Archaeopteris roemeriana (GÖPPERT) *sensu* STOCKMANS, 1948 from the Upper Famennian of Belgium: anatomy and leaf polymorphism

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Abstract

The anatomy of the lateral system of *Archaeropteris roemeriana* is described based on specimens in the STOCKMANS collection. New collections from Langlier Quarry, in the Bocq valley, Belgium, provided additional morphological information. Leaves are more abundant on one side of some axes; on vegetative ultimate axes a marked difference in leaf size on opposite sides of the branch is inferred from bilateral symmetry of the xylem tissue. In contrast, fertile ultimate axes resemble strobili and the xylem tissue is radially symmetrical. The number of sporophylls per cm and the number of orthostiches is also greater than on comparable vegetative axes. The anatomy of *A. roemeriana* is compared with that of *A. macilenta* from North America, the only other species for which anatomy is known. The use of leaf size for specific delimination in *Archaeopteris* is discussed with reference to the leaf size polymorphism inferred for *A. roemeriana*. These considerations also raise the question of wether *A. roemeriana* is synonymous with *A. halliana*.

Key-words: *Archaeopteris* – anatomy – leaf polymorphism – Famennian – Belgium.

Résumé

L'anatomie du système de branches latérales d'*Archaeopteris roemeriana* est décrite sur base des échantillons de la collection STOCKMANS. De nouveaux spécimens provenant de la carrière Langlier, vallée du Bocq, Belgique, ont permis des observations morphologiques complémentaires. Les feuilles sont plus abondantes sur un côté de certains axes; sur les branches végétatives ultimes, une différence notable dans la taille des feuilles situées de part et d'autre du rameau est indiquée par la symétrie bilatérale du tissu ligneux. Par contre, les axes fertiles ultimes ressemblent plutôt à des strobiles et leur stèle est à symétrie radiaire. Le nombre de sporophylles et d'orthostiches par cm y est également plus élevés que sur les axes végétatifs d'ordre analogue. L'anatomie d'*A. roemeriana* est comparée à celle d'*A. macilenta* d'Amérique du Nord, la seule espèce dont l'anatomie soit connue. L'utilisation de la taille des feuilles comme caractère spécifique chez *Archaeopteris* est discutée en fonction du polymorphisme foliaire décélé chez *A. roemeriana*. Ces considérations soulèvent également la question de la synonymie entre *A. roemeriana* et *A. halliana*.

Mots-clefs: *Archaeopteris* – anatomie – polymorphisme foliaire – Famennien – Belgique.

Introduction

Large, leafy axes known as *Archaeopteris* are the prominent element in many Upper Devonian plant assenblages and for many years were thought to be bipinnate leaves from a fern-like plant of uncertain affinity. This interpretation persisted because of the frondlike appearance of the compression fossils as well as a lack of information on leaf (pinnule) arrangement and branch (rachis and pinna) anatomy. The systematic position of the genus and its importance in vascular plant evolution were clarified with the discovery of *Archaeopteris* foliage attached to gymnospermous type wood known as *Callixylon* (BECK, 1960a, b). This novel combination of features led BECK (1960a, b) to erect a new class, Progymnospermopsida. Since 1960 our knowledge of plants at the progymnosperm grade has increased enormously, and their role in seed plant evolution is the subject of much debate (BECK, 1976, 1981; BECK & WIGHT, 1988; ROTHWELL, 1981, 1982; MEYEN, 1984). The extensive literature on the group and the status of included taxa have recently been reviewed by BECK & WIGHT (1988); three orders of progymnosperms are currently recognized: Aneurophytales, Archaeopteridales, and Protopityales.

Archaeopteris is the only genus of Archaeopteridales that is understood in any detail. However our concept of this plant is based mainly on studies of the lateral branch systems of *A. halliana* (GÖPPERT) DAWSON, emend. ARNOLD, 1939 and *A. macilenta* LESQUEREUX, 1884 from North America (BECK & WIGHT, 1988). These studies include detailed description of anatomy and morphology, as well as attempts to correlate anatomical and morphological observations. There has been no comparable detailed study of *Archaeopteris* outside North America, and as a consequence our knowledge of this important genus is based on a geographically restricted set of material. In this study we present the first anatomical description of European specimens of *Archaeopteris*. Material of *A. roemeriana* (GÖPPERT) sensu STOCKMANS 1948 was examined and the anatomy of the lateral branch system is described. These observations include the first detailed description of the anatomy of the ultimate vegetative axes of *Archaeopteris* and they allow a more complete evaluation of the degree of specialization of vegetative and fertile ultimate branches. Some aspects of leaf variation are re-examined from anatomical and morphological viewpoints.

Systematics and nomenclature of *Archaeopteris roemeriana*

The *Archaeopteris* specimens described here belong to *A. roemeriana* (GÖPPERT) sensu STOCKMANS, 1948, but there is some doubt over the delimitation of this species. *A. roemeriana* was described originally from an axis fragment (GÖPPERT, 1860) so the nature and extent of the morphological variation in the species were poorly understood. ARNOLD (1939) considered *A. roemeriana* to be the closest European species to *A. halliana* from North America and doubted the significance of the characters used to separate the two: the degree of leaf (pinnule) overlap and the acute angle of departure of the penultimate branches (pinna) in *A. roemeriana*. Subsequently, KRÄUSEL & WEYLAND (1941) introduced a key based on leaf size, nature of the leaf margin, density and degree of leaf overlap, and shape of vegetative leaves, and in their treatment *A. halliana* and *A. roemeriana* were synonymised. STOCKMANS (1948) described new Belgian material but did not discuss the earlier work of KRÄUSEL & WEYLAND (1941) and may have been unaware of it. STOCKMANS noted the similarity in leaf form and arrangement between *A. roemeriana* and *A. halliana* but he followed ARNOLD (1939) in retaining separate species because of the generally narrower axes and the apparent fusion of some of the vegetative leaves in *A. halliana*. Both of these characters are problematic. The size criterion, a difference of a few mm in axis diameter between the two species, is not a convincing character in what may have been a large tree. PHILLIPS *et al.* (1972) cast doubt on the existence of fused leaves in *A. halliana* and in this paper we present evidence for a leaf size polymorphism on the ultimate axes of Belgian specimens of *A. roemeriana*. In view of these difficulties we consider that an in depth, comparative study of the European and American species is necessary to resolve the question of synonymy and is beyond the scope of this paper. We use the name *A. roemeriana* in the sense that it was used by STOCKMANS (1948) because we whish to avoid the inference that the results from the Belgian material also apply to *A. halliana* from North America in which leaf polymorphism has not yet been reported.

Localities and material

All specimens were collected from the upper Famennian "Psammites du Condroz" group which is well exposed in Belgium south of the Brabant Massif. They were obtained from four localities, Moresnet, Booze-Trembleur, Evieux and Durnal which are located within the three main tectonic units that are distinguised within the group: the allochtonous Dinant Synclinorium, the Namur Synclinorium, and the Vesdre Synclinorium (Text-Figure 1).

Five specimens from Moresnet, Booze-Trembleur and Evieux were borrowed from the large STOCKMANS collection of *Archaeopteris roemeriana* housed in the Royal Institute of Natural Science of Belgium, Brussels. They yielded 28 fragments of anatomy and 370 sections (see Appendix 1). New specimens were collected by the authors from Durnal. All specimens were identified as *A. roemeriana* on leaf size and shape: the leaves are entire or very slightly uneven at the edge, spatulate, and less than 2 cm long according to STOCKMANS (1948).

