

Stanwoodia, a new genus of probable early gymnosperms from the Dinantian of East Kirkton, Scotland

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ABSTRACT: A new taxon of probable early gymnosperms is described from permineralised specimens showing excellent preservation of the tissues, from the late Lower Carboniferous (Dinantian), Brigantian, deposits of the Midland Valley of Scotland. *Stanwoodia* gen. nov., represented by the single species *S. kirktonensis* sp. nov., shows the combination of a primitive protostelic organisation with a dense secondary wood. It closely compares to the enigmatic genus *Bilignea* which was formerly referred with some reservations to the Cordaitales. Another interest of the new plant concerns the excellent preservation of the phloem with at least three different types of constituent cells including fibres. *Stanwoodia* also exhibits the oldest well-documented evidence of a sequent periderm or rhytidome in fossil plants.



KEY WORDS: Plant, stem, Lower Carboniferous, Brigantian, gymnosperm, protostele, phloem, periderm.

The Lower Carboniferous sequence at East Kirkton, near Bathgate, West Lothian has been the subject of a major international research investigation following the discovery of an important terrestrial fauna by Stan Wood (Wood *et al.* 1985). During 1987 and 1988 the site was excavated by a large number of workers under the direction of W. D. I. Rolfe and his team at the Royal Museum of Scotland. This work was in part funded by the Nature Conservancy Council. In addition to the abundant and important terrestrial fauna, the locality has yielded an important flora. The plants are preserved as compressions, permineralisations and as fusain. The plant assemblages change throughout the sequence (Rolfe *et al.* 1990). Some plants show a combination of preservational types. The flora will be described in a series of papers by the authors.

1. Geological setting

The late Lower Carboniferous of the Midland Valley Basin is characterised by a major sequence of oil shales deposited in a lake called Lake Cadell (Loftus & Greensmith 1988). The East Kirkton sequence is in the south-west of the Oil Shale outcrop. The Oil Shale Group has been dated as late Viséan age (Asbian & Brigantian) (Neves *et al.* 1973). The East Kirkton Limestone is one of a series of limestones within the Oil Shale Group and occurs near the top of the sequence. This limestone is considered to be of Brigantian age (Rolfe *et al.* 1990). Associated with this sequence is a series of volcanic rocks which interdigitate with the oil shales and limestones (Francis 1983; Leeder 1987; Jameson 1987). Basaltic lavas and ashes are abundant and cover an area of over 100 km² (Cadell 1925). The Oil Shale Group has long been famous for its plant compressions (Kidston 1923–5). In addition the associated volcanic sequences have yielded diverse anatomically preserved floras (Scott *et al.* 1984, 1986; Scott 1990, 1991; Scott & Rex 1987; Rex & Scott 1987). Many of the best-known anatomically preserved plants are from slightly older, Asbian, volcanics and include

the famous floras of Pettycur, Kingswood and Weeklaw (Rex & Scott 1987; Scott 1990a). The East Kirkton flora represents the youngest Lower Carboniferous anatomically preserved flora to be described not only in the Midland Valley Basin but anywhere in western Europe.

The sequence exposed at the East Kirkton Quarry comprises a series of limestones which have been interpreted as being deposited in volcanic hot springs (Muir & Walton 1957). These are overlain by oil shales which in turn are overlain by basaltic ashes and lavas. A description of the sequence and its preliminary interpretation has been given by Rolfe *et al.* (1990). In addition to the specimens collected in the bed by bed excavation, numerous plants have been collected as loose blocks either in the quarry spoil tips or in limestone walls surrounding the quarry. Permineralised stems and trunks (up to 1 m in diameter) occur in stromatolitic nodules and in the massive and laminated limestones of the basal limestone sequence. The genera preserved in this way include *Pitus* and *Eristophyton*. Two specimens of a new plant have been collected, one by Stan Wood and one by ourselves, which represent a new genus of gymnosperm. This is the subject of the present paper.

2. Description of *Stanwoodia* gen. nov.

The two specimens have been collected as loose blocks in the quarry spoil tip and their exact location is unknown. However they probably originate from one of the laminated limestones recorded by Rolfe *et al.* (1990). Specimen 1 (Pb 4860 Hunterian Museum, Glasgow University) collected by Stan Wood was originally about 0.1 m long. It has been cut into several pieces and one thin section (HM TS 22197) has been prepared and used in exhibits by him. The present study mainly concerns the proximal and best preserved portion of the stem (Fig. 1a–c) which has been cut into four slices. Two additional blocks, about 0.1 and 0.4 m long respectively, represent the other extremity of the specimen with only a small portion of the tissues preserved; they have

