ASPECTS OF PERMIAN PALAEOBOTANY AND PALYNOLOGY. III. A NEW RECONSTRUCTION OF *LILPOPIA RACIBORSKII* (LILPOP) CONERT ET SCHAARSCHMIDT (SPHENOPSIDA)

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ABSTRACT

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The Early Permian plant *Lilpopia raciborskii* (Sphenopsida) has been found for the first time outside its type region, the Karniowice area (Poland). On the basis of this new material, collected in the "Waderner Gruppe" of Sobernheim (Nahe area, German Federal Republic), *L. raciborskii* is described and discussed in the light of previous concepts of this species; a new and more complete reconstruction of the taxon is presented. For the first time epidermal features are described. The heterophyllous leaves of *L. raciborskii* are compared with *Sphenophyllum thonii* var. *minor* Sterzel.

KURZFASSUNG

Die unterpermische Pflanzenart *Lilpopia raciborskii* (Sphenopsida) ist zum ersten Mal ausserhalb des Typusgebietes, die Karniowice-Gegend (Polen), gefunden worden. An Hand dieses neuen Material, aufgesammelt in der Waderner Gruppe von Sobernheim (Nahe-Gebiet, B.R.D.), wird *L. raciborskii* zusammenfassend beschrieben unter Berücksichtigung der früheren Auffassungen; es wird eine neue vollständigere Rekonstruktion präsentiert. Zum ersten Mal werden Epidermisstrukturen beschrieben. Es werden Vergleiche mit anderen *Lilpopia*-Arten gezogen. Die heterophylle Blätter von *Lilpopia raciborskii* werden verglichen mit denen der *Sphenophyllum thonii* var. *minor* Sterzel.

INTRODUCTION

In 1937, Lilpop described the new monotypic genus *Tristachya* and placed it within the Sphenopsida. The type material originated from the Karniowice travertine at Karniowice (35 km west of Krakow, Poland). The age of these sediments is supposed to be Early Autunian (Lipiarski, 1971).

The material Lilpop studied was earlier described as *Sphenophyllum* sp. (Roemer, 1870) and *S. emarginatum* (Raciborski, 1891). Based on fertile structures, discovered by Lilpop, the genus *Tristachya* was established. The most complete specimen of Lilpop's fragmentary material consisted of an

articulated axis, holding one or two sterile and three fertile verticils. Each fertile verticil consists of three wedge-shaped *Sphenophyllum*-like leaves and three strobili with peltate sporangiophores. The arrangement of the strobili in verticils differs from the usual terminal attachment of strobili in *Sphenophyllum*. Lilpop's reconstruction shows the strobili as inserted in the axils of the wedge-shaped leaves.

Emberger (1944) considered *Tristachya raciborskii* as the member of a new family, the Tristachyaceae.

A problematical fossil was described and figured by Remy (1955) as *Tristachya* sp., from the Westphalian D of Friedrichsthal (German Federal Republic), but unfortunately the photograph does not show enough details for the justification of this identification.

A second, formally named, species of the genus *Tristachya* from the Autunian of Crock (Thuringia, German Democratic Republic) was described by Remy and Remy (1961). The type material of their new species, *T. crockensis*, was also fragmentary. In general their reconstruction of *T. crockensis* corresponds with Lilpop's reconstruction of *T. raciborskii*.

Conert and Schaarschmidt (1970) replaced the generic name *Tristachya* by *Lilpopia*: *Tristachya* appeared to be a later homonym of the name *Tristachya* Nees von Esenbeck 1829, which was used for the description of an extant grass from southern Africa.

Lipiarski (1972a) reexamined Lilpop's type material and he also collected new material in the type locality. He concluded that Lilpop's generally accepted reconstruction of *Lilpopia* was wrong. He demonstrated that in the fertile verticils the strobili alternated with the leaves, instead of being inserted in the axils of the leaves. Lipiarski's conclusions were mainly based on the examination of the lectotype, chosen by Conert and Schaarschmidt (1970).

A third species (*L. polonica*) was described, again from the Karniowice travertine, by Lipiarski (1971, 1972b). Although only small specimens of *L. polonica* were found, the new conception of the reconstruction of *Lilpopia* appeared to be correct.

The present material of *Lilpopia raciborskii* has been collected from the Lower Permian in the Nahe area, German Federal Republic. The material is reasonably preserved and includes the largest specimen so far known. Therefore the material has been studied in detail, in order to obtain a better insight in the morphological organization of this interesting species. A preliminary note on the material was earlier presented by Kerp (1981).

SOURCE STRATA

The material described in this report was collected in the brick-pit excavation of "Ziegelei Eimer" at Sobernheim, Nahe area, German Federal Republic. The predominantly red clay- and siltstones excavated at Sobernheim are intercalated between breccio-conglomerates of the Waderner Gruppe (= Nahe Gruppe of Boy and Fichter, 1982). Plant remains occur in some grey-green siltstone levels, but occasionally also in the red clay- and sandstones.