MORESNET (specimen IRScNB b 2420 a and 2420 b) *Archaeopteris roemeriana*, was collected for the first time in the vicinity of Moresnet (ROEMER, 1855). Many outcrops of the "Psammites du Condroz", Evieux Formation facies, are known from near this small village (STOCKMANS, 1948) and they all belong to the Vesdre Synclinorium. One of these upper Famennian beds corresponds to the stratum typicum for *A. roemeriana* but the exact location of the original collection was inadequately described (ROEMER, 1855).

Specimen IRScNB b 2420 is from the Suermondt quarry at Moresnet (details of the geographic position and geology of this quarry are described in STOCKMANS, 1948, p. 32). It is part of a fertile lateral branch system (Pl. 4, Fig. 10). Sporophylls and sporangia are clearly visible on the ultimate axes, but there are no well exposed vegetative leaves so identification at the specific level is still uncertain.

BOOZE-TREMBLEUR (specimen IRScNB b 2416) This locality, situated 12 km NE of Liège belongs to the Namur Synclinorium where the upper Famennian sediments are rarely exposed. A flora and fauna characteristic of the Evieux Formation facies was reported by ANCION *et al,* (1943). A precise description of the location of the outcrop is given by STOCKMANS(1948, p. 28) who collected the specimen IRScNB b 2416. It is a long penultimate axis with the basal parts of eight ultimate axes visible on one side and six on the other (Pl. 4, Fig. 8). Six separate fragments of anatomy were removed from the penultimate axis and basal parts of several of the ultimate axes. Although labelled *Archaeopteris roemeriana* by STOCKMANS, this designation probably refers to a specimen on the back which has relatively well preserved leaves. Leaf preservation on the specimen from which the anatomy was taken is very poor. Some impressions of leaves and veins can just be made out towards the top of the specimen and are enough to indicate that this is a species of *Archaeopteris*. It would appear from the size of the axes that this specimen is part of a distal portion of a lateral branch.

EVIEUX (specimens IRScNB b 2417, IRScNB b 2418, IRScNB b 2419) Evieux lock quarry (la carrière de l'Ecluse d'Evieux) is located near Esneux, a small village about 15 km south of Liège, in the Dinant Synclinorium. A detailed description of this fossil plant locality is to be found in BOUCKAERT *et al.*, 1968. It belongs to the Evieux Formation and biostratigraphycally, it is in the VCo spore
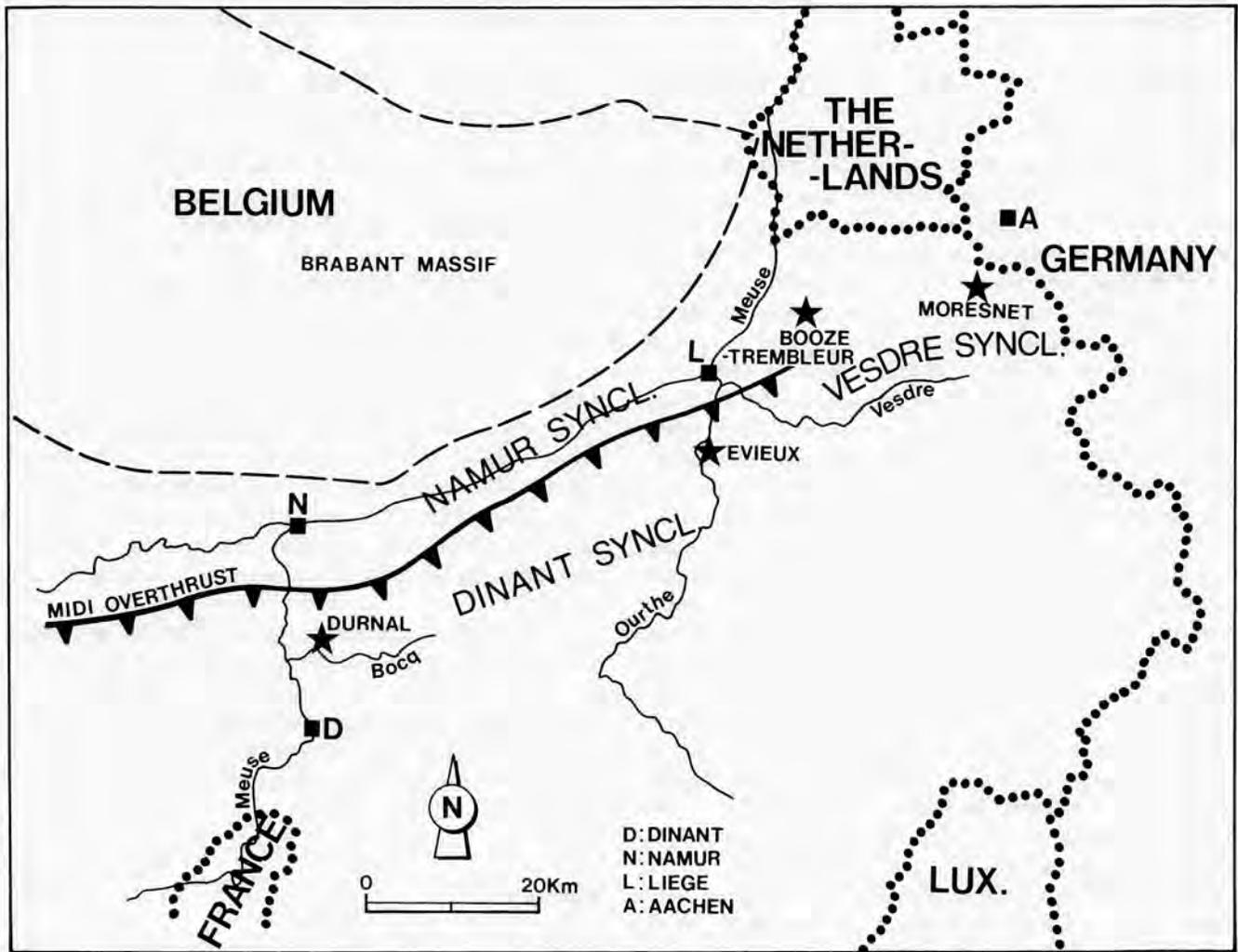
Fig. 1. – Location map of the river valleys and studied fossil plant localities in the Vesdre, Namur and Dinant Synclinoria.

zone, Fa2c in age (STREEL *in* BECKER *et al.*, 1974; STREEL *et al.*, 1987).

Anatomical information was obtained from three specimens collected at Evieux. Specimen IRScNB b 2417 is a small fragment of penultimate axis with an attached basal portion of ultimate axis (Pl. 4, Fig. 9). Below this is a similarly oriented leafy compression of an ultimate axis. This is not attached to the permineralization but from their orientation there can be little doubt that both belong to the same plant. The leaves are characteristic of *Archaeopteris roemeriana*. The specimen was labelled *Palaeopteris hibernica* SCH. var. *minor* by CREPIN, 1874, which is a synonym for *A. roemeriana* (GILKINET, 1922; STOCKMANS, 1948).

Specimen IRScNB b 2418 was collected in the year 1874 (Pl. 4, Fig. 7). It is part of a lateral branch consisting of a permineralized penultimate axis and coalified vegetative ultimate axes. The ultimate axes bear leaves that are of the *Archaeopteris roemeriana* type. The size of the axes suggests that this fragment came from a region some distance from the distal end of the lateral branch.

Specimen IRScNB b 2419 is a large vegetative lateral

branch with leaves of the *Archaeopteris roemeriana* type (Pl. 4, Fig. 6). Parts of the ultimate axes, particularly the distal ends, are permineralized and cellular preservation is good.