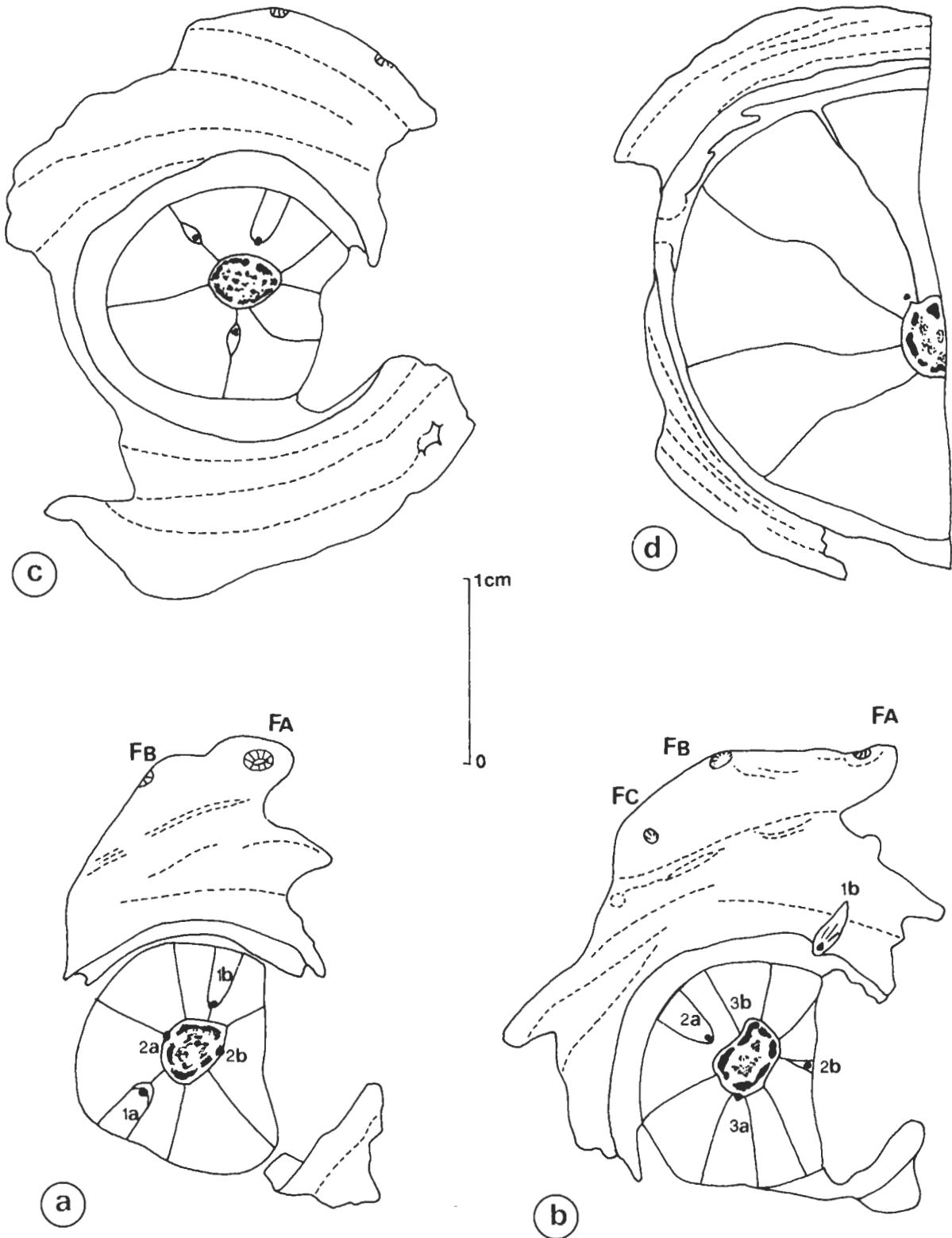


Figure 1 *Stanwoodia kirkitonensis* gen. et sp. nov. Camera lucida drawings of the transverse sections of stems of the holotype (a–c) and specimen 2 (d) at the same magnification, showing from outside to inside; the periderm with layers (broken lines), phloem zone, secondary xylem and central stele. (a) The lowermost section of the series; leaf traces in the wood are numbered 1a, b and 2a, b and those in the cortex as FA, FB. Slide 4860 DT 16. (b) Same stem 2 mm higher up; an additional leaf trace (FC) is visible in the cortex; note that trace 1b is now entering the inner cortex. 4860 CB 03. (c) Same stem about 20 mm higher up, showing a more complete cortex. 4860 AT 18. (d) Incomplete transverse section of specimen 2 showing the greater development of wood. EK DB 01.

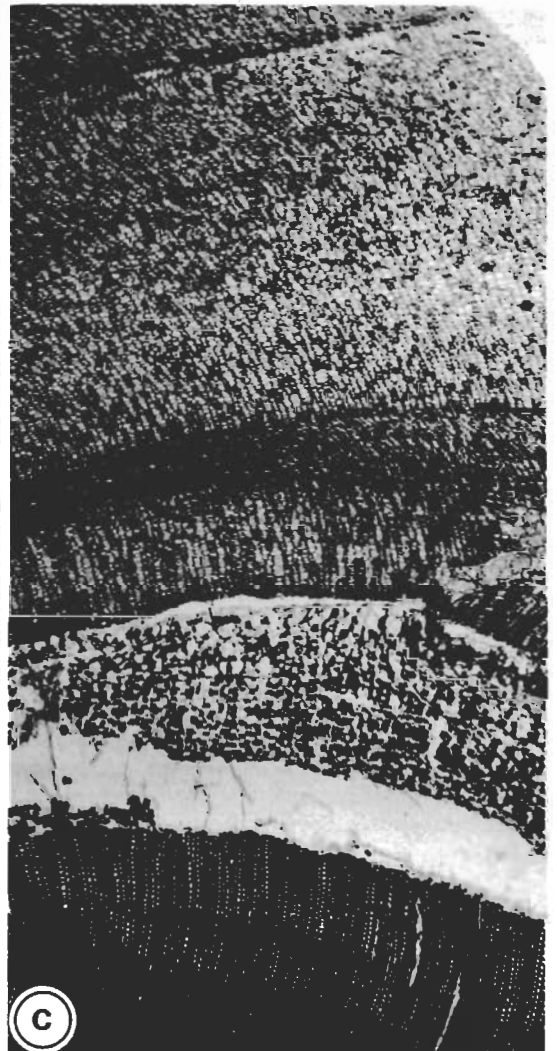
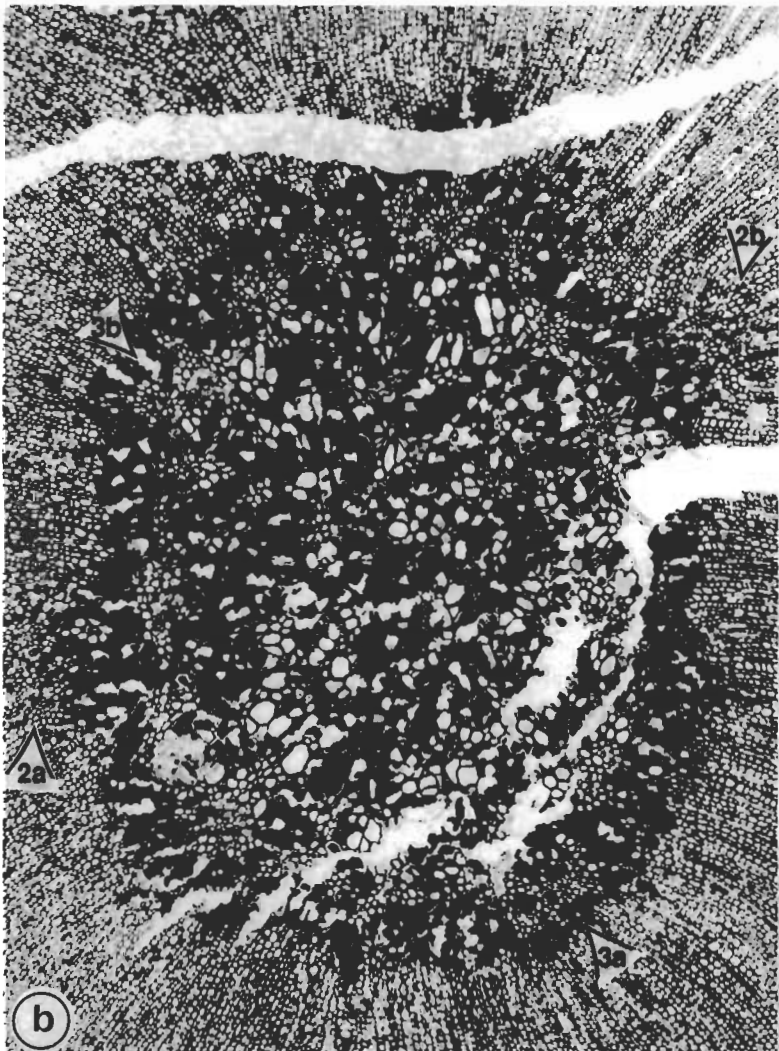
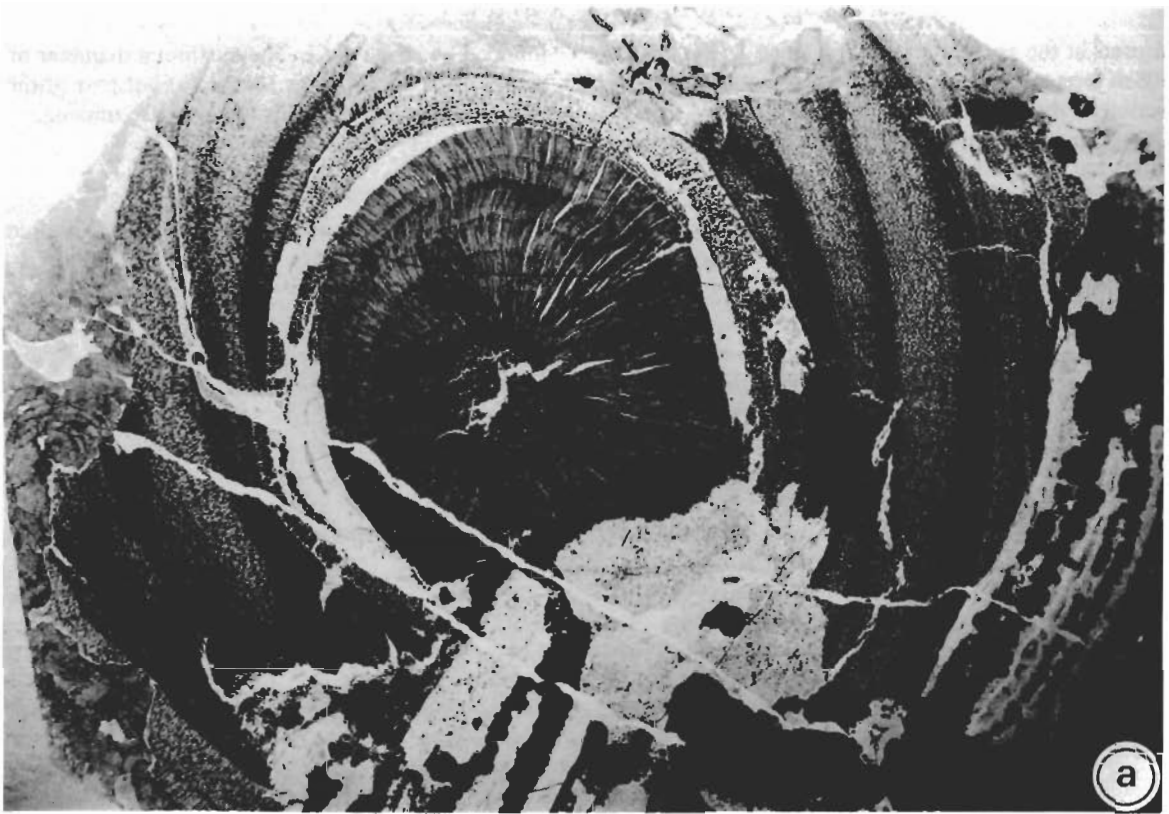


