***SPHENOPHYLLUM MIRAVALLIS* VETTER AND *BOWMANITES*
CUPULATUS SP.N. FROM THE "ILLINGER FLÖZZONE"
("HEUSWEILER SCHICHTEN", LOWER STEPHANIAN, SAAR BASIN,
GERMAN FEDERAL REPUBLIC)**

WILBERT L.A. HETTERSCHIED and LOUIS H. BATENBURG

Laboratory of Palaeobotany and Palynology, State University, Utrecht (The Netherlands)
Department of Systematic Botany, Groningen University, Biological Centre, Haren (The Netherlands)

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ABSTRACT

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This paper deals with a detailed study of *Sphenophyllum miravallis* Vetter, a member of the "*Sphenophyllum thonii* group". New material from the Reisbach colliery, working the "Illinger Flözzone" of the "Heusweiler Schichten" (Lower Stephanian, Saar Basin, German Federal Republic), is described morphologically and anatomically, and the species is discussed. The new material enlarges the known range of variability of the normal aspect of the foliage, i.e. the foliage of the thinner branches. Thicker stems with their aberrant polymorphous foliage, and cellular details, are described for the first time. An emended diagnosis is given. Comparisons with other species are made.

The new species *Bowmanites cupulatus* is introduced to accommodate fructifications most probably belonging to *Sphenophyllum miravallis*.

S. crenulatum Knight ex Wagner is considered to be a heterotypic synonym of *S. miravallis*, the latter name having priority.

KURZFASSUNG

Inhalt dieser Publikation ist eine detaillierte Untersuchung von *Sphenophyllum miravallis* Vetter, einem Vertreter der "*S. thonii* Gruppe". Neues Material aus dem Bergwerk Reisbach, das die "Illinger Flözzone" der "Heusweiler Schichten" (Unteres Stefan, Saarbecken, Bundesrepublik Deutschland) abbaut, wird morphologisch und anatomisch beschrieben und die Art wird diskutiert. Durch das neue Material wird der bekannte Variabilitätsbereich der Blätter auf die Beblätterung der dünneren Zweige ausgedehnt. Dickere Ächsen mit ihrer abweichenden polymorphen Beblätterung, sowie zelluläre Einzelheiten, werden zum ersten Mal beschrieben. Die Diagnose wird emendiert. Es werden Vergleiche mit anderen Arten durchgeführt.

Für Fruktifikationen, die mit größter Wahrscheinlichkeit zu *S. miravallis* gehören, wird die neue Bezeichnung *Bowmanites cupulatus* eingeführt.

S. crenulatum Knight ex Wagner wird als heterotypisches Synonym von *S. miravallis* angesehen und der letzte Name wegen der Priorität verwendet.

INTRODUCTION

In 1968 Vetter described the new species *Sphenophyllum miravallis*, including specimens previously identified as "*Sphenophyllum* du groupe de *S. thoni*" (Vetter, 1960) from some Stephanian—Autunian basins in France. A number of specimens assignable to *S. miravallis* was collected from the Reisbach colliery (Saar Basin, German Federal Republic) by Dr M. Boersma (Utrecht). He already discussed some of the specimens at the Eighth International Congress on Carboniferous Stratigraphy and Geology, Moscow 1975, and in written communications with Dr D. Storch (Jena). In his paper on the fossil flora of the "Illinger Flözzone" Boersma (1978) figured and described a specimen of the collection. In the present paper the new material of *S. miravallis* is described in detail and the species is discussed in order to contribute to a better understanding of this relatively rare and unknown element of the European Late Carboniferous flora. Special attention is given to the observed heterophyllous nature of the species.

The present study was carried out in the Laboratory of Palaeobotany and Palynology, Utrecht, as an integral part of a project aimed at the taxonomic, stratigraphical and palaeo-ecological evaluation of latest Carboniferous—Early Permian floras from Western Europe.

SOURCE STRATA

The "Illinger Flözzone" is situated in the middle part of the "Heusweiler Schichten", which are conventionally considered to be of "Stephanian B" age. A thorough study of the total megaflora of the "Illinger Flözzone" and comparisons with floras from the underlying "Dilsburger Schichten" and overlying "Breitenbacher Schichten" were carried out by Boersma (1973, 1978, 1979). Boersma (1979) concluded that the megafloras of the "Dilsburger Schichten" and "Heusweiler Schichten" are essentially of the same composition; those of the "Breitenbacher Schichten" are clearly different.

The first author (W.L.A.H.) also investigated some palynological assemblages from the "Illinger Flözzone" with the aid of Drs P.M. van Veen (Utrecht). The assemblages are typical for the *Angulisporites splendidus*—*Latensina trileta* (ST) Zone *sensu* Clayton et al. (1977). According to Clayton et al. the palynofloras of both the "Dilsburger Schichten" and "Heusweiler Schichten" belong to this zone.

Both megafloral and palynological studies prove that the flora of the "Illinger Flözzone" does not represent a separate phase in the Stephanian floral evolution of the Saar Basin but is clearly part of the phase represented by the floras of the underlying "Dilsburger Schichten".

MATERIAL AND METHODS

The present material was sampled from the Reisbach colliery during numerous collecting trips from 1965 to 1978 and is stored in the Laboratory

of Palaeobotany and Palynology, Utrecht. The specimens are numbered: U6014, U6118, U8586, U8597 and U8623—8657. Pieces from one lump of rock (e.g., part and counterpart) and separate fossils on one slab are indicated by a capital letter following the collection number. Transferred compressions from one piece of rock received an additional lower-case letter. All specimens are preserved as compressions/impressions. Most material originates from the roof of the mine (Boersma, 1978). These specimens, in fine grey siltstones, are the best preserved. Specimens from the blackish-grey coaly “Zwischenmittel”-shales show a more “weathered” condition and are more fragmentary. Some specimens are reddish brown; these are suitable for transfer techniques.

Uncovering was carried out with a small hammer and delicate chisels of varied types under a Wild M3 stereomicroscope. Clinging dust and debris were removed by brushing, washing with water, or both in combination. For sketching a drawing tube was attached to the microscope. In order to obtain anatomical information a transfer technique modified by Batenburg (1981a, p.278) was used.