DURNAL (specimens IRScNB b 2421 a, IRScNB b 2422 a, IRScNB b 2423 a, IRScNB b 2423 b, IRScNB b 2424) Compression fossils (Pl. 1; Text-Figure 2) were collected by the authors from the disused Langlier Quarry, at Durnal, near Dorinne and Spontin in the Bocq valley. Precise geographic details are given in FAIRON-DEMARET & SCHECKLER (1987) who described remains of *Moresnetia* from this locality. The plant horizon belongs to the Evieux Formation; it is in the lower part of the VCo biozone, Fa2 c in age (DI CLEMENTE, 1985).

Morphological information was obtained from these recently collected compression fossils of *Archaeopteris roemeriana*. Four of these speciemens (IRScNB b 2421 a, IRScNB b 2422 a, IRScNB b 2423 a and IRScNB b 2423 b) are illustrated Pl. 1. Text-Figure 2 is based on IRScNB b 2424 a, part, and IRScNB b 2424 b, counterpart of the same specimen.

Techniques

Anatomical details of *Archaeopteris* lateral branches are preserved in a dark, red-brown mineral thought to be goethite (FeO(OH)). Permineralizations were cut or picked from the rock surface, embedded in plastic (Palatal P4) and cut at approximately 0.7 mm intervals. The cut surfaces were found to be very porous, so the following, original, re-embedding procedure was adopted.

Cut sections were immersed in catalized plastic (Palatal P4, plus the usual additives, catalizer and hardener, the concentration of which has to be tested before in order to manage at least a five minute delay before the beginning of the solidification process) and a mild vacuum was applied for several minutes using a water driven vacuum pump attached to the top of a large dessication jar to provide a vacuum chamber. On removal, the sections were placed in a pool of catalized plastic between two sheets of glass wrapped in aluminium foil and a weight placed on top. Once the plastic had begun to set (firm but not yet brittle) the glass sheets were removed from the aluminium foil and each section was cut from the surrounding pool of plastic using a pair of scissors. Once the plastic has fully hardened the aluminium foil was easily peeled away. A fast setting plastic is recommended for this re-embedding stage.

The thin layer of plastic now coating the surface of each section was carefully removed by grinding on 600 or 800 grit carborundum paper. 1200 grit carborundum paper was used to finally expose the mineral and to carefully remove saw marks. Sections were hand polished using 1 μ aluminium oxide paste and the back (non-emulsion side) of a piece of photographic paper as a lap. Each surface took about one minute to polish.

These rather crude but quickly made thin sections were photographed in reflected light (bright field) using an Olympus BH2 microscope.

Large specimens were photographed dry. For higher magnification photography, the part of the specimen to be photographed was immersed in ethanol and covered with a coverslip to reduce reflection and to retard evaporation. The use of crossed polaroid filters significantly enhanced contrast. Leaves were uncovered using fine steel sewing needles and a small hammer (LECLERCQ, 1960).

Gross morphology

The vegetative leaves are spatulate, less than 2 cm long, have open dichotomous venation and are entire or nearly so (Pl. 1, Fig. 3). Leaf arrangement is difficult to determine in compression fossils but leaf bases can sometimes be seen on penultimate axes and this is facilitated by careful removal of coalified material from the axis surface, as demonstrated by BECK (1971) for *Archaeopteris macilenta*. For at least part of the penultimate axis there are more leaves on one side than the other (Text-Figure 2), and in this respect *A. roemeriana* is similar to

A. macilenta. Typically, on the side with fewer leaves (Text-Figure 2 b) there is a repetitive sequence involving a pair of leaves mid-way between consecutive ultimate branches followed by a single leaf at the branching point. No such repetitive sequence is discernible on the counterpart (Text-Figure 2a), and attempts to work out a phyllotactic sequence were unsuccessful because of the difficulty of determining the number of orthostiches as well as the fragmentary nature of the material.

Fully formed fertile leaves dichotomize at three levels and are not obviously lamellate (Pl. 1, Fig. 4). Numerous sporangia are attached to the adaxial surface but their exact number and arrangement have not yet been determined. Fertile leaves are confined to a distinct zone on ultimate axes between a few basal vegetative leaves and a vegetative distal region (Pl. 1, Figs. 1, 2). Observations of ultimate axes of comparable width and position (Pl. 1, Fig. 1) show that the sporophylls are more densely arranged than vegetative leaves: rough measurements indicate that there are nearly twice as many per cm of axis.
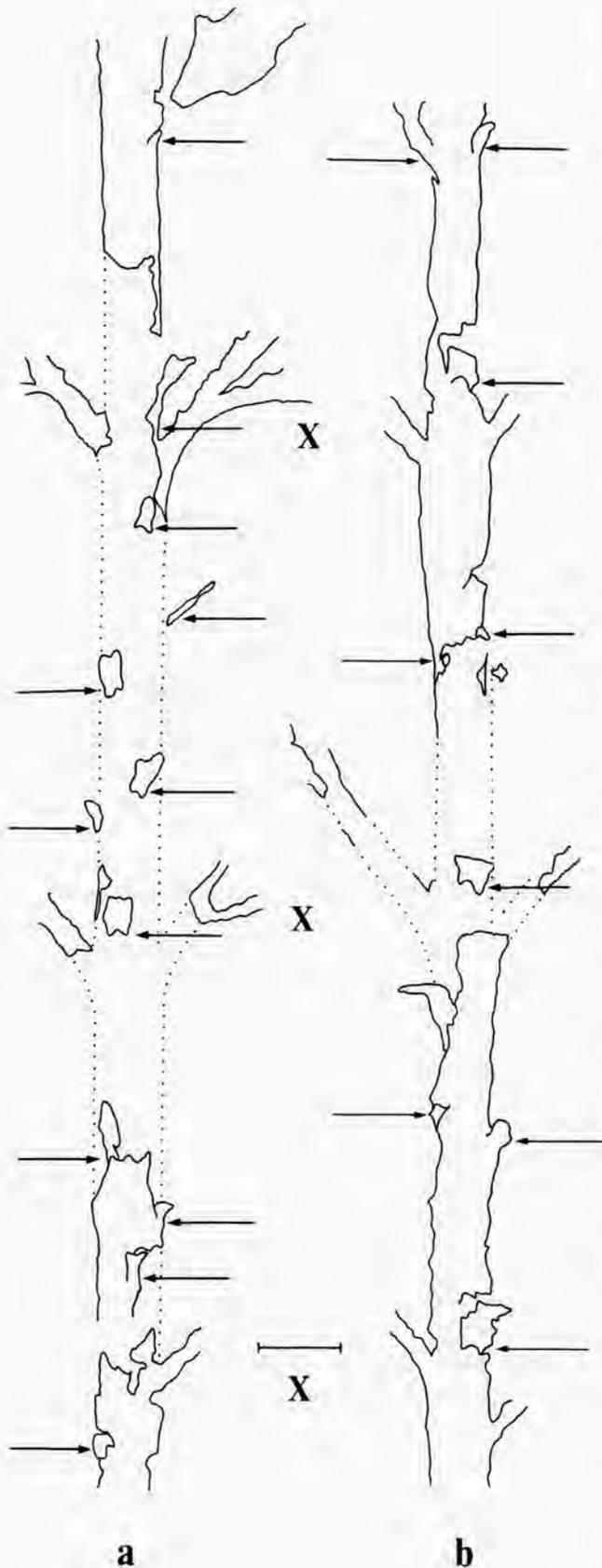
On ultimate axes, between the fully formed vegetative and fertile leaves, there is a short transition zone containing leaves of intermediate morphology. These interesting leaves bear sporangia that are confined to one half or less of the leaf. The part of the leaf that bears the sporangia is dissected whereas the other part is planated (Pl. 1, Fig. 5).