Figure 2 *Stanwoodia kirktonensis* gen. et sp. nov. (a) General transverse section of stem showing from outside the periderm with well marked layers, phloem, secondary xylem with rings and the protosteles. HMST 22197 ($\times 4.5$). (b) Transverse section of the parenchymatised protosteles showing the nearly complete ring of symphyloids separated from the secondary xylem by parenchyma cells with dark contents. Two 'pairs' of leaf traces are numbered 2a-b and 3a-b according to Fig. 3b. 4860 DT 05 ($\times 30$). (c) Transverse section of a portion of secondary xylem with visible 'growth rings', phloem and two inner layers of periderm. HM TS 22197 ($\times 18$).

not been used in the present study. Specimen 2 (Fig. 1d) is about 0.08 m long and is very incomplete. It shows only half of the section of the original stem.

In both specimens, the organic matter is preserved and peel sections have been made on all surfaces using standard 40% HF. The irregularity of the outer layers of specimen 1 is striking (Fig. 1a-c) and is difficult to explain by a simple mechanical erosion process. The following description is

founded on specimen 1. The maximum diameter of the stem preserved is 30 mm (Figs 1c and 2a) but part of the external tissues (outer cortex and leaf bases) are missing.

2.1. Stele

The stelar tissues measure about 3 mm in diameter. In transverse section (Figs 2b and 3a-c) there is a nearly

