



The late Palaeozoic tree fern *Psaronius* — an ecosystem unto itself

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Abstract

Stimulated by new observations, this contribution presents a summary of the current knowledge of different plants that grew closely associated with *Psaronius* trunks in the Early Permian petrified forest of Chemnitz (Saxony, Germany). The role of *Psaronius* tree ferns was to provide a frequently-used substrate for colonization by other plants. The massive root mantles protected different developing plants, and they may have improved the possibility of preservation of smaller plants and plant organs in particular. These are climbing axes of the fern *Ankyropteris brongniartii*, small epiphytes of the fern *Tubicaulis* sp., different isolated petioles of the fern *Anachoropteris*, small ?*Grammatopteris* axes, roots of the pteridosperm *Callistophyton*, and *Dadoxylon* specimens representing *Amyelon* roots of *Cordaites* and conifer stems. Further, plant-animal interactions demonstrate the role of *Psaronius* as an ecosystem unto itself. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The tree fern genus *Psaronius* Cotta was widely distributed during late Palaeozoic times. These homosporous, eusporangiate ancestors of the marattialean ferns are known from the earliest Pennsylvanian (DiMichele and Phillips, 1977) up to Triassic times (Frentzen, 1914), and they constitute an important part of the Upper Carboniferous and Lower Permian floras in particular (Pfefferkorn and Thomson, 1982; DiMichele and Phillips, 1994). The genus *Psaronius* occurred in several floral realms of both the Northern and Southern hemispheres. Contrary to the extant marattialean ferns that are exclusively (sub)tropical

and, therefore, narrowly confined geographically, *Psaronius* tree ferns show a wide distribution. They are commonly and contemporaneously known from Euramerica, Cathaysia and Gondwana. *Psaronius* tree ferns represent a large and ecologically heterogeneous group. Different species grew in both clastic hygrophile lowland communities (Phillips et al., 1985; DiMichele and Phillips, 1994), peat-forming hygrophile forested mires, and even up to mesophile periodically drier habitats (Barthel and Weiss, 1997).

The majority of the fossil record of *Psaronius* consists of silicified trunks (Cotta, 1832; Renault, 1869; Morgan, 1959; Mickle, 1984a), coal balls (Smoot, 1984; Galtier and Phillips, 1985; Millay, 1997), and of pyroclastic/tuffitic material that may have been deposited over forested mires (Corda,

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1845; Rößler and Barthel, 1998). The research history of *Psaronius* reaches back to the early days of palaeobotany (Sprengel, 1828; Cotta, 1832; Corda, 1845; Stenzel, 1854). In more recent years Morgan (1959), Stidd and Phillips (1968), Stidd (1971), Ehret and Phillips (1977), and Mickle (1984a,b) provided valuable new information on the genus.

The aim of this contribution is to present new observations on material from the petrified forest of Chemnitz, and to integrate long-known, isolated data on different plants or plant organs that grew on *Psaronius* trunks or embedded in the *Psaronius* free root zone, more or less hidden below the surface. There is a considerable number of plant–plant or plant–animal interactions worth focusing on in light of new evidence, which comes mainly from the Permian of Chemnitz.

To date we know of several taxa belonging to different systematic groups ranging from zygopterid ferns (Galtier and Phillips, 1996) and sphenopside up to gymnosperms that grew on the (sub)surface of *Psaronius*, including vines, epiphytes and even scrambling shrubby plants. The upright *Psaronius*-stems, especially their lower parts with thick mantles of adventitious roots, apparently formed an ideal host for other plants. The large root mantle firstly offered mechanical support, and secondly it may have protected the development of such plants. Renault (1869) and Stenzel (1889) have already reported examples of multiple plant-to-plant interaction in the fossil record. New examples allow us to recognize a much greater diversity of plant life strategies on *Psaronius* and permit reinterpretation of all examples in the light of plant interactions within a small Permian hygrophile community.

The current investigation focuses on the climbing axes of *Ankyropteris brongniartii*, small *Tubicaulis* sp. epiphytes, isolated *Anachoropteris* petioles, ?*Grammatopteris* axes, *Callistophyton* roots, and *Dadoxylon* axes representing both *Amyelon* roots of *Cordaites* and conifer stems growing closely associated with *Psaronius* trunks. Records of the genera *Anachoropteris* and *Callistophyton* from Chemnitz are presented for the first time.

Finally, the root mantle may have played a

noteworthy role in preserving the different, sometimes delicate, plant organs during various clastic and volcanic fossilization processes. In most cases, axes, petioles and roots of other plants were found within the outer root mantle (free root zone) of the *Psaronius* trunks. They are firmly anchored aided by their own adventitious roots. Only a few examples (Plate II, 1) show remains of free-growing climbers on the surface of *Psaronius*, possibly at positions higher up on the trunk.

2. Materials and methods

The material studied, described and illustrated in this contribution comes from the Permian petrified forest of Chemnitz, the type locality of *Psaronius*. The plant-bearing layer was found at the base of the Zeisigwald tuff horizon (Leukersdorf Formation, Erzgebirge Basin, eastern Germany). This pyroclastic sequence was deposited during several phreatomagmatic-influenced volcanic eruptions of the Zeisigwald volcano that was responsible for incorporating and preserving a rich Permian plant community (Fischer, 1990; Rößler, 1995, 1996). Specimens under study are stored in the following collections:

MfNC — Museum für Naturkunde, Chemnitz

MMG — Museum für Mineralogie und Geologie, Dresden

BAF — Freiberg University of Mining and Technology, Geological Institute.

Specimens are preserved as siliceous cellular permineralizations. They were examined from ground/polished surfaces and thin sections, and subsequently observed/photographed under reflected light using a Zeiss SV 11 binocular microscope.

For comparative purposes, the Bolsovian age type material of *Anachoropteris* Corda, stored at the palaeobotanical collection, National Museum, Prague, Czech Republic, and the Permian age type material of *Tubicaulis* Cotta, *Psaronius* Cotta, and *Grammatopteris baldaufii* (Beck) Hirmer, housed in the palaeontological collection of the Freiberg University of Mining and Technology, Freiberg, Germany, were additionally examined.

3. Observations, descriptions and discussion

3.1. The genus *Psaronius* Cotta 1832

Although *Psaronius* material is to be found in many palaeobotanical collections, a revision of the genus is still lacking. The genus *Psaronius*, originally introduced by Cotta (1832) for permineralized trunk segments, is used today to refer to the entire plant. *Psaronius* is considered as having upright, unbranched stems that reach a basal diameter of more than 80 cm (Sterzel, 1887). The largest *Psaronius* specimen known so far (*Psaronius weberi* Sterzel, 1887; MfNC K 620), measures 80 cm in diameter, but the extreme asymmetry of the trunk, interpreted as taphonomic (see Rößler, 1996), may allow basal diameters up to 1.5 m to be predicted.

The stem increases in size and stelar complexity towards the crown, which carried large tri- to quadripinnate fronds. This obconical construction develops from a small siphonostele at the base of the trunk expanding upward to a polycyclic dictyostele at the apex (Morgan, 1959; Stidd and Phillips, 1968). A dense mantle of adventitious aerial roots, which show an actinostelic tracheidal bundle embedded in parenchymatous, sometimes aerenchymatous, ground tissue, supports the false stem. An inner bound zone (inner root mantle) composed of smaller roots of regular spherical to elliptical shape is characterized by the appearance of secondarily derived parenchyma. The outer free zone (outer root mantle) shows larger roots of different shape free of parenchyma (Ehret and Phillips, 1977). The large fronds are normally three to four times pinnate, bilaterally symmetrical, and reach a length of up to 3 m. They had pectopterid-type pinnules. The arrangement of leaf traces varies from two vertical rows up to spiral sequence. Petioles have C-shaped adaxially opened vascular traces. Fertile frond portions exhibit some different synangiate types found on the abaxial surface of pectopterid pinnules. The most familiar genus is *Scolecopteris* Zenker (Millay, 1979; Barthel and Weiss, 1997).