Anatomy

Reconstructing ontogenetic changes in the stelar anatomy of fossil plants is often hampered by the fragmentary nature of the remains, and in this study the reconstruction of *Archaeopteris roemeriana* has been pieced together based on fragments from a number of localities. Unless otherwise stated, these fragments were identified as *A. roemeriana* using leaf shape and size (see above).

ANATOMY OF ULTIMATE VEGETATIVE AXES

Anatomical information was obtained from specimens IRScNB b 2419, IRScNB b 2418, IRScNB b 2417 and IRScNB b 2416 (Pl. 4, Figs. 6-9; Appendix 1). The series of anatomical changes through the ultimate vegetative axis is reconstructed in Text-Figure 3 a. At its point of departure from the xylem of the penultimate axis the branch trace is terete to elliptical in transverse section and protostelic (Pl. 3, Fig. 6), but by the time it enters the ultimate axis it has four distinct sympodia. At a distance of 1.5 cm along the ultimate axis five sympodia are fully developed (Pl. 2, Figs. 1, 3). This condition persists for about 2.5 cm and then reverts to four sympodia (Pl. 2, Figs. 5, 7). The loss of the fifth protoxylem pole is accompanied by medullation. At a distance of 11 cm along the ultimate axis three sympodia are present and the xylem has reverted to a protostele (Pl. 2, Fig. 2). In all instances, except for the three sympodia stage, transverse sections show that the xylem is elongate in the

horizontal plane (Pl. 2). This is most conspicuous in the five sympodia stage (Pl. 2, Figs. 1, 3), but in both the five and the four sympodia stages it is clear that the two sympodia on the lower side are larger than those on the upper side (Pl. 2, Figs. 1, 3, 5, 7). This is a consistent feature taking into account the periodic enlargement of sympodia before leaf trace divergence. The two large sympodia on the lower side also give rise to leaf traces that are twice the size of those derived from the small or upper sympodia (Pl. 2, Fig. 3; Pl. 4, Figs. 1-5), and these large leaf traces also dichotomize almost immediately (Pl. 4, Fig. 3). This asymmetry in the vascular tissue of the ultimate axes can be traced back more tentatively to its origin in the penultimate branch. The first leaf traces of the ultimate branch develop while the stele is still within the penultimate axis from what appear to be two large protoxylem poles on one side of an asymmetric protostele (Pl. 2, Figs. 4, 6, 8).

The sequence of changes illustrated here (Text-Figure 3a) have been pieced together from separate lengths of axis. The change from five to four sympodia was observed along a single axis, but the development of xylem in the lateral branch up to the four sympodia condition was seen only on a single specimen. The transitions from four to three sympodia at the distal end, and from four to five sympodia at the proximal end, are inferred from the relative position of other segments of anatomy. Likewise, the orientation of the distal three sympodia and the proximal two sympodia stage with respect to the middle region with four and five sympodia has not been directly observed. The sections through the xylem (Pl. 2, Text-Figure 3) are orientated perpendicular to the observed horizontal plane formed by the lateral branch system and bedding plane of the rock. However, it is not known which of the two surfaces was uppermost. Taking the five sympodia stage, and orientating the whole branch from this segment (Text-Figure 3b), we interpret the side with the two large sympodia as being lowermost with the three small sympodia being on the upper side. We argue that the marked difference in size of leaf traces on the two sides of the axis reflects a marked difference in leaf size. Because of the effects of shading the larger leaves would be expected on the lower surface and would project outwards further than the smaller leaves on the upper surface.

ANATOMY OF ULTIMATE FERTILE AXES

Anatomical information was obtained from specimen IRScNB b 2420 a (Pl. 4, Fig. 10; Appendix 1) from Moresnet, the type locality of *Archaeopteris roemeriana*. Sections were made from three branches covering a length of axis 2.8 cm from the base to 7.0 cm. These sections fall well within the zone of sporophylls and are outside the basal and apical vegetative regions. Although

Fig. 2. – Line drawing of part (a) and counterpart (b) of a penultimate axis of *Archaeopteris roemeriana* illustrating leaf base number and position (arrows) (specimen IRScNB b 2424 a & b). 'X' marks level of departure of paired ultimate branches. Note that there are more leaf bases on side 'a' than on side 'b'. Scale bar = 8 mm.
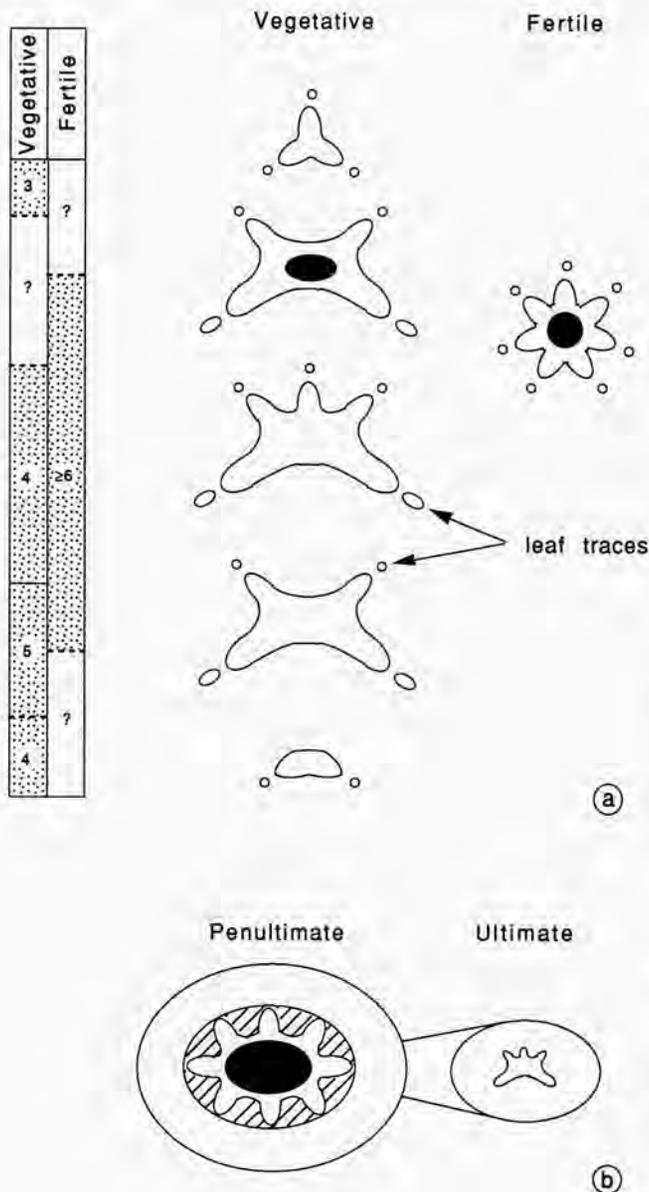
Fig. 3. – Diagrammic representation of stelar changes through comparable vegetative and fertile ultimate axes of *Archaeopteris roemeriana* (a), and the orientation of the ultimate vegetative axis with respect to the ultimate branch (b): medullation (black) and secondary xylem (diagonal shading). (a) In the vegetative axis, observed protoxylem pole number changes acropetally (bottom to top of diagram) through 2, 4, 5, 4, 3. Larger protoxylem poles on the lower side produce larger leaf traces over part of the axis. In the fertile axis only the six or seven protoxylem pole stage was observed. Medullation (black) occurs in the distal four pole stage of the fertile axis. The two columns on the left represent a 12 cm length of vegetative and fertile ultimate axis and the shaded segments indicate the position along the ultimate branch the various protoxylem pole (numbered) stages were observed. Note that the 2 pole stage occurs as a branch trace in the penultimate axis. Broken lines indicate uncertainty about the length of the segment; '?' indicates no observations.

anatomical details are poorly preserved within this zone, several consistent features can be made out. The xylem is more or less radially symmetrical and has six to seven sympodia of equal size (Pl. 3, Figs. 3, 5), and the absence of cellular preservation in a small central area in all sections indicates that it is medullated.

