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# *Archaeopteris* from the Upper Famennian of Belgium: heterospory, nomenclature, and palaeobiogeography

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## Abstract

New fertile specimens of *Archaeopteris roemeriana* from Upper (but not uppermost) Famennian strata of Belgium have been studied. Crowded sporangia are borne on non-laminate, three times bifurcate fertile leaves helically arranged around the fertile ultimate axes. Vegetative leaves occur both proximal and distal to the fertile leaves. Heterospory is demonstrated with miospores belonging to the *Geminospora*–*Aneurospora* complex and macrospores most probably to *Contagisporites* genus. The established morphological traits allow us to substantiate a synonymy between *A. roemeriana* and *A. halliana*. The apparent dominance of *A. halliana* on the eastern side of the Acadian mountains during Late Famennian times is discussed. © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** Famennian; *Archaeopteris*; spores; synonymy; palaeobiogeography; progymnosperms

## 1. Introduction

Remains of large leafy branching systems, the so-called penultimate and ultimate branches of *Archaeopteris*, are the predominant element in several Upper (but not uppermost) Famennian plant assemblages in Belgium. These specimens are usually referred to *A. roemeriana* (Goepfert) Lesquereux 1880 despite the fact there is some doubt over the delimitation of this species (Stockmans, 1948; Kenrick and Fairon-Demaret, 1991). In 1941, Kräusel and Weyland put *A. roemeriana* from Europe in synonymy with *A. halliana* from North America on the basis of leaf size, nature of leaf margin, and density and degree

of leaf overlap. Both species share similarities in leaf form and arrangement, as well as degree of leaf overlap and insertion on the penultimate or ultimate axes. Kenrick and Fairon-Demaret (1991), and Fairon-Demaret and Leponce (2001) retained them as separate because the known morphological details are not equivalent for both. The anatomy of *A. halliana* has not yet been described but the morphology of its fertile leaves, arrangement of sporangia, and details of mega- and microspores are known; a reconstruction of a fertile ultimate axis of *A. halliana* has been proposed (Phillips et al., 1972). No comparable morphological information on the fertile parts was available for *A. roemeriana* before this work, but the anatomy of its penultimate and ultimate axes, both vegetative and fertile, had been described (Kenrick and Fairon-Demaret, 1991). Anisophylly on the ultimate vegetative branches has more recently been demonstrated (Fairon-Demaret and Leponce, 2001).

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The purpose of this paper is to provide the results obtained by working out recently collected fertile specimens of *A. roemeriana*, to offer details of the branching of the fertile leaves, number and disposition of sporangia and spore morphology, and finally to discuss if both species, *A. halliana* and *A. roemeriana*, may be regarded as synonymous.

## 2. Nomenclature note on the genus *Archaeopteris*

The genus *Archaeopteris* has a long and complicated nomenclature history. A detailed review of the pertinent literature is beyond the scope of this paper. Complete references and citations are to be found in Kräusel and Weyland, 1941. Only the critical steps in the formal definition of the genus are evoked as even a brief survey of the literature reveals discrepancies in citations: e.g. *Archaeopteris* (Dawson) Stur 1875–1877 (in Carluccio et al., 1966), *Archaeopteris* Dawson 1882 (e.g. Andrews in Boureau, 1970) *Archaeopteris* Dawson 1871 (e.g. Gensel and Andrews, 1984).

1843: Hall shortly describes and produces a drawing of *Archaeopteris* remains collected in the 'Chemung Group' strata in western New York. He designates them as *Sphenopteris laxus* Hall.

1852: Goeppert remarks that *laxus* (*laxa* is correct) is a species name already pre-occupied in the genus *Sphenopteris* and he makes the new combination *Sphenopteris halliana* Goeppert for Hall's specimens.

1853: Forbes in an abstract mentions as *Cyclopteris hibernicus* Forbes the first specimen of *Archaeopteris* he discovered in Ireland in 1852; the description is minimal; no illustration is provided.

1859: Goeppert produces diagnoses and illustrations of several species, particularly of *Cyclopteris hibernica* Forbes and of *C. roemeriana* Goeppert, the first discovery of which was recorded (but neither named nor described) by Roemer, 1855 from Moresnet (Vesdre Synclinorium, Belgium). Goeppert also changes his *Sphenopteris halliana* Goeppert to *Cyclopteris halliana*.

1869: Schimper describes and illustrates the species *hibernica*, moving it to his new genus *Palaeopteris* that includes five species, including *P. halliana*

(Goeppert) Schimper and *P. roemeri* (Goeppert) Schimper.

1871: Dawson notices that *Palaeopteris* Schimper is invalid, already being pre-occupied for remains of tree-ferns described by Geinitz (1855). He discusses the genus *Cyclopteris*, demonstrating it had to be divided into several sub-genera; a new sub-genus *Archaeopteris*, with *A. hibernica* as the type, is erected to designate the Devonian remains. Unfortunately in this 1871 publication, Dawson establishes sub-genus names only, and gave no element to circumscribe them.

1875: Stur raises the name *Archaeopteris* to generic status and produces a formal diagnosis in Latin; in his paper (p. 57) subgenus *Cyclopteridis* (sic), the fourth of the subgenera mentioned by Dawson 1871 is raised to generic status, under the name *Archaeopteris*, including only with doubt the type-species *A. hibernica* (loc. cit., p. 57, footnote). In such conditions, Article 49 of the International Code of Botanical Nomenclature is not applicable.

1880: Lesquereux makes a different move. He provides a generic diagnosis (p. 303) for '*Archaeopteris* (Dawson)' as he puts it, referring to the subgenus *Archaeopteris* of Dawson 1871; he cites among other species, *A. hibernica* (p. 305), *A. halliana* (p. 304) and *A. roemeriana* (p. 303).

Lesquereux's 1880 paper fulfils the requirements for valid publication of *Archaeopteris* as a genus name. Accordingly citations should read *Archaeopteris* (Dawson) Lesquereux 1880, *A. halliana* (Goeppert) Lesquereux 1880 and *A. roemeriana* (Goeppert) Lesquereux 1880.

## 3. Material and methods

This study is based on 10 specimens (part and counter-part) housed in the Palaeobotany collections of the University of Liège, Belgium (ULg 13020, ULg 13119, ULg 13171, ULg 13172, ULg 13174, ULg 13497, ULg 13499, ULg 13502, ULg 13503, ULg 13509) and on three specimens in the Palaeobotany collections of the Royal Institute of Natural Sciences at Brussels, Belgium (IRScNB b 2421, IRScNB b 2422, IRScNB b 2423). They were selected as showing promising fertile ultimate branches. All were

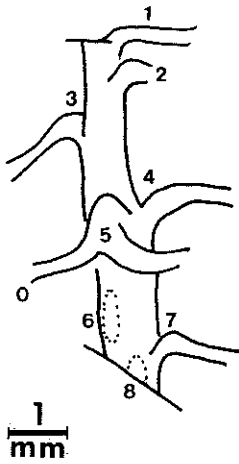


Fig. 1. Sketch drawing of the arrangement of the eight sporophylls (1–8) around the axis; stippled lines indicate attachment of fertile leaves disposed behind the axis compression; compare with Plate II, 7 (Specimen ULg 13503c).

collected during several trips to the disused Langlier quarry at Durnal near Dorinnes and Spontin in the Bocq valley (Province of Namur, Belgium; precise geographic information is given in Fairon-Demaret and Scheckler, 1986 who described remains of *Moresnetia* from this locality). The best results were obtained from material recently collected, particularly from specimens ULg 13502 and 13503, both parts and counter-parts of penultimate branch fragments with fertile ultimate axes attached. They are preserved as dark to light-brown compressions in a gray micaceous fine-grained matrix. The fracture plane of the rock matrix usually splits through the thickness of the compression so that both complementary pieces, part and counter-part, appear as mirror images of each other.

In the Langlier quarry a series of stacked sequences of the Famennian 'Condruz Sandstones' or 'Psammities du Condruz' group is exposed including lenticular sandstones, the overall architecture of which corresponds to a point bar or estuary channel (Thorez et al., 1994) more than 150 m wide. The channel fill includes a 'clay plug' indicative of a switch from tide-influenced estuary deposits with lateral arenaceous accretion structures to alluvio-fluvial deposits of horizontal gray to dark mudstone beds (Fagnant, 1999) containing, in one horizon, a rich concentration of plant debris. This plant horizon belongs to the VC0

(*Diducites versabilis*–*Grandispora cornuta*) spore Biozone (Maziane et al., 1999) and is regarded as late Famennian (Fa2c, Late but not latest Devonian) in age.