3.2. Plant interactions with *Psaronius* trunks

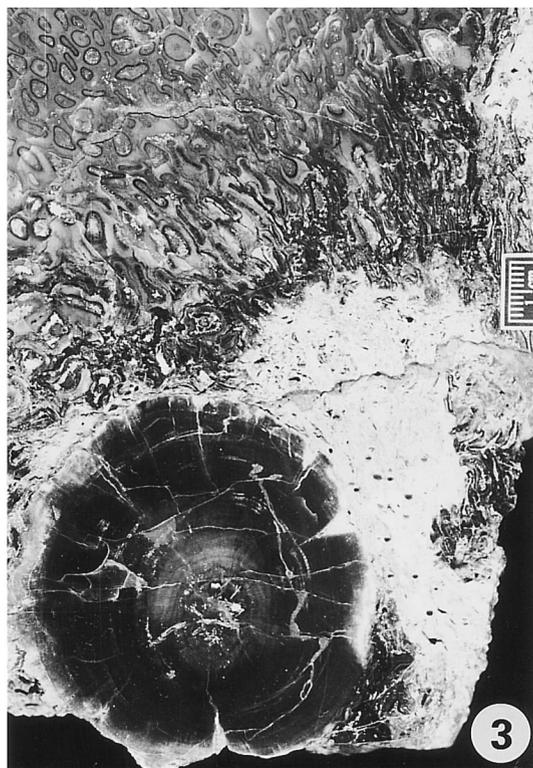
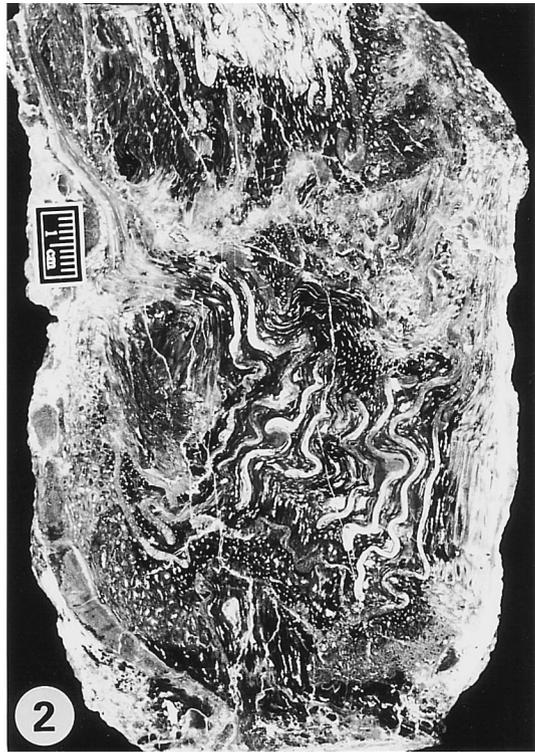
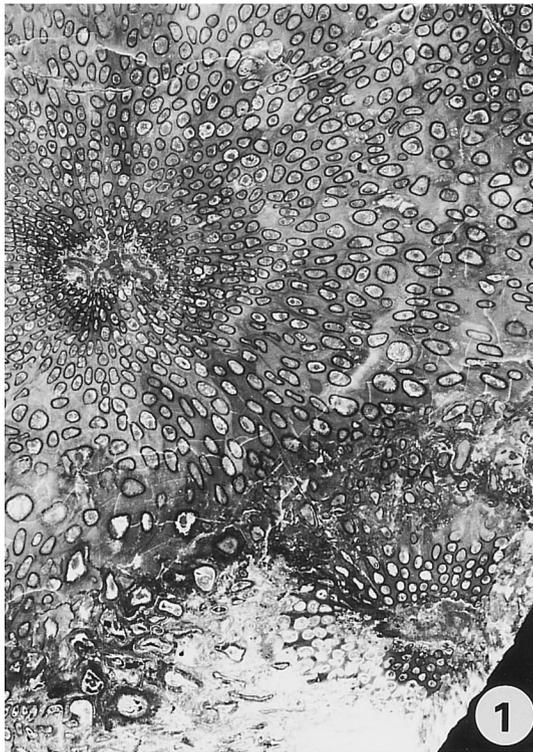
Although many examined *Psaronius* specimens exist, plants or plant organs growing on *Psaronius*

trunks were not frequently mentioned. For that reason it seems curious that the material, on which Cotta (1832) erected the genus *Psaronius*, showed several climbing axes of *Ankyropteris brongniartii* growing in between the root mantle. However, this was not noted until Sterzel (1887) re-examined the largest known *Psaronius* specimen, and compared it with Cotta's type specimen. Since that time a lot of anatomical work has been done and, consequently, a variety of examples showing other plants growing on *Psaronius* trunks have been mentioned in the literature (Strauß, 1920; Sahni, 1931, 1935; Mamay, 1952; Urban, 1974; Mickle, 1984a; Rothwell, 1991).

The large root zone of *Psaronius* trunks may have provided a frequently used substrate that guaranteed safe development of juvenile epiphytes, and offered mechanical support for the frond-bearing adults. Our developing knowledge reveals an increasing number of plants that were able to use these possibilities. Mickle (1984a) figured a triarch protostele belonging to *Sphenophyllum* Brongniart preserved among the adventitious roots of *Psaronius*. Rothwell (1991) reconstructed *Botryopteris forensis* Renault as an epiphyte on a *Psaronius* trunk. Recently there has been a growing awareness of alternative growth patterns among ferns or pteridosperms in Late Palaeozoic ecosystems (Behrensmeyer and Hook, 1992). Indirect evidence of a liana-like plant was shown by Gradzinski and Doktor (1995), who figured an upright *Sigillaria* trunk with an imprint of a winding axis on its surface, from the lower Westphalian of Upper Silesia, Poland. Kerp and Krings (1998) reported three basically different types of climbing organs on Late Carboniferous pteridosperms from the Blanzky-Montceau Basin, France, on the basis of cuticular material.

Observations of different plant interactions on extant tree ferns show us the variety of life strategies among small ferns, which exist on tree fern trunks, and facilitate the reconstruction of growth patterns and life strategies of Palaeozoic ferns. Metaphorical descriptions by Christ (1910) represent an outstanding guide to tree ferns, such as species of well-known *Dicksonia*, *Cyathea* or *Alsophila*, as substrates for colonization by other plants: "Eine ganz besondere Zierde älterer

PLATE I



Farnstämme sind die Luftwurzeln, welche am Stamm in dichter Fülle hervorbrechen, zur Erde herabsteigen und ihn mit einem festen Geflecht umgeben, das einer Schar zierlichster Epiphyten als Zuflucht dient". Several *Hymenophyllum*, *Asplenium*, *Polypodium*, *Davallia* and *Trichomanes* fern species showing epiphytic growth were reported from northern New Zealand, Costa Rica, Brazil and Teneriffa Island (Christ, 1910). Impressive liana-like climbers among extant ferns include species of *Polypodium*, *Drynaria*, *Stenochlaena* and *Oleandra*.

Several examples of plant interactions involving Permian *Psaronius* tree ferns may be demonstrated as follows.

3.2.1. *Psaronius*–*Psaronius*

A first, and unusual, example of tree-fern interactions is an intraspecific one. Sometimes, two *Psaronius* individuals may have grown as close together (Plate I, 2). This resulted in dense penetration of the downward growing free roots forming a single mantle of free adventitious roots, which contains two axes each independently surrounded by its own dense inner root mantle (Plate I, 1). There is no indication as to whether the two examples shown represent bifurcating axes of one tree.

