Frasnian plants from the Dra Valley, southern Anti-Atlas, Morocco

BRIGITTE MEYER-BERTHAUD*†, MARTIN RÜCKLIN‡, AUDE SORIA*,
ZDZISLAW BELKA§ & HUBERT LARDEUX¶

*Botanique et Bioinformatique de l'Architecture des Plantes, UMR 5120 CNRS-CIRAD, PS2/TA40,
Boulevard de la Lironde, 34398 Montpellier Cedex 5, France
‡Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13, 76133 Karlsruhe, Germany
§Institute of Geology, Adam Mickiewicz University, ul. Maków Polnych 16, 61-606 Poznań, Poland
¶Le Verger-Beaucé, 35 520 Melesse, France

Abstract – Anatomically preserved plant fragments are reported from Devonian marine deposits exposed in the Dra Valley of southern Anti-Atlas, Morocco. Associated conodont and tentaculite faunas indicate that the sediments yielding plants, which consist of black shales with intercalated calcareous concretions, are early Frasnian in age and most probably represent Zone 2 of the conodont zonation. This is the first record of Frasnian plants in North Africa. The specimens found all correspond to decorticated portions of axes. Six are referable to *Callixylon*, the organ genus corresponding to anatomically preserved axes of the progymnosperm tree *Archaeopteris*. Based on wood characters, especially ray structure, they are assigned to the species *C. henkei*, formerly described from the Famennian of Europe. One single specimen is compared to *Xenocladia*, a cladoxylopsid genus previously known from the Middle Devonian of Europe, USA and Kazakhstan. Interestingly, Archaeopteridales and Cladoxylopsida are two groups that dominate the younger plant assemblages of Famennian age recently described from the eastern Anti-Atlas. *Callixylon henkei*-type axes occur both in the Frasnian and in the Famennian deposits of the Anti-Atlas and they are all devoid of growth rings. These results are in accordance with a close position of Gondwana and Euramerica during Late Devonian times.

Keywords: Devonian, Anti-Atlas, Morocco, palaeobotany, fossil wood.

1. Introduction

Most accounts of Middle and Late Devonian plants based on macro-remains concentrate on records from northwestern Europe and North America that together formed the palaeocontinent of Euramerica (=Laurussia) during the Devonian Period. In the last twenty years, however, increased efforts to complete this record have been made with the study of fossils from localities of other palaeocontinents: China, Kazakhstan, Siberia and Gondwana (Anderson, Hiller & Gess, 1995; Berry *et al*. 2000; Cai & Wang, 1995; Chambers & Regan, 1986; Cingolani *et al*. 2002; Hilton, Geng & Kenrick, 2003; Iurina, 1988; Snigirevskaya & Snigirevsky, 2001). Short-term objectives of such investigations consist of describing new taxa or completing information on those already known from Laurussia, inferring environmental information from the functional and autecological study of the taxa, and investigating the composition of plant communities. In the long term, a more complete record of plants of Middle and Late Devonian age is required (1) to elucidate the patterns of origination and early diversification of three major groups of plants: the ferns, sphenopsids, and seed plants (Pryer *et al*. 2001;

Rothwell, 1999); (2) to test contradictory hypotheses about the cosmopolitan/provincial nature of the vegetation at this time and use this information for resolving palaeogeographical scenarios (Briggs, 1995; Hill *et al*. 2000; Talent *et al*. 2000; Wnuk, 1996); (3) to compare evolutionary patterns with those exhibited by faunas and assess the effects on terrestrial organisms of the major crises that affected the marine benthos during late Frasnian times (Anderson *et al*. 1999; DiMichele & Hook, 1992; Raymond & Metz, 1995).

Most research conducted on Middle and Late Devonian Gondwana plants in the past ten years relates to South America, especially Venezuela, as well as Morocco. It has resulted in the identification of ten new species, better assessment and emendation of six genera previously described from Europe and/or North America, and the first reports of accurately dated and unambiguously identified plant remains in North Africa for this period (Anderson *et al*. 1999; Berry *et al*. 2000; Berry & Stein, 2000; Meyer-Berthaud, Wendt & Galtier, 1997; Soria & Meyer-Berthaud, 2004; Soria, Meyer-Berthaud & Scheckler, 2001). In the present paper we report the first record of fossil plants from the Dra Valley of the Anti-Atlas and the first plant remains of Frasnian age in Morocco. These fossils, anatomically preserved in marine deposits, are only represented by a few specimens, but the general rareness of Frasnian

---

† Author for correspondence: meyerberthaud@cirad.fr

plant records in western Gondwana justifies this report. Six specimens consist of fragments of woody axes referable to *Callixylon*, the organ genus corresponding to anatomically preserved axes of *Archaeopteris* and related to the Progymnospermopsida. One small specimen is referred to the Cladoxylopsida, a group of plants affiliated with the ferns, which flourished in Middle Devonian times. These remains are compared to those recently found in the Famennian localities of the Mader and Tafilalt areas of the eastern Anti-Atlas. The latter yielded abundant but moderately diversified remains including several species of *Callixylon*, two species of the cladoxylopsid genus *Pietzschia*, and much rarer fragments of lycopsids, which are currently under study (Galtier, Paris & El Aouad-Debbaj, 1996; Meyer-Berthaud, Scheckler & Wendt, 1999; Soria & Meyer-Berthaud, 2004; Soria, Meyer-Berthaud & Scheckler, 2001).