SPHENOPHYLLUM MIRAVALLENSIS VETTER 1968 NOV. EMEND.

Synonymy, references

- Sphenophyllum miravallis* Vetter 1968, pp.15, 46—48, 161; table 6; fig.6A, B; pl. VIII, 6, 7, 11—13, IX, 1, 2, 4
 1971 Germer, pp.68, 69—70, 78, 80; fig.83 and pl. XVI, 2 [apparently the same specimen as in pl. II, 4 of Germer et al. (1968), Germer et al. (1966, pl. XI, 9) though provided with the same collection number, shows another fragment]
 1978 Boersma, pp.41, 45, 47, 52, 69; pl. VII, 1
 1978 Wagner, pp.565, 572, 573
 1979 Boersma, pp.160, 161, 167, 168
 1979 Storch, pp.675, 676 (*S. miravalle*)
 1980 Storch, pp.197—198, 210, 226; pl. XV, 7, 8 (= Germer et al., 1968, pl. II, 4) (*S. miravallense*)
 1981a Batenburg, pp.309, 311, 312
 1981b Batenburg III, pp.309, 311, 312; IV, p. 119 (*S. miravallense*)
 1982 Batenburg, p. 347 (*S. miravallense*)
S. crenulatum Knight ex Wagner 1978, pp.565, 572
 1975 Knight, pp.577—584; fig.26; pl. L, 1—4a (unpublished)
S. thonii auct. non Von Mahr: Bode 1936, pp. 68—70, 80 p.p.
 1964 Guthörl, p.641
 1966 Germer et al., pp.325, 326; pl. XI, 9
 1967 Germer and Kneuper, pp.5, 10
 1970 Lütkehaus, p.31
S. cf. thonii Von Mahr: Knight 1974, p. 303; pl. IV, 4, 5
S. aff. thonii Von Mahr: Germer and Kneuper 1970, pp. 801, 804
S. n.sp. aff. thonii Von Mahr: Germer et al., 1968, p.60; pl. II, 4
Sphenophyllum du groupe de *S. thonii*: Vetter 1960, p. 693
S. thonii var. *minor* auct. non Sterzel: Wagner and Artieda 1970, p.107; pl. XVIIIa.
 ?1978 Langiaux, pp. 57, 60.
S. verticillatum auct. non Von Schlotheim sp.: Zeiller 1885, pp.140, 145; pl. VIII, 4, 4a.
Specimen excludendum: *S. miravallis* or *S. thonii* var. *minor*: Boersma 1973, p.10 (*nomen*).

Type material

Holotypus: The specimen figured by Vetter (1968) in pl. IX, 1, 2, 4 and fig.6AB, stored in the collection of the Service Géologique des Houillères du Bassin d'Aquitaine, Decazeville (France) under the number H.B.A.407. The text-figures appear somewhat inaccurate (*vide* Storch, 1980, p.197).

Locus typicus: Decazeville Basin, France; drilling D.13, no. 9, at 10 m.

Stratum typicum: "Assise de Bourran", Upper Stephanian.

Original diagnosis

The following diagnosis of *Sphenophyllum miravallis* was given by Vetter (1968, p.46):

"Rameaux larges de 1,5 à 2 mm, avec côtes et sillons nettement marqués; entre-noeuds longs de 15 à 20 mm. Feuilles à limbe assez épais, groupées au nombre de 6 par verticille, entières, sans franges et non dentelées, pouvant se rapporter à deux types:

a) feuilles très oblongues, rétrécies dans leur tiers inférieur; longues de 15 à 20 mm mesurant 4 à 8 mm dans leur plus grande largeur.

b) feuilles plus arrondies, longues de 18 à 20 mm et larges de 8 à 12 mm.

Nervures fines, se divisant par dichotomies successives à partir de deux nervures initiales. Les nervures secondaires, réparties en deux champs nervuraires symétriques atteignent le bord du limbe sur tout le pourtour de la feuille, y compris dans sa partie inférieure."

Previous emendations

The following description, here treated as an emended diagnosis, was given by Germer (1971, pp.69–70):

"*Sphenophyllum miravallis* hat verhältnismäßig große Einzelblätter, die zu je 6 in einem Wirtel zusammenstehen und die bis zu 15 mm lang werden können. An der breitesten Stelle, die etwas oberhalb der Mitte liegt, werden sie zu 6 mm breit, so daß die Blättchen viel großflächiger sind als die der anderen Sphenophyllenarten, wenn man von *Sphenophyllum toni* MAHR absieht. Von der breitesten Stelle des Blättchens an ist sein Rand über das freie Ende hinweg fein gesägt. Dadurch unterscheidet sich *Sph. miravallis* von *Sph. thoni*, denn bei dieser Art sind die Blättchen am freien Ende zerschlitzt und ausgefranst. Vom Stengel führen mehrere Adern in die Blätter, die sich dichotom so zerteilen, daß jedes Zähnchen des Randes eine Ader erhält. Die Internodien sind etwa ebenso lang wie die Blättchen."

Boersma (1978, p.52) wrote:

"Vetter (1968) in his original diagnosis did not mention the denticulate margin of the leaves of *S. miravallis*. On the other hand, he identified the specimen from Reischbach, figured in Germer (1971a) as *S. miravallis* (R. Germer, oral communication, 1976). It must be admitted that quite often this margin is hidden in the matrix. I propose to emend the diagnosis of *S. miravallis* by adding: 'Upper margin and part of lateral margins of the leaf denticulate'."

Correct notation of specific epithet

Storch (1979) has used the name *Sphenophyllum miravalle*. He apparently considered "*miravallis*" to be adjectival in form and not used as a substantive,

and thus "corrected" the termination in order to make the epithet agree grammatically with the generic name (ICBN art.23 and 32). However, Vetter (1968) did not give a *derivatio nominis*; the possibility may not be excluded that he meant his epithet to be, or used it as, a substantive.