3.2.2. *Psaronius*–*Ankyropteris*

Ankyropteris is an extinct genus of zygopterid fern that exhibits a five to six-lobed medullose actinostele and H-shaped petiolar xylem (Bertrand, 1907; Mickle, 1980). This taxon probably provides the earliest evidence of plants growing on *Psaronius* trunks. The type species, *Ankyropteris brongniartii* (Renault, 1869) Mickle from the Lower Permian of France, is very frequent at Chemnitz and also is known from Nova Paka

(Podkrkonose Basin, Czech Republic). In almost all occurrences of the plant in the Permian it was found climbing within *Psaronius* root mantles or on their surfaces (Plate II, 1–4). The most conspicuous characters of this plant are the presence of axillary branching, which is frequently seen, and the dense overlapping vascularized aphanopodia covering the climbing axis. Comparisons of this vine-like plant with vegetative structures of *Senftenbergia* (Jennings and Eggert, 1977) seem to be confirmed by specimens obtained from a Lower Permian crystal tuff horizon of the Döhlen Basin, eastern Germany (Rößler and Barthel, 1998: pl. 6, 2). The *A. brongniartii* vines are not only reported as growing on *Psaronius*. From Chemnitz, *A. brongniartii* was noted as growing on a calamite stem (*Calamodendron striatum* Cotta, unpublished observation), favouring the reconstruction of that calamite by Remy and Remy (1978) against that of Hirmer (1927).

Some of the Chemnitz specimens of *Ankyropteris brongniartii* display a delicate example of plant–animal interactions (see also below). Within stem or petiole parenchyma (mostly around the phloem tissue) there are small hollows densely filled up with arthropod coprolites (Plate 7, 1–5). These are egg-like spherical to slightly elongated bodies of two distinct sizes. This feature is also clearly seen in some figures of Mickle (1980: figs. 12, 13, 15, 16) and Smoot (1985: fig. 27) involving North American coal ball specimens of *A. brongniartii*, although it was not mentioned by the authors.

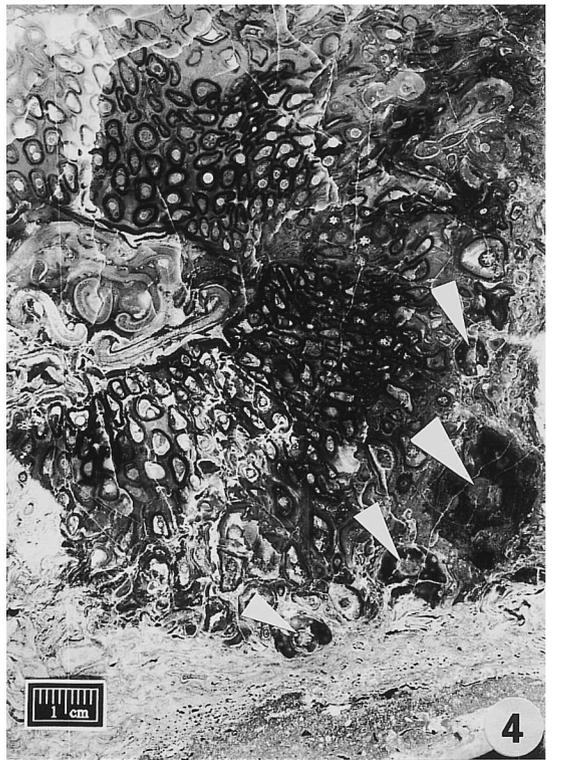
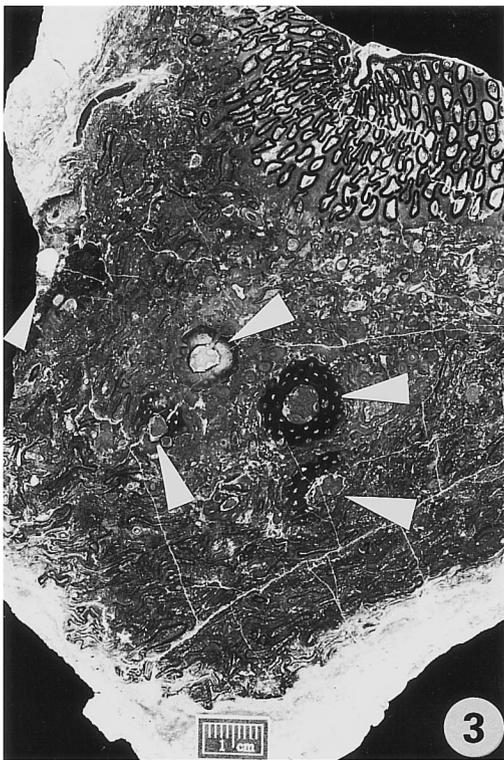
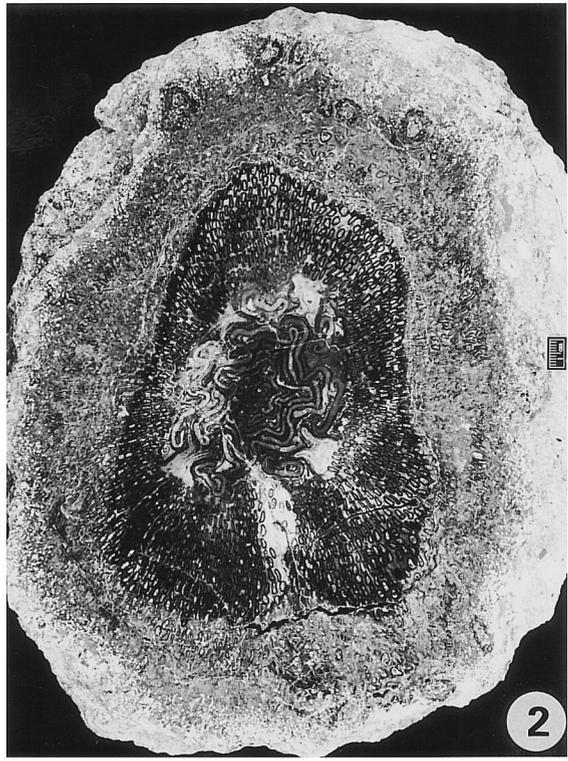
3.2.3. *Psaronius*–*Tubicaulis*

Tubicaulis was established by Cotta (1832) to accommodate exarch protostelic stems with a C-shaped petiolar xylem. Among the *Tubicaulis* species known to date, there are different stelar types that produced the same type of petiole. This

PLATE I

1. Two distichous stems of *Psaronius cotta* Corda within a single outer root mantle, MfNC K 4561, $\times 0.5$.
2. Two distichous *Psaronius* stems within a small single root mantle, MfNC K 4562.
3. *Amyelon* root of *Cordaites* preserved in close association with a basal *Psaronius* trunk, MfNC K 4561.
4. Preservation proximity of a gymnospermous stem preserved by a fragment of thick secondary xylem to the root mantle of *Psaronius*, MfNC K 669.

PLATE II



very artificial genus may represent at least two different evolutionary lines from the Lower Langsettian to the Permian, each of which exhibits the same variability in size, internal anatomy and growth habit (Phillips, 1974). The type specimen, *Tubicaulis solenites* Cotta from Flöha near Chemnitz, represents a small free-growing tree fern and, along with *T. sutcliffii* Stopes, may have had an unbranched erect axis with a solid protosteles and multiseriate circular bordered metaxylem pitting. The other line of the genus shows vitalized (mixed) protosteles and multiseriate scalariform metaxylem pitting, represented by *T. stewartii* (Eggert, 1959), *T. multiscalariformis* (Delevoryas and Morgan, 1952) and *T. africanus* (Holden and Croft, 1962). The latter group exhibits interconnections between *Tubicaulis* and *Anachoropteris involuta*-petioles, as was first demonstrated by Hall (1961). Phillips (1974) also reported small *Tubicaulis* shoots borne on *Anachoropteris*. This was confirmed by Galtier and Holmes (1984: pl. 2) studying material from Grand Croix, France, that resembled *T. stewartii* Eggert from the Upper Pennsylvanian of Illinois.