2. Geological background

During Devonian times, the Anti-Atlas constituted a fragment of a broad shelf area of Gondwana, expanding over the northern continental margin of the West African Craton. This most probably mid-latitude (30–40° S) temperate water carbonate province is characterized by extremely rich fossil faunas that have attracted the interest of many palaeontologists in the last decades.

The depositional and tectonic evolution of the Anti-Atlas shelf were controlled by regional, E–W-trending strike-slip faults that influenced the subsidence pattern and occasionally were sites of volcanic activity (Belka, Kazmierczak & Kaufmann, 1997). As a consequence, a complex pattern of carbonate platforms and small intracratonic basins formed during Devonian times (Wendt, 1988). Moreover, at least one large island with an exposed Precambrian basement existed in the northern part of the Anti-Atlas (J. Dopieralska, unpub. Ph.D. thesis, Univ. Giessen, 2003). On the platforms, the Upper Devonian sediments are usually represented by very fossiliferous carbonates, whereas monotonous shales predominate in the basinal successions. Clastic material, only occasionally transported into the basins, was supplied both from the south (West African Craton) and from the north (islands). Recently, Dopieralska (J. Dopieralska, unpub. Ph.D. thesis, Univ. Giessen, 2003) provided the first neodymium isotopic signatures for the Devonian seawater on the Moroccan shelf and showed a complex seawater circulation pattern. During middle Frasnian times, a general seawater flow from the southwest towards the east was recognized, while during the middle Famennian, the seawater circulated mostly westwards, that is, in the opposite direction. The Dra Valley, located in the southern part of the Anti-Atlas, belongs to the northern margin of the Tindouf Basin. It has been less intensely investigated in terms of palaeontology, sedimentology and tectonics than the long-studied eastern part of the range. Upper Devonian
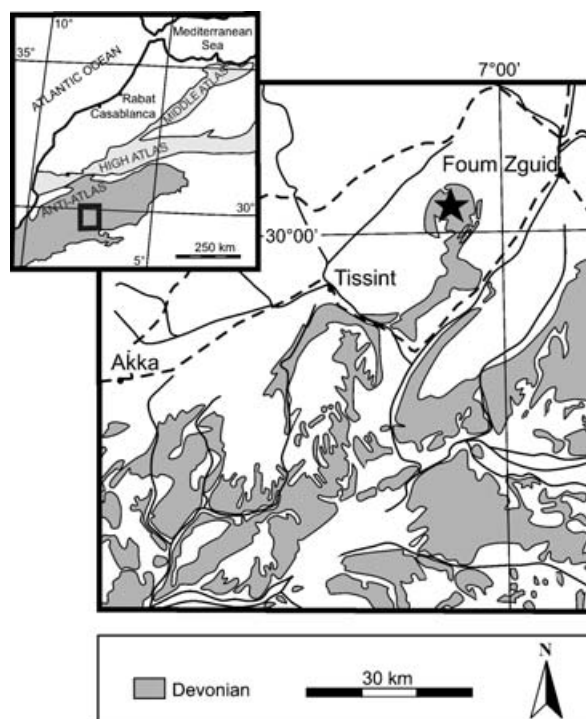

Figure 1. Simplified geological map of the Dra Valley near Foum Zguid showing distribution of Devonian rocks and location of the El Gara section (star).
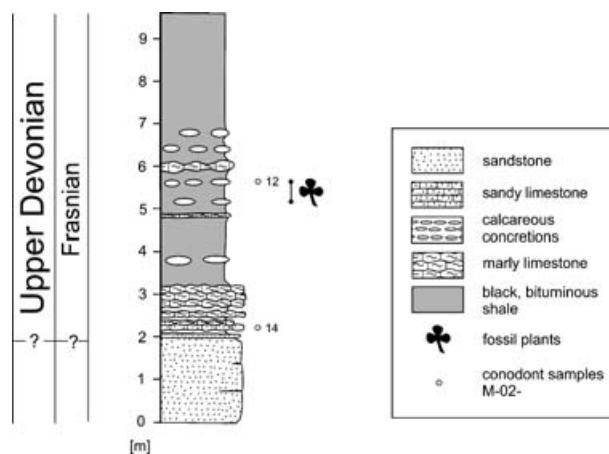

Figure 2. Section at El Gara (southwest of Foum Zguid, Dra Valley, southern Morocco).

sediments crop out here only in a few places and are mostly represented by black shales with interbeds of carbonates and sandstones.

3. Material and methods

Seven anatomically preserved fragments of axes were collected at El Gara, a locality about 20 km west of Foum Zguid and 30 km northeast of Tissint, in the Dra Valley (southern Anti-Atlas; Fig. 1). The fossiliferous beds are black, bituminous shales intercalated with calcareous concretions (Fig. 2). They are associated

with an abundant marine fauna of bivalves, styliolinids and orthoconic nautiloids, together with remains of a large arthrodire (placoderm). These sediments crop out on the western side of the Gara (='flat relief'), on a gently inclined plateau that overlies the 11.5 metre thick, conspicuous sandstone of the Megsem Medersam Formation, forming a cliff about half way up the hill (Fig. 2). Three specimens (GA1/2, GA3, GA6) were found *in situ*, included in a calcareous concretion. Two (GA4, GA7) were loose and occurred nearby. The smallest specimen (GA5) was found loose but a few metres below the others, and closer to the base of the black shale deposit. Whether it came from the same beds as the larger fragments and rolled down or it was weathered from a bed lower in the section, closer to the level of conodont sample M-02–14 (Fig. 2), is unknown.