In 1980 Storch "corrected" the epithet into *miravallense*, referring to ICBN art.23, 32 and 73, and apparently assuming the epithet to be derived from a geographical name. Batenburg (1981b, 1982) accepted this view. However, again Vetter did not give a *derivatio nominis*. We could not find any "Miraval" or something like it on detailed maps of his localities and their surroundings¹. Moreover, the use of a termination not formed in accordance with ICBN recommendation 73D is not listed in art.73 as an error which should be corrected.

In view of the above-mentioned objections against these "corrections" we prefer to retain the original notation, the more so since "The liberty of correcting a name is to be used with reserve, . . ." (ICBN art.73 note 2).

Description of the present material

The Reisbach material of *Sphenophyllum miravallis* mainly consists of detached leaves and small fragments of leafy stems. Longer portions of leafy axes (Plates I, II, III, 1 and VII, 1), specimens showing ramification (Fig. 1A, B) and portions of very thick leafy stems (Plate I) are scarce. Roots have so far not been found. Detached strobilar bracts, small fragments of fructifications and one more complete strobilus (Plate VIII, 1), though most likely belonging to *S. miravallis*, are here described under the name of *Bowmanites cupulatus* sp.n. (see pp. 288–290).

Stem morphology

The internodes are 5–33 mm long and 1–14 mm wide (Fig. 1A, B, Plates I–III and VII, 1). The length/width ratio varies from 1 to 15. Some internodes are equipped with up to 1.5 mm long outgrowths (Fig. 1B, Plate III, 1, arrows). The surface of thicker stems shows a very fine longitudinal striation. Occasionally, up to eight faint ribs are visible. Thinner axes mostly show two rather prominent ribs as well as the fine longitudinal striation. The nodes are only slightly swollen, with small rounded scars when leaves are detached. In detached leaves the base is always missing; probably it remained on the node, the scars thus representing the veins in the leaf bases.

Leaf morphology

The most common type of leaves in the present material (Fig. 1A, above left, Fig. 3-1, Plate I, at the thinner axes, Plates II, IV, 2, V, 1, 2 and VII, 2) is characterized by the following features:

¹ During the last congress (1983) on Carboniferous Stratigraphy and Paleontology in Madrid, P. Vetter told J.H.F. Kerp that the epithet *miravallis* was indeed used as a substantive and did not have any geographical meaning.

Fig.1. A, B. *Sphenophyllum miravallis* Vetter. Branching specimens; the more incised leaves at the thicker stems. A. Leaves of type 1 (above left) and 10a (right) in combination, demonstrating the heterophylly of the species. U8626C. B. Rather abrupt decrease of leaf incision from stem (leaf of type 11a, with climber hook: Fig.2-11 and Plate IV, 3) to side branch (leaves of type 3a). U8645B. C. *Bowmanites cupulatus* sp.n. Detached strobilar bract, with marginal outgrowths (left). U8645B. Scale bars 5 mm.

(a) An arrangement in usually six-leaved and trizygoid whorls (Plate II). In the upper whorl at Plate II (arrow), an anomalous very small seventh leaf is present. In one case a “pseudo-trizygoid” condition was observed: leaves of equal dimensions, but one of the angles between them much wider than the other ones.

(b) An oblong to obovate or obliquely obovate (Plate V, 2) shape.

(c) Length 5.5–25 mm, maximum width 3.7–10 mm, length/width ratio 1–4.

(d) One vein entering the leaf, dichotomizing close to the base. (This could only be confirmed with certainty in the specimen figured by Boersma,

1978, pl. VII, 1; in all detached leaves the base is missing and in the attached ones the base is mostly too strongly coalified to reveal any detail.) Number of successive dichotomies at most seven. Median veins running to the distal margin, lateral veins curved towards the lateral margins.

(e) Rounded distal and straight or slightly convex lateral margins gradually merging into one another; margin sinuate, except in the basal third of the leaf. Per leaf 16—41 teeth; each tooth entered by one ultimate veinlet; teeth obtuse, up to 1 mm long and 0.5 mm wide at the base. Clefts between the teeth mostly more or less obtuse; some acute.

(f) Basal toothless part of the lateral margin in some cases with small outgrowths (Fig.3-1). Transfer preparates show outgrowths on the margins of the teeth as well (Plate X, 2, 4, 5), but here they are even smaller, and thus are hardly visible under the stereomicroscope.

The branches bearing leaves of this type are 1—4 mm wide. Some branching specimens show ordinary foliage in combination with leaves of different forms, thus clearly demonstrating the heterophyly of the species (Fig.1A). With regard to their length these different leaves may be arranged in two groups: (1) leaves measuring 16 mm or less (Fig.2), and (2) leaves exceeding 20 mm (Fig.3). Intermediate lengths were found amongst the above-described ordinary leaves only. No specimen in our collection shows leaves from both groups attached to one axis.

In order to describe the polymorphous foliage, leaftypes have been designated arbitrarily. These are coded as follows: the smaller leaves mentioned have been given the suffix a, the larger ones suffix b; within both groups the leaves are arranged according to the rate of incision: the higher the numeral the more incised the leaf. No suffix a or b is added to the ordinary foliage, leaftype 1, since all intermediate lengths are found here.

Table I illustrates the relationship between leaftype and width of the axis to which the leaf is attached, the trend being that the more incised leaves are attached to the thicker stems. This is also demonstrated by some branching specimens (Fig.1A, B). If leaves of more than one type are present on one axis, the more incised leaves are attached more basally (Plate III, 1). The present material thus indicates that the plant produced leaves with decreasing incision in apical direction along an axis, as well as from an axis to its side branches. The decrease of incision may be gradual (Plate III, 1) or rather abrupt (Fig.1B); in the latter case several leaftypes are "passed over". At the thickest stem fragments found and at the ultimate twigs, respectively showing the extremes in the leaftype series, no change of type is observable (Plate I).

The material, however, is too fragmentary to exclude the occasional occurrence of a reverse sequence of leaftypes at a branch; it is not possible to state whether the heterophyly showed any plasticity in adaptation to external factors. The ultimate twigs probably were determinate. Since apical portions of thick stems have not been found, we cannot state that these stems were either twig-like apically, or that they had strongly incised leaves throughout and a rather unlimited growth potential.