Several examples from the fossil record, however, exhibit small slender rhizomatous plants growing as epiphytes that probably found ideal conditions for mechanical support among adventitious roots on *Psaronius* trunks. Noted features are characteristic for *Tubicaulis scandens* Mamay, for instance, based on one single coal ball specimen from the Upper Pennsylvanian of Illinois. Comparable epiphytic growth habit on a *Psaronius* trunk was recently reported for *Botryopteris forensis* (Rothwell, 1991).

More than 40 *Tubicaulis* shoots penetrating the free root zone of *Psaronius* were newly discovered from the Permian of Chemnitz (Plate II, 3;

Plate III, 1–4 IV, 1–7). These allow us to recognize some more *Tubicaulis* plants as true trunk epiphytes, and to confirm the observation of Mamay (1952).

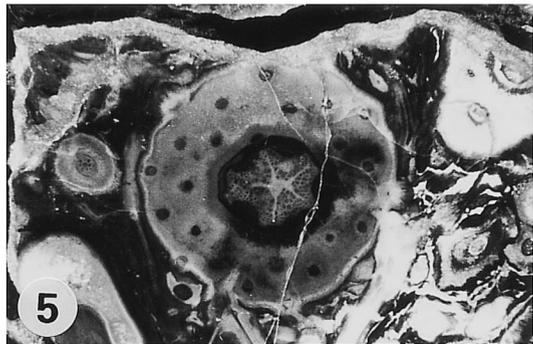
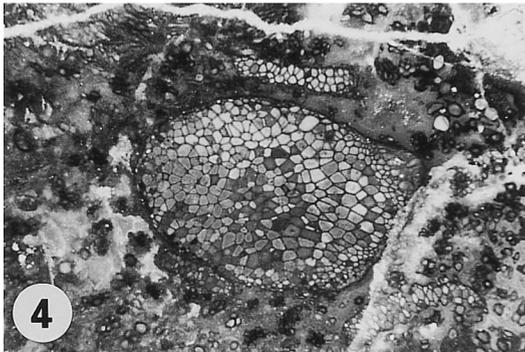
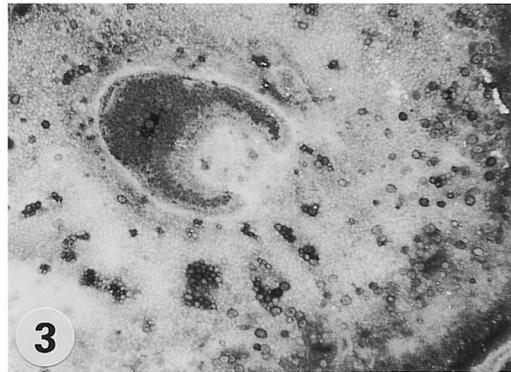
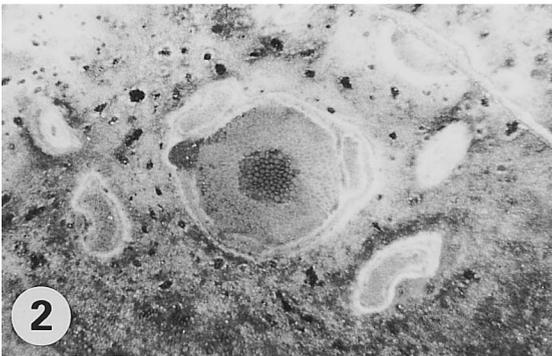
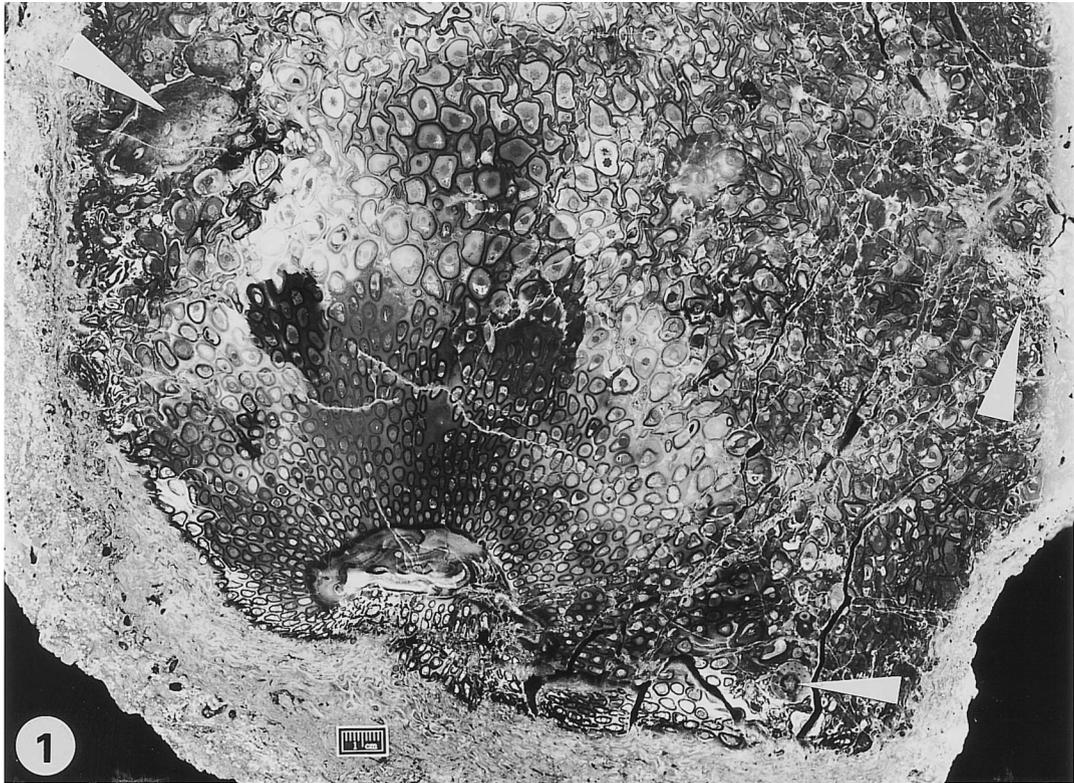
The slender sometimes branched axes show a thickness of between 15 and 35 mm. The central solid protosteles measures 2.3 to 6.5 mm, and is encircled by cortical parenchyma up to 12 mm wide. The vascular system is a simple tracheidal mass, and shows exarch maturation of the protoxylem groups. The surrounding cortical parenchyma consists of isodiametric cells with thin walls. Further, randomly distributed discrete patches of dark-brown to black thick-walled cells could be observed (Plate III, 2, 3; Plate IV, 3, 7). They may represent sclerotic nests. Leaf traces are spirally arranged in a 2/5 phyllotaxy. Axillary branching, as noted for the first time by Galtier and Holmes (1984), is very commonly seen. Numerous adventitious roots could be traced at the periphery of the axes. They have the typical coenopterid diarch xylem strands surrounded by the cortex, and dichotomize in their downward course.

Bertrand (1909) was first drawn to epiphytic *Tubicaulis* specimens after studying the Chemnitz material. Later, Bertrand and Bertrand (1911) established *Tubicaulis berthieri* for a single specimen from the Permian of Autun, France. Sahni (1931) reported epiphytic specimens of *Tubicaulis* from Chemnitz, and he confirmed the noteworthy frequency of these plants. He mentioned one specimen with seven *Tubicaulis* axes from Chemnitz. I believe that this important specimen, although never described in detail or figured, was recently traced in the collection of the Museum für Naturkunde Chemnitz (MfNC K 3475, Plate IV, 1–7). Sahni (1935) focused on one more Chemnitz specimen showing several *Ankyropteris* axes and

PLATE II

1. Bifurcating axes and petiole traces of *Ankyropteris brongniartii* on the upper part surface of a *Psaronius* trunk, MfNC K 228, $\times 0.5$.
2. *Psaronius* trunk showing eight *Ankyropteris brongniartii* axes on the periphery of the outer root mantle MfNC K 228, $\times 0.25$.
3. Cross-section of a *Psaronius* trunk containing four *Ankyropteris brongniartii* axes and one *Tubicaulis* sp. on the left margin, counterpart of the specimen drawn by Sahni (1935, fig. 1), MfNC K 2.
4. Cross-section of a *Psaronius* trunk containing one *Tubicaulis* sp. axis (big arrow) and three *Ankyropteris brongniartii* axes (small arrows), MfNC K 31.