Portions of some wood fragments are strongly recrystallized. Thin-sections of the best preserved parts were made in transverse, radial and tangential planes. An Olympus BX60 microscope was used for observations and cell measurements, the latter realized on a minimum of 50 elements whenever possible. The terms 'wood' and 'secondary xylem' refer to the same tissue in the following description.

4. Stratigraphy

The calcareous concretions yielding plants (Fig. 2) contain high densities of tentaculite (styliolinid) shells, which comprise the largest component of the rock. These are rarely associated with specimens of homoctenids. Despite a generally poor state of preservation which prevents the definite determination of specific species, it is possible to assign a Frasnian date for this calcareous horizon. The styliolinids are strongly reminiscent of *Striatostyliolina striata* (Richter, 1854) of Frasnian age, known from pre-Saharan Morocco (Lardeux, 1969). This is a diminutive species with a longitudinal ornamentation of extremely fine, barely visible furrows. The homoctenids belong to the group *Homoctenus tenuicinctus* (Roemer, 1850), well represented in the Frasnian with a very broad geographic distribution (Lardeux, 1969). A specimen examined in thin-section reveals a form of initial chamber characteristic of the type: an apical prolongation in the form of a very fine tube. The El Gara specimens possess a very straight, narrow shell. The transverse rings are few; in contrast, *Homoctenus tenuicinctus* (Roemer) has twice as many. The most similar species seems to be *Homoctenus kikinensis* Ljashchenko (Frasnian), which has an identical apical angle (3°), but which has a slightly larger number of transverse rings (Ljaschenko, 1959). The El Gara species also resembles *Homoctenus acutus* Ljashchenko (Frasnian) in its number of transverse rings. However, *H. acutus* has a wider apical angle, which means that the number of transverse rings on a length of shell equal to its diameter

is less: about 3 to 5, while the equivalent figure for the El Gara specimen is 6 to 7 (Ljaschenko, 1959).

Two rock-samples, M-02–14 and M-02–12, yielded conodonts (Fig. 2). The conodont elements recovered from a sandy limestone (sample M-02–14, Fig. 2) belong to four species: *Polygnathus pennatus*, *P. dubius*, *P. dengleri?* (juvenile) and *Polygnathus cf. P. pollocki*. This assemblage is indicative of the interval from the Givetian *disparilis* Zone to the Frasnian conodont Zone 4 (conodont zonation after Klapper, 1997). The second conodont sample M-02–12 was taken from a limestone bed containing a placoderm specimen and fragments of plants (Fig. 2). Its conodont fauna includes four species of the genus *Ancyrodella* (*A. rotundiloba* (early form), *A. rotundiloba* (late form), *A. alata* and *A. recta*) and *Mesotaxis falsiovalis*, indicating the upper part of the Frasnian conodont Zone 2 (Klapper, 1997, 2000). The sample, however, also contains a fragmentarily preserved ancyrodellid element which bears some features characteristic for the species *Ancyrodella rugosa*. Although a determination at species level is rather unreliable, it cannot be excluded that the sample M-02–12 represents the lowest part of Zone 3. Thus, the sediments which yielded the plants are Frasnian in age, probably corresponding to Zone 2 (*rotundiloba*). The interval of black bituminous shales, marly limestones and calcareous concretions represents the so-called Frasne-event, ranging from Zone 1 (*pristina*) to Zone 4 (*transitans*), during which black shales and/or limestones were deposited in the Anti-Atlas area (Wendt & Belka, 1991; Belka *et al*. 1999). In the Dra Valley the black facies overlies the 11.5 m thick sandstones of the Megsem Medersam Formation, presumably Givetian or even earliest Frasnian in age (Hollard, 1967).

5. *Callixylon* stems

5.a. Description

The six specimens described in this section share a similar wood structure; none shows any evidence of growth rings. In radial section, walls of the wood tracheids exhibit the diagnostic features of *Callixylon*, that is, bordered pits arranged in groups separated by unpitted portions of walls (Fig. 3j). All specimens show secondary xylem tracheids with square to rectangular transverse sections whose dimensions vary somewhat within individual rows of elements, especially in the radial direction (Fig. 3b, e, h). Rays are uniseriate, relatively short and homogeneous. They comprise parenchymatous cells only. Measurements are summarized in Table 1. Characters particular to the best preserved specimens are described below.