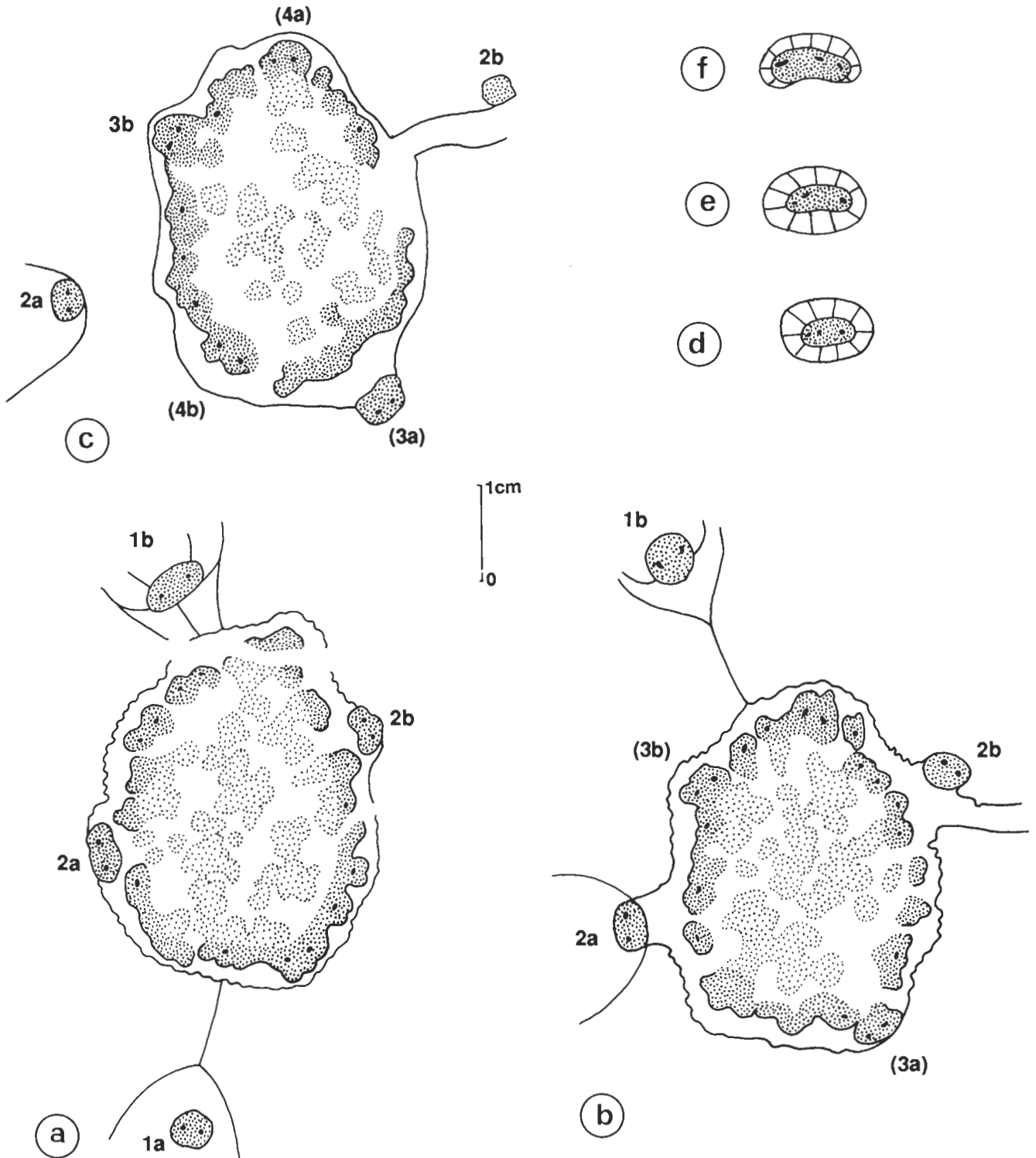


Figure 3 *Stanwoodia kirktonensis* gen. et sp. nov. (a)-(c) Camera lucida drawings of three successive transverse sections of the stelar system; inner limit of the secondary xylem indicated by a continuous line; primary xylem tracheids are stippled with dense stippling in peripheral lobes or strands and leaf traces; protoxylem in black. Successive leaf traces are numbered 1a, 1b, 2a, 2b, 3a, 3b, 4, etc. They do not conform to a helical phyllotaxy. Slides 4860 DT 16, DT 02, CB 03. (d)-(f) Camera lucida drawings, at the same magnification, of leaf traces in the outer cortex showing three protoxylem poles and surrounding sheath of wood. The most distal (f) corresponds to FB on Fig. 1b. 4860 DT 08, BB 07, CB 03.

continuous ring of primary xylem strands comprised of small tracheids (10–40 μm in diameter) which are continuous with larger metaxylem tracheids (40–80 μm wide and exceptionally up to 140 μm) which are scattered in groups throughout the central region of the stele (Figs 2b and 4a). The primary xylem tracheids are separated from the secondary xylem by four to eight layers of parenchyma cells with dark contents (P, Fig. 4a). These cells are small (30–60 μm in diameter and 30–80 μm high) and vertically aligned as shown in longitudinal section (P, Fig. 4d). Twelve to 16 protoxylem poles are present which correspond to mesarch sympodial strands. The protoxylem and the smaller metaxylem tracheids have helical to scalariform thickenings. These central tracheids are short (less than 300 μm long) and highly contorted in longitudinal section, with scalariform to multiseriate bordered pitting on all walls (Fig. 4b–c). The central region of the stele is composed of approximately equal volumes of tracheids and intermixed parenchyma cells with black contents (Fig. 2b). These parenchyma cells are nearly isodiametric, often in vertical files (Fig. 4c) and similar to those separating the primary xylem strands from the secondary xylem. This stele may be interpreted as a parenchymatised protostele (Beck *et al.* 1982). It has distinct xylem ridges producing leaf traces interpreted as sympodial strands at the periphery of the xylem and parenchyma which is irregularly intermixed with tracheids at the centre of the stele. There is a clear distinction between tracheids of the peripheral strands and those of the central region in terms of diameter, length and pitting.

2.2. Leaf traces

Successive stages in the origin and divergence of leaf traces may be followed by comparing leaf traces 1, 2, 3, 4 on Fig. 3a–c. Incipient leaf traces are recognised by the radial elongation of one protruding ridge at the surface of the stele (for example leaf traces 3a and 3b, Figs. 3b–c). At this stage one leaf trace is about 300 μm wide and two protoxylem strands are already present (see also Figs 2b and 4a). The sympodial pattern, which is the production of one leaf trace and a continuing cauline segment by the bifurcation of the sympodial strand, has not been clearly observed. However, evidence is suggestive of a division in a tangential plane resembling the situation in *Lyginopteris*, *Lyginopitys* and living conifers. This differs from the radial division of the sympodial strand found both in progymnosperms like *Callixylon* and in some calamopityan pteridosperms. The successive leaves do not conform to a normal helical phyllotaxis. The leaves may be interpreted as arranged suboppositely considering that:

- (1) There is generally one trace slightly in advance of the other (e.g. trace 1a with regard to 1b, Fig. 3a);
- (2) The angle between the two traces of one 'pair' is not 180° but 150–160°.
- (3) The arrangement of successive opposite pairs is not decussate but rather irregular as shown by the comparison of the position of 1a–1b with regard to 2a–2b and 3a–3b on Figure 3a–b.

We suggest this plant exhibits a deviant pattern of the bijugate condition which occurs in some living conifers (Camefort 1956; Nambodiri & Beck 1968). Complementary data from longitudinal and transverse sections are represented in the diagram (Fig. 5) of the vertical distribution of the leaf traces in a short portion of the stem. It must be noted that the leaves are distributed along two spirals which may represent contact parastichies or which

should be consistent with Camefort's (1956, Figs 50, 88 and 90) interpretation of two helices in the bijugate condition. However, the irregularity of the spacing of the leaves on each spiral cannot be explained. The vertical distance between two successive leaf traces is 1 mm on average (Fig. 5).

Leaf traces are observed within the cortex as far as 10 mm from the secondary xylem (FA, FB, FC, Fig. 1a, b). In each trace the primary xylem bundle is surrounded by a sheath of secondary xylem (Fig. 3d–f). One leaf apparently remains undivided distally (Fig. 6j) but shows a significant increase in tangential width (up to 700 μm) and three to four protoxylem poles (Fig. 3d–f) instead of the initial two. The outermost part of the stem is not preserved and we lack information about the petiole anatomy.

2.3. Secondary xylem

The total diameter of the cylinder of wood slightly exceeds one centimeter. This tissue consists of tracheids and ray parenchyma. Its irregular thickness (3–5 mm, Fig. 2a) suggests the specimen may have been a branch.

The tracheids are small, 20–50 μm in diameter, more commonly 30 μm in both radial and tangential dimensions. The radial walls show two to three alternating rows of crowded circular-bordered pits (Fig. 4e, f). The pore opening is slit-shaped and oblique. The apertures are crossed between pits of adjoining tracheids. The ray field of contact between ray and tracheids show six to nine oblique oval pits. The tangential walls are unpitted.

The rays are numerous, separated by one to eight files of tracheids in transverse section. They are all uniseriate but of varying height (Fig. 4g); 63% are very small rays, one to three cells high; 12% have four to six cells but 25% are seven to 10 cells high. Individual ray cells are about 20 μm in tangential width, 30 μm height and up to 100 μm long in radial longitudinal section (Fig. 4f).