Plant fossils from the brick-pit were mentioned for the first time by Geib (1950), who gave a short list of floral and faunal remains occurring at Sobernheim. The age of the fossiliferous beds was presumed to be "Upper Rotliegendes". This age was based on the co-occurrence of typical Autunian taxa together with *Ullmannia*, which normally occurs in Upper Permian strata. Several other authors (e.g., Falke, 1972; Remy and Remy, 1975) followed Geib's suggestion, attributing a Saxonian age to the Waderner Gruppe. Visscher et al. (1974) argued that the use of the Saxonian Stage has to be rejected, because no adequate biostratigraphical characterization of this stage could be given.

A rich collection of plant fossils from Sobernheim has been assembled by staff members and students of the Laboratory of Palaeobotany, Utrecht. Detailed studies on the fossil flora of Sobernheim, carried out during the last five years, convinced the present author of the absence of Late Permian elements. Moreover, a revision of Geib's original Sobernheim collection, stored in the Karl Geib Museum at Bad Kreuznach, was included in the investigations. Geib's *Ullmannia* appeared to be a misidentification based on poorly preserved material (Dr. K.W. Geib, Mainz, pers. commun., 1981). Also other reports on the occurrence of *Ullmannia* in the Rotliegendes of the Saar-Nahe Basin (Schuster, 1908) can be questioned, because the coniferalean fragments are too fragmentary for an accurate identification.

Up to the present time some forty taxa of plant megafossils are known from Sobernheim. An updated list of taxa so far identified is given by Kerp (1982). The macroflora has a typical Autunian character. Also the palynoflora indicates an Autunian age (Visscher et al., 1974). The presence of *Crucisaccites* allows a correlation with the oldest Permian deposits in the Donetz Basin (Dr. H. Visscher, pers. commun., 1982). It should be pointed out that the definition of the Carboniferous/Permian boundary is still one of the major problems of Upper Palaeozoic stratigraphy (Kozur, 1978).

The rich macroflora of Sobernheim is dominated by *Pecopteris cyathea*. Other characteristic floral elements include *Callipteris conferta*, *C. scheibei* and several species of the genus *Walchia*. Nearly all the specimens of *Lilpopia raciborskii* were found in an assemblage with *Pecopteris cyathea*, *Calamites* sp., *Annularia spicata* and *Calamostachys spicata*.

MATERIAL AND METHODS

The material present in the collection of the Laboratory of Palaeobotany and Palynology has been sampled in 1970 (the specimens with the collection numbers 4344A and 4344C), 1972 (6907), 1973 (6918A–6918H) and 1981 (8337–8347 and 13171). A well preserved isolated leaf is stored in the collection of the Forschungsinstitut Senckenberg at Frankfurt (B 13483).

The material is preserved as compressions/impressions. Unfortunately several attempts to isolate spores from the strobili and to make transfer preparations of the leaves were not successful. However, in a few cases epidermal features are preserved as impressions in the fine-grained rock matrix.

Careful preparation proved to be a prerequisite. The preparations were carried out under a binocular dissecting microscope with delicate chisels and needles. A drawing tube was attached for sketching. Photographs were made under polarized light.

Since epidermal features are preserved in the rock matrix rubber latex casts were prepared. These casts were subjected to scanning electron microscopy (cf. Chaloner and Gay, 1973; Chaloner and Collinson, 1975), which yielded important information on the cuticular anatomy.

DESCRIPTION

Lilpopia Conert et Schaarschmidt 1970

Type species: Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt 1970.

Original diagnosis: The following combined diagnosis for the genus *Lilpopia* and the species *L. raciborskii* was given by Lilpop (1937, p. 9): "Stems articulated, sixangular. Leaves to 6 in one verticil, superposed, wedgeshaped, bilobed, with rounded lobes and denticulated frontal edge. Leafy bracts triangularly ovoid, 3 in one verticil. Sporophylles peltate, disposed in 4 verticils on the central axis, alternating."

The generic diagnosis of *Lilpopia* was emended by Lipiarski (1972a, p. 102): "Three cones occur in a node together with the leaves, alternating with them."

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt 1970

Synonymy

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt: 1970, *Taxon*, 19: 793–795.

1971 Lipiarski, *Pr. Państw. Inst. Geol.*, 58: 30–31, 64, 72–73, 83–84, 100, 111; pl. IV, 6–21, pl. V, 1.

1972 Lipiarski, *Acta Palaeobot.*, 13: 101–109; figs. 1–4 (fig. 1A after Lilpop).

1981 Kerp, *Cour. Forsch.-Inst. Senckenberg*, 50: 17–21; fig. 1.

Tristachya raciborskii Lilpop: 1937, *Bull. Int. Acad. Pol. Sci. Lettr.*, Sér. B, 1: 1–10; pl. I, figs. 1–3.

Sphenophyllum emarginatum (Brongniart) Brongniart: 1891, *Raciborski, Rozpr. Wydz. Mat. Przyr.*, 21: 378; pl. V, 20–30; pl. VII, 23(?).

Sphenophyllum sp.: 1870 Roemer, *Geologie von Oberschlesien*, p. 117; pl. IX, 4.

Type material

Lectotype: The specimen figured by Lilpop (1937, pl. I, 1–2 and pl. I, 3–4 (gelatine casts) was chosen as the lectotype (Conert and Schaarschmidt, 1970).