5.a.1. Specimen GA1/2

GA1/2 is a 31 cm long specimen consisting of a 5.5 cm broad triangular sector of wood from a trunk or a
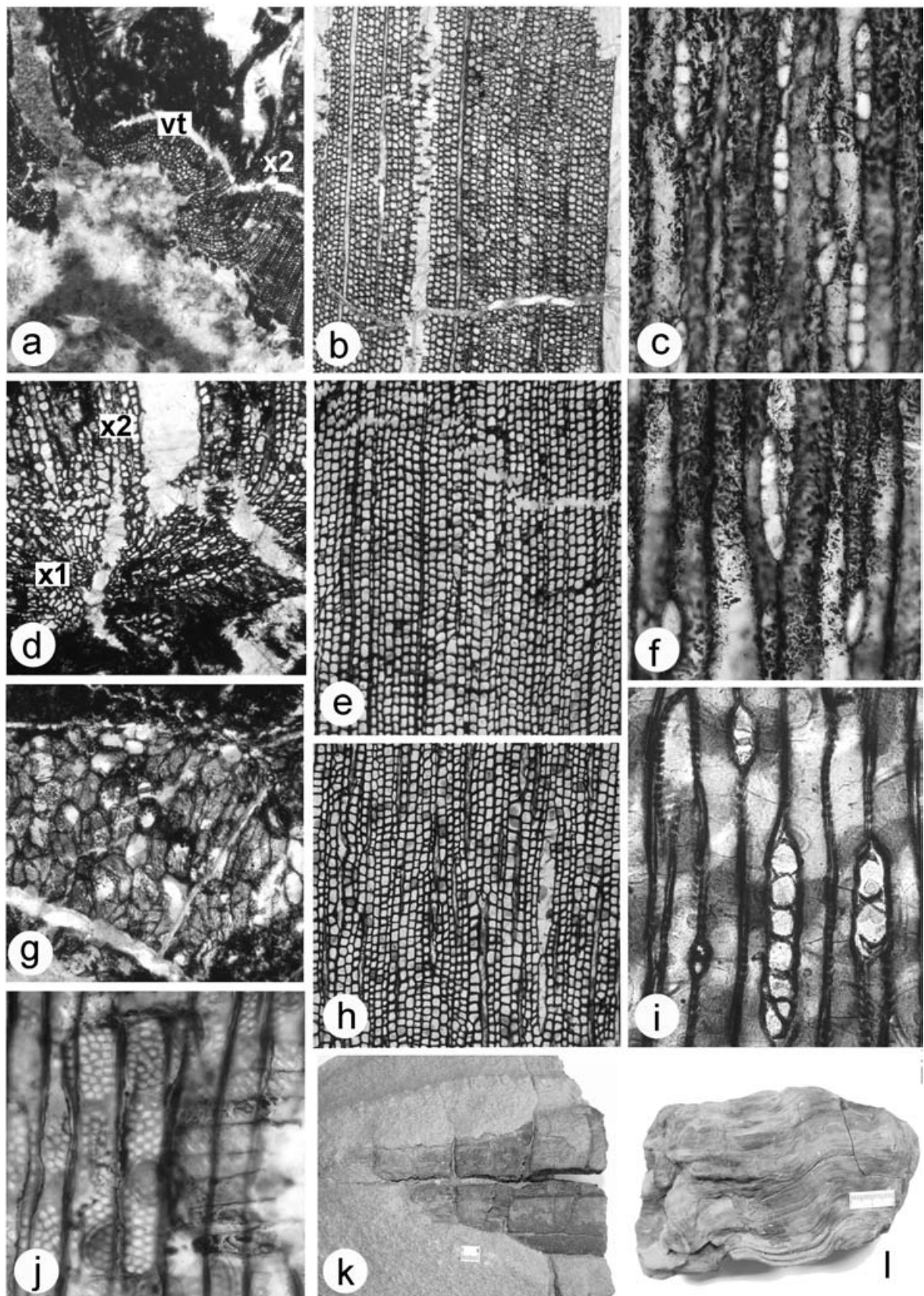
Figure 3. *Callixylon henkei*, Frasnian from El Gara. (a) Vascular trace on the inner edge of the wood, transverse section. GA2AI1. × 16. (b) Secondary xylem, transverse section. GA2AI1. × 40. (c) Short uniseriate rays, tangential section. GA2AT1. × 150. (d) Primary xylem strand on the inner edge of the wood, transverse section. GA4CS1. × 37. (e) Secondary xylem, transverse section. GA4CS1. × 40. (f) Short uniseriate rays, tangential section. GA4BT1. × 150. (g) Parenchymatous cells of central pith, transverse section. GA6BI1. × 37. (h) Secondary xylem, transverse section. GA8A1. × 40. (i) Short uniseriate rays, tangential section. GA8A2B. × 150. (j) Tracheid walls showing groups of bordered pits separated by unpitted zones, radial section. GA8A1aR1. × 150. (k) Part of specimen GA1/2, external view. × 0.3. (l) Specimen GA8, external view. × 0.37. vt – vascular trace; x1 – primary xylem; x2 – secondary xylem/wood.