The growth rings cannot always be traced all around the stem. Their development appears to have been irregular; the smaller and thicker-walled tracheids are 20 μm radially and the larger are 50 μm . Despite the excellent preservation of the specimen, the vascular cambium is not as distinct as in other Lower Carboniferous gymnosperms such as *Calamopitys* (Galtier & Héban 1973).

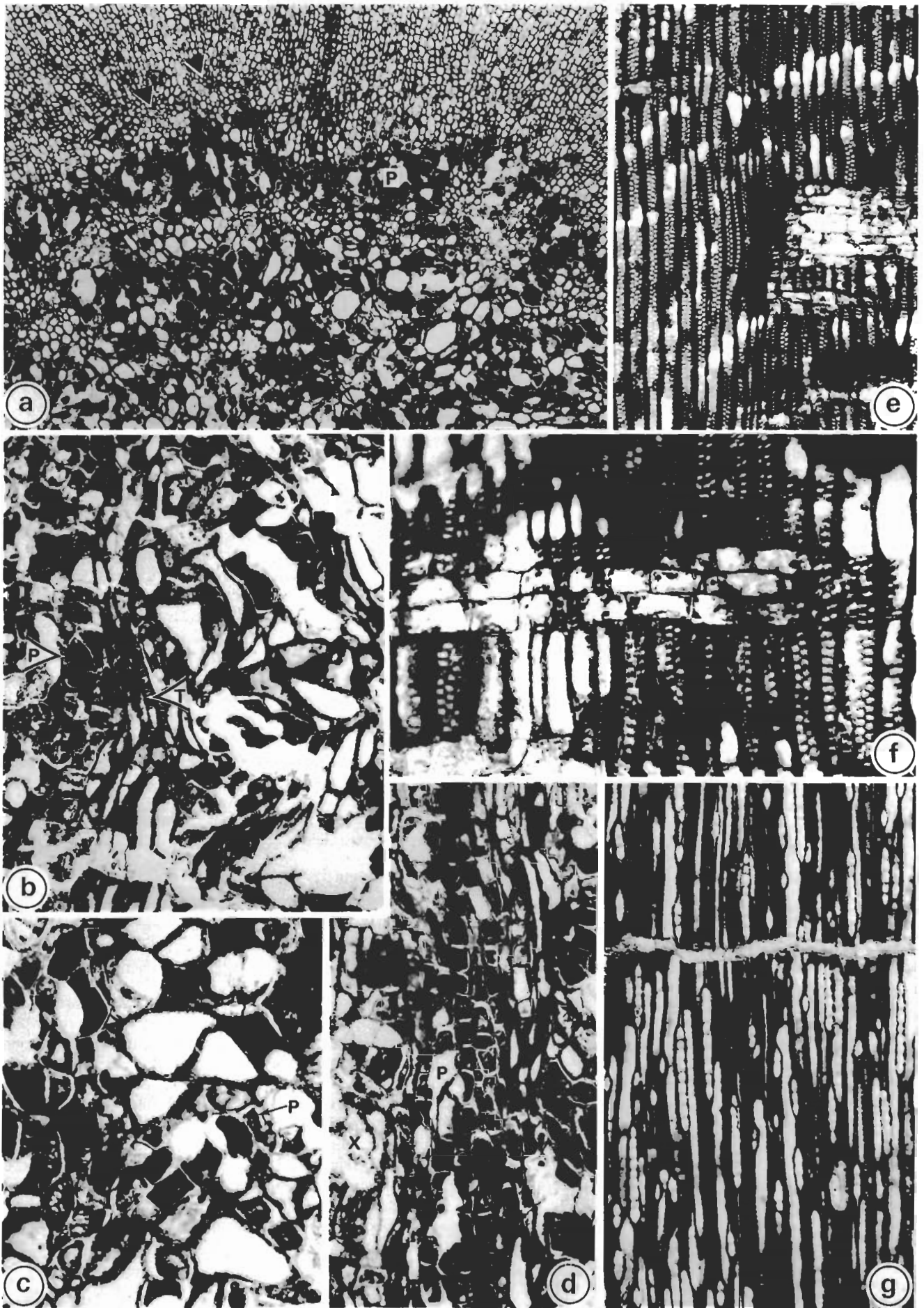
2.4. Phloem

The secondary phloem is a complex tissue up to 1.5 mm thick. It consists of fibres, different types of thin-walled cells and rays. The elongated thick-walled fibres are 20–45 μm in diameter and more than 1 mm long (F, Fig. 6a–d). Some thin-walled cells (30–80 μm in diameter) are arranged in tangential rows (C, Fig. 6a) alternating with fibres. These cells are devoid of content and generally poorly preserved in longitudinal section. Some are elongate and may correspond to sieve cells but evidence of sieve areas has not been observed.

Other thin-walled cells scattered through the phloem have a characteristic dark opaque content; they are 20–90 μm in diameter, slightly elongate and sometimes arranged in vertical columns which are a few cells high (P, Fig. 6a, c). They resemble the supposed 'tanniferous' cells described by Scheckler & Banks (1971a, b) in the phloem of several aneurophytalean progymnosperms. The phloem ray cells (R, Fig. 6b) are generally very poorly preserved.

2.5. Cortex

External to the phloem there is a well-developed periderm, about 10 mm in thickness, which has the appearance of a



rhytidome with overlapping scale-like layers (Figs 1c and 2a, c). The inner layers of periderm are in contact with an apparently active secondary phloem (Fig. 6d–e) but it is not possible to identify phellogen and phelloderm cells. The cells are tangentially flattened and rectangular both in transverse (Fig. 6e–h) and in longitudinal radial (Fig. 6d, i) sections; they are 40–75 μm in height and tangential diameter and only 20–30 μm in radial diameter. Elongated thick-walled fibres, identical to those found in the secondary phloem are scattered in the periderm (F, Fig. 6d, f). Small spherical groups of dark (perhaps sclerotic) cells are also present (S, Fig. 6h, i).

More commonly, vertical files of large parenchyma cells with dark contents (P, Fig. 6g–i) occur intermixed with periderm cells. They constitute distinct dark layers alternating with lighter homogeneous periderm layers (Figs 2a, c; 6f, g). These parenchyma cells are similar to the so-called 'tanniferous' cells of the secondary phloem.

The occurrence within the periderm of both fibres and parenchyma cells identical to those found in the phloem is suggestive of a deep place of origin of phellogen, i.e. within the phloem. In this plant the sequent periderms arise in discontinuous layers which have the shape of scales curved towards the inside so that the successive outer layers overlap the deeper ones unlike the situation generally observed in sequent periderm of living plants (Esau, 1977).

