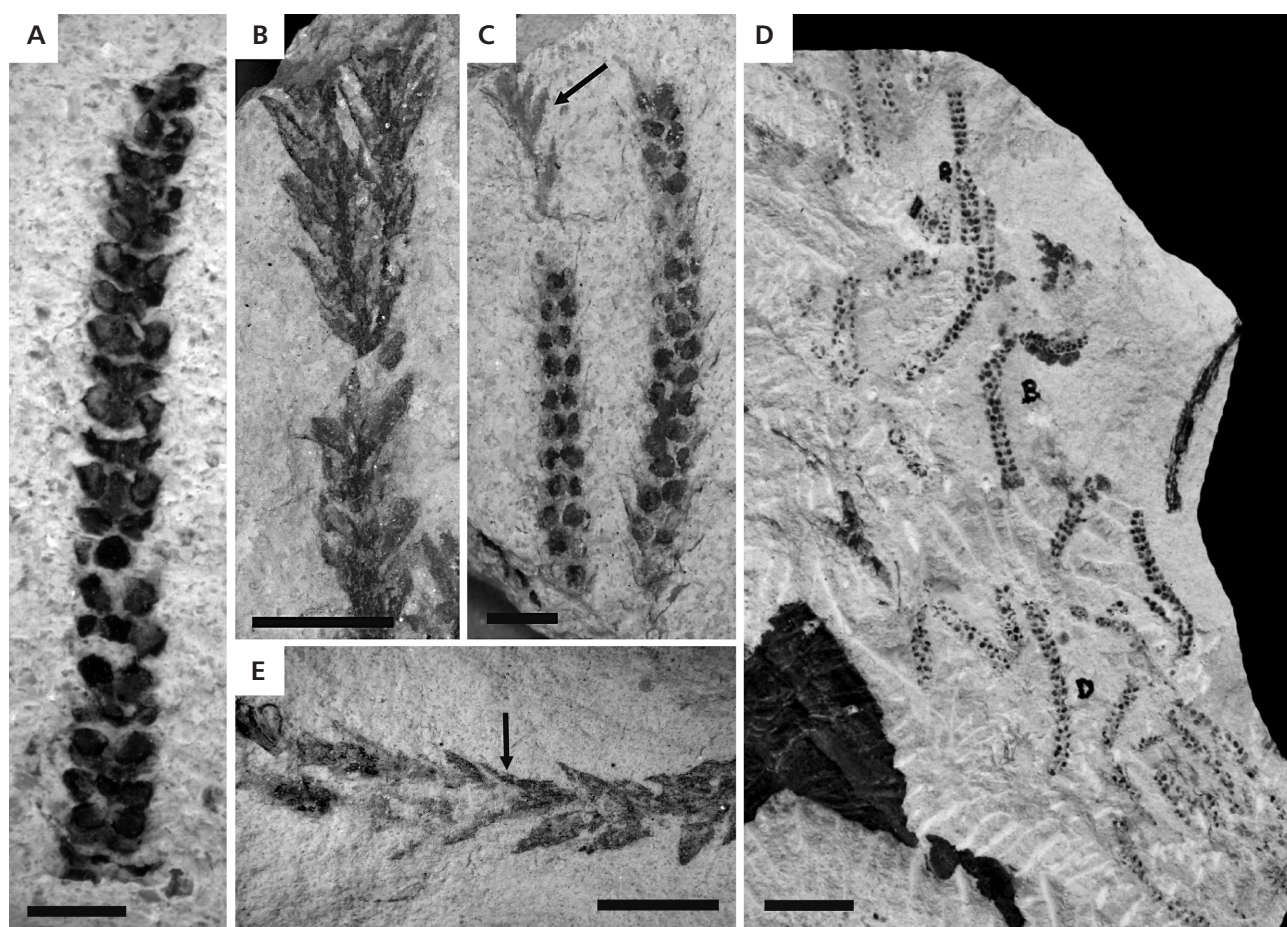


Figure 4. *Selaginella* sp. 1. • A – fertile specimen F1341; middle part of strobilus with microsporangia. Scale bar 3 mm. • B – sterile specimen F9702; shoots with the lanceolate lateral and medial leaves. Scale bar 5 mm. • C – fertile specimen F9690; two fragments of strobili with sporangia and visible sporophylls (arrow). Scale bar 3 mm. • D – large fertile specimen F16109; with many fragments of strobili. Scale bar 20 mm. • E – specimen F16110; two strobili arise from sterile shoots (arrow). The shoot dichotomizes into two terminal strobili. Scale bar 5 mm.

(Sternberg) Němejce, *Oligocarpia lindsaeoides* (Ettingshausen) Stur, *Eusphenopteris nummularia* (Gutbier) Novik and the *Selaginella*-like plants described herein.

The clustering of branches, foliage and fertile organs belonging to the same parent plant, some of which are in organic connection (Opluštil *et al.* 2009a) in the middle ash layer is informative as regards plant organ affinities and suggests that they were broken from a tree together under the weight of volcanic ash (Opluštil *et al.* 2009a). Leaves are often attached to branches indicating that these plants were alive when the eruption occurred. The remains of *Selaginella* sp. 2 were found physically connected to a lycopsid trunk in growth position.

Selaginella sp. 1

Selaginella sp. 1 is known from both sterile shoots and fertile strobili. *Selaginella* sp. 1 occurs in excavations O2, O3 and S3.

Description. – Sterile shoots are preserved very rarely and are poorly preserved. Shoots have a typical anisophyllous arrangement of leaflets with several leaf morphologies, but with only the lateral and medial leaves visible (Fig. 3B, E). Leaves are lanceolate, 0.5–0.8 mm broad and usually about 6 mm long (Fig. 4B). Sterile shoots quickly dichotomize in the distal part of plants.