Table 1. Anatomical features of the *Callixylon* axes from El Gara

Specimen	GA1/2	GA3	GA4	GA6	GA7	GA8
X2 tracheid tang dim (µm)	**31.9** Sdv 6.7	**32.3** Sdv 5.8	**37.7** Sdv 7.7	**32.4** Sdv 6.1	**42.5** Sdv 10.9	**44.3** Sdv 12.2
X2 tracheid rad dim (µm)	**34.1** Sdv 7.5	**40.8** Sdv 7.5	**44.4** Sdv 8.8	**37.5** Sdv 6.4	**45.9** Sdv 9.0	**47.3** Sdv 9.5
Ray cell width (µm)	**20.3** Sdv 2.7	**21.3** Sdv 4.4	**33.6** Sdv 6.5	**25.2** Sdv 3.6	–	**25.2** Sdv 4.4
Ray cell height (µm)	**23.6** Sdv 4.4	–	**38.6** Sdv 7.1	**31.6** Sdv 7.2	–	**31.1** Sdv 5.6
Ray height (µm)	**101.2** Sdv 41.4	–	**101.2** Sdv 36.8	**86.9** Sdv 31.5	–	**129.4** Sdv 64.5
Ray height (nb. cells)	1–11	–	1–6	1–4	–	1–8
Ray density (nb/mm^2)	52		28.2	32.1		33.2

Numbers in bold represent mean values. Sdv – standard deviation; tang dim – tangential dimension; rad dim – radial dimension.

large branch whose original diameter exceeded 11 cm (Fig. 3k). The innermost part corresponds to a zone close to the pith which is not preserved. Pith width is estimated to have been about 1 cm. One large vascular trace is present on the inner edge of the wood (Fig. 3a). It includes metaxylem tracheids ranging from 29 to 58 µm (mean: 41.3 µm; standard deviation: 7.7 µm) and two mesarch poles of protoxylem.

In transverse section, the mean tangential diameter of secondary tracheids is 28 µm in the innermost part of the wood, 32 µm in the external part (Fig. 3b); mean radial diameter similarly increases from 28 to 34 µm outwardly. Rays exhibit a long horizontal course.

In tangential section, rays have a mean height of 101.2 µm and comprise 1–11 cells; most are 2–5 cells high (Fig. 3c). Ray cells are relatively small (mean width: 20.3 µm; mean height 23.6 µm), those at the end of the rays being higher (mean height: 34.1 µm). Ray density is relatively high at 52 rays/mm^2. Features of the secondary xylem in radial section are not easily observed due to mineralization of the cell walls. Pitting is commonly biseriate, occasionally triseriate. Pits are polygonal, 8–12 µm wide, and densely packed in groups of 12 to 16 separated by 15–25 µm long unpitted wall areas. Cross-field pits are not preserved.

5.a.2. Specimen GA4

GA4 is a 11 cm long flattened specimen representing about one half of a decorticated axis, the original diameter of which exceeded 10 cm. Maximal wood thickness is 3.8 cm. The central pith is 2 × 20 mm wide. Its elements are not preserved. Ten discrete strands of primary xylem occur at the periphery, all located directly against the secondary xylem (Fig. 3d). They measure 200–400 µm in transverse section. Each contains one mesarch pole of protoxylem. With a mean diameter of 45.3 µm, metaxylem tracheids are larger than the neighbouring tracheids of secondary xylem.

In transverse section, secondary tracheids increase outwards, from 33 to 38 µm in mean tangential dimensions, and from 38 to 44 µm radially (Fig. 3e). Rays have a long horizontal course. In tangential section, rays are comparable in height to the rays in specimen GA1/2 (mean height: 101.2 µm), but they comprise fewer elements (one to six cells, most with one to three cells only) (Fig. 3f). Ray cells in this specimen are large (mean width: 33.6 µm; mean height: 38.6 µm). Ray density is low (28.2 rays/mm^2 on average). In radial section, pitting of the tracheid walls is commonly bi- and triseriate. Pitted zones comprise 12–14 bordered pits and are separated by 10–13 µm long unpitted areas. Pits range from 9 to 14 µm in diameter. There are up to six pits per cross-field; these show an inclined oval aperture.

5.a.3. Specimen GA6

This 11 cm long, heavily recrystallized, specimen consists of the central part of an axis that exceeded 6 cm in diameter originally. Its main interest lies in the partially preserved pith, which comprises large polygonal cells of parenchyma ranging from 82 to 202 µm in diameter and 62 to 121 µm vertically (Fig. 3g). Close to the pith border, these cells tend to be radially elongated in transverse section. In tangential section, preserved rays in the secondary xylem are relatively low (mean height: 86.9 µm) compared to those of other specimens.

5.a.4. Specimen GA8

This specimen represents a 13 cm long portion of wood which differs from the previous ones by its contorted outline, indicating that tracheids are not

straight (Fig. 3l). In transverse section, tracheids show various outlines, the ratio of polygonal/rectangular elements being higher than in the other specimens; local variations in both radial and tangential dimensions of the tracheids are also more conspicuous (Fig. 3h). Small groups of thinner-walled elements are scattered throughout the specimen in transverse section. This feature may correspond to groups of tracheids ending at the same level. Rays exhibit a relatively short horizontal course. One false growth ring occurs, which does not extend the full tangential width of the specimen.

In tangential section, rays are higher than those of the other specimens (mean height: 129.4 μm) but most comprise only one to three cells (Fig. 3i). Wall pitting is well-preserved in radial section (Fig. 3j). It is mostly bi- and triseriate. Pits are arranged in groups of 10 to more than 40, separated by unpitted areas ranging from 15 to 75 μm in length. Opposite bordered pits show crossed apertures. In cross-fields, pit number ranges from four to six. Their aperture is oblique and narrow.