2.6. Remarks

Specimen 2 provides little additional information. It represents a slightly larger and older stem with a stele 4 mm in diameter and a thickness of secondary xylem up to 11 mm. Accordingly the total diameter of the cylinder of wood (24 mm) (Fig. 1d) is twice that of specimen 1. The stelar tissue shows the same features as in specimen 1 with a central column of short tracheids of irregular shape, pitted on all their faces and intermixed with parenchyma cells. Characteristics of the secondary xylem and phloem are also similar to those found in specimen 1. The periderm conforms to a rhytidome with scale-like layers and although it appears to be less developed (5 mm thick), this may be due to incomplete preservation.

3. Nomenclature

3.1. *Stanwoodia* gen. nov.

Diagnosis. Stem with parenchymatised protosteles; leaf-trace-producing bundles (sympodial strands) in a nearly continuous ring at the periphery of the xylem, separated

from the secondary xylem by several layers of parenchyma. Protoxylem mesarch; metaxylem tracheids with scalariform to multiseriate bordered pits on all walls. Central column consisting of large, pitted tracheary elements mixed with parenchyma cells. Plane of divergence of leaf traces tangential-oblique. Leaves subopposite, arranged along two spirals. Leaf trace initially with two protoxylem poles, remaining undivided in the stem cortex. Secondary xylem pycnoxylic; tracheids with multiseriate bordered pits on radial walls only. Rays short, uniseriate. Secondary phloem complex with alternating bands of parenchyma cells, fibres and probable sieve cells. Considerable development of periderm forming a rhytidome with overlapping scale-like layers.

Derivation of the generic name. In honour of Mr Stan Wood who collected the type specimen. Type species: *Stanwoodia kirktonensis* sp. nov.

3.2. *Stanwoodia kirktonensis* sp. nov.

Diagnosis. Stem with parenchymatised protosteles 3–4 mm wide; central column consisting of short-contorted tracheids, 10–140 μm in diameter and less than 300 μm long, intermixed with parenchyma cells with black contents, 30–60 μm in diameter and 30–80 μm long, sometimes vertically aligned. Numerous sympodial strands and incipient leaf traces at the periphery of the stele with metaxylem tracheids 10–40 μm in diameter and more than 1 mm long. The primary xylem is separated from the secondary xylem by four or more layers of parenchyma cells. Leaf trace about 300 μm wide with two protoxylem poles at point of entering wood; in the stem cortex the leaf trace remains undivided but enlarges up to 700 μm , with 3–4 protoxylem poles. Leaf traces irregularly subopposite, do not conform to a simple helical phyllotaxy. Secondary xylem with small tracheids (20–50 μm , more commonly 30 μm in diameter) and rays one cell wide, commonly one to three but up to 10 cells high. Ray parenchyma cells about 20 μm in tangential width, 30 μm high and up to 100 μm in radial dimension. Secondary phloem constituted of tangential bands of long thin-walled cells (probably sieve cells) 30–80 μm in diameter, alternating with thick-walled fibres 20–45 μm in diameter, more than 1 mm long and scattered parenchyma cells with dark contents 20–90 μm in diameter, generally in vertical columns. Sequent periderm with alternating layers of tangentially flattened cork cells 40–75 μm in vertical and tangential diameter and 20–30 μm in radial width. Dark layers constituted of larger parenchyma cells with dark contents in vertical files and fibres similar to the phloem elements intermixed with other periderm cells.

Derivation of the specific epithet. Refers to the name of the type locality, East Kirkton quarry.

Holotype. Specimen Pb 4860 and the corresponding thin and peel sections, palaeobotanical collections, Hunterian Museum, University of Glasgow.

Paratype. Specimen 2, geological collections, Royal Museum of Scotland.

Type locality. East Kirkton quarry, near Bathgate, West Lothian, Scotland.

Stratigraphy. East Kirkton Limestone, Upper Oil Shale Group, Late Viséan, Brigantian, Lower Carboniferous.

4. Discussion

4.1. Comparison with the genus *Bilignea* Scott

Among Lower Carboniferous plants of gymnospermous affinities, *Stanwoodia* most closely resembles the genus

Figure 4 *Stanwoodia kirktonensis* gen. et sp. nov. (a) Detail of protosteles and inner secondary xylem, transverse section showing the continuous layers of parenchyma cells with dark contents (P) separating the primary xylem from the wood. Double arrow on upper left designates a leaf trace entering the wood. 4860 DB 08, ($\times 43$). (b) Longitudinal section of the central column, showing on the left, several layers of parenchyma cells (P) surrounding the protosteles, a few narrow elongate tracheids (T) of the axial strands and, on the right, contorted and wide tracheids of the central protosteles. 4860 CALR, 13, ($\times 84$). (c) Detail of the large and short tracheids of the central column with intermixed parenchyma (P), longitudinal section. 4860 CALR 14, ($\times 130$). (d) Longitudinal section showing the transition from the secondary xylem (X), on the left, to the primary xylem separated by four or five layers of parenchyma cells (P) in vertical files. 4860 CALR 06, ($\times 84$). (e, f) Longitudinal radial sections of secondary xylem showing multiseriate pitting of tracheids and detail of ray cells. 4860 CALR 04, ($\times 84$); 4860 CALR 14, ($\times 180$). (g) Tangential section of secondary xylem showing uniseriate rays of various height. 4860 CALT 03, ($\times 84$).

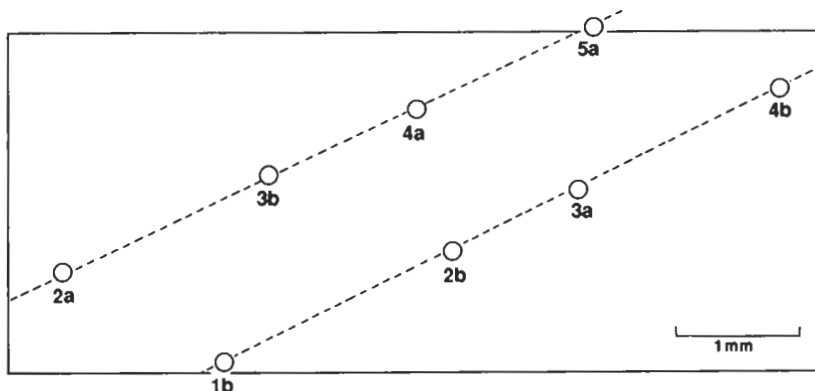


Figure 5 Diagram representing the leaf traces of *Stanwoodia* in the secondary xylem as if spread out in one plane. Reconstructed partly from tangential peel sections. Note the irregular distribution of traces along two spirals. Numberings correspond to those in Figs 1 and 3.

Bilignea Scott (1924) of which two species were initially described. These include *B. solida* from the Carboniferous of Ayrshire (exact age unknown) and *B. resinosa* from the Cementstone Group of Loch Humphrey Burn, Lower Carboniferous, probably early Visean (Scott *et al.* 1984). Both species are founded on decorticated specimens with a cylinder of wood which is up to 40 mm diameter in *B. resinosa*.