Fragments of narrow strobili (Fig. 4A, C, D), 3 mm in diameter and more than 200 mm long, arise from sterile shoots where the strobilus dichotomizes into two (maybe more) terminal strobili (Fig. 4E arrow). Sporophylls are arranged in whorls (Fig. 4A) each whorl bearing four sporophylls with sporangia. Sporophylls are not well preserved but appear to be lanceolate (Fig. 4C arrow). Both micro- and megasporangia are present. Megasporangia are situated in the lower short part of the strobilus while microsporangia are borne in a longer upper part of strobilus. Sporangia of both types are slightly oval to circular in outline about 1.0–1.5 mm in diameter. Microsporangia bear *Cirratriradites*-type

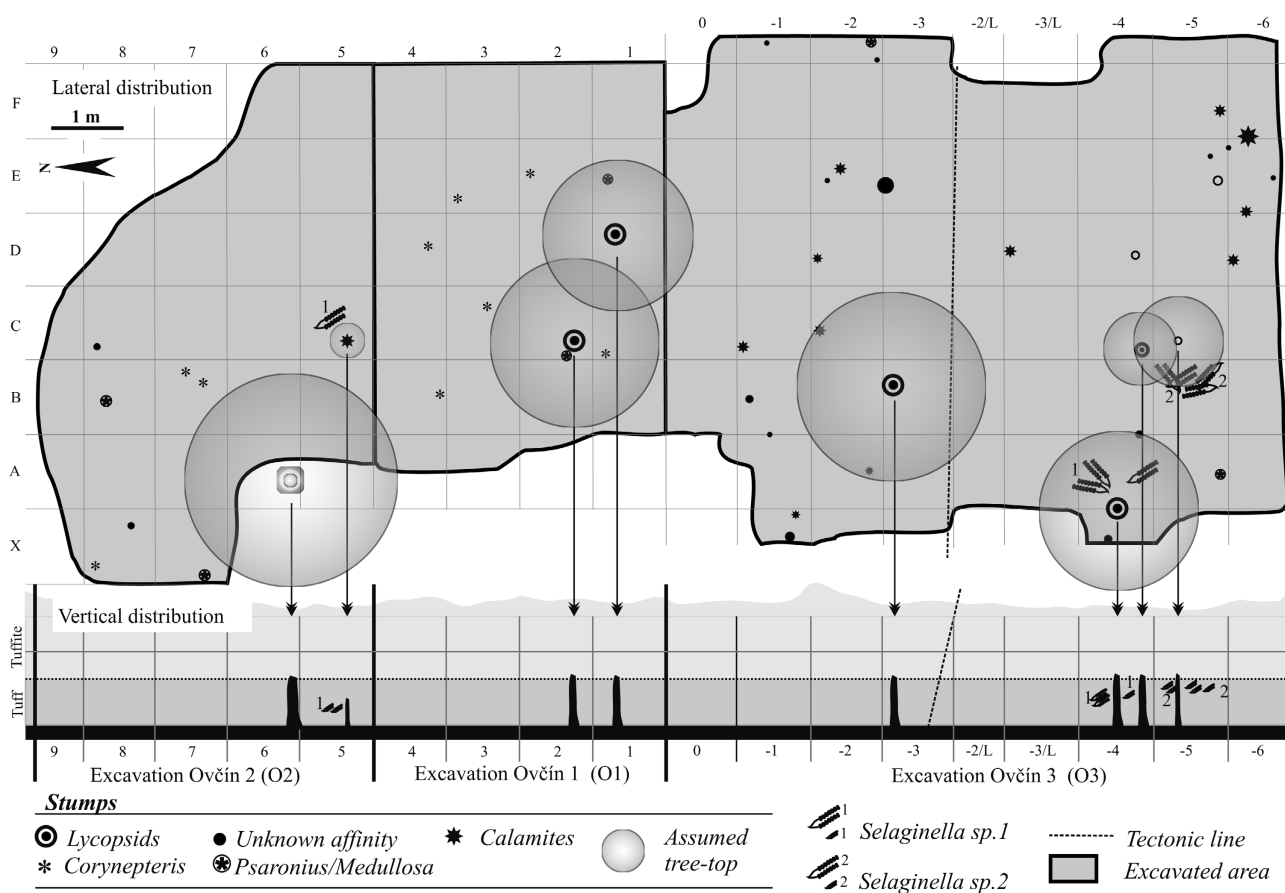


Figure 5. Horizontal and vertical distribution of *Selaginella*-like remains in the excavations O1–O3.

of spores and megasporangia bear *Triangulatisporites*-type of spores.

Horizontal distribution. – *Selaginella* sp. 1 is rare in comparison to other species known from the locality, with a normalized contribution only 0.1% (Opluštil *et al.* 2009b). Strobili are more common than sterile shoots. They occur also near a calamitalean axes in the grid C5-O2 (where C5 is the grid in excavation O2) (Fig. 5), however it is assumed that the remains probably grew on one of the adjacent lycopsids in A6-O2 (Fig. 5), A-O3 (Fig. 5), C5-S3 (Fig. 6) or B2-S3 (Fig. 6). *Selaginella* sp. 1 is associated with leafy shoots of the arborescent lycopsid *Lepidodendron lycopodioides* Sternberg in the excavation O2 (Fig. 7), *Lepidophloios* cf. *acerosus* Lindley & Hutton in the excavation O3 (see Opluštil *et al.* 2009b, p. 731, fig. 3) and “*Lepidodendron*” (= *Paralycopodites*) *simile sensu* Němejc in excavation S3. Besides the tree plants, *Selaginella* sp. 1 remains are often associated also with liana-like sphenopsid *Sphenophyllum* sp. and ferns *Corynepteris angustissima* and *Oligocarpia lindsaeoides* (Fig. 7).