ANATOMY OF PENULTIMATE AXIS

Sections of penultimate axis were made from four specimens: IRScNB b 2416, IRScNB b 2417, IRScNB b 2418 and IRScNB b 2419 (Pl. 4, Figs. 7-9; Appendix 1). The greatest number of sections came from specimen IRScNB b 2418 (Pl. 4, Fig. 7) in the mid region of a lateral branch. At this point, the xylem is a large eustele and up to seven sympodia were seen (Pl. 3, Figs. 1, 2). Preservation of one side of the eustele was too incomplete to allow an analysis of leaf and branch trace phyllotaxy. As in the ultimate axes, leaf traces depart radially and divide at least once before entering the leaves (Pl. 3, Fig. 1). Branch traces are easily distinguished by their large size. In the more distal regions of this series of sections some radial files of cells, interpreted as secondary xylem, develop on one side of the xylem (Pl. 3, Figs. 2,4). In the more distal region of the lateral branch system (specimen IRScNB b 2418) the xylem reverts to a protostele with four large sympodia. Two of these give rise to opposite branch traces, while the other two produce opposite leaves (Pl. 3, Fig. 6).

Comparison of vegetative and fertile ultimate axes

The most important features of the ultimate vegetative and fertile axes are summarized in Table 1. The maximum number of sympodia is greater in the fertile axes, and this is consistent with the greater observed density of sporophylls in compression fossils as compared to vegetative leaves. Medullation is a common feature of both axis types and was also observed in penultimate axes. In transverse section the xylem in vegetative axes is noticeably flattened and this is unlikely to be due to compression because individual cells are uncompressed. The leaf size polymorphism on the vegetative axis in inferred from the consistent differences in sympodium and leaf trace size on different sides, as observed in permineralized axes. This is most noticeable in the four and five sympodia stages, but size differences disappear by the distal three sympodia stage. No comparable leaf size polymorphism was detected in fertile axes, but there is a marked shape polymorphism involving the vegetative and fertile leaves both of which occur on fertile ultimate branches. The sporophylls are flattened, dichotomously branching axes that bear sporangia, whereas the vegetative leaves are spatulate and entire or very slightly uneven at the edge. In the transition zone between sporophylls and vegetative leaves there are transitional forms where both types of morphology are expressed in the same leaf. One half of the leaf is vegetative and spatulate, the other half is dissected and bears sporangia.

Table 1

Feature / Axis type	Vegetative ultimate axis	Fertile ultimate axis
maximum number of sympodia:	5	at least 6 or 7
leaf / sporophyll density:	0.34 mm^{-1} (13 measurements)	0.59 mm^{-1} (36 measurements)
medullation:	yes, in 4 sympodia stage	yes, at least in 6/7 sympodia stage
symmetry of strand:	noticeably flattened in transverse section until 3 sympodia stage	radial, at least in fertile zone
leaf size polymorphism on opposite sides of axis (inferred from anatomy):	lower surface leaves twice the size of upper surface leaves over part of axis	none observed
leaf shape polymorphism:	none observed	vegetative leaves at base and apex entire; sporophylls dichotomously branched, non-laminate axes

Table comparing anatomical and morphological features in the ultimate fertile and ultimate vegetative axes of *Archaeopteris roemeriana* from Belgium.

Comparison with North American species

As noted by ARNOLD (1939), KRÄUSEL & WEYLAND (1941), STOCKMANS (1948), and PHILLIPS et al. (1972) *Archaeopteris roemeriana* is very similar to *A. halliana* in its leaf morphology. Anatomical information presented here suggests a marked difference in leaf size on different sides of the ultimate axes of *A. roemeriana*; this has not been shown for *A. halliana*. A similar difference in leaf size on the penultimate axes of *A. macilenta* was inferred from a difference in leaf base size (BECK, 1971). In both *A. roemeriana* and *A. macilenta* (BECK, 1971) the differences in leaf size may correlate with differences in the number of orthostiches. In both penultimate and ultimate axes there are more orthostiches on one side, at least over part of the axis.

If leaf polymorphism is common in *Archaeopteris* it is not obvious from compression fossils. Neither STOCKMANS(1948) nor NATHORST (1902) observed a difference in leaf size on different sides of the ultimate axis in their studies of *A. roemeriana*, nor dit PHILLIPS et al. (1972) in their review of the literature pertaining to leaf variation in this and other species of the genus. The absence of obvious leaf size differences in leafy compression fossils is puzzling but may be due in part to the rarity of completely exposed leaves on fractured surfaces.

Prior to this study, knowledge of the anatomy of the lateral branch system of *Archaeopteris* was based entirely on *A. macilenta*, or specimens identified as *Archaeopteris* sp. (BECK, 1971; CARLUCCIO et al., 1966; SCHECKLER, 1978). Anatomically the penultimate axis of *A. roemeriana* is similar to that of *A. macilenta*. It is eustelic but becomes protostelic at its distal end and contains some secondary xylem. Little more useful information was obtained from the poorly preserved specimens examined in this study. The sections of ultimate fertile axis of *A. roemeriana* come from the mid region

of a branch and are identical in overall shape, number of sympodia, and medullation to those obtained from equivalent regions of *A. macilenta* by CARLUCCIO et al., (1966) and SCHECKLER (1978). One of the new findings in this study is the anatomy of the ultimate vegetative axis of *Archaeopteris* which has not previously been described in detail. CARLUCCIO et al. (1966) illustrated the early stages of xylem formation for the vegetative ultimate branch but were unable to trace development into the ultimate axis. They figured a four-lobed stage which develops soon after departure from the eustele of the penultimate axis. This study confirms the suspicions voiced by these and other authors that the vascular construction of the vegetative ultimate axis might be different to that in the fertile ultimate axis (CARLUCCIO, 1966; BECK, 1971, 1976; SCHECKLER, 1978).

Conclusion

Comparison of the anatomy of vegetative and fertile axes of *Archaeopteris roemeriana* illustrates the degree to which both structures are specialized in different ways, perhaps in relation to the functions they perform. The bilateral symmetry and leaf size polymorphism in the vegetative ultimate axes could be interpreted as adaptations to the photosynthetic role of this branch. The bilateral symmetry of the vascular tissue in transverse section reflects the orientation of the vegetative leaves in one plane, and this arrangement of smaller leaves on the upper surface would reduce the shading of the lower leaves. Larger and more prominent leaves on the lower surface would have a similar effect. Similar features were recognized by BECK (1971) in the penultimate axes of *A. macilenta*. The radial symmetry, similar size of leaves on opposite sides of the axis, and the greater number of sporophylls and orthostiches per unit length of axis in the

fertile ultimate branches could be interpreted as adaptations to a reproductive role. Considerations of shading and orientation with respect to the light may be less significant with highly divided sporophylls, and a relatively tightly packed strobilus might also result in increased spore production. In these respects *A. roemeriana* is very similar to *A. macilenta*.

The observations made in this study do not resolve the question of whether *A. roemeriana* is synonymous with *A. halliana*. In fact, they raise more questions than they answer because the anatomy of *A. halliana* from North America is unknown and the possibility of leaf size polymorphism, a potential specific character, has not been investigated in this species. Careful uncovering of leaves on part and counterpart of penultimate and ultimate axes of *A. roemeriana* from Belgium and *A. hal-*

liana from North America is the obvious next step to address this issue and test the utility of leaf size as a specific character. Future investigations into inter specific leaf variation and its causes should also consider within species variation, particularly between vegetative leaves and sporophylls.