The main method of study of this compression material has been that of *dégagement* (Fairon-Demaret et al., 1999). Photographs were taken (using polarised light) and camera lucida drawings were made to record the successive stages of uncovering of the fertile appendages. Specimens were also embedded in cold-setting polyester resin in order to produce transfers of the preserved organic matter after HF digestion of the embedding matrix. Sporangial fragments and spores recovered were air-dried, mounted on a stub using carbon conductive adhesive, and gold-coated. Observation and photographs were made using a Jeol JSM-5800 scanning electron microscope. Maceration of the embedding sediment was performed using the standard palynological procedure.

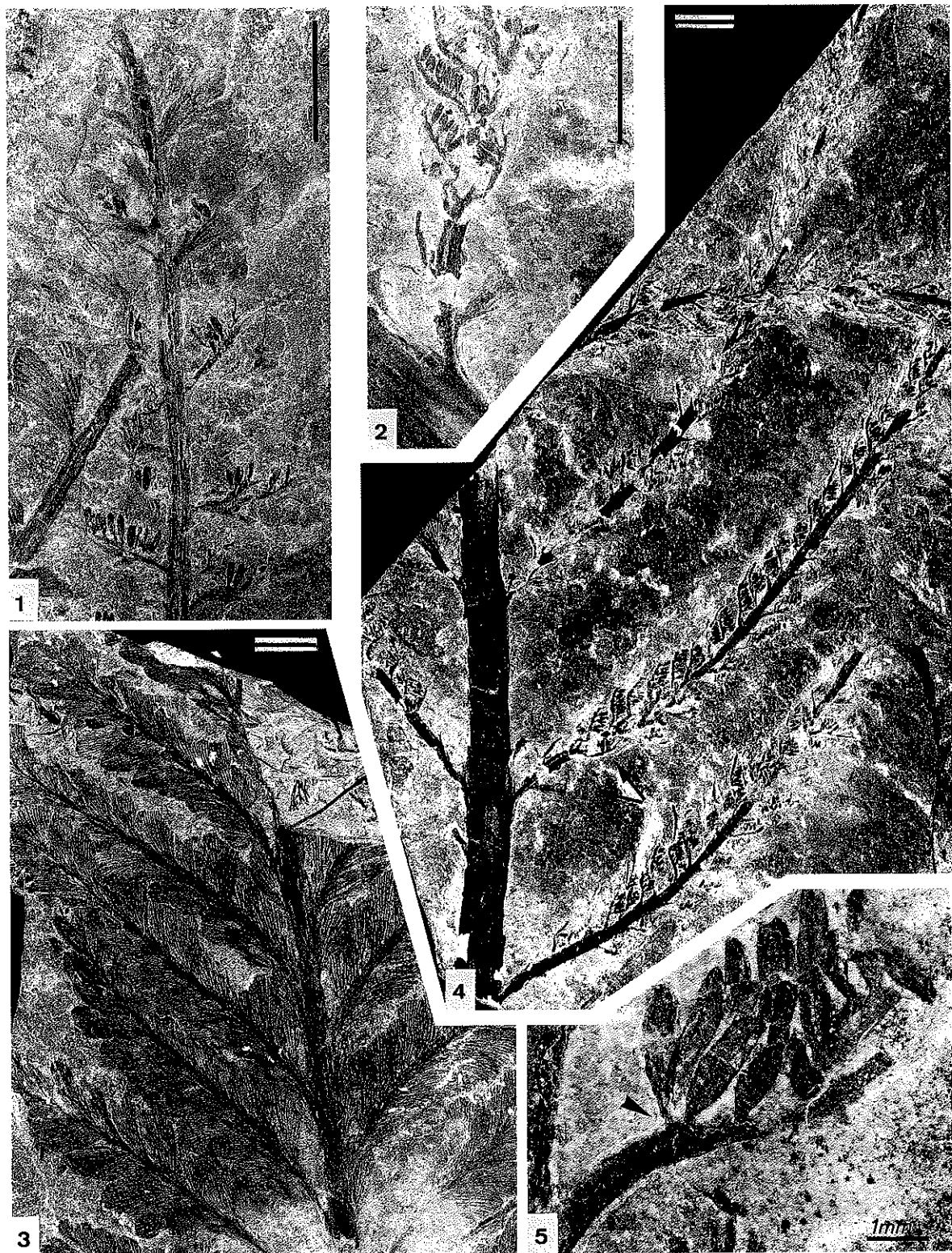
## 4. Results

### 4.1. The fertile ultimate branches

Complete penultimate branching systems of *Archaeopteris roemeriana* are rarely preserved. Most often, they are fragmentary with proximal and distal ultimate branches absent (Plate I, 4). Nevertheless, several specimens clearly show that on a fertile branching system the middle area only is fertile with basalmost and apical branches being vegetative, as on other *Archaeopteris* species (Phillips et al., 1972; Beck, 1981; Beck and Wight, 1988). Occurrence of wholly fertile lateral branch systems, without intervening basal sterile ultimate branches, cannot be ruled out.

Fertile ultimate branches bear sporophylls on most of their length but they are bound proximally (Plate I, 2, 4) and distally (Plate I, 1) by apparently helically arranged vegetative leaves of the usual spatulate shape of 'standard' *A. roemeriana* leaves (Plate I, 3). These vegetative leaves are highly variable in number, depending on the position of the fertile branch in the lateral branching system. In the mid-region vegetative leaves are usually 2–3 in number at the base of the fertile branches (Plate I, 2, 4) but are up to ten when the fertile branch is borne at the base of

PLATE I



the lateral branching system. Two to three vegetative-fertile leaves make the transition between wholly vegetative spatulate leaves and sporophylls. These show both morphologies with, on the one hand, a part consisting of a flattened vegetative blade more or less deeply dissected, very variable in extent, and, on the other hand, a part appearing as more or less flattened, forking axes bearing sporangia on about half of their length (an illustration of such a transitional leaf is provided in Kenrick and Fairon-Demaret, 1991, Plate I, 5). Uncovering of these transitional leaves shows that they bear a highly variable number of sporangia, from a few (3–9, Plate III, 7) up to more than twenty. Transitional forms adjacent to wholly fertile leaves have a blade reduced to a minimum and may appear similar to sporophylls but as a rule they are less bifurcated. Towards the apex, a few transitional forms are also observed; the distalmost leaves are vegetative again (Plate I, 1) and are usually reduced in size, as are the apical leaves on vegetative branches (Fairon-Demaret and Leponce, 2001). Thus, from the base towards the apex fertile ultimate branches of *A. roemeriana* are showing typical allomorphy *sensu* Jones, 1999.

Sporophylls are more densely arranged when compared to vegetative leaves (Kenrick and Fairon-Demaret, 1991). Their arrangement around the axis is difficult to ascertain but a regular decussate insertion is not suggested as they rarely appear opposite or subopposite along the axis (Plate I, 1, 2, 4; Plate II, 2; Plate III, 4). They are rather borne according to a helical pattern, as demonstrated by dégaging a fragment of a fertile ultimate branch, 15 mm long and 1 mm wide (Plate II, 7; Fig. 1; specimen ULg 13503). Both ends are broken and it is not possible to specify the position of this fertile fragment on the ultimate branch. Eight fertile leaves are borne according to a peculiar pattern with two successive fertile leaves attached close together (leaves 1 and 2, 4 and 5,

7 and 8), followed by a more isolated one (leaf 3 and leaf 6). Leaves 1 and 3 are attached behind the compressed remain of the axis, as well as leaves 6 and 8; they are completely embedded in the sediment but their attachment on the axis is shown by oval, thick, carbonaceous areas; leaf 4 is borne laterally; leaves 2, 5 and 7 are attached in front (Plate II, 7; Fig. 1). A phyllotactic fraction belonging to the Fibonacci series could not be determined.