Locus typicus: Karniowice, 35 km west of Krakow, Poland.

Stratum typicum: Karniowice travertine, Autunian.

The specific diagnosis of *Lilpopia raciborskii* was emended by Lipiarski (1972a, p. 102): "In a fertile verticil there occur three leaves with anterior

margins rounded or with a heart-shaped concavity. In a sterile verticil there occur six leaves with the anterior margins rounded, incised or covered with teeth.

Cone consists of 18 to 24 sporangiophores developed as peltate heads set perpendicularly to the cone and forming verticils."

Description of the present material

The largest specimen, 4344A and its counterpart 4344C [Plates I—III, Plate IV, 1 and Plate VI, 1, 3 (latex casts)], consist of an axis of the ultimate order with portions of three axes of ultimate order, two of them being distinctly fertile. One axis of the ultimate order is only partially preserved. The connection of the lowermost axis of the ultimate order with the axis of penultimate order is missing. The two other axes of the ultimate order are directed apically, having an angle of approximately 40° with the axis of the ultimate order. The axis of the penultimate order shows five nodes. Apically the length of the internodes decreases. The length of the internodes and their width at the nodes are given in Table I.

Axes of the penultimate order are principally triangular in transverse section, but hexangular at the thickened parts near the nodes.

Eight nodes of the lowermost axis of the penultimate order are preserved, three of them distinctly bearing fertile verticils. The middle axis of the ultimate order is only fragmentarily preserved as a portion with one internode. Three nodes of the uppermost axis of the ultimate order are preserved, the uppermost one bearing the strobili. In shape the axes of the ultimate order resemble the axis of the ultimate order. The attachment of the uppermost axis

TABLE I

Length and width of nodes and internodes of the axis of penultimate order and the three axes of ultimate order of the specimens 4344A and 4344C (part and counterpart) (all measurements are given in millimeters)

Axis of penultimate order	1st	2nd	3rd	4th	5th	6th		
Length of the internode	—	48	40	37.5	37.5	—		
Minimum width of the internode	4.5	3	4	4	4	3.5		
Maximum width of the node	5	6	6	6	6	4		
Lowermost axis of ultimate order	1st	2nd	3rd	4th	5th	6th	7th	8th
Length of the node	?11	13	9.5	8.3	9	7.5	10	9
Width of the internode	2.5	3.4	2.6	2.3	2.3	2.6	2.6	2.3
Middlemost axis of ultimate order	1st	2nd	Uppermost axis of ultimate order		1st	2nd	3rd	
Length of the internode	?8	—			6	11	7	
Width of the node	3	—			2.5	3	1.7

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt

1. Specimen 4344 ($\times 1$). Axis of penultimate order with portions of three axes of ultimate order. Arrows: A = fragment of middlemost axis of ultimate order; B = strobilus of the uppermost axis of ultimate order.

PLATE II

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt

1. Specimen 4344A ($\times 1$). Counterpart of specimen 4344C (Plate I, 1). Arrow C indicates the uppermost axis of ultimate order with two leaves and one strobilus at the third node.

PLATE III (p. 245)

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt

1. Specimen 4344C ($\times 3$). The two strobili and two leaves of the third node of the uppermost axis of ultimate order.
2. Specimen 4344C ($\times 2$). Uppermost axis of ultimate order with attachment to the axis of penultimate order.
3. Specimen 4344A ($\times 3$). Counterpart of the same axis as shown on Plate III, 3. The arrow indicates a strobilus. Under alcohol.
4. Specimen 4344A ($\times 6$). The fourth verticil of the lowermost axis of ultimate order showing three strobili and three leaves. Under alcohol. Arrows: C = middlemost strobilus; S = front side of peltate sporangiophore with in the centre a small shallow cavity.

PLATE IV (p. 246)

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt

1. Specimen 4344C ($\times 2$). The lowermost axis of ultimate order with the 2nd—7th node.
2. Specimen 8337B ($\times 4$). Portion of an axis with a fertile and a sterile verticil. The arrow indicates a strobilus. The leaf of the sterile verticil is also figured on Fig.3. Under alcohol.
3. Specimen 8341A ($\times 3$). Two incomplete sterile verticils with a portion of an axis. Notice the heterophylly within a single verticil. The leaf indicated by an arrow is also figured on Fig.5.

PLATE V (p. 247)

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt

1. Specimen 8338 ($\times 4$). Part of an axis with a fertile verticil with two leaves and two strobili preserved. The arrows indicate the positions of the strobili. Compare with Fig.2. Under alcohol.
2. Specimen 8339 ($\times 4$). Part of an axis with a sterile verticil. The leaf in the upper left quadrant is also figured on Fig.4. Under alcohol.
3. Specimen 13171 ($\times 2$). Complete sterile verticil with six leaves.