Table I further shows that a trizygoid configuration of whorls is most obvious at the thinner branches with the less incised leaves, which no doubt

PLATE I (p. 271)

Sphenophyllum miravallis Vetter. Large slab showing twigs, with leaves of type 1, and two very thick stems, with strongly incised leaves (arrow: longest leaf in the present material). U8627B.

PLATE II (p. 272)

Sphenophyllum miravallis Vetter. Portion of twig with leaves of type 1 in six-leaved trizygoid whorls (arrow: anomalous very small seventh leaf). U8623.

PLATE III (p. 273)

Sphenophyllum miravallis Vetter (scale bars 5 mm)

1. Portion of branch showing gradual decrease of leaf incision in apical direction: leaves of types 7a, 5a and 4a at lower, middle and upper node, respectively (arrows: outgrowths). U8646A (Fig.2-4, 5, 7).
2. Branch fragment with leaf of type ?8a. U8645B.

PLATE IV (p. 274)

Sphenophyllum miravallis Vetter (scale bars 2 mm)

1. Leaf of type 10a, with climber hooks. U8626B.
2. Rather small leaf of type 1. U8640.
3. Leaf of type 11a, with climber hook. U8645B (Fig.1B below and Fig.2-11).
4. Leaf of type ?9a. U8645B.
5. Whorl of twelve incomplete leaves, belonging either to type 4b, 5b or 6b, some of them with climber hooks. U8627A.

PLATE V (p. 275)

Sphenophyllum miravallis Vetter (scale bars 2 mm)

1. Leaf of type 1. U8623 (Fig.3-1).
2. Obliquely obovate leaf of type 1. U8623.
3. Leaf of type 2a. U8639.
4. Leaf of type 3b. U8645B (Fig.3-3).
5. Leaf of type 9a. U8626C (Fig.2-9).

PLATE VI (p. 276)

Sphenophyllum miravallis Vetter (scale bars 2 mm)

1. Leaves of type 5b (in the middle) and 7b (right-hand portion). U8641 (Fig.3-5 and Fig.3-7, respectively).
2. Leaf of type 2b. U8645A (Fig.3-2).

PLATE VII (p. 277)

Sphenophyllum miravallis Vetter (scale bars 2 mm)

1. Portion of branch bearing leaves of type 6b, with climber hooks. U8636B.
2. Leaf of type 1. U8645B.
3. Detail from 1: climber hook.

Description on p. 270

PLATE I

PLATE III

Description on p. 270

PLATE IV

Description on p. 270

PLATE V

Description on p. 270

PLATE VI

Description on p. 270

PLATE VII

Description on p. 270

PLATE IX

Description on p. 281

PLATE X

Description on p. 281

PLATE VIII (p. 278)

Scale bars 2 mm

- 1, 2, 4. *Bowmanites cupulatus* sp.n.
1. Large strobilus fragment. U8624B.
2. Strobilar fragment; teeth of bracts are obtuse or more acute. U8645B.
4. Detached strobilar bract, with rather acute teeth. U8625B.
3. *Sphenophyllum miravallis* Vetter. Leaf of type 4b. U8623 (Fig.3-4).

PLATE IX (p. 279)

Sphenophyllum miravallis Vetter. Transferred compressions (scale bars 100 μ m)

1. Epiderm of a branch. U8643Ad.
- 2-4. Leaf of type 1, showing epiderm, mesophyll remains and sheath cells of veins; marginal translucent band and epidermal cells at the bottom of clefts between teeth (2, 3); ordinary epidermal cells and stomata (4). U8643Aa.

PLATE X (p. 280)

Sphenophyllum miravallis Vetter. Transferred compressions (scale bars 100 μ m)

1. Detail from Plate IX, 4: stomata, ordinary epidermal cells with coarsely sinuous anticlinal walls.
- 2, 4. Teeth at a leaf of type 1, showing projecting acroscopic parts of marginal cells and relatively thin marginal free walls. U8643Aa.
3. Multicellular hairs or little spines at the margin of a leaf of unknown type. U8643Ab.
5. Detail from 4 (left).

TABLE I

Relationship between type of the leaf, width of the axis to which it is attached, and configuration of the whorl it forms part of. (t = trizygoid whorl(s); d = detached leaves only)

Leaftype	Width of axis (mm)							
1	1.0(t)	2.5	2.5(t)	2.75(t)	3.0	3.0(t)	3.5(t)	4.0
2a	4.5(t)							
3a	d							
4a	5.0(t?)							
5a	5.0(t?)	6.0	9.0	10.0				
6a	d							
7a	5.0(t?)	6.0	8.0					
8a	8.0							
9a	d							
10a	8.0(t?)							
11a	9.0							
2b	d							
3b	2.5							
4b	d							
5b	d							
6b	5.0	6.0	8.0					
7b	5.0	7.0						

is a reflection of the growth pattern of the plant. Now that the heterophylly of *S. miravallis* is discussed along general lines, the two series of leaf types will be described in more detail.

The main tendencies in both series are the decrease of the number of teeth and vein dichotomies and the increase of the depth of the clefts between the teeth. In type 2a (Fig.2-1, 2, Plate V, 3) some of the clefts are deeper than those in type 1. Types 3a (Fig.1B, at the sidebranch, Fig.2-3) and 4a (Fig.2-4, Plate III, 1, at the upper node) show somewhat longer teeth; here the margin is more coarsely lobed than in the foregoing types. A few deeper clefts are present in leaves of types 5a (Fig.2-5, Plate III, 1, at the middle node), 6a (Fig.2-6) and 7a (Fig.2-7, Plate III, 1, at the lower node), making these leaves lobate; the individual teeth are increasingly longer, thus taking the form of narrow lappets. Leaves of types 8a (Fig.2-8, Plate III, 2?) and 9a (Fig.2-9, Plate IV, 4? and V, 5) have six teeth or lappets only; those of types 10a (Fig.1A, at the thicker axis, Fig.2-10 and Plate IV, 1) and 11a (Fig.1B, at the thicker axis, Fig.2-11 and Plate IV, 3) only four. The median cleft is increasingly deeper and the middle two lappets are increasingly longer; the lateral lappets are usually shorter.