#### 4.2. The fertile leaves

The morphology of the fertile leaves, which are on an average 10 mm in length, is more complex than might appear on first sight, as demonstrated by uncovering both part (ULg 13502a; Plate II, 2) and complementary counter-part (ULg 13502b) of a fragment of a penultimate branch, 150 mm long and 4 mm wide, bearing four pairs of oppositely arranged ultimate branches, the two basalmost ones being fertile. An additional fifth, proximal fertile branch, preserved over a length of 55 mm, was originally attached to this penultimate branch, but its connection is now missing. A well preserved fertile leaf, attached at an estimated distance of 40 mm from the supposed insertion of this ultimate branch, was dégaged on both the part (Plate III, 1–3, 5; Fig. 2a'–d' Fig. 3) and the complementary counter-part (Plate II, 1, 3; Fig. 2a–d). This peculiar leaf was chosen because it was positioned in the wholly fertile mid-region of the fertile ultimate branch and, most importantly, is not entangled with other ones as is usually the case.

Initially this fertile leaf 9.5 mm long, showed a distal fork, observable only on the counterpart, and appeared to fork once near its mid-length (better seen on the counter-part ULg 13502b; Fig. 2 at big arrow); occurrence of another more proximal bifurcation was suspected on both part and counter-part

PLATE I. (Scale bar = 1 cm, except when otherwise indicated).

1. Apex of a fertile ultimate branch showing transitional leaves between the fertile area and wholly vegetative apical leaves (Specimen ULg 13499b).
2. Detail of 4; base of a fertile ultimate branch with two basal vegetative leaves.
3. General view, natural size, of a vegetative lateral system with overlapping, spatulate leaves with typical nervation (Specimen ULg 13179).
4. General view, natural size, of a fertile lateral system; the arrows point to the area detailed on 2 (Specimen ULg 13172a).
5. Detail of a fertile leaf showing crowded sporangia, three of them being borne at the same level (arrow head); (Specimen ULg 13171b).

(Fig. 2a–a' at small arrow). The progressive uncovering of this leaf on the part (Plate III, 2, 3, 5; Fig. 2a'–d') and on the counterpart (Plate II, 1, 3; Fig. 2a–d) is illustrated. On the part, the sporangia were completely removed in order to clearly reveal the morphology of the leaf (Plate II, 2, at arrow, 5; Fig. 3). At the end of the process, the fertile leaf was demonstrated to be actually three times bifurcated, resulting in eight terminal segments (H–O). Five (J, K, L, M and O) are visible on the part (Fig. 3; Plate II, 5); segments H and I are preserved on the counter-part (Fig. 2a–d). The bifurcations occur in a single plane, more or less perpendicularly to the longitudinal axis of the branch. The splitting of the matrix cut the compression at the level of the second bifurcation, between segments I and J. Segment N was unfortunately destroyed during the uncovering process but the photographic record of the successive uncovering steps allows to ascertain its occurrence. All segments are 1 mm wide, being only slightly enlarged immediately before a bifurcation. They most often appear tubular (Plate I, 5; Plate II, 5–7; Plate III, 6). On several segments (but never in the proximal and distalmost areas of a fertile leaf) a narrow, thin flange is occasionally seen along both sides of the thick carbonaceous middle area (Plate III, 1–5). It cannot be decided if such an aspect results from compression or if it is actually indicative of the slight development of a very reduced lamina.

#### 4.3. The sporangia

The pedicellate sporangia are fusiform in shape. On an average they (more than 200 sporangia measured)

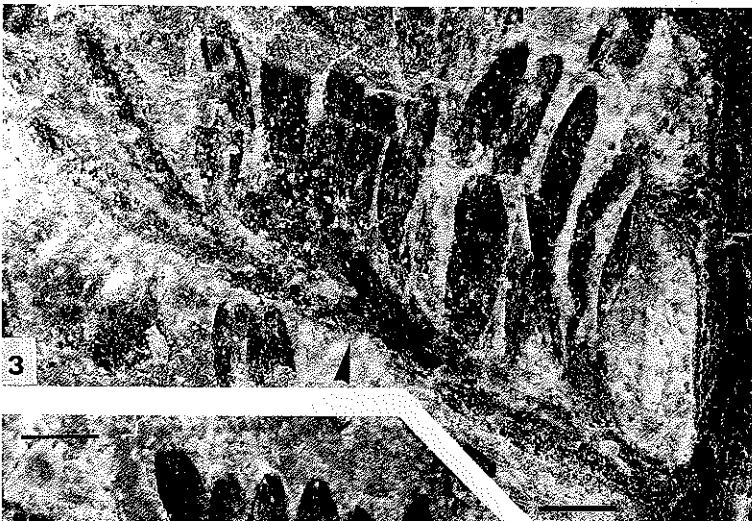
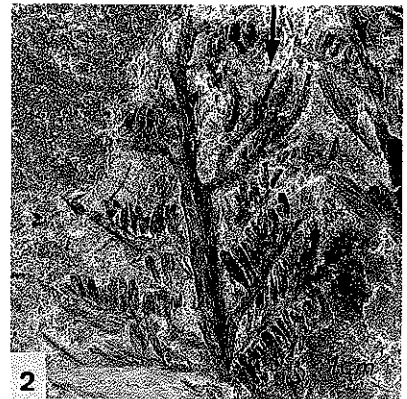
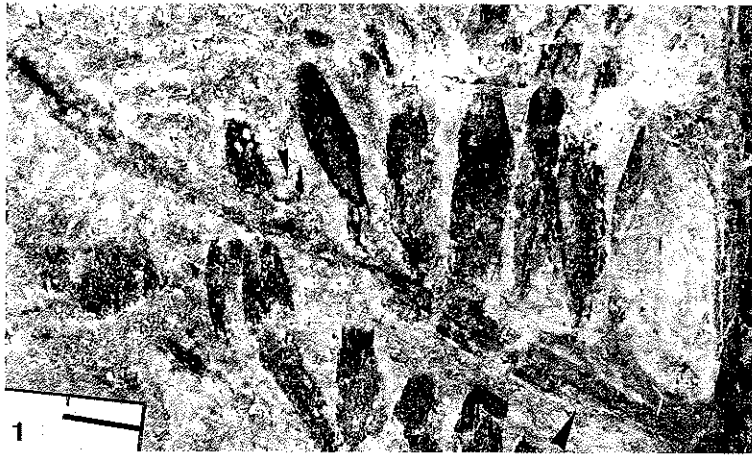
measure 1.94 mm in length (min.: 1.34 mm; max.: 2.9 mm) and 0.62 mm in greatest width (min.: 0.4 mm; max.: 0.78 mm). Longer and slender sporangia progressively merge into shorter and broader ones without clear-cut differences between two size classes. Dehiscence occurs through a longitudinal slit, as usual in *Archaeopteris*. (Plate II, 6).

The sporangia are borne upright, standing in two alternate rows (Plate II, 4–6; Plate III, 6). Just before a bifurcation, where a segment is enlarged, three sporangia can be observed borne side by side (Plate I, 5). While uncovering the above described fertile leaf, sporangia were counted (Fig. 4, a–c). They were not numbered according to a logical sequence; they were given a number as the degagement proceeded. No sporangia were noticed on the basal part A. On segment B, seven sporangia are borne, six in a row (5, 6, 10, 20, 21, 23) and an additional one occurs at the level of the enlargement preceding the bifurcation. On segment C, seven sporangia are inserted in alternate rows (1, 2, 4, 34, 35, 36, 39). On segment D, six sporangia are noticed, arranged in two rows (18, 19, 25, 26, 27, 28) and on segment E, they are ten (11–17, 24, 30, 31) with possibly three of them (17, 30, 31) standing side by side before the J–K bifurcation. Five sporangia occur on segment F, three in a line (7, 8, 9) and two side by side (32, 33) and on segment G, two sporangia are seen in a line (37, 39). The distalmost segments H, I, J, K, L, M, N and O have no sporangia. One (29) is present on segment J. Thus on this fertile leaf, 39 sporangia were present. Their insertion point was not always clearly visible. A reconstruction made of three complementary drawings is proposed to

PLATE II. (Scale bar = 1 mm except when otherwise indicated).