PLATE III



one *Tubicaulis*, which he received from Max Güldner, a local private collector. During the present investigation, the counterpart of this specimen (MfNC K 2, Plate II, 3) was found in the Chemnitz collection. Most of the newly discovered material exhibits coexistence of these two genera on the same tree fern trunk. Although it seems obvious that the *Tubicaulis*-axes were frequent epiphytes on *Psaronius* trunks, it still remains unclear which sterile/fertile frond type belongs to *Tubicaulis* ferns and what the entire plants looked like.

3.2.4. *Psaronius*–*Anachoropteris*

Anachoropteris is an organ genus that was instituted by Corda (1845) for isolated petioles exhibiting a U-shaped to inrolled vascular strand with abaxially located protoxylem groups. Consequently, it represents the petiole of a heterogeneous group of ferns, and it is characterized by diversity in size, branching pattern and growth habit.

Until now there is multiple evidence of *Anachoropteris* petioles growing close to *Psaronius* trunks (Sahni, 1931; Mickle, 1984a: fig. 46; Doubinger et al., 1995: fig. 92). The material presented here shows three more anachoropterid axes within the outer root zone of *Psaronius*. One of them, specimen MfNC K 3475, is 15.5 mm × 9.2 mm wide and possesses a U-shaped vascular strand of 5.1 mm × 4.9 mm width. Comparing certain anatomical cortex details that are frequently seen in *Tubicaulis* specimens (groups of small thick-walled cells with dark content, large isolated cells with light content), it seems likely that it represents a free petiole of one of the *Tubicaulis*-plants, which are visible in cross-section (Plate IV, 1). It may be taken for granted that the specimen studied

(Plate IV, 2) is the same as the one that was reported, but not described or figured, by Sahni (1931).

Specimen MMG SaP 1900 (Plate V, 2, 3) two small anachoropterid petioles. The first measures 6.3 mm in diameter with a 4.1 mm × 2.5 mm wide vascular strand and several adaxially located protoxylem groups. The second measures 3.5 mm in diameter with a 2.0 mm × 1.4 mm wide vascular strand. Because of the typical inrolled vascular strand, it may be identified as *Anachoropteris pulchra* Corda. After comparisons with material of the Corda-collection stored in Prague, Czech Republic, the species *A. involuta* Hoskins is regarded as synonymous with the latter. A separate species seems unjustified from the current point of view, because the description presented by Hoskins (1930) does not note any clear differences. Although the new Chemnitz specimen exhibits two *Tubicaulis* axes, no direct connection between both organs, as shown by Hall (1961) and Galtier and Holmes (1984) for '*A. involuta*', could be identified.

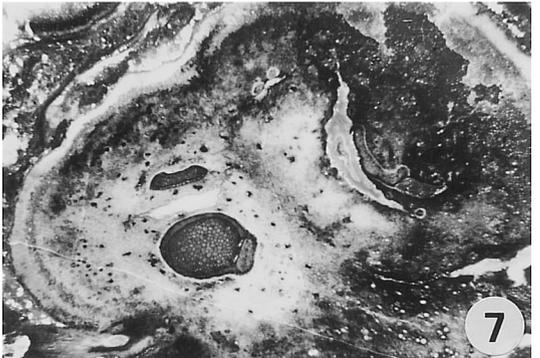
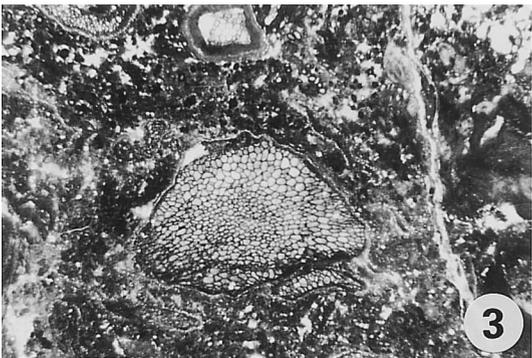
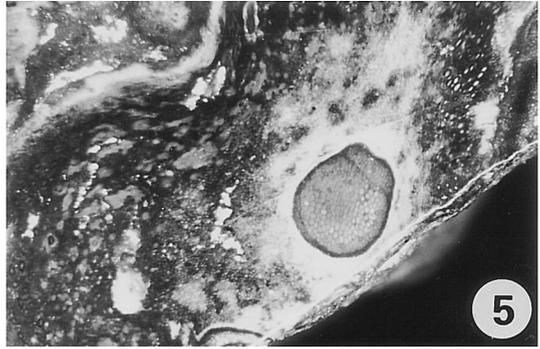
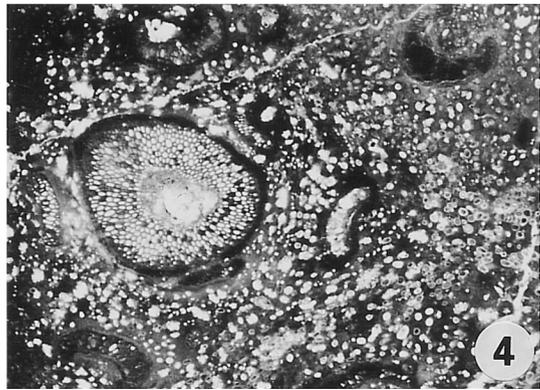
3.2.5. *Psaronius*–?*Grammatopteris*

Specimen SaP 1900 (MMG Dresden) exhibits a small slightly lobed solid protostele of 3.8 mm diameter surrounded by four probable petiole traces measuring ~1.0 mm in diameter (Plate V, 5). Both the protostele and the petiole traces are embedded in an insufficiently preserved ground tissue encircled by a few layers of ?cortical cells. The described questionable plant fossil with the entire width of 7.0 mm × 12.2 mm is densely surrounded by *Psaronius* adventitious roots. The mosaic of recognized characters closely resembles the genus *Grammatopteris* Renault. This genus was introduced by Renault (1893, 1896) to accommodate isolated protostelic stems that show spiral arrangement of the bar-shaped petiole traces with-

PLATE III

1. *Psaronius* trunk with two *Tubicaulis* sp. epiphytes (arrows) and one *Ankyropteris brongniartii* climber (arrow) embedded within the outer root zone of the tree fern, coll. Nestler 511.
2. Detail of the central protostele and leaf traces of the large *Tubicaulis* sp. (note the arrow on the left margin of 1), × 5.
3. Detail of a leaf trace of the large *Tubicaulis* sp. showing the axillary branching pattern and dark sclerotic nests of the cortical parenchyma, × 10.
4. Detail of the central protostele and leaf traces of the small *Tubicaulis* sp. (note the arrow on the right margin of 1), × 13.
5. Detail of the *Ankyropteris brongniartii* axis and associated aerial roots (note the arrow at the lower margin of 1), × 3.5.

PLATE IV



out any curvature. Based on their anatomical characters, it has been suggested that *Grammatopteris rigollotii* Renault and *G. baldaufii* (Beck) Hirmer (Plate V, 4) are closely related toosmundaceous ferns (Kidston and Gwynne-Vaughan, 1907; Beck, 1920). Both have been interpreted as small tree ferns.

If the identification of the present specimen can be accepted, the genus would be found within a *Psaronius* root mantle for the first time. Consequently, a different growth habit in comparison with the other known species of *Grammatopteris* is indicated.