Leaves belonging to series b are less common. This series, therefore, is less complete: in particular a gap is present between types 1 and 2b. Leaves of type 2b (Fig.3-2, Plate VI, 2) are lobate and comparable with those of type 6a. Types 3b (Fig.3-3, Plate V, 4) and 4b (Fig.3-4, Plate VIII, 3) may be compared with types 7a and 8a. Type 5b (Fig.3-5, Plate VI, 1, in the middle) resembles type 9a with regard to the depth of the median cleft, but shows four lappets like type 10a. Type 6b (Fig.3-6, Plate VII, 1) may be compared with type 10a. However, the leaves of types 5b and 6b have long lateral lappets, which is usually not the case in the respective leaves of series a. Finally, in type 7b (Fig.3-7, Plate VI, 1, right-hand portion) the leaves are once-forked only.

Leaves of type 9a (Fig.2-9) may show marginal outgrowths, but these are more common in series b (Fig.3-4, 5, 7, Plate VI, 1 and VIII, 3). From types 8a and 5b onwards the leaves have climber hooks (Fig.1B, at the thicker axis, Fig.2-10, 11, Fig.3-6, Plate IV, 1, 3, 5 and VII, 1, 3): the vein protruding from the lappet forms an acutely pointed solid hook. However, well-preserved leaf tips and some luck in the process of uncovering are prerequisites to make this feature visible. The more incised leaves have thicker veins, and thus are stiffer (see under leaf anatomy), which is in accordance with their function as attachment organs.

Plate IV, 5 shows a whorl of twelve incomplete leaves belonging either to type 4b, 5b or 6b. Apart from the anomalous seven-leaved one figured in Plate II, this is the only verticil found consisting of more than six leaves. The longest leaf in the present material (Plate I, arrow) measures 29 mm and has a climber hook. It is attached to the stem with the longest internodes (up to 33 mm). Because of incompleteness its type, either 5b, 6b or 7b, could not be ascertained.

Fig.2. *Sphenophyllum miravallis* Vetter. Series a (small leaves): leaf types 2, 6, 8 (U8643A), 3 (U8639), 4, 5, 7 (U8646A); Plate III, 1), 9 (U8626C; Plate V, 5), 10 (U8623), 11 (U8645B; Fig.1B below and Plate IV, 3).

Stem anatomy

Only one stem-transfer could be prepared, by lack of more material showing adequate preservation (Plate IX, 1). The internodal epidermal cells have straight or nearly straight anticlinal walls. They are longitudinally elongated, up to $80\ \mu\text{m}$ long and $25\text{--}40\ \mu\text{m}$ wide. The end walls usually are not perpendicular to the lateral ones. Both the distal and the lateral anticlinal walls are $3\text{--}8\ \mu\text{m}$ thick. Some multicellular outgrowths were found.

Leaf anatomy

Several compressed leaves and leaf fragments of type 1 were transferred (Plate IX, 2–4, Plate X, 1, 2, 4, 5), together with one leaf fragment of

Fig.3. *Sphenophyllum miravallis* Vetter. Series b (large leaves): leaftype 1 and 4 (U8623; Plate V, 1 and Plate VIII, 3, respectively), 2 (U8645A; Plate VI, 2); 3 (U8645B; Plate V, 4), 5 and 7 (U8641; Plate VI, 1 in the middle and right-hand portion, respectively), 6 (U8646A).

unknown type (Plate X, 3). They all show, essentially, the same preservational state. The epiderms and the outer elements of the veins, with apparently rather resistant, probably cutinized or sclerified cell walls, are relatively well preserved. The vascular bundles themselves have disappeared. The mesophyll, if preserved, has changed into a mass of brown lumps without a definite structure. Remnants of mesophyll obscure the epidermal cell pattern in most portions of the intervein regions and areas between the most lateral vein and the lateral leaf margin. The margin of the leaf is generally devoid of mesophyll remains; thus, the entire leaf is usually skirted by a translucent band up to $70\ \mu\text{m}$ and two epidermal cells wide (Plate IX, 2, 3). At the bottom of the clefts between the teeth this band widens to about four cells. In non-

transferred leaves its reddish brown colour contrasts with the dark remainder of the leaf.

The ordinary epidermal cells (Plate IX, 4, Plate X, 1) are elongated parallel to the veins. They are up to $150\ \mu\text{m}$ long and $60\ \mu\text{m}$ wide. Both the distal and the lateral anticlinal walls are very coarsely sinuous and $3\text{--}6\ \mu\text{m}$ thick. Where two inward sinuses almost meet, the cells may be as narrow as $5\ \mu\text{m}$. The epidermal cells over the veins are equally long but usually somewhat narrower. Their anticlinal walls are more finely sinuous.

The marginal and near-marginal epidermal cells are elongated parallel to the margin rather than to the veins; this is particularly conspicuous at the bottom of the clefts between the teeth (Plate IX, 2, 3). Here the epidermal cells are usually somewhat shorter. The anticlinal walls of the marginal and near-marginal epidermal cells are less sinuous and slightly thicker than those of the ordinary epidermal cells. The marginal free walls, however, appear to be relatively thin (Plate X, 2, 4, 5). Outgrowths vary from mere projecting acroscopic parts of marginal cells, ca. $30\ \mu\text{m}$ long (Plate X, 2, 4, 5), to apparently multicellular hairs or little spines, up to $70\ \mu\text{m}$ (Plate X, 3) or even $1.5\ \text{mm}$ (Fig.3-4, Plate VIII, 3) long.