Vertical distribution. – The majority of specimens of *Selaginella* sp. 1 was found about 300 mm above the base of the

ash bed (Fig. 3C). The only exceptions are three specimens recovered from near the base of the tuff, 10 mm above the roof of Lower Radnice Coal in C5-S3 (Fig. 6), B2-S3 (Fig. 6) and C5-O2 (Fig. 5). These very small fragments probably fell down during the early phase of the ash-fall. *Selaginella* sp. 1 is missing in the uppermost part of tuff bed (Fig. 3C).

Interpretation. – The virtual absence of *Selaginella* sp. 1 from the base of the tuff bed indicates that this plant was not a component of the understorey. Instead the occurrence of the *Selaginella* sp. 1 specimens some 300–350 mm above the roof of Lower Radnice Coal, as well as their physical association with tree branches (Fig. 7) allows us to conclude that these plants grew in the crowns of arborescent plants well above the ground. Their association with the lianas *Sphenophyllum*-species, *Corynepteris angustissima* or *Oligocarpia lindsaeoides* (Opluštil *et al.* 2009a, b; Pšenička & Bek 2001; Fig. 7) is in agreement with this interpretation since these species also needed supporting plant to reach the upper forest storey. Also supporting this idea is the fact that the *Selaginella* sp. 1 remains occurred near the standing stumps, more or less occupying areas where the hypothetical tree-tops would be projected onto

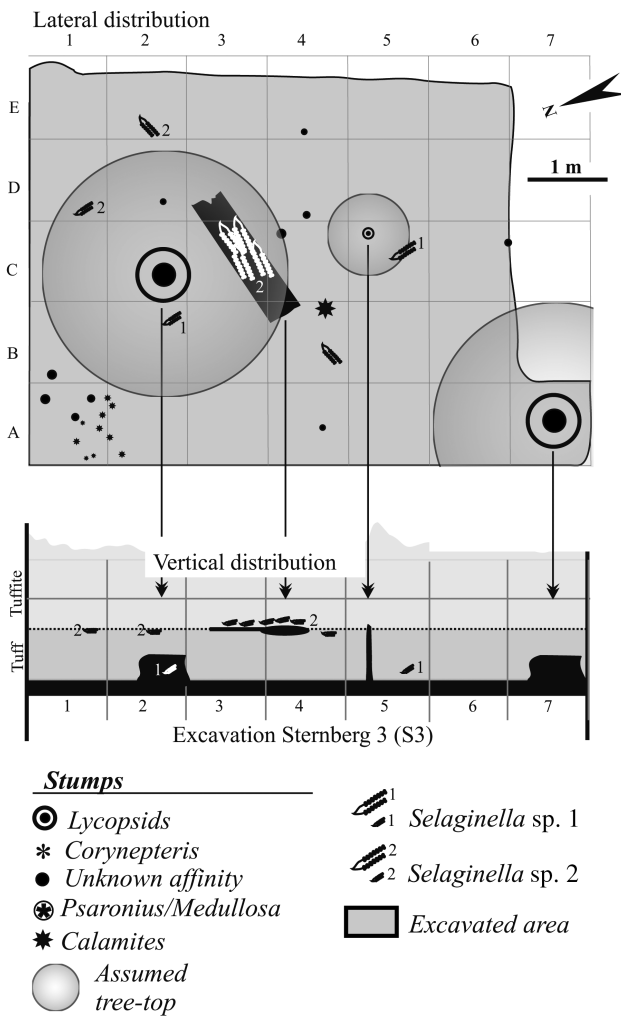


Figure 6. Horizontal and vertical distribution of *Selaginella*-like remains in the excavation S3.

the ground (Figs 5, 6). Nevertheless, nearly none of the *Selaginella* sp. 1 remains was found in close proximity to standing stumps (except one small specimen from B2-S3). Instead they were associated with terminal leafy shoots of *Lepidodendron lycopodioides* which suggests that *Selaginella* sp. 1 occupied distal part of tree crown and was buried as the fragile lycopsid branches composed mostly of parenchymatous tissue were broken due to volcanic ash load, some 300–350 mm above the tuff bed base. The very long fertile zones, perhaps because of their robustness and fragility (and perhaps also due to maturation) were separated from much tiny the vegetative part and buried separately. Based on this circumstantial evidence, it is possible to hypothesize that *Selaginella* sp. 1 represents an epiphyte, which was growing on terminal leafy shoots of some arborescent lycopsids. In this case, the species probably grew on *Lepidodendron lycopodioides* (excavation O2) (Fig. 8), *Lepidophloios* cf. *L. acerosus* (excavation O3) and perhaps “*Lepidodendron*” (= *Paralycopodites*) *simile* (excavation S3).

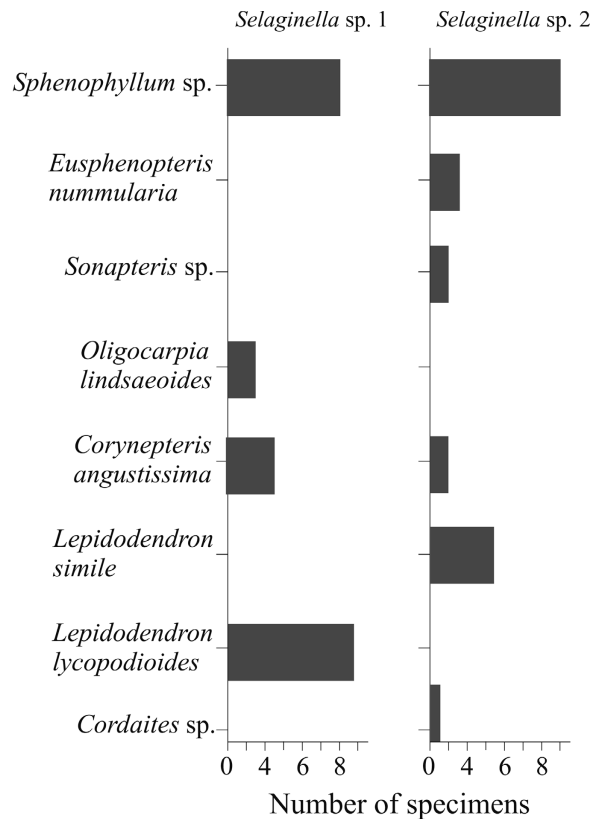


Figure 7. Associations of the *Selaginella*-like remains on specimens.