3.2.6. *Psaronius*–*Dadoxylon*

There are two specimens in the Chemnitz collection showing *Psaronius* trunks overgrown by axes of the *Dadoxylon* type. One of them (MfNC K 4561), already figured by Urban (1974), represents a root of a ?cordaite tree/shrub growing hidden within the outer root zone of *Psaronius cottaie* Corda (Plate I, 3). The root of the *Amyelon*-type measures 65 mm in diameter and consists of dense secondary xylem tracheid rows. The weak indication of growth rings may demonstrate irregular periodically interrupted growth. The ratio of inner to outer root mantle of the *Psaronius* specimen suggests that it may represent a segment near the base of the former trunk. The interpretation that the contact between both plants was caused while the *Psaronius* tree was still living and standing erect may be supported by the following two observations. Firstly, the *Dadoxylon* specimen is almost completely surrounded by *Psaronius* adventitious roots; secondly, both plants exhibit the same direction of growth. Penetration of the *Psaronius* root mantle by the cordaite root at a

later time is highly unlikely because there was no peat accumulation until a volcanic eruption destroyed the small community. This example illustrates that few *Psaronius* species were growing in the same communities as *Cordaite*s, within restricted hygrophile areas, as has been shown at other Permian age localities (Barthel and Rößler, 1996; Rößler and Barthel, 1998).

A second specimen (MfNC K 669, Plate I, 4) demonstrates the preservational proximity of a gymnospermous stem preserved by a fragment of thick secondary xylem to the root mantle of *Psaronius*. Although it remains difficult to distinguish cordaite and conifers on the basis of their secondary xylem, the specimen presented may be recognized as a conifer-like stem. There are several anatomical characters, such as the uniseriate circular pitting and the small uniseriate rays, that support this interpretation.

3.2.7. *Psaronius*–*Callistophyton*

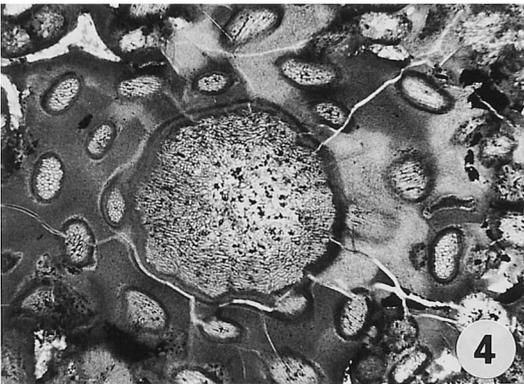
The genus *Callistophyton* Delevoryas and Morgan, 1954 was still unknown at the end of the last century, when most of the Chemnitz *Psaronius* specimens were collected. Some specimens from Autun, France, were firstly described by Renault (1879, 1880) as cordaitean material known as *Poroxydon boyssetii* and *P. edwardsii* (Rothwell, 1975). However, this group of gymnosperms quickly became the best understood Palaeozoic seed ferns. Rothwell (1975, 1980, 1981) reconstructed a scrambling understory plant with a slender eustelic stem and distantly spaced leaves, on the basis of three-dimensionally preserved coal ball material from the Late Pennsylvanian of North America.

The present study provides the first evidence of

PLATE IV

1. Portion of a *Psaronius* outer root zone containing seven epiphytic axes of *Tubicaulis* sp. (five of them are indicated by white arrows) and one petiole of *Anachoropteris* sp. (black arrow), MfNC K 3475.
2. Detail of 1, isolated petiole of *Anachoropteris* sp. that possibly belongs to one of the *Tubicaulis* stems of the specimen, $\times 5$.
3. Detail of 1, central protosteles of first *Tubicaulis* sp. with few C-shaped traces, $\times 6$.
4. Detail of 1, second *Tubicaulis* sp. with C-shaped traces, $\times 4.5$.
5. Detail of 1, third *Tubicaulis* sp. with C-shaped traces, $\times 7.5$.
6. Detail of 1, fourth *Tubicaulis* sp. with C-shaped traces, $\times 7.5$.
7. Detail of 1, fifth *Tubicaulis* sp. with C-shaped traces, $\times 4.5$.

PLATE V



permineralized *Callistophyton* plant remains from the Lower Permian age pyroclastics of Chemnitz. Several fragments of silicified *Psaronius* root mantles allowed the recognition of *Callistophyton*-like plant fragments. The material exclusively consists of roots.

In a fragment of the largest known *Psaronius* trunk (MfNC K 620), Stenzel (unpubl.) found a curious '*Psaronius* root' showing secondary xylem. Butterworth (1900) and Scott (1900: p. 275) described comparable features on *Psaronius cromptonensis* from the Coal Measures of Lancashire. Finally, Solms-Laubach (1911) dealt with that phenomenon, and he re-examined thin sections of Butterworth's and Scott's material. Moreover, he mentioned comparable observations on *Psaronius* specimens from Brasil (coll. Solms 581, 582, 588). However, he did not recognize the true nature of the small roots. The Chemnitz specimen mentioned by Solms-Laubach (1911) was re-examined, observations based on new finds were added, and both lines of evidence support the interpretation and identification as roots of *Callistophyton*. Moreover, the Chemnitz material exhibits different sizes of the roots from thin rootlets (Plate VI, 6, 7 to relatively thick ones (Plate VI, 1–5). As Rothwell (1975) has shown, *Callistophyton* roots are protostelic and diarch, with exarch maturation of the primary xylem. The smaller ones measure 0.5–0.9 mm in diameter, and consist of a diarch primary xylem surrounded by a continuous zone of primary cortex. Some of the isodiametric cells of the cortex contain dark contents. The outermost slightly darker cell layer may represent the rhizodermis. The larger mature roots measure 5.2–6.4 mm in diameter, and exhibit many radial rows of secondary xylem. Vascular cambium and secondary phloem surround the xylem. The phloem is surrounded by a few layers of cortical

cells and thin-walled cells of the ?periderm (Plate VI, 5). Additionally, figured material (Plate VI, 5) shows coprolites enriched within the phloem tissue of the *Callistophyton* roots.

Compression material of *Dicksonites pluckenettii* (Schlotheim) Sterzel that is suggested to be closely related to Callistophytales (Stidd and Barthel, 1979; Meyen and Lemoigne, 1986) is also noted from the Zeisigwald tuff horizon of Chemnitz. Besides, regarding the growth habit of the plant there exists a close relationship between the reconstruction given by Rothwell (1975), and Permian compression material of the Saar-Nahe Basin, Germany, figured by Barthel (1996: fig. 8). In the light of the new finds presented here, which show *Callistophyton* organs growing on *Psaronius* trunks, the observation of Zeiller (1888, pl. VIII, fig. 1) regarding the doubtful connection of *Psaronius* stems and *D. sterzeli* fronds becomes clearer, and may be regarded as solved now.