1. Detail of a fertile leaf (counter-part), last step in the uncovering process of the counterpart (Specimen ULg 13502b); one bifurcation at mid-length can be seen (small arrow head) as well as the proximal one (big arrow head); compare with Fig. 2d.
2. General view of the fertile ultimate branching system; the arrow points to the completely uncovered fertile leaf the sporangia of which having been removed (Specimen ULg 13502a). Scale bar: 1 cm.
3. Uncovering stage of the fertile leaf illustrated in 1; the second segment of the distalmost bifurcation is well shown, as well as the bifurcation located at about mid-length of the sporophyll (arrow head); compare with Fig. 2b.
4. Fertile leaf that has been flattened in the bedding plane showing the crowding of the sporangia apparently arranged into two (?three) alternating rows (Specimen ULg 13171b).
5. A fertile leaf with sporangia on one of the terminal segments, up to half of its length (Specimen ULg 13509).
6. Detail of sporangia with longitudinal dehiscence slit (Specimen ULg 13020).
7. Fragment of a fertile ultimate branch that was partially uncovered; eight sporophylls (1 to 8) are helically arranged; compare with the schema on Fig. 1 (Specimen ULg 13503c).

PLATE II



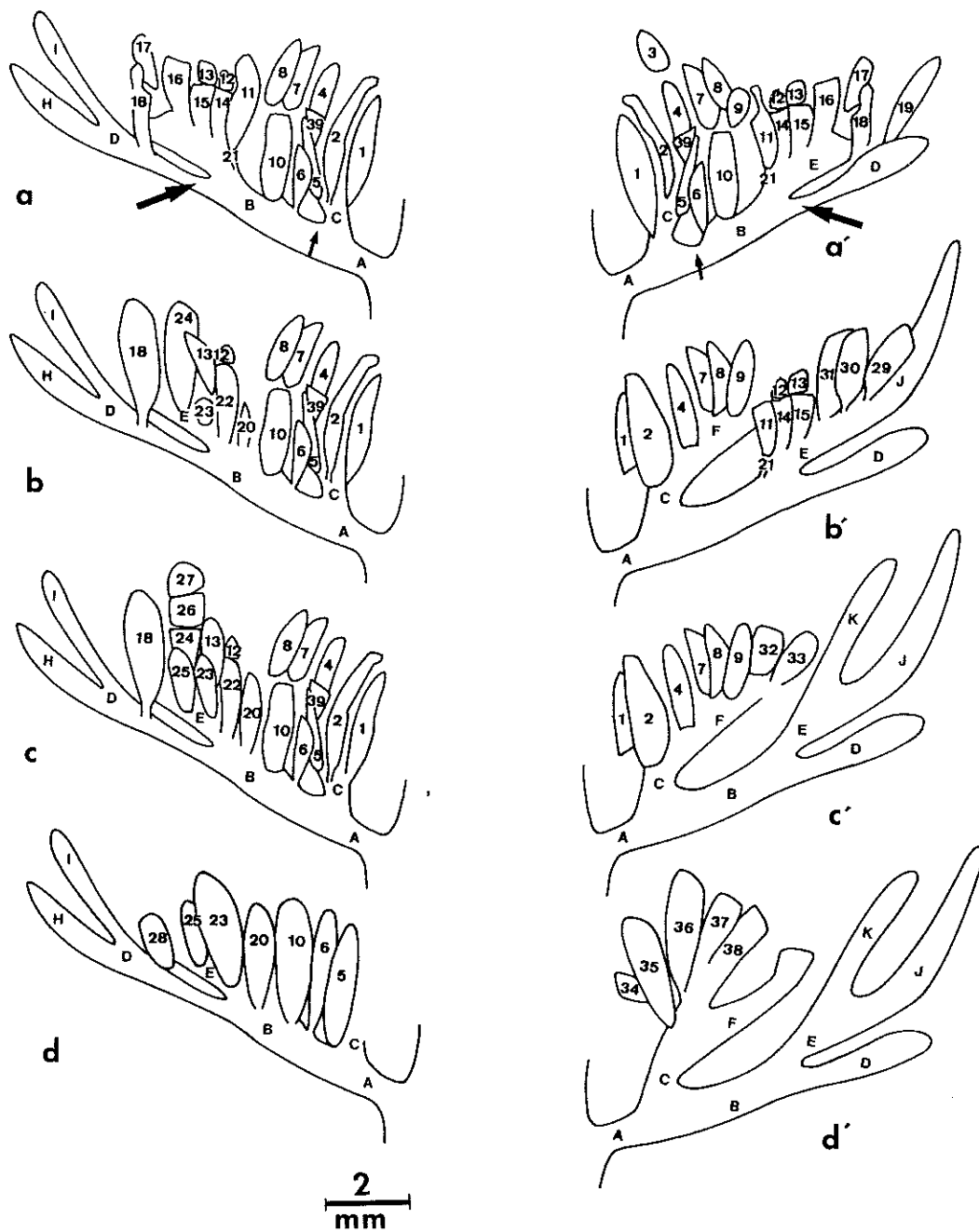


Fig. 2. Drawings corresponding to the successive stages of dégage ment of a single fertile leaf; a'–d' on the part (specimen ULg 13502a; see Plate III, 1–3) and a–d on the counterpart (specimen ULg 13502b; see Plate II, 1 and 3).



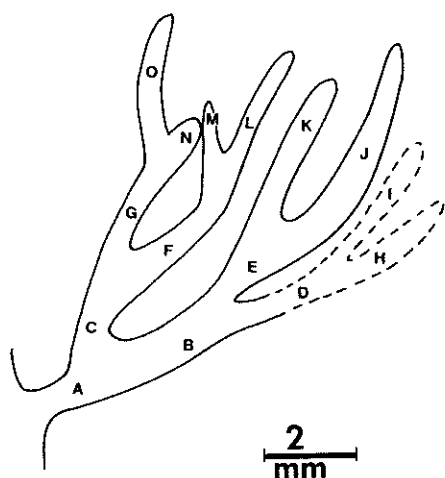


Fig. 3. Drawing of the last stage of dégage ment of a fertile leaf (specimen ULg 13502a); stippled lines indicate the distal segments that are preserved on the counterpart only; see Plate III, 5.

evidence the crowded arrangement of the sporangia (Fig. 4).

Other fertile leaves bear an even higher number of sporangia, as sporangia may exceptionally occur proximally, before the first bifurcation of the sporophyll and distalmost ones may be borne on several of the eight terminal segments for up to half their length (Plate II, 5).

The sporangia recovered by transfer (specimens ULg 13020) show the sporangium wall to be made up of rectangular cells arranged in longitudinal rows (Plate IV, 5).

#### 4.4. The spores

Transfers of fertile branches from four specimens (ULg 13020, 13119, 13497, 13509) revealed that most of the sporangium compressions were empty, and their remains usually crumbled to dust when freed from the matrix support. Several spores still adhering to sporangium fragments (Plate IV, 3, 8, 9) were nevertheless recovered. They display a wide variety of size, from 13 to 214  $\mu\text{m}$  in diameter and can be arranged into two size classes. The first one includes microspores, under 70  $\mu\text{m}$  in diameter. They are subtriangular in equatorial outline. On the distal face, they show an ornamentation of small cones densely arranged; on the proximal face, they have a slightly raised trilete mark and the cones are sparsely

distributed on the contact areas, which are delimited by a thin, imprecise ridge (Plate IV, 8). The second category includes the few remains of megaspores. No megaspore was observed showing the proximal face, and a trilete mark plus eventual curvaturae were not seen; the distal face possesses a distinct ornamentation made of small more or less prominent cones and rods. These sculptural elements are fused to varying extents to form small, irregularly reticulated, undulating crests or wart-like elements (Plate IV, 9).

Unfortunately these spores on sporangium fragments were too few in number to be regarded as conclusively contained in the sporangia, the more so as the matrix contains a rich assemblage of dispersed spores, including forms identical to the microspores described above. In addition palynological slides were prepared from: –1) sediment immediately around the sporangia, released during the transfer process of specimen ULg 13020 (type 1, palynological slides 53820, 53822, 53843), –2) the same amount of sediment cut off on specimen ULg 13497, a few centimetres away from the sporangia on a fertile ultimate branch (type 2, palynological slides 52521, 52562) and –3) an identical quantity of sediment from specimen ULg 13119 with compressions of vegetative branches only (type 3, palynological slides 54143, 54144). The most common morphological types of microspores [*Aneurospora greggsii* (McGregor) Streel, *Grandispora cornuta* Higgs and *G. gracilis* (Kedo) Streel being gathered under *Grandispora* sp., *Diducites versabilis* (Kedo) Van der Zwan and *D. plicabilis* Van der Zwan represented under *Diducites* sp., all the *Retusotriletes* together and all the *Auroraspora* sp.] were counted, plus the isolated megaspores (belonging to a single morphological type), as well as tetrads and agglomerated tetrads of *A. greggsii* (Table 1). Average percentages were compared (Table 2).