PLATE VI (p. 248)

Lilpopia raciborskii (Lilpop) Conert et Schaarschmidt

1. Specimen 4344A. Latex cast showing a sporangium of the right strobilus of the second fertile verticil of the lowermost axis of ultimate order. SEM $\times 75$, angle of the stub 30° .
2. Specimen B 13483. Latex cast showing adaxial and abaxial epiderm of the leaf. The elevated part in the centre represents the abaxial epiderm. SEM $\times 60$, angle of the stub 30° .
3. Specimen 4344A. Same sporangium as on Plate VI, 1. SEM $\times 47.5$, angle of the stub 15° .
4. Specimen B 13483. Latex cast showing the venation, the adaxial epiderm and a part of the abaxial epiderm (in the lowermost part of the picture). SEM $\times 7.5$, angle of the stub 30° .
5. Detail of Plate VI, 4 showing a single stoma. SEM $\times 900$, angle of the stub 30° .
6. Detail of Plate VI, 4 showing the adaxial epiderm with coarsely sinuous cells and narrow elongate cells over the veins. SEM $\times 400$, angle of the stub 30° .

PLATE III

Description on p. 244

PLATE IV

Description on p. 244

PLATE V

Description on p. 244

PLATE VI

Description on p. 244

of the ultimate order to the axis of the penultimate order is shown on Plate III, 2, 3.

All the leaves attached to the axis of the penultimate order are only fragmentarily preserved. The broad, wedge-shaped leaves are set perpendicularly to the axis or they are raised apically with their convex sides up. No anterior margins of leaves attached to the axis of the penultimate order are preserved. The longest leaf fragment of the axis of the penultimate order measures at least 11 mm.

Most of the sterile and fertile verticils of this specimen are incomplete. Leaves and/or strobili are missing or still hidden in the matrix.

The lowermost two nodes of the strobili-bearing axes are sterile. The second node of the lowermost axis shows two elliptical leaf scars between the two laterally directed leaves (Plate IV, 1). The fourth verticil of the lowermost axis of the ultimate order is the only one showing all the components of fertile verticil (Plate III, 4). It consists of three leaves and three strobili. The leaves alternate with the strobili. The alternation can also be observed in the third verticil of the uppermost axis of the ultimate order. Plate III, 1, 2 shows two strobili and two leaves. Both strobili are directed sideways. One leaf is directed frontwards and is inserted between the strobili. The other leaf is directed sideways, partially situated behind the strobilus on the left side.

Each strobilus consists of approximately 20 sporophylls. Each sporophyll shows a small shallow cavity on the front side (Plate III, 4, indicated by two arrows and S). They resemble the sporophylls of the extant genus *Equisetum*. On a latex cast of the right strobilus of specimen 4344A sporangia were identified. The sporangia are ovoid, 0.7–0.8 mm long and 0.45–0.5 mm wide. Cells of the sporangium wall are irregularly shaped, most being elongate, polygonal, 46.7–100 μm long and 26–41.6 μm wide, and arranged in more or less longitudinal rows.

Although only a few leaves of the fertile branches of specimen 4344A/4344C are completely preserved, heterophylly could be observed. The lowermost two verticils of a fertile axis bear narrow lobate leaves, whereas the fairly broad leaves of the higher situated fertile verticils are wedge-shaped.

Specimen 8337A (Fig.1) shows a portion of an axis with four fertile and two sterile verticils. Its counterpart, specimen 8337B (Plate IV, 3; Fig.2), shows two fertile and one sterile verticil. The impression of the uppermost verticil of specimen 8337B, corresponding with the fifth verticil of specimen 8337A, shows a nearly complete leaf. This is the only almost completely preserved leaf found in connection with a strobili-bearing axis. The leaf is 11 mm long and approximately 6 mm wide. The anterior margin is rounded with obtuse teeth. Each tooth is 0.4 mm long and 0.4 mm wide at the base. The basal part of the leaf is not preserved. Veins dichotomize 2–5 times, usually 4 times at equal intervals. Approximately 20 veins terminate at the anterior margin. Near the very base of the leaf faintly visible veins terminate at the lateral margins.

On specimen 8338 (Plate V, 1; Fig.2) a part of an axis with two strobili

Fig.1. *Lilpopia raciborskii* (Lilpop) Conert et Schaarschmidt. Specimen 8337A. Axis with six verticils, four of them being fertile. Scale bar 5 mm.

Fig. 2. Specimen 8338. Part of an axis with a sterile verticil with two strobili and two leaves. The arrow indicates a leaf scar. Scale bar 5 mm.

Fig.3. Specimen 8337B. A single leaf showing the venation. Scale bar 1 mm (also figured on Plate IV, 2).

and two leaves is preserved. On the front side of the node, between the two strobili a leaf scar is to be seen (on Fig.2 indicated by an arrow). One thick vein is entering the leaf which is situated at the right side of the axis.

Together with the fertile specimens mentioned above, several isolated strobili, isolated leaves and sterile verticils have been collected. Specimen 8339 (Plate V, 2; Fig.4) shows an incomplete sterile verticil, with well-preserved venation. Specimen 8341A (Plate IV, 3; Fig.5) consists of a portion of an axis with two incomplete sterile verticils. The leaves are wedge-shaped. The anterior margins are irregularly denticulate. Teeth obtuse, normally up to 0.4 mm long and 0.4 mm wide at their base, but also longer teeth, up to 1.3 mm long and 0.6 mm wide, occur on the same leaves. Specimen 13171 (Plate V, 3) shows a complete verticil of six leaves. In specimen B 13483, an incomplete sterile leaf of the normal wedge-shaped type, impressions of the abaxial and the adaxial epidermis are preserved in the fine-grained rock matrix. The epidermal features were studied from latex casts under the SEM. The cast shows the adaxial epidermis and some small parts of the abaxial epidermis. The elongate epidermal cells are arranged in longitudinal rows parallel to the veins. In the adaxial epidermis, apart from the guard cells of the stomata, two types of cells can be distinguished: (1) narrow

Fig.4. *Lilpopia raciborskii* (Lilpop) Conert et Schaarschmidt. A single leaf of specimen 8339 showing the venation. Scale bar 1 mm (also figured on Plate V, 2).