It is not clear from our slides whether a given stretch of epiderm represents the adaxial or the abaxial side of the leaf. Some patches of epiderm contain up to 130 stomata per mm^2 (Plate IX, 4, Plate X, 1) whereas other, quite similar patches do not show any stomata at all. Thus, probably the leaves are not amphistomatic, and adaxial and abaxial epiderms are not obviously different except for the presence of stomata. Stomata are less numerous over the veins. Apart from that, the stomatal distribution does not show a special pattern. The stomata do not appear to be raised or sunken. The stomatal pores are closed or open, ca. $16\ \mu\text{m}$ long. The two guard cells are elongated-reniform, ca. $35\ \mu\text{m}$ long and $7\ \mu\text{m}$ wide; they appear to be slightly thicker-walled than the ordinary epidermal cells. The long axis of pores and guard cells is usually approximately parallel to the veins. Most stomata are enclosed by a pair of similarly oriented neighbouring cells. They may be termed paracytic, although many of them are touched at one or both poles by additional neighbouring cells. Occasionally, other configurations occur (e.g., the middle stoma at Plate X, 1: dia- or anisocytic?). In many cases stomata share a neighbouring cell.

The sheath cells of the veins (Plate IX, 2–4, Plate X, 4) are strongly longitudinally elongated, angular to fusiform, $65\text{--}120\ \mu\text{m}$ long and ca. $20\ \mu\text{m}$ wide, with straight and thick (up to $15\ \mu\text{m}$) anticlinal walls. At the apex of a tooth the sheath may be slightly distended.

Comparison with previously described material

According to Vetter's original diagnosis (1968) the leaves of *Sphenophyllum miravallis* would have entire margins. However, some leaves in his Plate IX, 2 (holotypus!) appear to be finely toothed. Moreover, Vetter identified the specimens from Reisbach shown to him, including the one figured by Germer

et al. (1968) and Germer (1971), as *S. miravallis* (Germer, 1971; Boersma, 1978): these specimens show clearly toothed leaves. Most likely, in the larger part of the original material the teeth are either hidden in the rock matrix, like in many of the present specimens, or are not preserved. The necessary emendation of the diagnosis was carried out by Germer (1971) and Boersma (1978).

The specimens from Reisbach up till now described and figured show obovate leaves only (Vetter's type b). In the present material oblong leaves (Vetter's type a) were found as well. This apparently eliminates the possibility mentioned by Storch (1980) that Vetter would have based his diagnosis on two separate species. Trizygioid whorls, like figured by Vetter (1968) and Boersma (1978), are predominant in our material. A "pseudo-trizygioid" condition, like in the specimens figured by Germer et al. (1966, 1968), Germer (1971) and Storch (1980), was found only once. Clearly isophyllous verticils occur as well. According to previous authors more than one vein would enter the leaf. In the present material, as far as we could observe, there is only one basal vein. However, we do not think that this feature has any value for species delimitation.

The present material enlarges the known range of variability of the ordinary leaves, i.e. the foliage of the thinner branches. Thicker stems with their aberrant polymorphous foliage, and cellular details, have not been described previously¹. The new information on *S. miravallis* makes a re-emendation of the diagnosis desirable.

Emended diagnosis

Large-leaved strongly heterophyllous species. Internodes ca. 1–15 mm wide and 0.5–3.5 cm long, may bear up to 1.5 mm long multicellular outgrowths. Thicker stems not prominently ribbed. Nodes only slightly swollen; detached leaves leave small rounded scars.

Normally six leaves per iso- or anisophyllous whorl, ca. 0.5–3 cm long and 3.5–12 mm wide. Leaves with decreasing incision in apical direction along axis and from axis to side branch. Nervature open-dichotomous; up to seven successive dichotomies. Leaves of all types may bear marginal outgrowths varying from extensions of epidermal cells to up to 1.5 mm long multicellular hairs or little spines.

Ordinary leaves oblong to obovate or obliquely obovate; length/width ratio ca. 1–4. Straight or slightly convex lateral margins gradually merging into rounded distal ones; margin sinuate in upper 2/3 of leaf, with ca. 15–40 obtuse teeth, each entered by one ultimate veinlet; clefts between teeth mostly more or less obtuse.

More incised leaves with fewer teeth and vein dichotomies; the most dissected ones with somewhat concave lateral margins, lappet-shaped teeth and climber hooks.

¹Some preliminary notes on the heterophylly in the present material were given by Storch (1980) and Batenburg (1981a).

Internodal epidermal cells longitudinally elongated, up to 80 μm long, ca. 25–40 μm wide, with straight or nearly straight ca. 3–8 μm thick anticlinal walls; end walls usually not perpendicular to lateral ones.

Ordinary cells of leaf epiderm elongated parallel to veins, up to 150 μm long and 60 μm wide, with coarsely sinuous ca. 3–6 μm thick anticlinal walls. Marginal cells elongated parallel to margin, slightly thicker- and less sinuously walled, but marginal free walls relatively thin. Stomata up to 130 per mm^2 , probably restricted to one side of leaf, usually paracytic, with two ca. 35 μm long and 7 μm wide elongated-reniform guard cells; pores ca. 16 μm long; long axis of pores and guard cells usually approximately parallel to veins.

Sheath cells of veins strongly longitudinally elongated, angular to fusiform, ca. 65–120 μm long and 20 μm wide, with straight and up to 15 μm thick anticlinal walls.

Discussion of synonymy

Sphenophyllum thonii resembles *S. miravallis* with regard to the shape, dimensions and venation of the leaves but differs from the latter by its typical ragged lacinate leaf margins. The citations of *S. thonii*, *S. aff. thonii* and *S. n.sp. aff. thonii* from the Saar Basin (see list on p. 265) all refer to specimens in reality belonging to *S. miravallis* (Germer, 1971; Boersma, 1978; Storch, 1980).

According to Sterzel (1895) the leaves of his *S. thonii* var. *minor* have an entire distal margin and lateral veins which are thinner than the other ones. The taxon would thus be clearly different from *S. miravallis*. Kerp (1981, 1984), emphasizing among other characters the relative thinness of the lateral veins, considers Sterzel's specimens to belong to *Lilpopia raciborskii* (Lilpop) Conert et Schaarschmidt, which shows this feature as well. In our opinion the specimen figured by Wagner and Artieda (1970) under the name *S. thonii* var. *minor* resembles *S. miravallis* rather than Sterzel's material. According to Mr J. Langiaux (Montceau-les-Mines) (pers. commun., 1981) the specimens of *S. thonii* var. *minor* mentioned in his 1978 paper may very well belong to *S. miravallis*.