Selaginella sp. 2

Selaginella sp. 2 sterile shoots and strobili were found in the excavations O3, S1, S2 and S3.

Description. – The sterile leafy shoots appear to be isophyllous with leaves closely adpressed to the axis, arranged in four rows. Leaves are lanceolate, 0.2–0.5 mm broad and ca 4 mm long (Fig. 9C). Sterile shoots are dichotomizing (Fig. 9A). Some sterile leafless shoots are also present (Fig. 9B).

Fertile parts are represented by narrow, short strobili (Fig. 9A arrow), which are monosporangiate. Some specimens show that *Selaginella* sp. 2 probably had distinct strobili each to produce mega- or microsporangia. Each sporophyll bears only one sporangium. The megaspores can be compared with dispersed species *Bentzisporites tricollinus* (Zerndt) Potonié & Kremp.

Remark. – The systematic study of this species is still at the beginning. The sterile leafy shoots appear to be isophyllous, which is different of anizophyllous foliage of true *Selaginella* species. It will be probably a new *Selaginella*-like plant genus or subgenus. Nevertheless, this paper is not taxonomic research, and due to this we are using the artificial name *Selaginella* sp. 2.

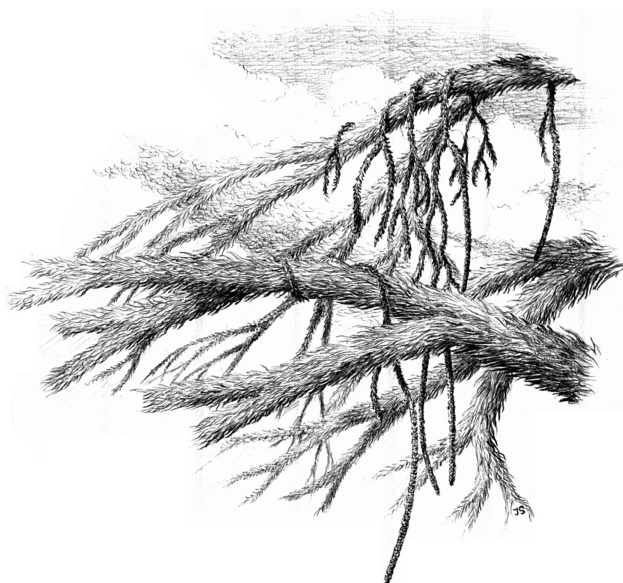


Figure 8. A reconstruction of *Selaginella* sp. 1 growing on terminal shoots of *Lepidodendron lycopodioides*.

Horizontal distribution. – *Selaginella* sp. 2 is also a rare element of the flora excavated from tuff at the Ovčín locality. Material is often fragmentary. Sterile parts are more common than fertile strobili. The best specimen is from the excavation S3 where *Selaginella* sp. 2 was preserved in “living position” still attached to the host plant, in this case a lycopsid trunk (Fig. 9D–F). The trunk was entombed at a low angle, starting from the roof of the Lower Radnice Coal and continuing throughout the tuff to its top (Fig. 9D, TT) where it is only partly compressed (ellipsoid in cross section). Above the tuff unit the trunk consists only of a few fragments, which are greatly compressed. The three-dimensionally preserved trunk in the tuff shows that the plant had to be leveled during the volcanic eruption otherwise dead prostrate plants would be quickly decomposed in tropical climate, especially when the major part of the plant consists of parenchymatic tissues as in the case of lycopsids (DiMichele & Phillips 1994). The remaining part of the trunk that protruded above the tuff unit was decomposed shortly after the volcanic event. The *Selaginella* had to grow on standing or leaner trunk because the *Selaginella*’s shoots are preserved around the trunk. This specimen was found in C3–S3 (Fig. 6) attached to a prostrate trunk of an arborescent lycopsid located at the top of the tuff bed, *i.e.* about 600 mm above the roof of the Lower Radnice Coal. Remains of this form are often found densely concentrated around prostrate trunks as in C3–S3 (Figs 6, 9D–F), 1E1, 1E2, and 1E3 in excavation S2 (Fig. 10). Although the concentrated remains occur near the base of stumps as seen in 1D (Fig. 6), some isolated fragments of this species were found in some areas like in 1D5–S2 (Fig. 10), 1C5–S2 (Fig. 10), E5–S1 (Fig. 10),

D1–S3 (Fig. 6) and B5–O3 (Fig. 5) and in C5–S1 (Fig. 10). *Selaginella* sp. 2 is often associated with leafy shoots of “*Lepidodendron*” (= *Paralycopodites*) *simile* (Fig. 7) in O3 (see Opluštil *et al.* 2009b, p. 731, fig. 3), S1 (based on Opluštil *et al.* 2009a, p. 239, fig. 6), and partly S3. The remains of this species are also associated with leaves and branches of *Cordaites borassifolius* (Sternberg) Unger (Fig. 7) in O3 (see Opluštil *et al.* 2009b, p. 734, fig. 6) and S1 and S2 (see Opluštil *et al.* 2009a, p. 250, fig. 17). *Selaginella* sp. 2 is further associated with some lianas such as *Sphenophyllum*-species, *Eusphenopteris nummularia*, *Corynepteris angustissima* or *Sonapteris*-species (Fig. 7).