Acknowledgements

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APPENDIX 1

Working n°	Locality	Specimen n°	Axis	Status	Ts/Ls	Sections
1	Booze-Trembleur	IRScNB b 2416	Pen + Ult	Veg	Ts	1-32*
2	Booze-Trembleur	IRScNB b 2416	Pen	Veg	Ts	2*-26
3	Booze-Trembleur	IRScNB b 2416	Ult	Veg	Ts	1*-13
4	Booze-Trembleur	IRScNB b 2416	Ult	Veg	Ts	2*-12
5	Booze-Trembleur	IRScNB b 2416	Pen + Ult	Veg	Ts	2*-16
6	Booze-Trembleur	IRScNB b 2416	Ult	Veg	Ts	uncut
7	Evieux	IRScNB b 2417	Pen	Veg	Ts	1-17*
8 a	Evieux	IRScNB b 2417	Ult	Veg	Ts	2-25*
8 b	Evieux	IRScNB b 2417	Ult	Veg	Ts	26-39*
9	Evieux	IRScNB b 2417	Pen	Veg	Ls	1-6*
10 a	Evieux	IRScNB b 2418	Pen	Veg	Ts	2-43*
10 b	Evieux	IRScNB b 2418	Pen	Veg	Ts	1*-6
11	Evieux	IRScNB b 2419	Ult	Veg	Ts	1-10*
12	Evieux	IRScNB b 2419	Ult	Veg	Ts	1-15*
13	Evieux	IRScNB b 2419	Ult	Veg	Ts	1*-3
14	Evieux	RScNB b 2419	Ult	Veg	Ts	1-5*
15	Evieux	IRScNB b 2419	Pen	Veg	Ts	1*-4
16	Evieux	IRScNB b 2419	Ult	Veg	Ts	1*-8
17	Evieux	IRScNB b 2419	Ult	Veg	Ts	1*-4
18	Evieux	IRScNB b 2419	Ult	Veg	Ts	1-15*
19	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1-6*
20	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1-6*
21	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1-4*
22	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1-5*
23	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1*-13
24	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1-5*
25	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1-5*
26	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1-4*
27	Moresnet	IRScNB b 2420 a	Ult	Fer	Ts	1*-16
28	Moresnet	IRScNB b 2420 a	Pen	Fer	Ts	1*-38

Detail of anatomical preparations of *Archaeopteris roemeriana*. Pen = penultimate branch, Ult = ultimate branch, Veg = vegetative axis, Fer = fertile axis, Ts = transverse section, Ls = longitudinal section, * = distal end of section.

Compression fossils of *Archaeopteris roemeriana* collected from Durnal, Belgium.

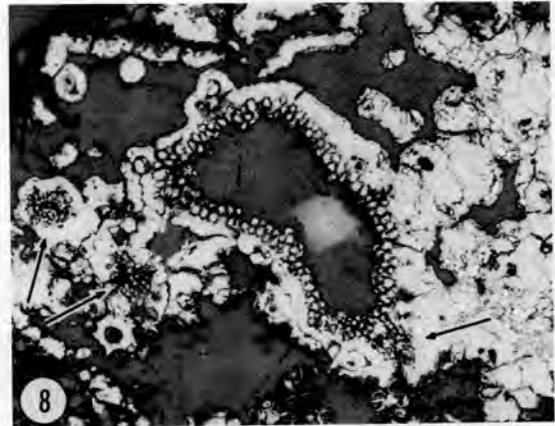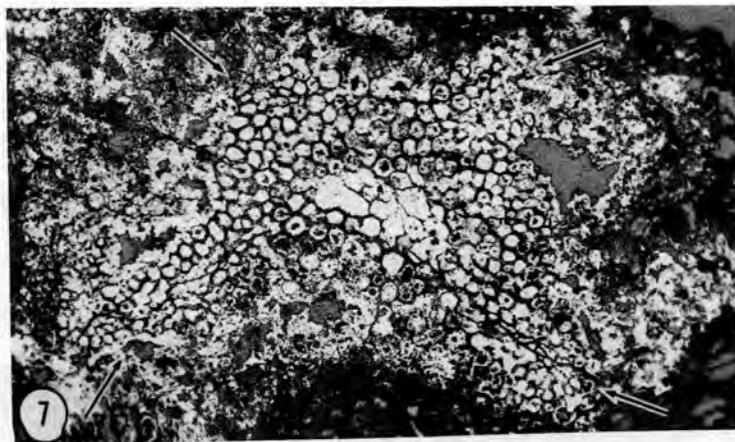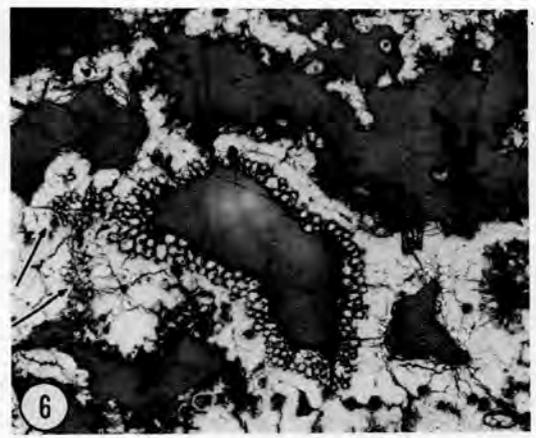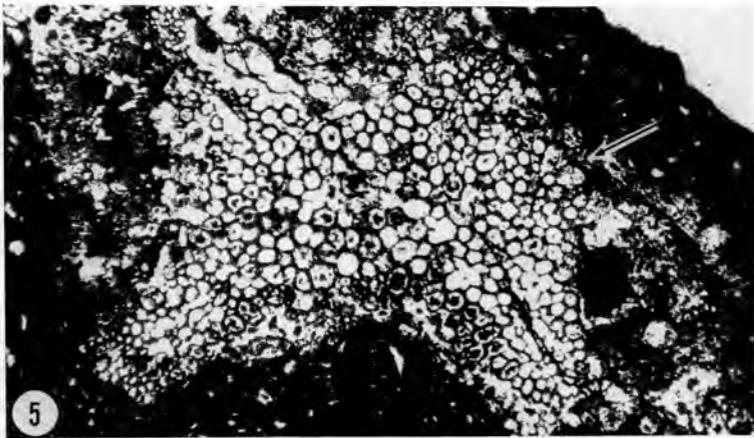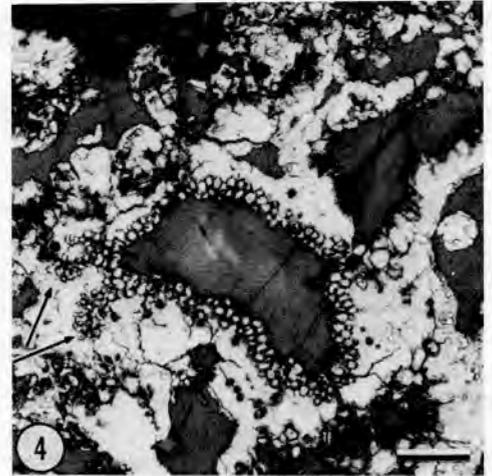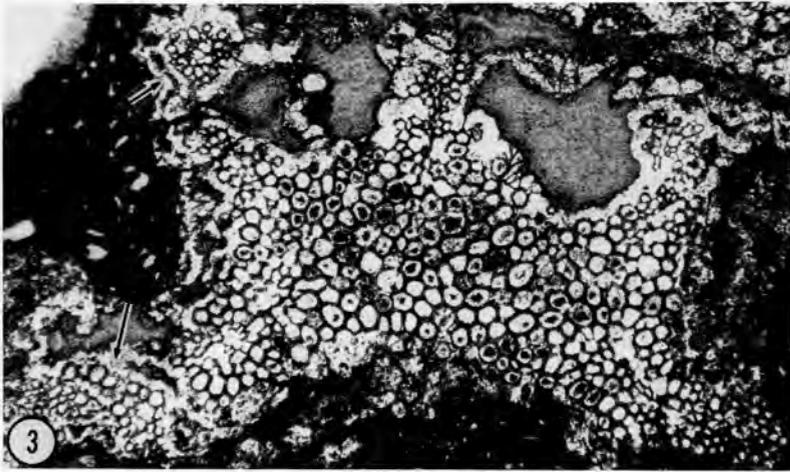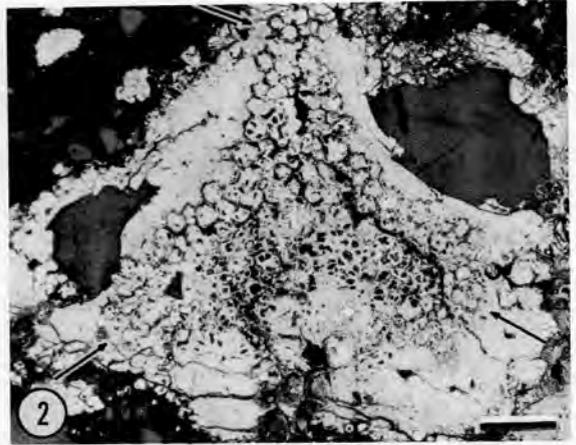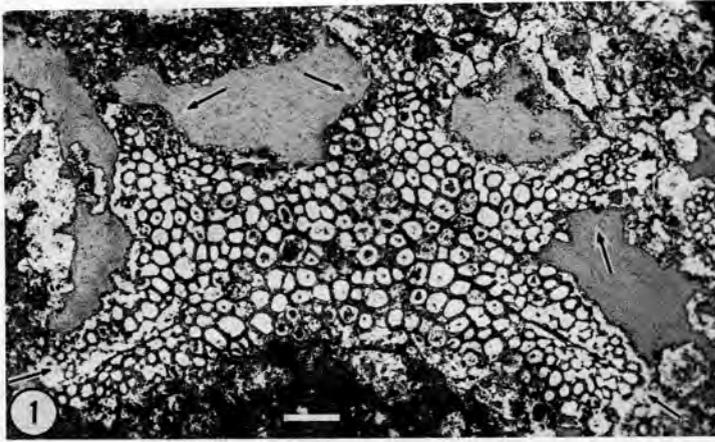Fig. 1. – Ultimate fertile and vegetative axes attached to a penultimate axis. The middle fertile axis shows a transition from vegetative leaves at the base, through a zone of sporophylls in the middle and back again into a zone of vegetative leaves towards the apex. Scale bar = 1 cm (specimen IRScNB b 2421 a).