5.b. Comparison and affinities

The most distinctive specimens of the sample are: (1) GA1/2, which exhibits the smallest dimensions of tracheids and ray cells, and the highest density of rays; (2) GA4, which possesses the largest ray cells; and (3) GA8, which shows large contorted tracheids, and rays that are both short in transverse section and high longitudinally. Differences between the specimens of El Gara are essentially quantitative and difficult to interpret due to the small size of the sample. In addition, almost nothing is known about the inter/intra-specific patterns of variation in the wood of *Callixylon*. On the basis of ray characters shared by all specimens (predominantly short uniseriate rays devoid of ray tracheids), we regard all the specimens from El Gara as referable to a single species. Specific features reported for GA8 may be related to its position within the tree, the shape of the tracheids suggesting that it was part of the basal part of a trunk.

Specific diagnoses for the organ genus *Callixylon* generally focus on secondary xylem features, the primary xylem and associated ground tissues forming the stele being less often preserved. Arnold (1934) recognized that features such as cell wall thickness, patterns of pit grouping on the radial walls of secondary tracheids, and thickness of growth rings are poorly diagnostic. The most widely used features for characterizing species of *Callixylon* are related to the structure and height of the rays. However, these characters must be carefully considered since ontogenetical variations may occur, higher rays being added in more external portions of wood, for example, and because dimensions may have been altered by compression during fossilization (Lemoigne, Iurina & Snigirevskaya, 1983).

The Moroccan specimens that possess uniseriate rays resemble the type-species *Callixylon trifilievii*, first described by Zalessky (1909, 1911) from the Famennian specimens of the Donetz Basin (Ukraine), and then revised by Lemoigne, Iurina & Snigirevskaya (1983), who provided the first formal diagnosis of the species. Other wood fragments assigned to *C. trifilievii* include specimens of Famennian age from the Tuva district of Siberia (Lemoigne, Iurina & Snigirevskaya, 1983). The El Gara specimens and these axes of *C. trifilievii* share several characters including dimensions of wood tracheids and ray cells, number and shape of pits in cross-fields, absence of ray tracheids, and parenchymatous pith cells that are similar in shape and dimensions. However, they differ in the length of the rays, those in the type-species being higher and up to 80 cells at only 6.5 cm from the pith. In addition, thick-walled cells like those scattered in the pith of *C. trifilievii* were not observed in the Moroccan material. As far as brief description indicates, specimens assigned to *C. trifilievii* and recently collected from the lower Frasnian (Gnevashevskaya Formation) of the Andoma Mountain in northwestern Russia have higher rays (1 to more than 25 cells) than the El Gara wood fragments (Snigirevskaya & Snigirevsky, 2001). Rays in the remains labelled '*C. timanicum*' in Zalessky's collection (Famennian of Timan, Pokajama Formation; S. Snigirevsky, unpub. Ph.D. thesis, Saint Petersburg State Univ., 1997) and those in *C. velinense* (Frasnian of Belgium), all tentatively synonymized with *C. trifilievii* (Lemoigne, Iurina & Snigirevskaya, 1983), are short, not exceeding 15 cells. Rays in *C. velinense* are commonly three to four cells high and their density is comparable (25–30/mm^2) to that of most Moroccan specimens (Marcelle, 1951), but unlike the latter, they are composed of horizontal tracheids. Two other species reassigned to *C. trifilievii* by Lemoigne, Iurina & Snigirevskaya (1983), *C. zalesskyi* from the Frasnian of New York and *C. whiteanum* from the Woodford chert of Oklahoma (presumably early Tournaisian), differ from the El Gara specimens by the partial biseriation of their rays. Other differences include the occurrence of abundant ray tracheids in the wood of *C. zalesskyi* and higher rays (3–80 cells) in that of *C. whiteanum*.

A form of wood structure very similar to that of the Moroccan specimens is displayed by five species characterized by rays that are predominantly short, uniseriate and devoid of ray tracheids. These are *C. henkei* from the Famennian of the Dortmund area, Germany; *C. clevelandensis* from the Famennian of Ohio, USA; *C. cf. clevelandensis* from the Frasnian of the Junggar basin in Xinjiang, China; *C. huronensis* from the Famennian of Ohio; and *C. brownii* from the Tournaisian of Kentucky, USA (Cai, 1989; Chitaley, 1988; Chitaley & Cai, 2001; Hoskins & Cross, 1951; Kräusel & Weyland, 1929). Rays may be partly biseriate in the four latter species and bordered pits were reported on the tangential walls of tracheids in *C. clevelandensis*

and *C. henkei*. When all characters are considered, it is with *C. henkei* that the Moroccan specimens have most wood features in common. However, differences between the five species are small, and a revision is needed to assess more accurately their affinities and possible synonymy.

Two species of *Callixylon* have been described to date from Famennian outcrops of the Anti-Atlas: *C. erianum* (Meyer-Berthaud, Scheckler & Wendt, 1999) and *Callixylon sp.* (Galtier, Paris & El Aouad-Debbaj, 1996). The latter is represented by a 30 cm long portion of trunk with an original diameter of about 15 cm. Its wood is similar, in terms of structure and cell dimensions, to that of the El Gara specimens except that rays are a little higher, some up to 32 cells. Galtier, Paris & El Aouad-Debbaj (1996) emphasized its resemblance to both *C. velinense* and *C. henkei*.