Vertical distribution. – The major occurrence of *Selaginella* sp. 2 is around the top of the tuff bed about 500–600 mm above the Lower Radnice Coal (Fig. 3C), *i.e.* around the boundary between tuff and tuffite (Fig. 3C). This species is completely absent in the lower and middle part of the tuff unit.

Interpretation. – The most informative specimens are attached to the trunks (in C3–S3) (Fig. 5) and/or concentrated around the trunks [1E3, 1E2 and 1E1–S2 (Fig. 10) and B5–O3 (Fig. 5)]. Isolated “islands” of several specimens [1D5 and 1C5 in S2 (Fig. 10)] may have fallen away from some standing trunks not discovered during the fieldwork.

Direct position of *Selaginella* sp. 2 on the trunk of “*Lepidodendron*” (= *Paralycopodites*) *simile* arises suggestion that this plant was probably attached to this lycopsid trunk (Fig. 11). Up to 1 m long shoots of *Selaginella* sp. 2 are concentrated into a cluster along one side of the trunk and point roughly to the upper part of the cluster where we assume the plant was attached to the trunk. In S3 several small *Selaginella* sp. 2 remains occur (E2, D1 and B4) (Fig. 6) which are probably parts of the specimen attached to the trunk and were detached during the eruption. A similar situation was uncovered in S2 where the *Selaginella* sp. 2 remains were also concentrated around a prostrate trunk (Fig. 10). This portion of a trunk was in the uppermost part of the tuff bed and is also three-dimensionally preserved, though not as well as the above-mentioned specimen, and continued to the lower part of the tuffite where it was quite compressed and poorly preserved. Due to the position of the trunk in upper part of the tuff bed it is unlikely that the tree was dead and prostrate before the eruption. Instead we assume that it was probably leveled due to volcanic ash load when the lower part was already buried in ash.

Close proximity of *Selaginella* sp. 2 remains to standing cordaitalean trunks (based on associated *Cordaites borassifolius* leaves) was encountered also in the B5 square unit of the O3 excavation (Fig. 5) where isolated clusters