First of all complete megaspores are rare. They only occur in type 1 slides (type 2 slides only contains a few broken fragments of megaspores). Under the light microscope they are subcircular in equatorial outline, varying from 110 to 403  $\mu\text{m}$  (average 214  $\mu\text{m}$  in diameter; 43 spores measured). They are trilete, highly carbonised and often cracked (Plate IV, 10). Even after clearing treatment (Schulze solution), details of the lips of the trilete mark or of the contact areas on the proximal face could not be observed.

Table 1  
Spore taxa/morphotypes-number of specimens in the three types of slides

Taxon/morphotype	Slide Number/type						
	53820/1	53822/1	53843/1	52521/2	52562/2	54143/3	54144/3
<i>Aneurospora greggsii</i>	904	842	1092	466	468	95	122
<i>Grandispora</i> sp.	840	78	85	52	60	72	106
<i>Diducites</i> sp.	42	46	64	22	47	47	67
<i>Auroraspora</i> sp.	20	20	22	18	12	25	18
<i>Retusotriletes</i> sp.	10	12	10	16	10	19	30
Total	1060	998	1273	574	597	258	343
Megaspore	9	10	19	0	0	0	0
<i>A. greggsii</i> tetrads	106	106	106	21	25	2	9
Packets of tetrads	7	5	7	0	0	0	0

Nevertheless ornamentation of cleared megaspores obtained from the enclosing matrix (Plate IV, 6, 7) is not significantly different from uncleared ones seen attached to sporangium fragments (Plate IV, 9) with conii, grana and rods that are 1–2.5  $\mu\text{m}$  high in side view. The variable coalescence of these ornaments results in typical, irregularly winding, rugulae similar in appearance to the external ornamentation of the dispersed megaspores of the *Contagisporites* complex but no apparent inner body could be observed. As occurrence of isolated intact megaspores is restricted to the matrix directly enclosing the sporangia of *A. roemeriana* (type 1 slides), it may reasonably be assumed that they were shed by these.

One morphological type of microspore is dominant in all three palynological samples, however in different proportions. From an average of 85 and 79% respectively in sample types 1 and 2, they drop to 36% in type 3 (Table 2). They are identical to the small spores observed in the transfers, with a dense ornamentation of small conii or grana on the distal

face. The proximal face is less coarsely ornamented, resulting in distinct contact areas, which are delimited by a slight, poorly defined thickening (Plate IV, 1, 2). They fall within the concept of the *spora dispersae* taxon *Aneurospora greggsii*. (Mc Gregor) Streel. Tetrads of this type of microspores occur in sample types 1 and 2 with a significantly higher number in the type 1 sample which also contains several packets of agglomerated tetrads (Plate IV, 5). All these observations also point to occurrence of *A. greggsii* type of microspores in the *Archaeopteris roemeriana* sporangia which are heterosporous.

### 5. Comparison and synonymy with *Archaeopteris halliana*

*Archaeopteris roemeriana* actually shares many characteristics with *A. halliana* from North America. The last comprehensive analysis of this species was performed by Phillips et al., 1972. They demonstrated

PLATE III. (Scale bar = 1 mm except when otherwise indicated).

1–3 and 5. Several steps in the dégage ment of the fertile leaf on the part (Specimen ULg 13502a).

1. The proximal bifurcation and a second one near mid-length of the sporophyll are visible; compare with Fig. 2a'.

2. Two terminal segments are uncovered plus the second one of the bifurcation near mid-length of the sporophyll, this incompletely shown segment being overloaded with sporangia; compare with Fig. 2c'.

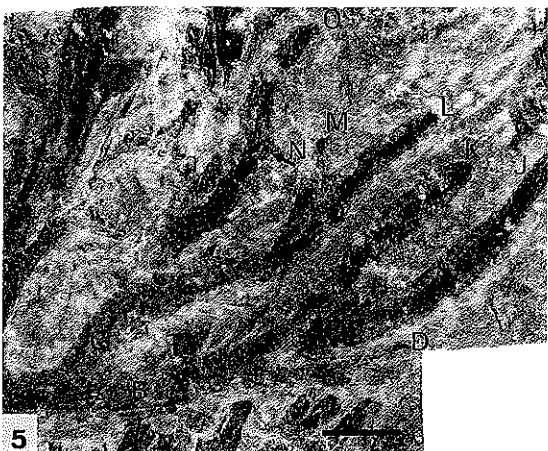
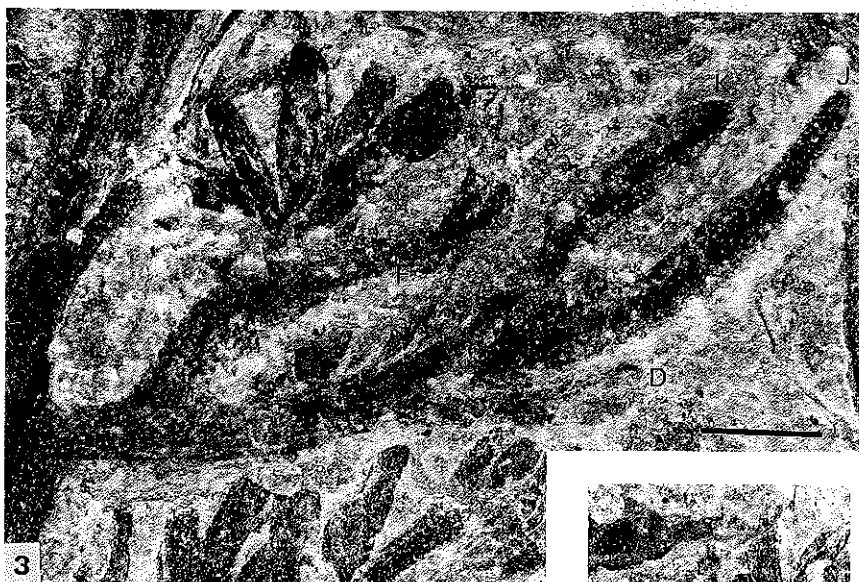
3. Occurrence of additional sporangia inserted at a lower level is shown; compare with Fig. 2d'.

4. General view of a fertile ultimate branch; the sporophylls rarely appear opposite or subopposite along the axis (Specimen ULg 13020a that was transferred). Scale bar = 1 cm.

6. Fertile leaf that has been exceptionally flattened in the bedding plane; the two-ranked sporangia are locally folded back along both sides of a segment (Specimen ULg 13171b).

7. 'Transitional' leaf uncovered showing crowded sporangia (Specimen ULg. 13171b).