6. Cladoxylopsid axis

6.a. Description

Specimen GA5 is a 2.4 cm long, 3×1.7 cm wide, decorticated fragment of axis, which is composed of a large number of vascular strands embedded in a tissue of disorganized, isodiametric, parenchymatous cells, many of which have a black infilling (Fig. 4b, e, j). In transverse section 31 vascular strands are preserved, some only partially. All strands share a similar structure (see below), but they are variable in shape and size (Fig. 4a). In transverse section, small strands are circular and measure 1.2–2 mm in diameter; large ones are oval-elongate and range from 3×1.5 to 4.5×3 mm in length (Fig. 4a, b). Longitudinally, these strands unite and divide forming a reticulum rather than representing discrete entities. Spacing and distribution of small/large strands appear random and do not show any conspicuous pattern in this incomplete fragment of axis.

Each vascular strand comprises a small circular to elongate core of primary xylem surrounded by a relatively wide ring of secondary xylem (Fig. 4c, d). In transverse section, primary xylem strands rarely exceed 300 μm in their smallest dimension and 2.5 mm in the largest. Secondary xylem ranges from 1.2 to 2 mm in thickness and is relatively evenly distributed around the primary strands. Protoxylem poles are not always distinctive. Small primary xylem strands possess one centrarch protoxylem pole (Fig. 4d); elongate ones have more protoxylem strands in a mesarch position. Primary tracheids range from 18 to 60 μm (mean: 30 μm) in diameter. Secondary xylem consists of tracheids and rays (Fig. 4g, k). In transverse section, tracheids measure 20–43 μm (mean: 29 μm) radially and 19–54 μm (mean: 32 μm) tangentially (Fig. 4f, g). Their radial walls exhibit circular to oval bordered pits closely arranged in one to three rows (Fig. 4j, k). A large number of rays are one to eight cells high and uniseriate (Fig. 4h). Some rays that are partly or entirely

multiseriate and up to 43 cells high may contribute to the tangential enlargement of the secondary xylem (Fig. 4h, i). Tangential enlargement is also accommodated by an increase in the number of radial files of tracheids and by a slight enlargement of the tracheid diameter outwards (Fig. 4f, g). All ray cells are parenchymatous and relatively high (34–109 μm; mean: 68.2 μm) (Fig. 4h, i, l). Their width in tangential section ranges from 26 to 53 μm. The secondary xylem does not show any growth rings and there is no evidence of a cambium or secondary phloem outside this tissue (Fig. 4e, f).

6.b. Comparison and affinities

In the Devonian, axes with a multi-stranded vascular system characterize the Cladoxylopsida. This group was particularly successful in Middle Devonian times and decreased in importance until the early Mississippian when it became extinct. Discoveries of new taxa and reconstructions of entire plants recently brought forward new information that clarified the group and renewed interest in these complex plants related to the ferns (Berry, 2000; Berry & Fairon-Demaret, 2002; Soria & Meyer-Berthaud, 2004; Soria, Meyer-Berthaud & Scheckler, 2001).

Secondary xylem occurs in some cladoxylopsid taxa known from anatomically preserved axes, and the extent of this feature is not necessarily related to the size nor to the age of the organ considered. Indeed, current reinvestigations of *Pietzschia schülleri* from new specimens from the Famennian of Morocco demonstrate that trunks exceeding 15 cm in diameter consist entirely of primary tissues (A. Soria, unpub. Ph.D. thesis, Univ. Montpellier, 2003). Cladoxylopsid axes possessing secondary xylem belong to the genera *Duisbergia* and *Xenocladia* (Middle Devonian), *Polypetalophyton* (Frasnian), *Steloxylon* (uppermost Devonian or lowermost Mississippian), *Volkelia* and Mississippian species of *Cladoxylon*. None of these taxa has ever been reported from Gondwanan localities.