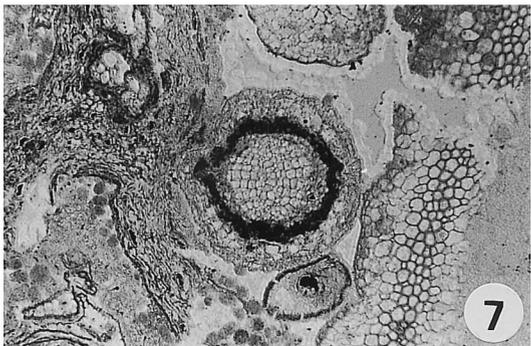
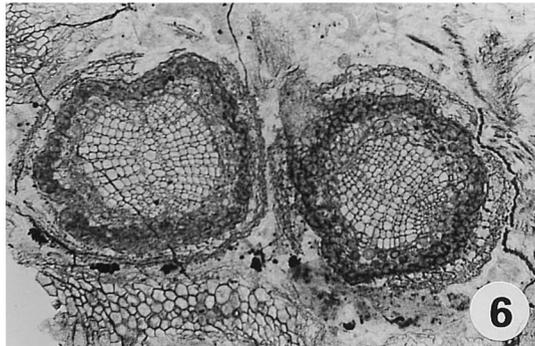
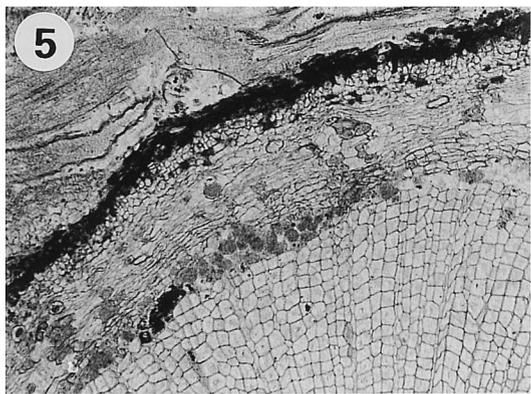
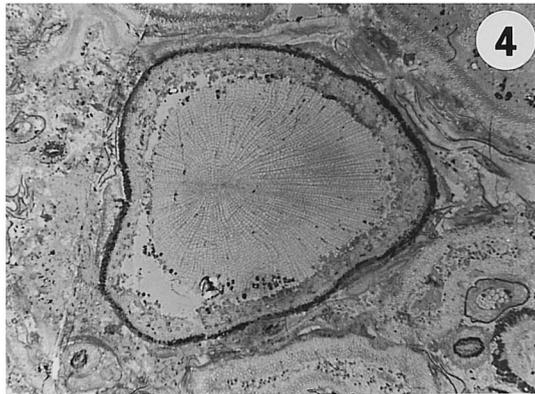
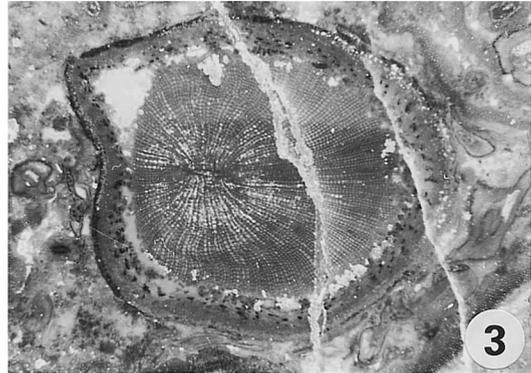
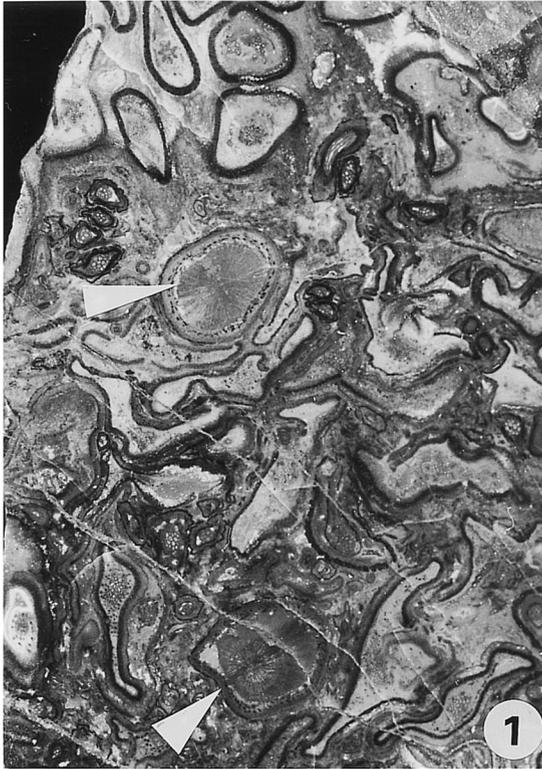
3.3. *Psaronius* and evidence of animal life

As several authors recently showed, different arthropods play an important role in Permian-Carboniferous ecosystems (Todd, 1991; Dunlop, 1994; Labandeira et al., 1997). The frequent presence of numerous predators, such as trigonotarbid and phalangiotarbid suggests highly developed food webs. Representatives of the lowest level may be some detritivores or herbivores such as mites, collembolan hexapods or isopods that played an important role in decomposing plant litter (Scott, 1977). Many arthropod groups produce faecal pellets of distinctive sizes that may be fossilized. Therefore, coprolites of different size, shapes and contents are very abundant in the fossil record. Nevertheless, faecal pellets of most fossil arthropod groups are less well known.

PLATE V

1. Portion from the outer root zone of a *Psaronius* trunk containing two *Tubicaulis* sp. specimens (white arrows), two *Anachoropteris pulchra* petioles (small black arrows) and one ?*Grammatopteris* sp. axis (big black arrow), MMG SaP 1900.
2. Detail of 1, isolated *Anachoropteris pulchra* petiole, $\times 10$.
3. Detail of 1, isolated *Anachoropteris pulchra* petiole, $\times 12$.
4. Protostele and leaf traces of *Grammatopteris baldaufii* (Beck) Hirmer from Chemnitz for comparison with 5, BAF 171/1, $\times 6$.
5. Detail of 1, ?*Grammatopteris* sp. axis, $\times 6$.

PLATE VI



Re-examination of several thin sections of the Chemnitz collection resulted in multiple indirect evidence of arthropod life. This may be demonstrated by small coprolites, oval faecal pellets of two significant size orders. First averages about 54.14–73.53 μm , second reaches 30.15–42.05 μm in length. As well as the major vegetation elements, *Psaronius* tree ferns and related epiphytes/vines/scramblers are affected in particular. Rothwell and Scott (1983) reported enrichment of coprolites within Marattiaceous fern ground tissue from the Upper Pennsylvanian Monongahela Group of Ohio. Labandeira and Phillips (1996b) or Labandeira (1998) considerably extended our knowledge of plant–animal interactions by demonstrating instructive examples of insect herbivory during the Late Carboniferous. Most interesting seems the evidence of insect fluid-feeding on Upper Pennsylvanian tree ferns. Moreover, they suggest the possibility that the widespread distribution of *Psaronius* forests during the Late Pennsylvanian (DiMichele and Phillips, 1994) may have offered an important food source to sap-sucking insects, and affected development of piercing-and-sucking mouthparts of Palaeodictyoptera. These insects were able to feed on vascular tissues of living plants.