PLATE III



## PLATE IV

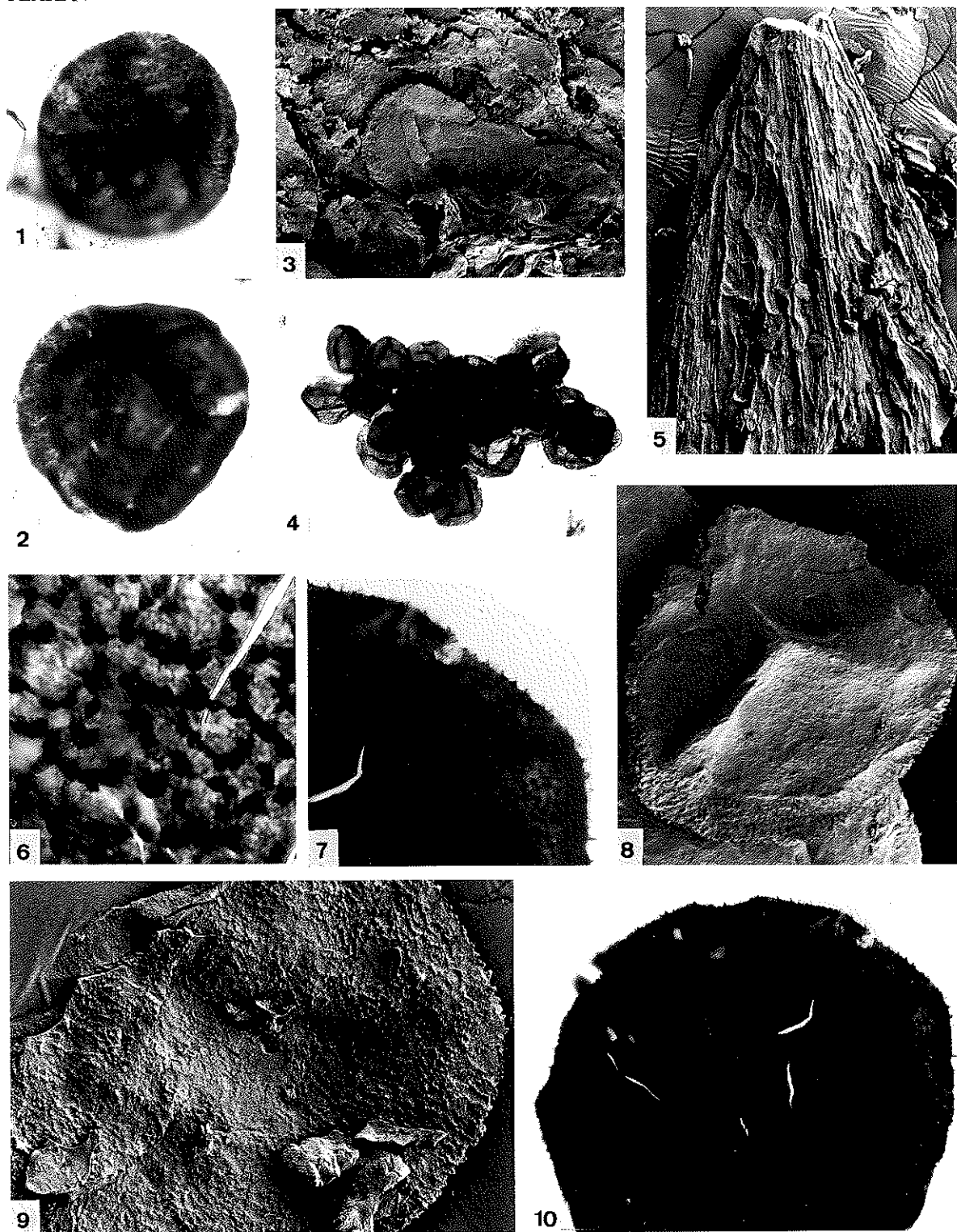


Table 2  
Abundance of the main morphotypes in the three types of slides

Spore morphotype abundances (%)			
	Type 1	Type 2	Type 3
<i>Aneurospora greggsii</i>	85.2	79.26	36.1
<i>Grandispora</i> sp.	7.41	9.56	29.61
<i>Diducites</i> sp.	4.56	5.89	18.97
<i>Auroraspora</i> sp.	1.86	2.56	7.15
<i>Retusotrilletes</i> sp.	0.96	2.22	8.15

that fertile ultimate branches of *A. halliana* bear sporophylls, both proximal and distal to which also commonly occur gradual transitional forms followed by strictly vegetative leaves, as in *A. roemeriana*. Both species thus show occurrence of 'allomorphy' (Jones, 1999). In both species, also, the sporophylls are three times forked, ending in eight tips, and sporangia of the same shape and size are borne on the segments resulting from the basal and middle bifurcations. These sporophylls also have similar dimensions, being shorter than usual 'standard' (as opposed to the reduced ones occurring on the adaxial side of vegetative axes of *A. roemeriana*) vegetative leaves.

On *Archaeopteris*, leaves are thought to be borne on the ultimate axes according to an anomalous series of fractions most of which lie outside the usual Fibonacci series of numbers (Scheckler, 1978). Although Phillips et al., 1972 suggest a four rowed arrangement of the leaves on the ultimate branches of *A. halliana*, their reconstruction (loc. cit., Text-figure 3, p. 55)

presents some sort of compromise between helical and four-ranked disposition of sterile and vegetative leaves. Two successive fertile leaves are locally very close together (loc. cit., Text-figure 2, p. 54), as in *A. roemeriana*. Thus 'paired' sporophylls are noticed on the fertile ultimate axes of both species. Nevertheless, a helical arrangement of the sporophylls is consistent with the more or less radially symmetrical xylem strand observed within the axes of the fertile area in *A. roemeriana* (Kenrick and Fairon-Demaret, 1991). Outside this zone, in the basal and apical vegetative regions of the fertile ultimate branch, the vascular strand, which has not yet been described, might be of a different shape. Likewise, the fertile fragment of *A. roemeriana* showing 'paired' sporophylls, the position of which along the fertile branch could not be specified, might also come from a region where the shape of the vascular strand is changing. Such a hypothesis may also apply to the proximal portion of the *A. halliana* fertile branch drawn by Phillips et al. (1972, Text-figure 2, p. 54). Interestingly, on *A. roemeriana* vegetative ultimate axes small 'paired' vegetative leaves inserted close together occur in areas corresponding to changing number of sympodia in the vascular strand (Fairon-Demaret and Leponce, 2001).

In both species, the sporangia are of the same shape and dimension. They are more numerous on *A. roemeriana* sporophylls with as many as, perhaps more, 59 sporangia per fertile leaf versus about 20 counted for *A. halliana*. Sporangia occasionally occur even on the basal segment and on half of the

#### PLATE IV

1. *Aneurospora greggsii*, distal surface (palynological slide 53822; type 1 prepared from the sediment immediately around the sporangia, released during the transfer process of specimen ULg 13020).  $\times 1000$ .
2. *Aneurospora greggsii*, proximal surface (palynological slide 53820; type 1 prepared from the sediment immediately around the sporangia, released during the transfer process of specimen ULg 13020).  $\times 1000$ .
3. *A. greggsii*, several specimens still enclosed in badly preserved sporangial tissue remains; transfer of specimen ULg 13509.  $\times 1000$ .
4. A packet of agglomerated tetrads of *A. greggsii* (palynological slide 53822; type 1 prepared from the sediment immediately around the sporangia, released during the transfer process of specimen ULg 13020).  $\times 400$ .
5. Fragment of one sporangium transferred from specimen ULg 13509.  $\times 120$
6. Detail of a megaspore ornamentation (palynological slide 53843; type 1 prepared from the sediment immediately around the sporangia, released during the transfer process of specimen ULg 13020).  $\times 1000$ .
7. Detail of the ornaments of the megaspore illustrated Fig. 10 (palynological slide 53822; type 1 prepared from the sediment immediately around the sporangia, released during the transfer process of specimen ULg 13020).
8. SEM of the proximal surface of an *A. greggsii* specimen isolated from the transfer of specimen ULg 13509.  $\times 1400$ .
9. SEM of a megaspore, distal surface, isolated from the transfer of specimen ULg 13509.  $\times 420$ .
10. General view of the megaspore, the ornamentation of which is illustrated on Fig. 7  $\times 250$ .