Fig. 2. – Details of fertile to vegetative transition towards the apex of an ultimate axis from Fig. 1. Scale bar = 5 mm (specimen IRScNB b 2421 a).

Fig. 3. – Partially uncovered vegetative leaf with open dichotomous venation. Scale bar = 2 mm (specimen IRScNB b 2422 a).

Fig. 4. – Partially uncovered, non planated, dichotomous branching sporophyll viewed from abaxial side. Scale bar = 2 mm. (specimen IRScNB b 2423 b).

Fig. 5. – Half fertile, half vegetative (planated) leaf taken from transition zone between fully fertile and fully vegetative leaves. Leaf viewed from adaxial side. Scale bar = 2 mm (specimen IRScNB b 2423 a).

PLATE 2

Transverse sections through different levels of the ultimate vegetative axis of *Archaeopteris roemeriana* from Evieux showing the shape of the xylem. All polished thick sections viewed in reflected light (bright field).
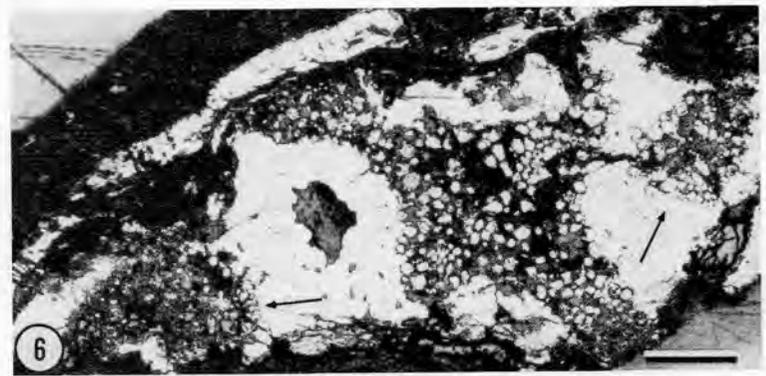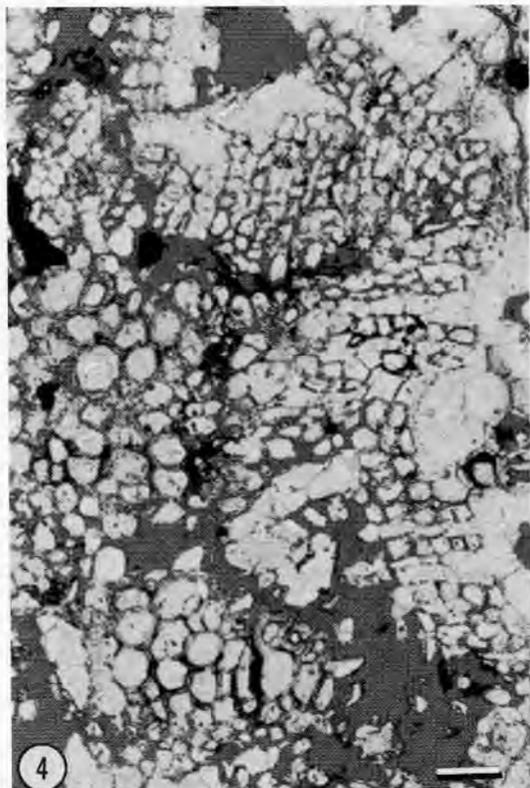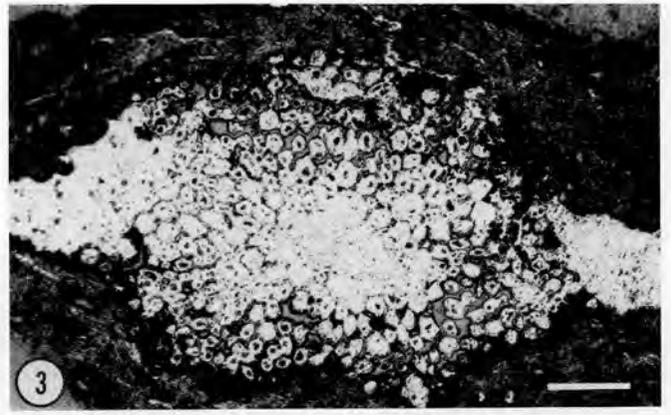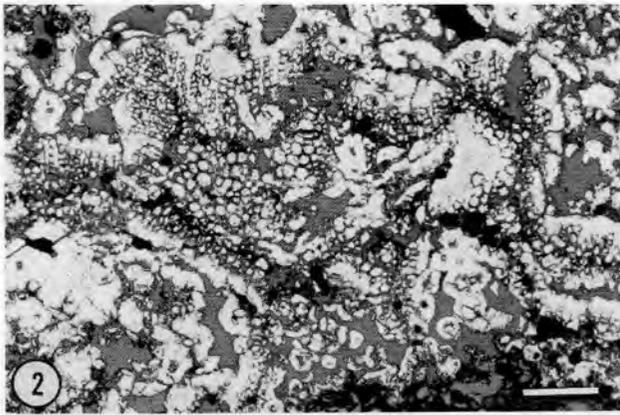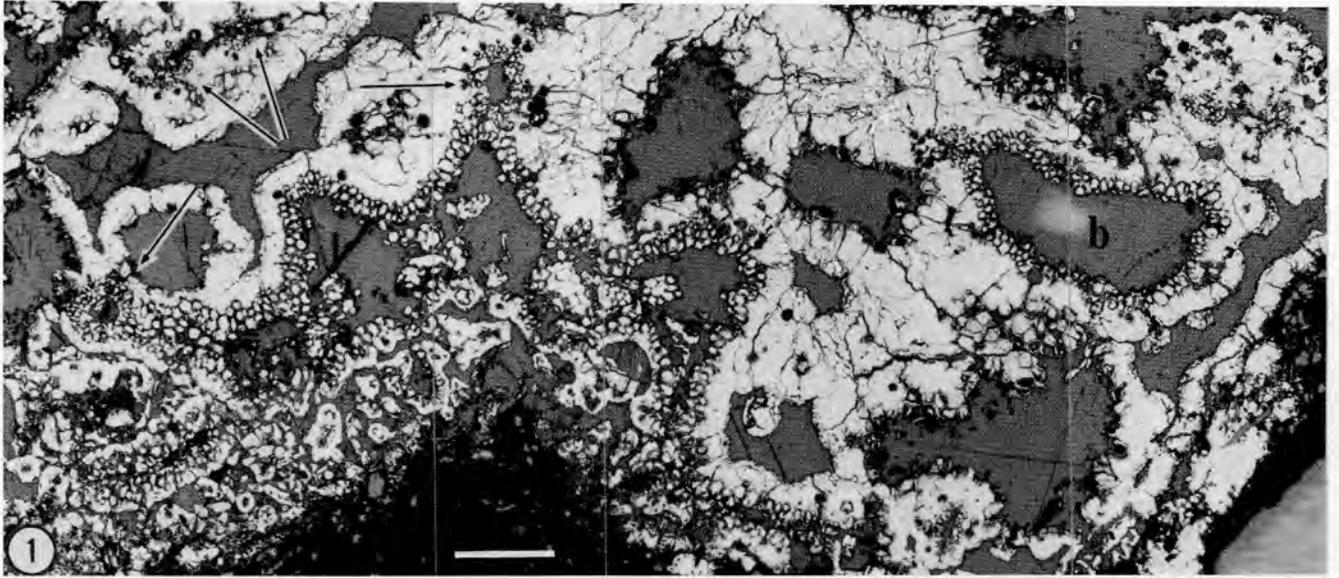
Figs. 1, 3, 5, 7. – Series through five and four protoxylem pole stages at the same magnification. Scale bar = 100μ. Fig. 1. Five pole stage: two large protoxylem poles (arrows) on lower side of xylem and three small protoxylem poles (arrows) on upper side (working n° 8 a, section 11 f). Fig. 3. Five protoxylem pole stage. Note the relative sizes of the leaf traces (arrows) derived from the large and small protoxylem poles. The large protoxylem pole on the lower left gives rise to a large leaf trace. Similarly, the small protoxylem pole on the upper left side gives rise to a small leaf trace (working n° 8 a, section 9 r). Fig. 5. Transition between five and four pole stage. The fifth pole is represented by an indistinct bulge on right side of the xylem (arrow) (working n° 8 a, section 17 f). Fig. 7. Four pole stage (between five pole and three pole) with medullation in the center. Protoxylem poles are indicated by arrows (working n° 8 a, section 19 f). Specimen IRScNB b 2417.

Fig. 2. – Three protoxylem pole (arrows) stage from distal end of the axis. Scale bar = 100 μ (working n° 12, section 4 f). Specimen IRScNB b 2419.

Figs. 4, 6, 8. – The two pole stage shortly after its departure from the eustele of the penultimate axis. A series showing the departure of the first two leaf traces. Scale bar = 200 μ. Fig. 4. First leaf trace (arrows) close to the point of origin but already divided in two (working n° 10 a, section 14 f). Fig. 6. First leaf trace (arrows) slightly distal to previous section (working n° 10 a, section 14 r). Fig. 8. Second leaf trace developing on right (arrow) and the two vascular traces of the first leaf clearly visible on the left (working n° 10 a, section 16 r). Specimen IRScNB b 2418.