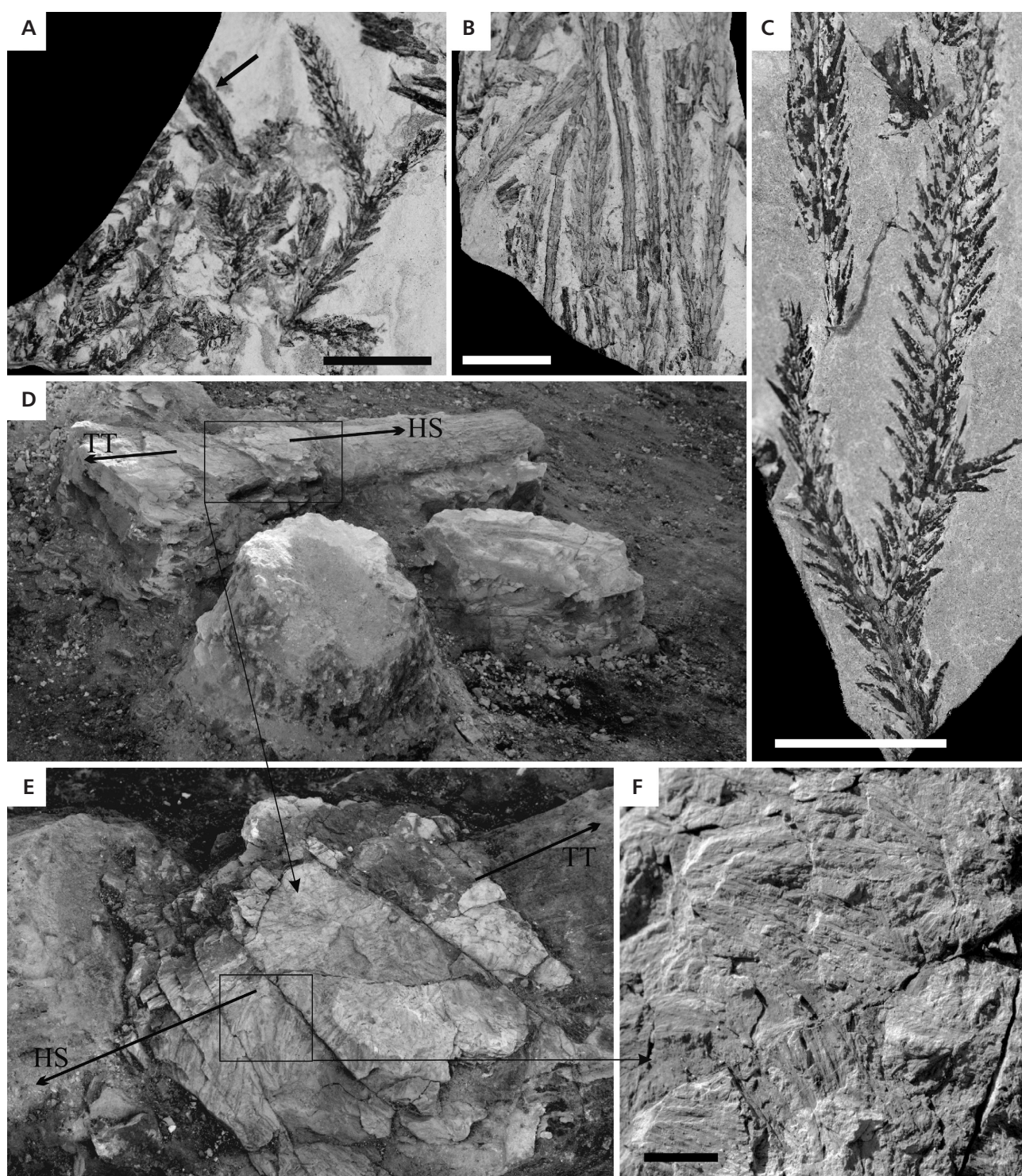


Figure 9. *Selaginella* sp. 2. • A – specimen F16112; dichotomizing sterile terminal parts together with fragment of strobilus (arrow). Scale bar 10 mm. • B – specimen sterile leafy and leafless shoots from the prostrate stem in the C3-S3. Scale bar 10 mm. • C – fertile specimen F16111; dichotomizing sterile shoots with lanceolate lateral leaves. Scale bar 10 mm. • D – Excavation Sternberg 3 (S3) with lying stem in C3 and the big tree stump at downstage. Arrows points to the tree-top (TT) and direction of hanging down of *Selaginella* sp. 2 plant (HS). • E – detail of hanging cluster of *Selaginella* sp. 2 plant still attached to lying stem. Arrows show direction to tree-top (TT) and direction of hanging down of *Selaginella* sp. 2 plant (HS). • F – detail of the cluster of sterile shoots of *Selaginella* sp. 2 plant. Scale bar 10 mm.

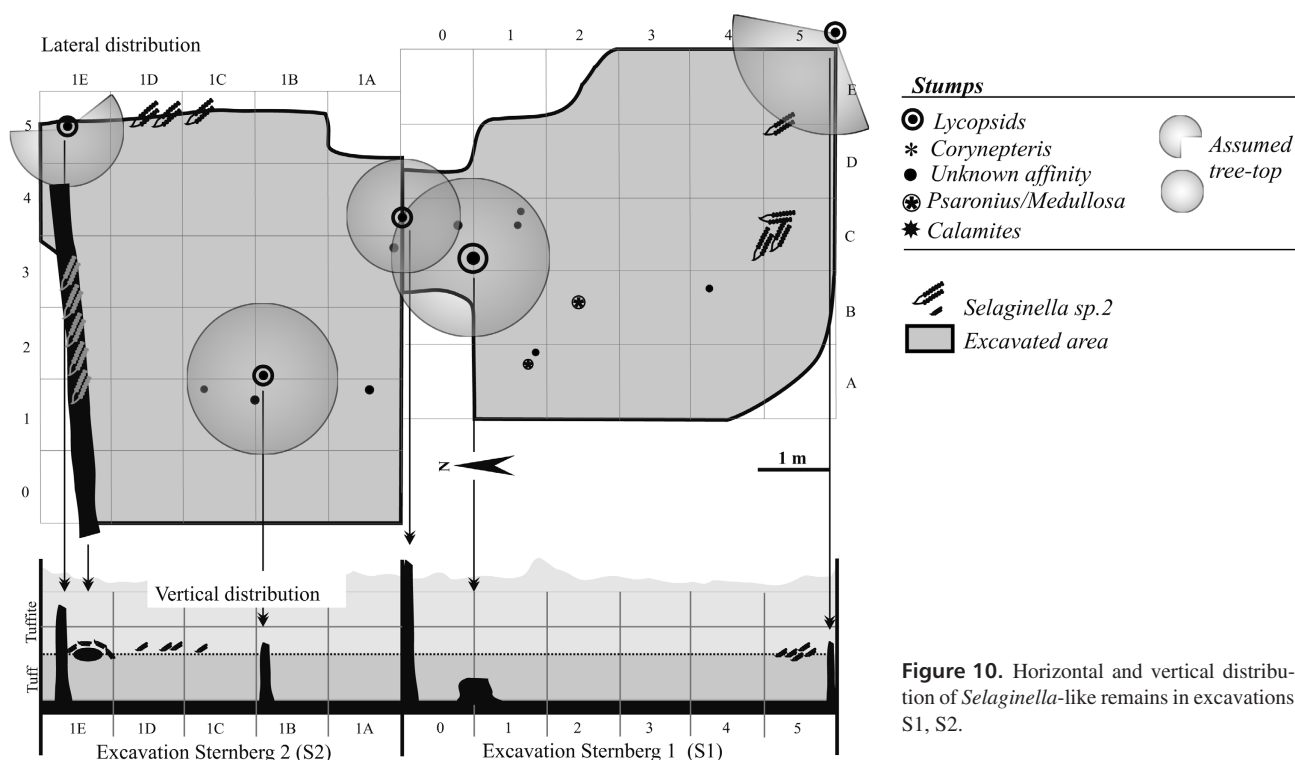


Figure 10. Horizontal and vertical distribution of *Selaginella*-like remains in excavations S1, S2.

occurred in the uppermost part of the tuff bed. We therefore assume that Cordaitalean trees may have also been a host plant for this *Selaginella* sp. 2. We can, however, only speculate, based on the circumstantial evidence, that the cordaitalean tree lost its leaves during the ashfall. The *Selaginella* sp. 2 plants were therefore less protected and were stripped from the trunks in the latest phase of the ashfall. Additionally, the surface of the cordaitalean trunks was smoother than those of the lycopsids with their densely arranged, embossed leaf cushion.

Unlike *Selaginella* sp. 1 that grew in the tree canopy, *Selaginella* sp. 2 probably grew on the trunks and thus was more protected from the weight of the volcanic ash by the tree canopy. *Selaginella* sp. 2 remains were thus buried by volcanic ash simultaneously with the host plant.