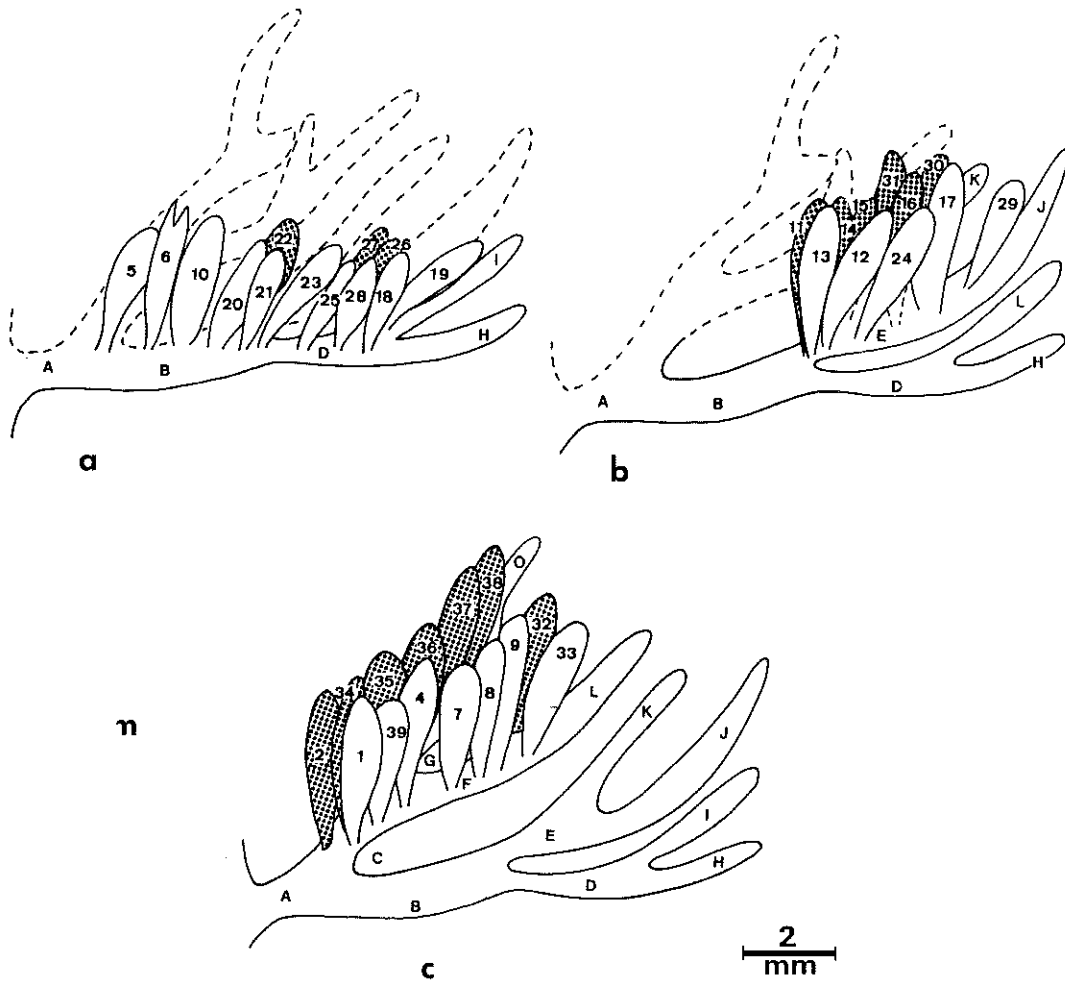


Fig. 4. Reconstructions of the arrangement of sporangia on a single fertile leaf, combining the data obtained from *dégagement* of the part and counterpart; the dashed sporangia are inserted at a lower level.

length of the terminal ones on *A. roemeriana*, a fact not noticed in *A. halliana*. The weight to be put on such a difference in the number of sporangia should not be over-emphasised. Actually, the crowding of sporangia on the fertile leaves might be highly variable according to the original growth position of the fragment when considered relative to what may have been a large tree; size of reproductive competence is often dependent also on the growth environment of the plant (Jones, 1999).

The trilete, circular to subcircular microspores described from *Archaeopteris roemeriana* are assigned to the *spora dispersae* taxon *Aneurospora*

*greggsii* and not to *Geminospora lemurata* Balme emend. Playford, as are the microspores of *A. halliana* and of other species of *Archaeopteris* (Gensel, 1980; Allen, 1980; Balme, 1995). Both taxa are similar in external ornamentation. They differ mainly in the number of visible exine layers. On *A. roemeriana* microspores no clear-cut separation between intexine and exoexine could be observed under the light microscope, but they show a tenuous, poorly delimited proximo-equatorial 'thickened' feature. When observed with the SEM this equatorial thickening appears as a slender raised line, not as a usual crassitude. It is probably indicative of a variation in

the internal construction of the spore eventually corresponding to a separation between both exine layers. *Geminospora* specimens are camerate and usually possess a well defined inner body. However, sometimes they show only a small separation between exoexine and intexine (Marshall, 1996) with intexine often adpressed to the exoexine and difficult to distinguish (Allen, 1980). Unfortunately miospores isolated from sporangia of *A. halliana* were not illustrated by Phillips et al., 1972 but those from *Archaeopteris* sp. appear indistinguishable from the *A. roemeriana* miospores (compare Phillips et al., 1972, Plate 45, Fig. 49, 50, 52, 54 and 55 with Plate IV, Figs. 1 and 2). A clear distinction between both exine layers eventually depends on the taphonomy and preservational history of the spores. Development of haptotypic features (as a more or less prominent crassitude on *Aneurospora*, also occasionally seen on *Geminospora*, Allen, 1980) varies with the level of maturity of the spores (Streel and Scheckler, 1990). Therefore we suggest that both morphographic taxa, *Aneurospora greggsii* and *Geminospora lemurata*, might belong to a single natural type of miospores. It seems likely that these were produced by the *Archaeopteris* plant as well as by earlier members of the Archaeopteridales such as *Svalbardia* (sometimes regarded as a junior synonym of *Archaeopteris*, Carluccio et al., 1966; Beck, 1971; Scheckler, 1978; discussion in Beck and Wight, 1988) and *Tanaites* (Krassilov et al., 1987; Balme, 1995). We thus confirm Streel and Scheckler's (1990) hypothesis about *Archaeopteris* being the *A. greggsii* mother plant.

Among the miospores abundant in the marine Fa2c (Upper but not Uppermost Famennian) deposits of the Dinant Synclinorium in Belgium, *Aneurospora greggsii* is the most abundant taxon (Streel and Scheckler, 1990). *A. greggsii* is also dominant in the more allochthonous part of the downstream flooding facies at Elkins in West Virginia, USA, and it was already suggested that *A. greggsii* 'might well represent *Archaeopteris*' (loc. cit., p. 322). Unfortunately as spore morphology cannot be used to distinguish between *Archaeopteris* species (Allen, 1980; Balme, 1995; Beck and Wight, 1988), the fact that the very same microspore morphon is recorded from both the Belgian and North American Famennian formations is useless for taxonomic purposes.

Megaspores of *Archaeopteris* are assignable to the *sporae dispersae* genus *Contagisporites* Owens, 1971 (Marshall, 1996 and reference therein) that is morphologically similar in optical microscopy to *Biharisporites* (Singh) Potonié, 1956, a dispersed megaspore genus with a Lower Permian type species (Balme, 1995). *Contagisporites* includes radial trilete camerate spores with a typical closely packed ornamentation made of a variety of small sculptural elements, coni, grana, rods, bacula, etc. Megaspores of *Archaeopteris halliana* are indistinguishable from those of *A. macilenta* (Phillips et al., 1972). Their external morphology is similar also to those of *A. roemeriana*. However, the poor state of preservation of the latter makes impossible to provide details on their internal construction and they are provisionally put in the *Contagisporites* complex on the basis of their sculptural elements.

Finally, European *Archaeopteris roemeriana* and North American *A. halliana* cannot be distinguished on morphological grounds by the characters of their vegetative nor their fertile parts. They are only separated by the persistent lack of information on the internal structure of *A. halliana* where anisophylly on vegetative ultimate axes still remains to be demonstrated, a characteristic which usually is not observable on compression remains without technical work (Fairon-Demaret and Leponce, 2001). Nevertheless, owing to the morphological similarities between both species, important, diagnostic differences in the internal construction are not expected. We rather suggest to consider the positive evidence identified above and apply the 'strong inference principle' (sensu Stein and Hueber 1989). Accordingly and considering the new information on the fertile parts of *A. roemeriana*, we propose to adopt the old proposal of Kräusel and Weyland, 1941 and to gather both categories of remains from Europe and North America, under a single species name. From now, they will be designated as *Archaeopteris halliana* (Goepfert, 1852) Lesquereux, this specific epithet established by Goepfert as early as 1852 having priority.

The nomenclatural type of *Archaeopteris halliana* was designated by Arnold (1939) who provided good photographic illustration (Plate V, Fig. 1) and a detailed description (pp. 299–300) of the terminal part of a branching system collected more than 150 yr ago from Pine Valley in Chemung County, New York, and previously drawn by Hall (1843, p. 275, Fig. 1).

Illustrated again by Beck (1971) the holotype is conserved in the paleobotanical type collection (n° USNM 41131) of the National Museum of Natural History, Smithsonian Institution, Washington DC.

## 6. Discussion and palaeobiogeographic considerations

*Archaeopteris* species are primarily distinguished by the morphology and degree of overlap of the leaves on the plagiotropic vegetative ultimate branches. On these grounds *A. halliana* is easily distinguished from *A. macilenta*. On the species where they are described, fertile leaves are three-dimensionally arranged around the axis. *A. macilenta* (Beck, 1981) however shows a decussate arrangement of the sporophylls as opposed to the helically disposed, non-laminated ones of *A. halliana*. Both species can thus be distinguished not only by the morphology their vegetative leaves but also by the characteristics of their sporophylls and strobili.