S. crenulatum was erected by Knight (1975) in an unpublished thesis; it includes Spanish specimens previously named *S. cf. thonii* (Knight, 1974) and the above-mentioned Saarland material. The species would differ from *S. miravallis* by having isophyllous whorls of toothed leaves instead of trizygoid verticils of leaves with entire margins. Wagner (1978) shared Knight's views in this regard and validated the name. Wagner's description must be treated as the original diagnosis of *S. crenulatum*. Since Wagner referred to Germer et al. (1968) and Germer (1971), but not to Knight's 1974 work, the type-specimen is the one figured by Germer et al. (1968), Germer (1971) and Storch (1980), i.e. one of the specimens identified by Vetter and Germer (Germer, 1971; Boersma, 1978) as *S. miravallis*. The present material shows both isophyllous and anisophyllous whorls; entire leaf margins in Vetter's original material are probably due to fossilization (see p. 266). Therefore,

without doubt we consider *S. crenulatum* a heterotypic synonym of *S. miravallis*, the latter name having priority.

Knight (1975) and Storch (1980) included some specimens described and figured by Zeiller (1885) under the name *S. verticillatum* Von Schlotheim sp. in the synonymy of *S. crenulatum/miravallis*, though with a question mark. In our opinion the specimens fall within the range of variability of *S. miravallis* as shown by the present material.

Storch (1980) included in the synonymy a specimen mentioned by Boersma (1973): "*S. miravallis* oder *S. thoni* var. *minor*". This, however, is an error: Storch himself identified the specimen, from a photograph sent to him by Boersma, as *S. verticillatum* and published the photograph under the latter name (pl. XVI, 2). We agree with Storch's identification.

Storch (1980) mentioned a certain similarity between *S. miravallis* and *S. nemejcii* Obrhel 1967. Indeed, of the few species bearing some resemblance with *S. miravallis*, *S. nemejcii* is the most similar one. The most obvious difference appears to be that of the leaf dimensions: according to Obrhel (1967) the leaves of *S. nemejcii* are only 7–10 mm long and 3–3.8 mm wide. Some of Obrhel's specimens (1967, fig. 1A, C, D, pl. I, 4, 5, 7, pl. II, 3, 4) show rather irregular teeth, a feature not yet found in material of *S. miravallis*. *S. nemejcii* too is heterophyllous; a number of leaves figured by Obrhel (1967, fig. 1A, B, E, F, G, pl. I, 2, 3, 6, pl. II, 1, 2) resemble leaftypes in *S. miravallis*. If new material would eliminate the mentioned differences, conspecificity would imply that the name *S. miravallis* should be rejected in favour of *S. nemejcii* for reasons of priority.

Stratigraphic and geographic distribution

Up till now material belonging to *Sphenophyllum miravallis* has been found in the: (a) Stephanian—Autunian of the Basins of Decazeville, Espalion-Lassouts and Dtroit de Rodez, mid-southern France (Vetter, 1960, 1968); (b) Stephanian B of the Cnra-Matallana and Sabero Coalfields, northwestern Spain (Wagner and Artieda, 1970; Knight, 1974, 1975; Wagner, 1978); (c) Lower Stephanian of the Saar Basin, German Federal Republic (e.g., Germer et al., 1966, 1968; Germer, 1971; Boersma, 1978); and (d) Stephanian of the Gard Basin, southern France (Zeiller, 1885).

The mention of *S. miravallis* from the Upper Stephanian of the Saar Basin ("Breitenbacher Schichten" at Hinzweiler) by Storch (1980), referring to Boersma (1973), is an error (see above).

BOWMANITES CUPULATUS SP.N.

Type material

Holotypus: The specimen figured in Plate VIII, 1, stored in the collection of the Laboratory of Palaeobotany and Palynology, State University Utrecht (The Netherlands) under the number U8624B.

Paratypus 1, 2 and 3: The specimens figured in Plate VIII, 2, VIII, 4 and Fig.1C, respectively, stored in the above-mentioned collection under the numbers U8645B (paratypus 1 and 3) and U8625B (paratypus 2).

Locus typicus: Saar Basin, German Federal Republic; Grube Dr A. Schäfer, Reisbach.

Stratum typicum: Fine grey siltstones in the roof of the mine; "Illinger Flözzone", "Heusweiler Schichten", Lower Stephanian.

Derivatio nominis: The specific epithet *cupulatus* refers to the cup-shaped bract-whorls.

Diagnosis

Strobili up to at least 65 mm long and 12 mm wide. Internodes ca. 3–5 mm long and 1 mm wide. Bracts probably six per cup-shaped whorl, ca. 5–10 mm long and 5 mm wide, orbiculate to obovate, with ca. 0.7 mm long obtuse or acute teeth, may bear up to 0.2 mm long outgrowths. Veins rather thin. Sporangia elliptic, reticulate, ca. 3.5–4 mm long and 3 mm wide, probably one per bract.

Description of the material

Along with fragments of *Sphenophyllum miravallis*, and in many cases intimately intermingled with detached leaves of this species, orbiculate to obovate, ca. 5.5–10 mm long and 4.5–5 mm wide, leaves were found (Fig.1C, Plate VIII, 4). Like in leaftype 1 of *S. miravallis* the distal and lateral margins gradually merge into each other and the margin is toothed throughout, except in the basal parts of the leaf which, here too, may be provided with small outgrowths (Fig.1C). The outgrowths are up to 0.2 mm long. The veins are generally somewhat thinner here and the teeth may be more acute. The teeth are ca. 0.7 mm long.

Also a large portion of a fructification was found of which the bracts proved to be identical with these small leaves (Plate VIII, 1). The specimen is 65 mm long and up to 12 mm wide; it gradually narrows to the base, which appears to be nearly complete; the apex is obviously missing. The internodes are ca. 3 (basally)–5 mm long and ca. 1 mm wide; they are not very prominently ribbed. The bracts are grouped in cup-shaped whorls, each whorl probably consisting of six bracts. It could not be ascertained whether the bracts are fused basally. Several smaller strobilar fragments of the same type were found (Plate VIII, 2).