Discussion and conclusion

Discussion on epiphytes from the Ovčín locality

The suggestion that the *Selaginella* plants were epiphytes is based on many indirect lines of evidence. The basic of them is the fact that the forest at the Ovčín locality was buried in a geological instant (a T^0 horizon) and none of the fossilized remains were transported. The distribution of the fossils therefore provides insight into the original vertical and spatial distribution of individual plants in the forest,

and in some cases provided evidence about the life strategies of some plant species (Opluštil *et al.* 2009a, 2009b; Libertín *et al.* 2009; Pšenička & Schultka 2009; Pšenička & Bek 2009). Preferential position of *Selaginella* sp. 1 remains in the upper part of the tuff bed and lower part of the tuffite in association with lycopsid or cordaitalean branches from the tree storey provides circumstantial evidence that this species was not growing on ground (understorey). Instead it is suggested that it occupied terminal leafy shoots of an arborescent lycopsids where it used its densely arranged leaves to hold onto the host plant (Fig. 8). The arborescent lycopsids were among the tallest trees in the tropical forest reaching heights of over 20 m (Opluštil *et al.* 2009a). Being positioned in the tree crown had the advantage of allowing more effective photosynthesis. The second example shows a *Selaginella* sp. 2, which probably attached itself to the trunks of certain arborescent species (Fig. 11) including *Cordaites borassifolius* and *Lepidodendron (Paralycopodites) simile*. The former grew to 15–20 m in height in the Radnice Basin (Opluštil *et al.* 2009a, Šimůnek *et al.* 2009). The latter was a polycarpic lycopsid with opposite rows of short, deciduous lateral branches arising from a pole-like trunk (DiMichele 1980, Phillips & DiMichele 1992). The branches did not overshadow the trunk significantly so that an epiphytic plant could grow there. It is assumed that *Selaginella* sp. 2 could therefore grow on stems of these host plants, which did not have a dense crown of leaves. This interpretation is supported by the finding of nearly a complete plant attached to the decorticated

lycopsid stem. The plant was relatively robust to grow on terminal leafy shoots like the *Selaginella* sp. 1.

Described epiphytes grew in the Pennsylvanian rainforest of an intermountane area in the heart of the Variscan Mountains. Extant epiphytes mainly occur in tropical rain forests. Fossil “presumable” epiphytes are also centred to a palaeotropical rainforest (Benzing 1990, Dubuisson *et al.* 2009). The latest knowledge on vascular epiphytes shows that these plants are not able to survive frost and do not occur at higher latitudes in temperate and boreal regions (Dubuisson *et al.* 2009). Due to this fact it can be expected that most of the Pennsylvanian epiphytes grew in the Euroamerican province located in the tropics (DiMichele 2009). The question is at what altitude forest was originally growing. The answer can be brought from Ovčín locality where two epiphytic *Selaginella*-like plants come. Opluštil (2005) believes that the altitude of this area was less than 1000 m based on the expected length of the drainage system and slope toward the northwest. The occurrence of epiphytes in this area supports this idea that the altitude was less than 1000 m.

General conclusions

The identification of a true epiphyte in the fossil record is problematic at best and the chance of finding anytime soon unequivocal evidence from the fossil record are slim. However, the existence of epiphytic plants in Late Palaeozoic times is based on indirect evidence from petrified material (Mamay 1952, Rothwell 1991, Rößler 2000) and volcaniclastic deposits in the present paper. We can thus speculate that they evolved in tandem with the development of early forests during Devonian times. As shown in the Fig. 12, distribution of potential epiphytic plants in the fossil record is stratigraphically uneven. While several species are reported from Pennsylvanian and Cenozoic strata, almost nothing is known from Mesozoic times. However, this pattern may probably be a result of missing-data from certain periods of Earth history rather than reflecting the actual pattern of evolution of epiphytic plants. Another reason for misinterpreting the evolutionary history of epiphytic plants is poor knowledge of fossil forests and their ecosystems throughout Earth history. We hardly ever find a conserved fossil forest with the vegetation structure preserved that more or less corresponds with original phytocenoses. Example of a really well preserved forest is described in Opluštil *et al.* (2009a, 2009b) and partly in this paper. But relevant data from other geological periods are still missing.

The problem with the correct identification of epiphytes arises from their definition – plants that are non-parasitic growing on other plants. Epiphytes do not have their own unambiguous morphological or anatomical characterization that allows them to be distinguished from other plants.

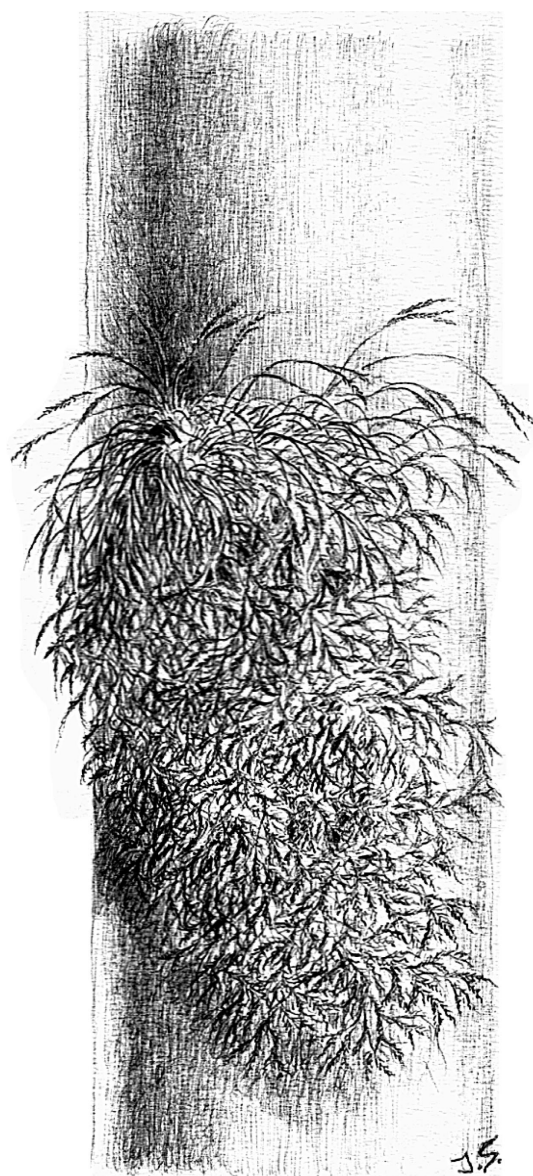


Figure 11. A reconstruction of *Selaginella* sp. 2 growing on lycopod stem.