Fig.5. A single leaf of specimen 8341A showing the venation and the irregular denticulation of the anterior margin. Scale bar 1 mm (also figured on Plate IV, 3).

elongate cells with rather straight or slightly sinuous anticlinal walls, situated over the veins, and (2) broader elongate cells with coarsely sinuous anticlinal walls situated between the veins. Five to ten longitudinal rows of elongate cells with coarsely sinuous anticlinal walls are situated between the veins; cells irregularly shaped, 120–167 (average 140) μm long and 31–56 (average 47) μm wide. Veins covered with 2–4 rows of narrower elongate cells with thicker and less sinuous anticlinal walls; cells 120–170 μm long and 22–31 μm wide. It is very difficult to recognize stomata under the SEM. Stomata do not appear to be elevated or sunken. Each stoma consists of two reniform guard cells, up to 42 μm long and 9.5 μm wide. The long axis of the pore is orientated approximately parallel to the veins. Stomata bordered by 3–4 epidermal cells of the normal type with coarsely sinuous anticlinal walls. The frequency of the stomata could not be determined. Only a small part of the abaxial epidermis is preserved. It shows fewer details than the adaxial epidermis, but the arrangement of two types of cells in longitudinal rows parallel to the veins is not principally different from the adaxial epidermis. Stomata appear to occur on both the adaxial and the abaxial epidermis.

DISCUSSION

The reconstruction of *Lilpopia raciborskii* published by Lilpop (1937) shows the strobili of the fertile verticils standing in the axils of the so-called “leafy bracts”. Subsequently this reconstruction became generally accepted and it was reproduced in several textbooks on palaeobotany (e.g., Kryshfovich, 1957); Němejč, 1963; Boureau, 1964; Gothan and Weyland, 1973).

New material of *Lilpopia raciborskii* was described by Lipiarski (1971). He collected several leafy stems of *L. raciborskii* from the Karniowice travertine, in which the plants were preserved in life position. In the natural position of growth the leaves are turned with their convex sides directed upwards (Lipiarski, 1972a). This means that the lectotype of *L. raciborskii* (Lilpop, 1937, pl. I, 1–4) is figured upside down. Further data which could be established from direct observation of the lectotype are: (1) the strobili become smaller apically if the plant is positioned correctly; (2) the length of the internodes increases apically; and (3) the size of the leaves diminishes apically.

Furthermore, it appears that the strobili alternate with the leaves in a fertile verticil instead of being inserted in the axils of the leaves as was suggested by Lilpop, or hanging under the leaves as it would appear if the lectotype is set correctly. Based on these new data Lipiarski (1972a) proposed a new reconstruction of *L. raciborskii*. The discovery of *L. polonica*, another species from the Karniowice travertine, already confirmed the accurate interpretation (Lipiarski, 1971, 1972b).

The present material from Sobernheim confirms the correctness of Lipiarski's interpretation. It gives an opportunity to draw a new and more complete reconstruction of the plant, which is presented here on Fig. 6. Some remarks concerning Lilpop's and Lipiarski's observations can be made.

Fig.6. Suggested reconstruction of *Lilpopia raciborskii* (Lilpop) Conert et Schaarschmidt drawn after the specimens 4344A and 4344C.

The natural position of the leaves is not at right angles to the axis (Lilpop's explanation of his pl. I, 7), but the leaves are slightly raised in an apical direction with their convex sides upwards.

Lipiarski (1972a, pp. 105, 107) presumed the presence of three successive fertile verticils preceded and followed by sterile verticils. The dark spot, visible on Lilpop's pl. I, 1, 2, is interpreted as a leaf of a sterile verticil. However, this is only a single leaf fragment at its attachment to the axis and is not preserved. Interpreting this dark spot as a leaf does not imply that it is a part of a sterile verticil. There is also a possibility that only a single leaf fragment of a fertile verticil is preserved, or that the strobili are detached.

Specimen 8337A from Sobernheim shows four successive fertile verticils followed by at least two sterile verticils. The lowermost axis of ultimate order of specimen 4344AC consists of eight verticils, three of them being distinctly fertile. The first two verticils are sterile. The third and the fourth verticil both are fertile. The fifth node shows only the attachment of two incompletely preserved leaf fragments. The sixth node shows one strobilus and the uppermost two verticils are sterile. Obviously the fifth verticil was also a fertile one. Probably the mature strobili have detached, which would explain the absence of strobili on the fifth and sixth node. The pedicels of the strobili of *Lilpopia polonica*, a comparable species of which the internal organization of the strobili is known, are abruptly narrowed near the attachment to the node. This could be interpreted as a kind of abscission mechanism for mature strobili. Several isolated and detached strobili have been collected at Sobernheim.