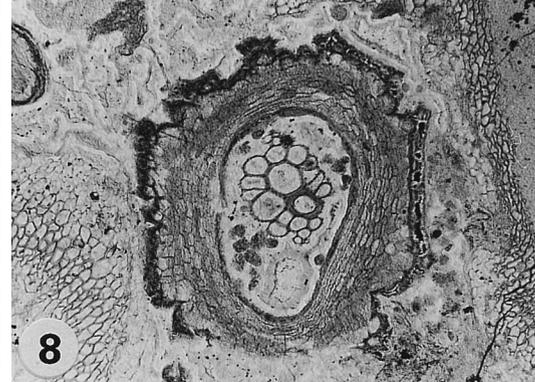
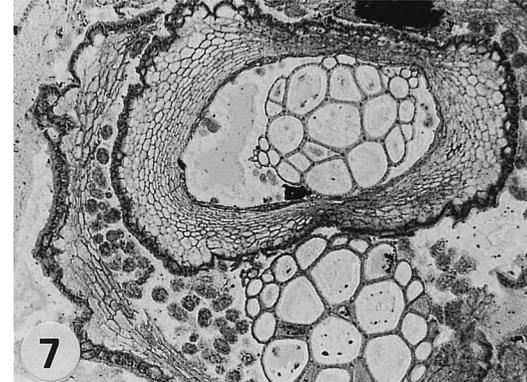
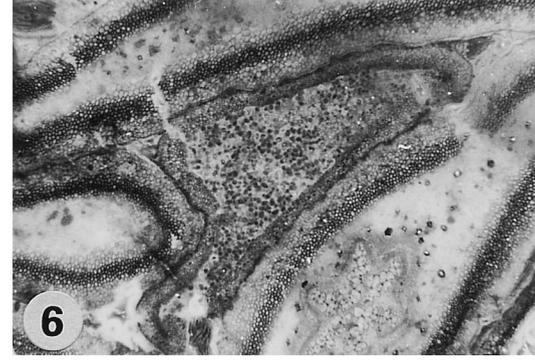
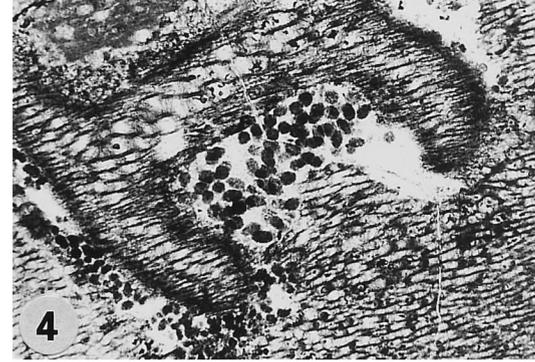
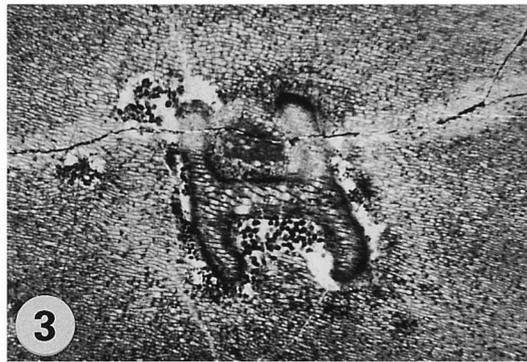
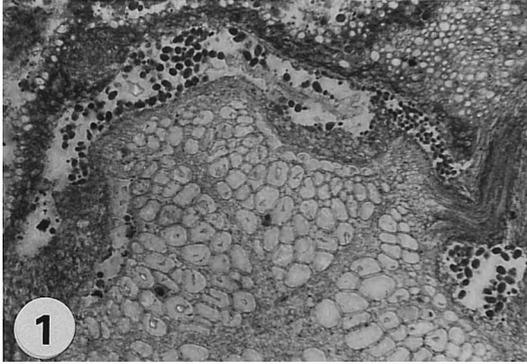
Recently, Labandeira and Phillips (1996a) presented an insight into the early ecological history of the holometabolous insects. They showed that by Late Pennsylvanian times larvae of such insects were galling the internal tissue of *Psaronius* tree fern fronds. Labandeira et al. (1997) reviewed the important role of oribatid mite detritivory affecting all major plant taxa including lycopsids, sphenopsids, ferns, pteridosperms and cordaites during a

17 million year interval from the Euramerican tropic coal swamp forests. Current investigation could extend this evidence into more restricted Permian age environments and to other plants. Whereas Labandeira et al. (1997) deduced that their coprolite producers consumed dead plant tissues and related fungi at ground level, based on Permian age material from Chemnitz I would like to suggest that not only rotted plant parts are used as a living area and coprolite store. Erect still-living plants may have been affected by small arthropods, as some taphonomic characters of the petrified forest material indicate (Rößler, 1996). Walter et al. (1994) reported evidence of facultative herbivores among extant oribatid mites. However, the general preference for soft tissues, such as thin-walled cortical parenchyma of the *Psaronius* root mantles or phloem of climbing and epiphytic ferns or pteridosperms by the herbivores can be confirmed by this study. Two distinct size orders of the coprolites indicate coexistence of different arthropods or different ontogenetic stages of them, as larva, nymphs or adults. There is no regular transition between the coprolite sizes that would allow their interpretation as products of growing individuals. Coprolites of the Chemnitz permineralizations occur within the small galleries of the ground tissue of the root mantle, and show groups of 5 to 60 ovoid bodies. Significantly, on *A. brongniartii* climbing axes the coprolite producers especially used the soft-porous tissue surrounding the pentarch stele or around the H-shaped vascular strands (especially at the phloem tissue) of the petioles (Plate VII, 1–4) parenchyma of the inner root mantle, as well as the aerenchyma of the larger adventitious roots of the outer root mantle,

PLATE VI

1. Broken fragment of the large *Psaronius weberi* Sterzel with several *Callistophyton* roots (arrows) in the outer root zone of the tree fern, ground and polished surface, MfNC K 620 c, $\times 3$.
2. Detail of 1, $\times 8$.
3. Detail of 1, $\times 8$.
4. Detail of 1, transverse section, $\times 7$.
5. Detail of 4, showing secondary xylem, phloem and cortex of the diarch root; on the interface between secondary xylem and phloem abundant coprolites are seen, $\times 35$.
6. Detail of 1, juvenile diarch *Callistophyton* roots, transverse section, $\times 35$.
7. Detail of 1, juvenile diarch *Callistophyton* root, coprolites within the *Psaronius* ground tissue, transverse section, $\times 35$.

PLATE VII



frequently show large groups of coprolites (Plate VII, 6). Comparable coprolites can also be noted from the phloem of *Callistophyton* roots (Plate VI, 5), from the parenchyma of the adventitious roots of coenopterid ferns (Plate VII, 7, 8) and from the dense secondary xylem of conifers. New observations may complete the poor information of plant–animal interactions during the Permian. Whereas the shape and size of the coprolites resemble those of oribatid mites mentioned by Labandeira et al. (1997), the identity of the organisms responsible remains uncertain until body fossils are found.

4. Conclusions

Considering the observations and comparisons above, I would like to conclude that *Psaronius* tree ferns exhibit an exceptional ecosystem by themselves, accommodating a variety of other, especially non-psaroneaceous, plants and plant organs. This assumption may be underlined by the frequent occurrence of plant–arthropod interactions in *Psaronius* trunks.

All examples of interactions mentioned above are interpreted as having happened on living tree ferns. The orientation of the climbers/epiphytes and their dense interaction with the host plant allows us to conclude there was rapid preservation, and to exclude the possibility that the interactions could have resulted during taphonomic processes.

It will be useful, in the future, to search not only for axes and their branching patterns and

different roots, but also for reproductive organs possibly embedded in *Psaronius* outer root mantles far more so than has previously been done. There still remain several foliage types of uncertain affinity among lower Permian Rotliegend floras.

The massive root mantles protected different developing plants, and they may have improved the possibility of preservation of smaller plants and plant organs in particular.

The *Ankyropteris*-vines, and especially the *Tubicaulis*-epiphytes, were astonishingly frequent, far more than commonly thought. Nearly every *Psaronius* of the Chemnitz collection that has a preserved free root zone shows at least one other plant growing in close association with the host plant. Certainly the closer investigation of *Psaronius* root mantles will provide further surprises in the future. In spite of dissimilarities in both environmental preferences and different growth habits in some cases, the comparison of *Psaronius* specimens with extant tree ferns and their living conditions may help to understand the variety of plant functional adaptations and to interpret their interactions in a palaeoecological context.

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PLATE VII

1. Transverse section of an *Ankyropteris brongniartii* axis showing two different sizes of coprolites in small cavities around the pentarch stele, MfNC K 4569, $\times 20$.
2. Detail of 1, $\times 40$.
3. Transverse section of a petiole of *Ankyropteris brongniartii* showing H-shaped trace. Coprolites have replaced former phloem and parenchyma tissues, MfNC K 4568, $\times 14$.
4. Detail of 3, $\times 35$.
5. Transverse section of an *Ankyropteris brongniartii* marginal axis showing partly destroyed cortex area densely filled with coprolites, MfNC K 4568, $\times 14$.
6. *Psaronius* adventitious root densely filled with coprolites, MfNC K 31, $\times 10$.
7. Transverse section of small diarch adventitious roots that are known from different coenopterid ferns, MfNC K 620 c, $\times 35$.
8. Transverse section of a small diarch adventitious root, MfNC K 620 c, $\times 35$.

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