Therefore many original epiphytic plants could be still hidden among other already described fossil plant species from Palaeozoic to Cenozoic times. Epiphytes are closely allied with their phorophytes and their fossilization depends on the fossilization of the phorophytes. Phorophytes are trees (or at least plants of tree size) and remains of them are generally fragmentary, in many cases detached and dispersed terminal shoots, fragments of branches, bark, wood, leaves or reproductive organs. It means that organic connection between epiphytes and phorophytes could be found in really specific cases. Generally, the preservation of epiphytes is the result of the coincidence of many factors. It has been mentioned that permineralized material is more suitable for recognizing parasitic plants and showing the close interaction between

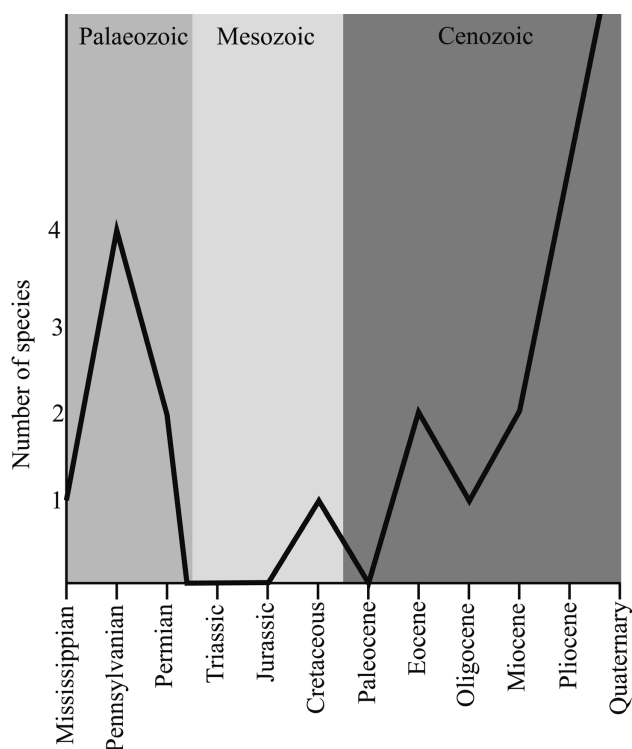


Figure 12. Distribution of potential epiphytic plants in the fossil record thought the geological time. Based on published papers.

the plants, while compression can show the general morphology with the potential of showing the connection or association of epiphytes with their phorophytes. Nevertheless, such connections could also be the result of other types of interactions, because aerial roots of some climbing plants can penetrate the tissue of the supporting plants (as with *Ankyropteris* Sterzel, *Anachoropteris* Corda and others). Scrambling plants also can intertwine with the adventitious roots of the dead or living plants. The result of these cases preserved in petrified specimens could be identical. It means that the presented interaction between *Psaronius* and *Tubicaulis* cannot be regarded as explicit evidence of the interaction between an epiphytic plant and its phorophyte. Probably the best possibility of finding concrete evidence of epiphytes is in so-called T_0 horizons/assemblages where it is possible to study plants in their original position with a minimum taphonimal bias.

Human factor and sampling bias

Besides the “natural” taphonomic processes, the understanding to which is of a crucial importance for correct ecological interpretations, there is also a taphonomical artifact related to sampling techniques (e.g. Falcon-Lang *et al.* 2009). Consequently, this sampling bias can influence the general view of the evolution of all plants and nature inclu-

ding the evolution of epiphytes. During palaeobotanical history many vascular (Mamay 1952, Rothwell 1991, Rößler 2000) and microphytic plants (Shao-lin & Wu 1986; Krings *et al.* 2010a, 2010b, 2011) have been interpreted as epiphytes. However, most of these attributions are based only on indirect evidence. It means that the affiliation to epiphytes was based on combination of subjective knowledge and experience of particular author. Such approach has resulted in the impression that we have unambiguous evidence of epiphytes from geological history although the opposite is true. In many cases the authors apply a “principle of actualism” to the fossil record. This approach, however, is applicable in relatively younger geological history (Cenozoic) where most of plants have their extant relatives. As we go deeper into geological history this principle subsides to work.

Another important factor affecting the general view on epiphytes is the uneven level of exploration of the individual stratigraphical units, which in turn arises from the exploration of individual localities and can be result of sampling bias (e.g. Falcon-Lang *et al.* 2009). The exploration level of stratigraphical units; a lot of information comes from stratigraphical intervals which bear economically important resources, usually coal. The intensity of paleobotanical exploration of such stratigraphic levels is therefore usually much higher than in cases of mineral-barren stratigraphic units. This is clearly shown in the work of Burnham (2009), who analyzed a number of published records of fossils of climbing plants of Mississippian through to Quaternary age (Burnham 2009, fig. 1). She clearly showed that the main occurrences are centred to strata of Pennsylvanian, Eocene and Miocene ages whereas the minimum occurrence of climbers is during Mesozoic times, probably as a result of absence of data of Mesozoic age. Burnham (2009) established the theory that the apparent absence of climbers during Mesozoic times was due to the dramatic reduction in plant biodiversity at the end of the Permian Period, but it could equally be just a consequence of the limited collected data from this stratigraphical interval or combination of both. In any case, over/under representation of fossil material from certain stratigraphic levels can affect the interpretation of existing data.

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