Stanwoodia is similar to *Bilignea* in its compact secondary xylem with small tracheids and rays. Furthermore, in both genera the pith is replaced by a central column of short tracheids which are pitted on all their faces and a ring of primary xylem strands consisting of elongated tracheids. However, the two genera differ in the following characters:

- (1) The occurrence of several layers of parenchyma cells with dark contents between the primary xylem strands and the secondary xylem is a feature of *Stanwoodia* which is absent in *Bilignea*.
- (2) Similar parenchyma elements, often in vertical files, are intermixed with short tracheids inside the central column in *Stanwoodia* but no parenchyma could be detected in *B. solida* according to Scott (1924). This feature is confirmed by our own reinvestigation of the original slides of this species in Glasgow. In *B. resinosa* large secretory sacs are present which have no equivalent in *Stanwoodia*.
- (3) The primary xylem strands are more distinct in *Bilignea solida* than in *Stanwoodia*. Furthermore, they vary much in size in the former species where the largest strands are about 1 mm in diameter. They do not exceed 0.3 mm in *Stanwoodia*.
- (4) The very regular arrangement of leaf traces in *B. solida* corresponds to a phyllotaxy of 5/13 according to Scott (1924). In contrast, there is no regular helical arrangement in *Stanwoodia* where an irregular bijugate pattern has been described.

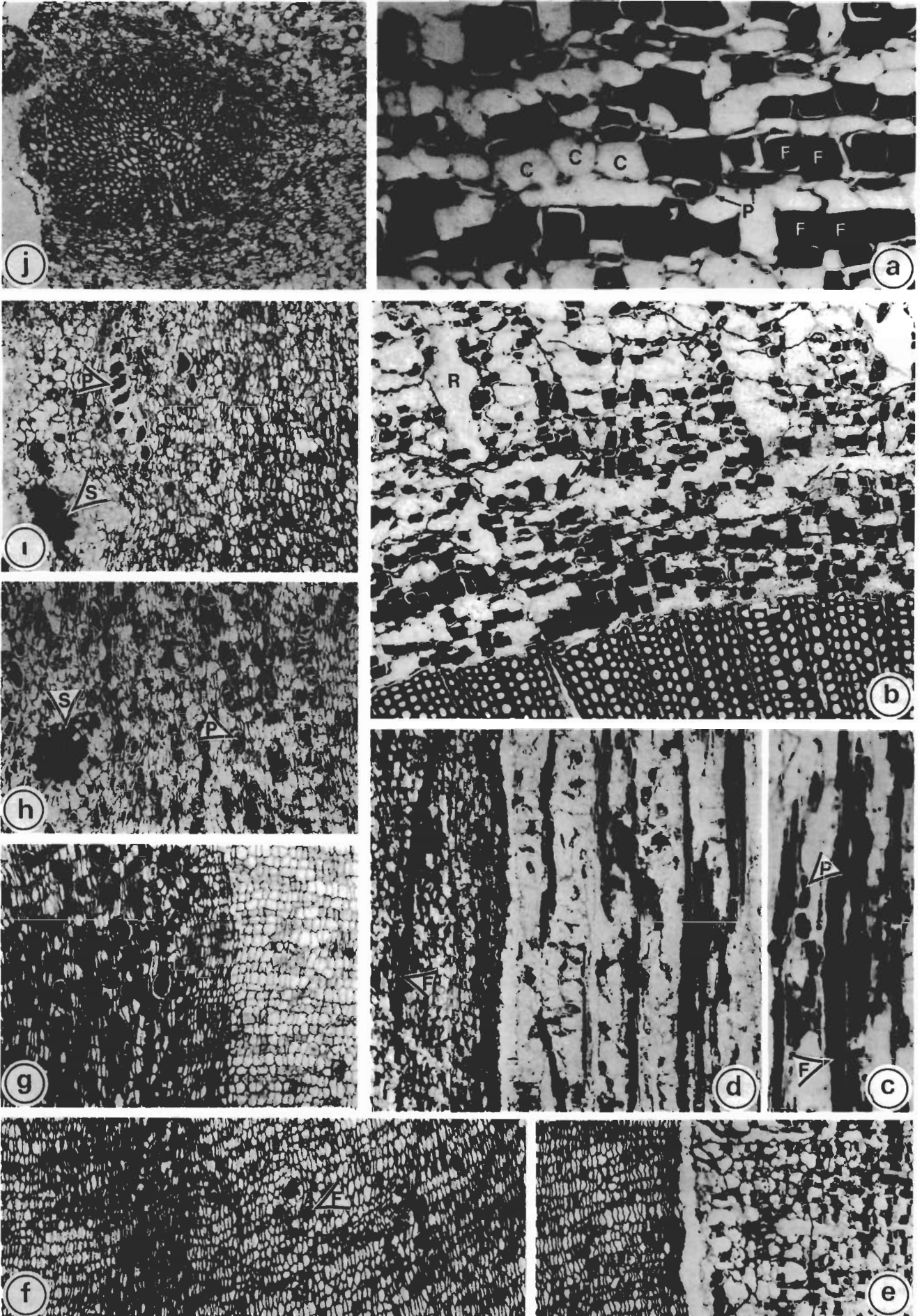
Other differences may reflect incomplete preservation and concern the structure of the phloem and periderm which are not known in *Bilignea*. The occurrence of faint growth rings is a common feature of *Bilignea resinosa* and *Stanwoodia* while it is not known to occur in *B. solida*. These rings may represent a reaction to a similar external stress such as nearby volcanic activity which was well documented in both original environments. It is significant that growth rings have been observed in other woody stems found in volcanosedimentary deposits of the same age in Scotland (Scott *et al.* 1986) and in Morocco (Chalot-Prat & Galtier 1989).

4.2. Comparison with other forms

There are several Lower Carboniferous genera resembling *Stanwoodia* in the pycnoxylic secondary xylem but differing in their stelar structure. One must mention *Eristophyton* Zalesky which has a more or less wide, wholly parenchymatous pith surrounded by discrete primary xylem strands conforming to an eustelic organisation (Lacey 1953; Galtier & Scott 1990). *Pitus* Witham is very similar to *Eristophyton waltonii* Lacey but differs in the possession of medullary primary xylem strands (Gordon 1935). *Endoxylon* Scott (1924) also possesses a wide parenchymatous pith and rather large primary xylem strands.

Other Lower Carboniferous plants resemble *Stanwoodia* in their protostelic organization and leaf trace origin but differ by having manoxylic wood. This is the case for several species of (the older) *Calamopitys* Unger or of *Heterangium* Williamson. However, the latter shows a regular grouping of central tracheids separated by well-marked parenchyma plates which are not observed in *Stanwoodia*. *Lyginopitys* Galtier (1970) shows a stelar structure similar to that of *Stanwoodia* but differs in the occurrence of medullary xylem strands and a wood with larger rays. Lastly, the younger *Megaloxylon* Seward (1899) shows perhaps the most similar stele with a central column of short tracheids and peripheral strands of more elongated elements.