In *L. raciborskii* the strobili alternate with the leaves in a fertile verticil. This was demonstrated by Lipiarski (1972a) and can be confirmed by the material from Sobernheim. The uppermost verticil of the uppermost axis of the ultimate order of specimen 4344C shows a leaf inserted between two strobili. The fourth node of the lowermost axis of the ultimate order of specimen 4344A shows a complete fertile verticil with three strobili and three leaves. Also from observation of specimen 8338, it is evident that the leaves alternated with the strobili. Both strobili are directed sideways, partially covering the two leaves. On the front side of the node, between the two strobili, the scar of a presumed leaf is evident. Six leaves are present in a sterile verticil. Only a few complete sterile verticils have been found. None of the sterile verticils of the strobilus-bearing branches is complete. The second verticil of the lowermost axis of the ultimate order of specimen 4344A shows two leaves, both directed sideways. On the front side of the node two elliptical scars are visible. Because in a fertile verticil the strobili alternate with the leaves, as is demonstrated above, this can only be a sterile verticil. The same reasoning can be given for the first, the seventh and the eighth node of the same axis. Thus the lowermost axis of the ultimate order of specimen 4344AC consists of eight nodes, the lowermost two bearing only sterile leaves, then four successive fertile verticils followed by at least two sterile verticils. This is the most complete fertile branch of *L. raciborskii* known to date.

In a strobilus the peltate sporangiophores are closely spaced. The internal organization of the strobili is unknown, although hypothetical schemes have been published by Remy (1955) and Lipiarski (1972a). The strobili of *L. polonica* consist of a whorl of four sporangiophores and one larger anterior sporangiophore (Lipiarski, 1972b). The strobili are attached to the axis with short stalks. If the strobili of *L. raciborskii* are comparable with the strobili of *L. polonica*, then the interpretation of Remy (1955) and Lipiarski (1972a) is correct. If the strobili of *L. raciborskii* are pedicellate, as in *L. polonica*, it is obvious that the strobili were pendant.

In the present paper the sporangia of *L. raciborskii* are described for the first time, but their exact mode of attachment to the sporangiophores is not clear. Because too little organic material has remained, no spores could be isolated. Remy and Remy (1961) isolated spores of the *Laevigatosporites*-type from the strobili of *L. crockensis*. For the first time the anatomy of the leaves of *L. raciborskii* could be studied. The leaves of *Lilpopia* are not principally different from the normal *Sphenophyllum* leaves (compare, e.g., Batenburg, 1981).

Lipiarski (1972a) already mentioned a heterophylly in *L. raciborskii*, based on isolated sterile material. The leaves of the lowermost axis of ultimate order of specimen 4344AC are narrow and lobate, whereas the other leaves are fairly broad and wedge-shaped. Also in the sterile material a variability in shape of the leaves could be demonstrated. Even in a single verticil (specimen 8341A) heterophylly could be observed.

Lilpop (1937, p. 5) stated that the internodes between fertile and sterile nodes are twice as long as the internodes between two fertile nodes. Although the internodes between two fertile verticils are somewhat shorter than the internodes between a fertile and a sterile node, the difference in length is not as great as Lilpop suggested. It is remarkable that the first internode of an axis of ultimate order is shorter than the following internodes. The width of the internodes does not gradually decrease apically, but probably this can be explained by deformation during the fossilization. In his description Lilpop (1937, p. 5) mentioned that the leaves of the sterile verticils are twice as long as the leaves of the fertile verticils. Although there is a small difference in size between the leaves of the sterile and the fertile verticils, again this difference is not so great as Lilpop suggested. All the leaves attached to the lowermost axis of ultimate order have about the same length. Nevertheless, there is a difference in size between the leaves attached to an axis of ultimate order and those attached to an axis of penultimate order. The only axis with both sterile and fertile verticils known from the literature is figured by Lilpop (1937, pl. I, 6—9). However, on Lilpop's illustrations no significant difference in size between leaves of fertile and sterile verticils can be observed.

Comparisons with other species of the genus Lilpopia

The other species of the genus *Lilpopia* (*L. crockensis* and *L. polonica*) are easily distinguished from *L. raciborskii*.

The leaves of *L. crockensis* have a laciniate anterior margin. All the veins terminate at the anterior margin. The leaves are more elongate than the leaves of *L. raciborskii*. The strongly laciniate leaves of *L. raciborskii* occur in sterile verticils, whereas in *L. crockensis* those leaves also occur in fertile verticils. In *L. crockensis* the number of sporangiophores in a strobilus is about 10, whereas the strobili of *L. raciborskii* consist of 18–24 sporangiophores.

Most leaves of *L. polonica* are smaller than those of *L. raciborskii*. Leaves of *L. raciborskii* with a similar size are as a rule more rounded. The fertile verticils of *L. polonica* consist of three strobili and six leaves. The strobili occur between pairs of leaves. The sterile verticils consist of six leaves. Each strobilus consists of five sporangiophores.