All the better known species of *Archaeopteris* are heterosporous, share the same general organisation and are thought to possess a similarly arborescent construction. The well known reconstruction of *Archaeopteris* tree is largely based on *A. macilenta* (Beck, 1962, 1981) that in addition allowed the establishment of connection between *Archaeopteris* and *Callixylon* (more precisely *C. zalesskyi* in Beck, 1960). A variety of developmental units have recently been described from logs of *Callixylon whiteanum* (Trivett, 1993) and *C. erianum* (Meyer-Berthaud et al., 1999, 2000) and presently the integration of the new anatomical information on the one hand, and of the observations derived from morphological studies of *Archaeopteris* compressions on the other hand, still appears premature. The isolated fertile systems of *A. halliana* described here are of no help. It is not known if these detached, determinate, fertile lateral branching systems are to be equated to the apically initiated branch type described in *Archaeopteris*, and probably shed as units (Beck, 1971, 1981; Beck and Wight 1988; Scheckler, 1978; type A branches of Meyer-Berthaud et al., 1999, 2000) or if they are borne on 'branch B' of Meyer-Berthaud et al. (1999, 2000), long-lived structures producing regularly arranged appendages.

The fact that the sporophylls of *Archaeopteris halliana* are shorter than the vegetative leaves is most probably developmentally driven. Sporophylls supported the weight of numerous sporangia crowded on the upper surface of narrow segments, and accordingly may have minimized external stress by reducing the length of the loaded lever arm (Mattheck and Kubler, 1997). In showing very restricted, if any, lateral growth of a lamina they are strikingly different from the laminated ones of *A. macilenta*. *A. halliana* fertile leaves obviously had reduced photosynthetic activity. When cleared from their sporangia, they appear made of bifurcated segments showing restricted, if any, dorsoventrality but with a proximodistal axis still clearly present. The successive bifurcations occurring in one plane are evocative of ancestral aneurophytalean fertile organs similar in construction as those of *Tetraxylopteris* (Bonamo and Banks, 1968) but with reduced size and less orders of branching. Such a 'conservative' view might be attractive on theoretical grounds but is not actually realistic. In seed plants it has been shown that a gradient with a source originating in the apex is responsible for determination of dorsoventrality in leaf initials. Subtle change in the strength or position of the 'dorsalising function' is sufficient to induce a variety of leaf morphologies, including radially symmetrical ones without lamina but still showing a proximodistal axis, determination of which remains independent of differentiation of a lamina (Waites and Hudson, 1995). As similar structure/function parameters apparently are active in plants regardless of geological period or phylogenetic affinities (Niklas, 1994, 1997), such subtle change may have operated in *A. halliana* during the transition to the reproductive phase of growth. Genetically fixed it resulted in the obvious morphological difference between *A. halliana* and *A. macilenta* fertile leaves.

The non laminated sporophylls of *Archaeopteris halliana* were more efficient for wind dispersal of the sporangium contents, facilitating dissemination but at the expense of protection and of more equable local micro-environment as eventually provided by *A. macilenta* laminated sporophylls. Water loss by evapo-transpiration was also reduced. Such a difference in fertile leaf morphology might correlate with difference in the biotopes both species colonised or in their geological age (or in a combination of both).

Up to now palynological studies do not help in



discussing on reliable grounds eventual differences in time or spatial distribution of *Archaeopteris* species as the same *sporae dispersae* complex, *Aneurospora greggsii*–*Geminospora lemurata*, encompasses the microspores isolated from several *Archaeopteris* species including both *A. macilenta* and *A. halliana* (Gensel, 1980; Allen, 1980; Balme, 1995; Streeel and Scheckler, 1990).

Upper Devonian compressions of both species are collected in Bear Island (Nathorst, 1902), China (Hao and Mei, 1987; Cai et al., 1987) and in North America where they occur together in Frasnian and Famennian localities (Banks, 1966; Carluccio et al., 1966; Phillips et al., 1972; Scheckler, 1986). Even if their relative abundance is rarely detailed, *A. macilenta* is recorded as being particularly abundant in north American Frasnian deposits (Phillips et al., 1972). In Belgium occurrence of *A. macilenta* pre-dates the fossil record of *A. halliana*: it is known from Frasnian non-marine sediments from a single locality in the Campine Basin (Booischoot borehole; Streeel and Loboziak, 1987), the poor record of this species being apparently distorted by the rarity of Upper Devonian fossil plant deposits older than the VCo spore zone in the Ardenne–Rhine regions. Nevertheless it remains that *A. macilenta* has never been recorded in the numerous late Famennian localities of the Dinant Basin and Vesdre Synclinorium where *A. halliana* is the only species of *Archaeopteris* found (Stockmans, 1948; Kenrick and Fairon-Demaret, 1991).

It has been suggested that *Archaeopteris* trees (in general, without distinction between species) grew at well-drained sites adjacent to river systems where they formed dense gallery forests (Algeo and Scheckler, 1998; Meyer-Berthaud et al., 2000). Studies of in situ tree stumps and root casts in the Appalachian foreland basin in Pennsylvania have shown that *Archaeopteris* trees grew along fluvial margins and also eventually on drier parts of the flood plain as indicated by more limited evidence (Driese et al., 1997). It has thus also been suggested that *Archaeopteris* trees had ‘a wide tolerance within a landscape’ (Scheckler et al., 1999, p. 13).

*Archaeopteris macilenta*, *A. halliana*, *A. hibernica* and *A. sphenophyllifolia* plus remains of *Callixylon erianum* and *Callixylon* sp. are recorded in alluvial and fluvial deposits of the Hampshire Formation in West Virginia and in Virginia, USA (Scheckler,

1986). Among these species *A. macilenta* and *A. halliana* are most common (Scheckler, personal communication). In contrast, on the West European side of the Acadian mountains, in the near-shore marine sediments of the Dinant Basin, *Archaeopteris* is represented by remains of a single species, *A. halliana*, and by drifted logs of *Callixylon* sp. Elimination of *Archaeopteris* species (and particularly of *A. macilenta*) other than *A. halliana* by differential survival during identical transport conditions is difficult to accept in the case of these closely related arborescent plants, the more so as transport conditions would have been identical if they actually occupied the same ecological niche along streams. The difference in *Archaeopteris* species richness between both sides of the Acadian mountains is still more striking when considering that both areas were almost contemporaneous [lower VCo in Dinant Basin versus VH (= former upper VCo) spore Biozone, sensu Maziane et al., 1999 in Hampshire Formation], that they both were located in a paleo-tropical belt at 15 or 25°S. lat., and that they both supported a similar vegetation cover on the same kind of continental environments (well drained alluvial plain with upstream and downstream ‘coal’ swamps) as demonstrated by similar miospore assemblages (Streeel and Scheckler, 1990). Either *A. halliana* was the only species actually growing on the eastern side of the Acadian mountains, or it was the only species occupying the stream banks, an environment with higher fossilisation potential than the flood plain. The first hypothesis appears more likely when considering the next paragraph.

During Late (but not latest) Famennian times seasonal changes occurred (also in the Dinant Basin, as demonstrated for example by faint but nevertheless obvious growth rings on *Callixylon* remains; personal observation). In addition quantitative palynology allows interpretation of wet intervals with strong episodic flooding, at a cyclic recurrence of 33–41 ka duration (Streeel, 1999). On the flood plain, during the drier intervals, the upland water-table was lowered, reducing upstream swamp extension as shown by a concomitant diminution of spore output from swamp and near swamp communities. *Aneurospora greggsii* nevertheless remained most often the dominant miospore species in the Upper Famennian assemblages of the Ardenne (Streeel, 1999), demonstrating

the persistence of *Archaeopteris* trees. *A. halliana* possesses several traits favouring good control of water loss by transpiration (e.g. anisophylly and non laminated sporophylls that were more efficient in wind dispersal of the sporangium content). These peculiar, adaptative morphological traits allowed *A. halliana* to cope with dry, stressful periods of lowered water-table eventually better than *A. macilenta* that was not present (even along the river banks). This last species apparently was restricted at that time to the Appalachian windward, western rainy side of the Acadian mountains (Paproth et al., 1986) where the contrast between wet and dry climatic cycles might have been more buffered.

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