Figure 6 *Stanwoodia kirktonensis* gen. et sp. nov. (a) Detail of the secondary phloem, transverse section showing tangential tiers of fibres (F) and thin-walled probable sieve cells (C), and scattered parenchyma cells with dark contents (P). HM TS 22197, ($\times 170$). (b) Transverse section of outer secondary xylem and phloem tissue. There is no well-preserved cambium. Note distorted rays (R) in phloem. HM TS 22197, ($\times 80$). (c) Detail of phloem, longitudinal section showing long thick-walled fibres (F) and vertical files of parenchyma cells with black contents (P). 4860 CALT 03, ($\times 180$). (d) Longitudinal section throughout inner periderm, at left, with one long fibre (F) and phloem with alternating bands of dark elongate fibres, long thin-walled cells and scattered parenchyma cells with dark content. 4860 CALT 03, ($\times 42$). (e) Corresponding transverse section with inner periderm at left and phloem. HM TS 22197, ($\times 42$). (f) Transverse section of the periderm showing one distorted layer and small groups of fibres (F). 4860 AB 01, ($\times 42$). (g) Transverse section of periderm with one dark layer corresponding to the occurrence of parenchyma cells with dark contents. HM TS 22197, ($\times 42$). (h) Transverse section of outer periderm near a leaf trace with a large number of parenchyma cells (P) and a group of small 'sclerotic' cells (S). 4860 CT 01, ($\times 42$). (i) The same elements in longitudinal section, note the parenchyma cells (P) in vertical file. 4860 CBLR 03, ($\times 42$). (j) Leaf trace in the outer periderm with a continuous ring of secondary xylem and three or four protoxylem strands. 4860 BB 07, ($\times 44$).



4.3. Morphological significance of *Stanwoodia*

The main interest centres firstly on the combination of a protostelic organisation with a dense wood and secondly on the features of the phloem and periderm which are exceptionally well preserved in this plant. The stelar structure may be interpreted as a new example of a primitive stage in the evolution towards an eustele through the longitudinal dissection of a protostele as speculated by Namboordiri & Beck (1968) and Beck (1970). Indeed *Stanwoodia* shows a parenchymatised protostele conforming to the stage observed in some *Calamopitys* used by Beck in his analysis.

The significance of pycnoxylic versus manoxylic organisation of wood is still not well understood. Pycnoxylic wood is a primitive feature of progymnosperms with regard to manoxylic wood with wide and high rays. The latter should be considered a derived character of lyginopterid, calamopityan and medullosan pteridosperms (Galtier 1988). Some genera like *Pitus* and *Eristophyton*, which are sometimes interpreted as pteridosperms, show a significant variation in the width of their rays but we do not consider that they have truly manoxylic wood (Galtier & Scott 1990).

Because phloem is rarely preserved in fossil gymnosperms this tissue is not generally considered to be of possible taxonomic or evolutionary significance. The oldest gymnospermous phloem has been described in Middle Devonian members of the Aneurophytalean progymnosperms (Wight & Beck 1984); it is a complex tissue consisting of four different types of cells including thick-walled fibres and isodiametric sclereids. A similar phloem has been described in Upper Devonian members of the same group (Beck 1957; Scheckler & Banks 1971a, b). In Lower Carboniferous calamopityan pteridosperms the phloem consists mainly of parenchyma and sieve cells (Galtier & Hébert 1973) but is devoid of sclerotic elements. It is therefore a less complex tissue than in the younger *Stanwoodia* where at least three types of constituent cells have been recognised including elongate fibres.

Periderm has been described in some Devonian Aneurophytalean progymnosperms as the earliest occurrence of this tissue (Scheckler & Banks 1971a, b). They show several stages in the development of periderm, interpreted to have been initiated by a periclinal division of parenchyma cells. This was located inside the fibrous outer cortex or deeper in the inner cortex but always nearly simultaneously around the whole circumference of the axis. This situation is different in *Stanwoodia* where the initiation is deeper and occurs in discontinuous layers. In the aneurophytalean progymnosperm *Triloboxylon*, the phellem cells have thick walls and a relatively extensive phelloderm developed. However, the two types of cells are hardly distinguishable in transverse section (Scheckler & Banks 1971a). In contrast, the periderm of *Stanwoodia* appears more complex and shows a mixture of typical phellem cells with fibres and parenchyma cells. In *Stanwoodia* the periderm has the appearance of a rhytidome, a feature not observed in progymnosperms.

Periderm occurs relatively rarely in early gymnosperms. There is no evidence of well-developed periderm in early pteridosperms or even in stems several tens of millimeters in diameter such as *Calamopitys* where the cortex results from primary growth (Galtier 1988). However, a periderm is common in the Medullosales where it has been interpreted as a phelloderm. Until now the best example of periderm in Lower Carboniferous gymnosperms was that described in *Endoxylon* by Scott (1924). The periderm of *Stanwoodia* actually represents the oldest well-documented occurrence

of a rhytidome in fossil plants.

4.4. Taxonomic position

Stanwoodia is another example of a decorticated stem which is difficult to classify in the absence of characters concerning leaf trace anatomy and fertile parts. As discussed above, we recognise some agreement between *Stanwoodia* and the genus *Bilignea*. Both have similar primary and secondary xylem; they differ in details of the stelar structure and phyllotaxis. In addition phloem and cortex are unknown in *Bilignea*.

Stanwoodia could also be tentatively grouped with *Endoxylon* which has a very similar dense wood but differs, like *Eristophyton*, *Pitus* and *Mesopitys*, in its parenchymatous pith. Lacey (1953) suggested 'without any strong conviction' that these genera should be associated with the Cordaitales emphasising common characters of the dense secondary wood. However, Lacey considered also the possibility that the same plants could represent either pteridosperms or pteridophytes. Since that time the class Progymnospermopsida has been defined for plants which associate a pteridophytic mode of reproduction and gymnosperm-like vegetative anatomy and morphology. If we take into consideration the available features of the stele and secondary xylem, we cannot exclude the idea that *Stanwoodia* may be a Progymnosperm. On the other hand, some genera like *Pitus* and *Eristophyton* have been more recently interpreted as pteridosperms (Long 1979, 1987) considering their leaf anatomy and variation in secondary xylem organisation with more or less broad rays. In *Stanwoodia* the leaves are not known but the leaf traces observed in the stem cortex are rather small and undivided. This is suggestive that this plant did not possess large leaves. However, previous and present studies of the flora from East Kirkton demonstrate that pteridosperm-type leaves (*Sphenopteridium*, *Spathulopteris*, *Sphenopteris*, *Rhodea*) occur in abundance but we have not yet discovered a single example of a pteridosperm stem with manoxylic wood. The only stems of gymnospermous affinities found at East Kirkton are *Pitus*, *Eristophyton* and *Stanwoodia*; we cannot exclude the possibility that the latter was the stem bearing one of these types of foliage.

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