Remarks on L. crockensis and L. polonica and an emendation of the generic diagnosis of Lilpopia

Remy and Remy (1961) published a reconstruction of *L. crockensis*, which shows the strobili extending above the leaves. Apparently these authors based their view on Lilpop's reconstruction of *L. raciborskii*. The illustrations of their fragmentarily preserved material shows no evidence for the correctness of their interpretation. Probably their illustration of the holotype should be turned upside down, as was already suggested by Lipiarski (1972a).

It is interesting to note the presence of strongly curved teeth at the anterior leaf margin of *L. crockensis*. On their plate II, 5, Remy and Remy (1961) figured a portion of an axis with a fertile verticil. A single leaf of this verticil is also figured on their plate I, 6. It shows a laciniate leaf with a strongly curved tooth at the anterior margin. This feature is strongly reminiscent of the hooks of *Sphenophyllum* leaves as described by Batenburg (1977, 1981). From the photographs it is not clear whether it really is a solid hook, or just a strongly curved tooth.

The present investigations indicate again that a reinvestigation and probably a revision of *L. crockensis* is needed. If it should appear that the strobili of *L. crockensis* indeed were situated in the axils of the leaves, this species should be transferred to a new genus.

L. polonica differs from both other species in the number of leaves in a fertile verticil. The six leaves of a fertile verticil of *L. polonica* are arranged in pairs; the strobili are situated between the pairs of leaves.

Lipiarski (1972a) emended the generic diagnosis of *Lilpopia* by adding: "Three cones occur in a node together with the leaves, alternating with them". However, in *L. polonica* the six leaves do not alternate with the three strobili. Only in *L. raciborskii* could a true alternation of strobili and leaves be demonstrated. Therefore, Lipiarski's emendation has to be replaced by: three strobili occur in a fertile verticil together with the leaves, the strobili are standing between the leaves.

Comparisons of the leaves of L. raciborskii with Sphenophyllum

Isolated leaves and sterile verticils of *L. raciborskii* from Karniowice were first described as *Sphenophyllum* sp. (Roemer, 1870) and subsequently as *S. emarginatum* (Raciborski, 1891). Based on the fructifications, which are different from types of fructifications correlated with foliage of the form-genus *Sphenophyllum*, Lilpop (1937) established the genus *Tristachya*; this name was later replaced by *Lilpopia*.

It is here considered that the isolated leaves and sterile verticils of *L. raciborskii* might indeed correspond to *Sphenophyllum*. A comparison of the leaves of *L. raciborskii* with the leaves of certain species of *Sphenophyllum* is therefore relevant.

The most obvious comparison is with *S. emarginatum*, because Raciborski (1891) first attributed isolated leaves, which later appeared to be the sterile foliage of *L. raciborskii*, to this species. However, this Late Carboniferous species *S. emarginatum* does not have a rounded anterior margin and the veins do not terminate at the lateral margins in contradistinction to the leaves of *L. raciborskii*.

The most interesting taxon for a comparison is *Sphenophyllum thonii* var. *minor* Sterzel, originally described from the Lower Permian of Oppenau, Baden, German Federal Republic (Sterzel, 1893). Sterzel gave the following description of *S. thonii* var. *minor*:

“Stengel kantig, bis 3 mm dick. Internodien bis zu 2 cm Länge beobachtet. Blattquirle sechsblättrig. Blättchen meist ziemlich gross, verkehrt-länglicheirund, verkehrt-breiteirund bis breitkeilförmig, häufig 14 mm lang und 10 mm breit, auch 14 mm lang und 15 mm breit, zuweilen bis 22 mm lang und 10.5 mm breit. Spitze der Blättchen abgerundet, zuweilen etwas abgeflacht oder etwas ausgeschweift, in den typischen Blättchen nie gezähnt oder gekerbt. Der obere Blattrand selten ausgefaset (Erhaltungszustand?). Erhaltungszustand der Nervation meist so, dass an der Basis mehrere (bis sechs) Nerven nebeneinander auftreten von denen die seitlichen schwächer sind. Die eigentliche Basis kommt aber infolge Umbiegung der Blättchen nicht klar zum Ausdruck, und es finden nahe derselben Gabelungen statt, so dass wohl eigentlich alle Nerven aus vier oder noch weniger Basalnerven ihre Ursprung nehmen. Es liegen deutlich bis vierfache Gabelungen vor ohne diejenigen, die wahrscheinlich noch tiefer statt finden. Nervenenden 22-26-33 vorhanden.”