PLATE 3

Transverse sections through the penultimate axis and the ultimate fertile axis (Figs. 3, 5) of *Archaeopteris roemeriana* showing details of the xylem.

Fig. 1. – Penultimate axis showing protoxylem poles, leaf traces (arrows) and branch trace (b). Scale bar = 300 μ (working n° 10 a, section 16 f). Specimen IRScNB b 2418 from Evieux.

Fig. 2. – Penultimate axis showing protoxylem poles and a small amount of secondary xylem development (files of cells) along one side. Scale bar = 200 μ (working n° 10 a, section 27 f). Specimen IRScNB b 2418 from Evieux.

Fig. 3. – Ultimate fertile axis with medullation in the center of the xylem. Scale bar = 100 μ (working n° 26, section 3 f). Specimen IRScNB b 2420 a from Moresnet.

Fig. 4. – Detail of secondary xylem development from Fig. 2. Scale bar = 100 μ.

Fig. 5. – Ultimate fertile axis with more or less radially symmetrical xylem and protoxylem poles (arrows). Leaf trace (long arrow) on left. Scale bar = 100 μ (working n° 24, section 2 f). Specimen IRScNB b 2420 a from Moresnet.

Fig. 6. – Penultimate axis at distal end of branch system. Four protoxylem poles and two branch traces (arrows). Scale bar = 100 μ (working n° 1, section 9 f). Specimen IRScNB b 2416 from Booze-Trembleur.

Plate 4

Archaeopteris roemeriana. Leaf trace formation in large and small protoxylem poles in the ultimate vegetative axis (Figs. 1-5; specimen IRScNB b 2417 from Evieux). Scale bar = 200 μ. Specimens from which anatomical information was obtained (Figs. 6-10).

Figs. 1-3. – Large leaf trace formation from large protoxylem pole.

Fig. 1. – Before leaf trace departure (working n° 8 a, section 8 r).

Fig. 2. – Leaf trace (arrow) departure (working n° 8 a, section 9 r).

Fig. 3. – Almost immediately new leaf trace divides in two (arrows) (working n° 8 a, section 10 f).

Figs. 4. 5. – Small leaf trace formation from small protoxylem pole.

Fig. 4. – Before leaf trace departure (working n° 8 a, section 9 f).

Fig. 5. – Leaf trace (arrow) departure (working n° 8 a, section 10 f),

Fig. 6. – Large vegetative lateral branch from Evieux. Scale bar = 5 cm. Specimen IRScNB b 2419.

Fig. 7. – Part of vegetative lateral branch from Evieux. Scale bar = 2 cm. Specimen IRScNB b 2418.

Fig. 8. – Part of vegetative lateral branch from Booze-Trembleur. Scale bar = 2 cm. Specimen IRScNB b 2416.

Fig. 9. – Fragment of vegetative lateral branch from Evieux. Scale bar = 1 cm. Specimen IRScNB b 2417.

Fig. 10. – Part of fertile lateral branch from Moresnet. Scale bar = 2 cm. Specimen IRScNB b 2420 a.