The sporangia are all hidden by the bracts. However, in some cases their elliptic shape and reticulate surface show through. They are ca. 3.4–4 mm long and 3 mm wide. Probably, each bract corresponds with one sporangium.

Discussion

The fertile remains described are attributed to the organ-genus *Bowmanites* sensu Hoskins and Cross (1943). These authors already discussed why the generic name *Sphenophyllostachys* Seward 1898 should be rejected in favour of *Bowmanites* Binney 1871.

The assignation of this type of sphenophyllalean fructification to *Sphenophyllum miravallis* might be disputed: specimens showing organic connection have not been found. However, the mode of preservation of the bracts, the shape of their margins, the presence of marginal outgrowths and the finds of such bracts in close association with vegetative remains of *S. miravallis* strongly suggest a relationship with this species rather than one of the other species in the extensive collection from Reischbach, viz. *S. oblongifolium* (Germar et Kaulfuss) Unger and *S. majus* (Bronn) Bronn. *S. oblongifolium* is the most common plant species in the Reischbach collection. Its generative parts, well known from literature (Barthel, 1976 described two types) and frequently found in the Reischbach material too (Boersma, 1978, pl. IX, 1, 2 shows three strobili of which at least two are attached), are quite different from the remains discussed here. The same applies to the fructification mentioned in literature as belonging to *S. majus*. Of this species only a few vegetative portions have been found in Reischbach.

FINAL CONSIDERATIONS

The *Sphenophyllum* species of the "thonii group", i.e. the Westphalian C—Upper Permian species with lanceolate, oblong or obovate leaves in which part of the veinlets ends at the lateral margins, are still insufficiently known. Data concerning the thicker stems and their foliage are scarce. The same applies for cellular details; the fructifications belonging to it are largely unknown.

Heterophylly (a generic character of *Sphenophyllum*, vide Batenburg, 1981a) has not been described in detail before in a member of the "thonii group", although Obrhel (1967, *S. nemejcii*) and Barthel (1976, *S. thonii*) figured specimens with polymorphous foliage. The heterophylly of *S. miravallis* is of the usual type within the "compression species" of *Sphenophyllum*: spreading leaves at the thinner axes, more incised leaves mainly at the thicker axes. The most dissected leaves have climber hooks. Such structures are known also from *S. cuneifolium* (Von Sternberg) Zeiller, *S. emarginatum* (Brongniart) Brongniart, *S. laciniatum* Storch, *S. saxonicum* Remy et Remy and *S. zwickaviense* Storch (Storch, 1966, 1980; Batenburg, 1977, 1981a, b, 1982), and are present in *S. oblongifolium* from Reischbach as well (preliminary notes by Batenburg, 1977, 1981a; Hettterscheid, unpubl.). Batenburg (1981a, b, 1982) has argued that they are widespread among the "compression species" of *Sphenophyllum* and has stressed the heterophylly in these species as an adaptation to a scrambling habit.

The two thick stems figured in Plate I belong to the thickest compressed *Sphenophyllum* axes known. The specimens show, like the other thick stems of *S. miravallis*, conspicuous nodes, internodal ribs and attached leaves and, thus, are neither decorticated nor defoliated. Batenburg (1981a, b, 1982) has emphasized this feature as a constant character of the "compression species" of *Sphenophyllum*, suggesting a connection with the development of the leaves at these stems towards attachment organs.

In *S. miravallis* a trizygoid configuration of whorls is most obvious at the thinner branches and those with the less incised leaves. The same feature is shown by *S. oblongifolium* (Barthel, 1976; Hetterscheid, unpubl.).

The cellular details of *S. miravallis*, as described in this paper, do not show principal differences with those of the other "compression species" of *Sphenophyllum* (compare with the compilation by Batenburg, 1981a, b, 1982).

Bowmanites laxus Halle has been associated questionably with *Sphenophyllum thonii* (Halle, 1927; Hoskins and Cross, 1943). However, the only fertile material found in organic connection with foliage assignable to the "thonii group" belongs to two species of the genus *Lilpopia* Conert et Schaarschmidt (syn.: *Tristachya* Lilpop), viz., *L. raciborskii* (with *S. thonii* var. *minor*: Kerp, 1981, 1984) and *L. crockensis* (Remy et Remy) Conert et Schaarschmidt (Remy and Remy, 1961). These species too show leaf polymorphism or heterophylly, and may have climber hooks (Remy and Remy, 1961, pl. I, 6, pl. II, 5). As far as our observations go, the rather robust fructifications described in this paper (*Bowmanites cupulatus* sp.n.) are of a quite different and much simpler type. If the identification of these strobili with *Sphenophyllum miravallis* is correct, the "thonii group", though consisting of species with rather similar vegetative parts, is an artificial unit.

In the Upper Carboniferous—Lower Permian of Europe the range of leaf variability of the "thonii group" is covered by the above-mentioned *Lilpopia* species, *Sphenophyllum miravallis* and *S. thonii*. Regarding its leaf dimensions *S. thonii* appears to be the "culminating" *Sphenophyllum* species in Europe. The "thonii group" disappears from the European record during earliest Permian (Autunian) times. In strata of presumed equivalent age in the Cathaysian realm [Taiyuan Formation, Shansi Formation and Lower Shihhotse Formation; for age assessment compare Asama (1970) and Li and Yao (1980)], a larger number of species assignable to the "thonii group" has been recognized (Halle, 1927; Asama, 1966, 1970), indicating a wider morphological spectrum. A striking example is the development of very large leaves, up to 6.5 cm long, in *S. shansiense* Asama (1966, 1970). However, the large number of species distinguished in Cathaysia might be, at least partly, the result of incomplete knowledge of heterophylly and individual variation within the species [compare, e.g., *S. spinulosum* Yabe et Oishi in Asama (1970, pl. III, 3) with *S. thonii*, or *S. rotundatum* Halle with *S. fimbriatum* Halle in Halle (1927, pl. X, 1–9)].

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