Sterzel (1893) figured several specimens of *S. thonii* var. *minor* (pl. X, 26, 27; pl. XI, 1-4), but unfortunately all these specimens appear to be incomplete. The only specimen showing the bases of the leaves is figured on his plate X, 26, but in this specimen the venation is not clear. The general shape and the dimensions of the leaves of *S. thonii* var. *minor*, as described by Sterzel, closely resemble those of *L. raciborskii* from Sobernheim. Also the vein pattern is very similar; compare e.g. Sterzel's plate XI, 4 with specimen 8337B (Plate IV, 2; Fig.3). The presence of weak veins leading to the lateral margins of the basal part of the leaf in both taxa is an important similarity. The main difference between the two taxa is the shape of the anterior margin of the leaf. According to Sterzel, *S. thonii* var. *minor* should be entire-

marginated, while the leaves of *L. raciborskii* can be either entire-marginated (Lipiarski, 1972a) or denticulate (Lilpop, 1937; Lipiarski, 1972a and the present material). It should also be noted that teeth commonly seem to be absent, being easily broken or embedded in the rock. Consequently the question remains as to whether *S. thonii* var. *minor* really is entire-marginated. It is clear that the specimens figured on Sterzel's plate X, 27 and plate XI, 1—2 are damaged at the anterior margins. The remaining specimens show an entire anterior margin (pl. X, 26; pl. XI, 3) or a denticulate anterior margin (pl. XI, 4). The denticulation of the last-mentioned specimen was interpreted by Sterzel as a result of preservation. In general plant remains from Oppenau are not well preserved (Mrs. I. Stepanek, Freiburg, pers. commun., 1982). Because in the opinion of the present author there exists no clarity about the shape of the anterior margin of *S. thonii* var. *minor*, the distinctive characters are restricted to: (1) the general triangular outline of the leaves, (2) the size of the leaves, and (3) the venation. Using these characters it is clear that *S. thonii* var. *minor* sensu Sterzel can be included in *L. raciborskii*. Sterzel already compared his *S. thonii* var. *minor* with *S. emarginatum* from Karniowice, as described and figured by Raciborski (1891). Raciborski's material later became the very type material of *L. raciborskii*! Sterzel discussed the value of distinctive characters such as the number of veins entering the leaf and the shape of the anterior margin, concluding that they were ambiguous. In his opinion it is possible that *S. emarginatum* from Karniowice could be included in *S. thonii* var. *minor*.

Another specimen agreeing with *S. thonii* var. *minor* was figured by Sterzel (1893, pl. XII, 8—10). Other specimens attributed to *S. thonii* var. *minor* were figured by Zalesky (1907) and Wagner and Artieda (1970). Later on Zalesky's material was identified as *S. verticillatum* (Zobel, 1910) and *S. emarginatum* (Jongmans, 1911). Subsequently Zalesky (1937) described his material as a new species, *S. amadokense*. The specimen figured by Wagner and Artieda (1970) is considered to belong to *S. miravallis* (see Hettterscheid and Batenburg, 1984). Other reports of occurrences of *S. thonii* var. *minor* in Europe could not be confirmed for lack of illustrations.

Halle (1927) figured some specimens from Central Shansi (China) under the name *S. thonii* var. *minor* (pl. IX, 1, 2, 5, 6; ?3, 4), but in the opinion of the present author these specimens essentially differ from Sterzel's type material. The leaves figured by Halle are longer than the leaves described by Sterzel. Moreover, contrary to Sterzel's type material, which shows a rather open venation, Halle's specimens show a remarkably dense venation. Also specimens from Japan, figured by Asama (1970) as *Parasphenophyllum thonii* var. *minor* show a dense venation that is different from Sterzel's type material. Obviously the East Asian material of *S. thonii* var. *minor* has to be transferred to a new and separate species.

The status of *S. thonii* var. *minor* sensu Sterzel is debatable. Authors such as Zobel (1910) and Jongmans (1911) believed that *S. thonii* var. *minor* represents a mode of preservation or a modification of the normal *S. thonii* var. *thonii* with fringed leaves. Arguments favouring this interpretation are

the fact that similar leaves have been found on axes of specimens with normal *S. thonii* leaves and the similarities in venation. However, during about fifteen years of collecting activities, the typical leaves of *S. thonii* var. *thonii* have not been found at Sobernheim, although this species was mentioned by Geib (1950). During a revision recently carried out of the original Geib collections, stored at the Karl Geib Museum at Bad Kreuznach, no specimens of *S. thonii* var. *thonii* were found. Probably Geib identified *Lilpopia* leaves as *S. thonii*. The leaves identified by Boersma (1975) as *S. cf. thonii*, stored in the collection of the Laboratory of Palaeobotany and Palynology Utrecht, appear to belong to *Lilpopia raciborskii*. The problem of whether *S. thonii* var. *minor* is only a mode of preservation or a modification of the normal *S. thonii* type is still not satisfactorily solved.

L. raciborskii furthermore can be compared with *S. miravallis*. An extensive description of the heterophylly of this species is given by Hetterscheid and Batenburg (1984). The normal type of leaves of this strongly heterophyllous species is obliquely obovate to obovate with rounded anterior margins; the upper two-thirds of the leaf margin is denticulated. *S. miravallis* can easily be distinguished from *L. raciborskii*. It should also be noted that *S. miravallis* may be correlated with a different type of fructification (*Bowmanites cupulatus* Hetterscheid et Batenburg).

Two species of *Sphenophyllum* from Upper Carboniferous outcrops in the Zwickau area (German Democratic Republic) were described and figured by Storch (1980), respectively as *S. gothanii* and *S. n.sp. 2*. Storch compared both species with *Lilpopia*; the first mentioned species especially with *L. crockensis*. However, there are no similarities between these species and *L. raciborskii*. The shape of the leaves and the venation are completely different.

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