There are many uncertainties concerning the morphology and anatomy of the plants assigned to *Duisbergia*, a genus recently reinvestigated by Berry & Fairon-Demaret (2002). Reports on *D. mirabilis* by Remy & Remy (1977) and Mustafa (1978) describe wide axes possessing a large number (more than 60) of radially elongated vascular strands embedded in a pith, each comprising a solid core of primary xylem surrounded by a thick ring of secondary xylem. Unlike those in specimen GA5, vascular strands in *Duisbergia* all appear similar in size and shape, and are strictly organized in a peripheral ring of elongated strands. A second genus with secondary xylem that necessitates revision is *Steloxylon*. The type species, *S. ludwigii*, is represented by one specimen whose origin, from a Permian locality in Siberia (Solms-Laubach, 1910) or an outcrop of possible Devonian age
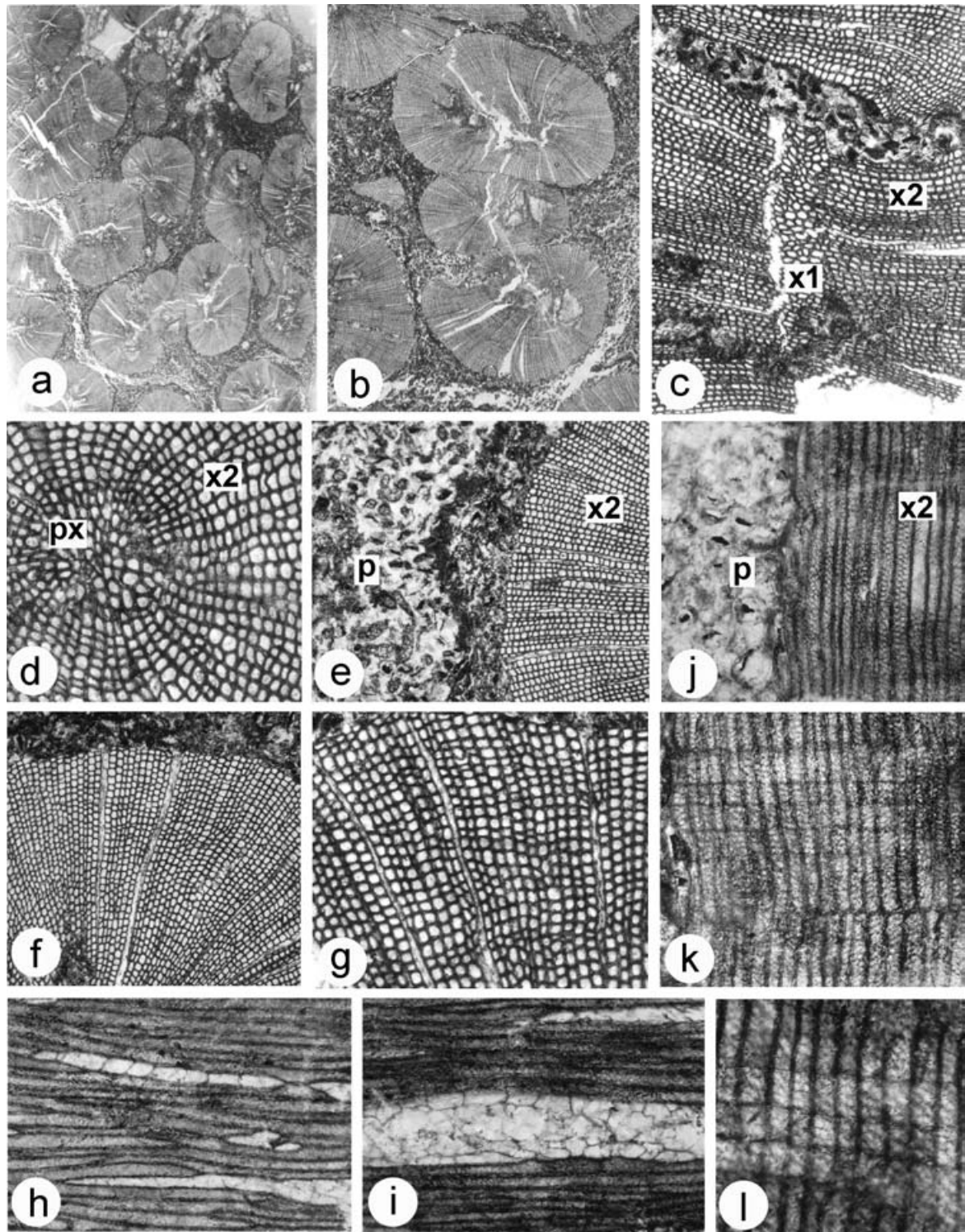
Figure 4. cf. *Xenocladia*, Frasnian from El Gara. (a) General view of the decorticated axis showing multiple vascular strands, transverse section. GA5A1. × 3.7. (b) Detail of preceeding view. GA5A1. × 7.6. (c) Detail of a vascular strand showing an elongate core of primary xylem surrounded by secondary xylem, transverse section. GA5A1. × 37. (d) Detail of a small vascular strand showing a circular core of primary xylem with a central pole of protoxylem surrounded by secondary xylem (X2), transverse section. GA5A1. × 74. (e) Disorganized tissue of parenchymatous cells lying against the secondary xylem (X2) of a vascular strand, transverse section. GA5A1. × 37. (f) Secondary xylem with no cambium layer on the outer edge, transverse section. GA5A1. × 33. (g) Detail of secondary xylem, transverse section. GA5A1. × 66. (h) Uniseriate (top) and partly multiseriate (bottom) rays, longitudinal section orientated horizontally. GA5AT2. × 63. (i) Multiseriate ray, longitudinal section orientated horizontally. GA5AT2. × 63. (j) Disorganized parenchyma lying against the secondary xylem of a vascular strand, longitudinal section. Note the biseriate ornementation of tracheid walls. GA5AT1. × 74. (k) Ray in secondary xylem, radial section. GA5AT1. × 74. (l) Detail of secondary xylem showing cross-fields. GA5AT1. × 120. x1 – primary xylem; x2 – secondary xylem/wood; px – protoxylem; p – pith.

in Kazakhstan (Lemoigne & Iurina, 1983), is uncertain. A character that distinguishes *S. ludwigii* from all other cladoxylopsid taxa with secondary xylem, including that represented by specimen GA5, is the frequency and complexity of anatomoses between the individual vascular bundles. Two other species, *S. irvingense* and *S. sancta-crucis*, were based on specimens from the New Albany Shales of northeastern USA, of latest Devonian or earliest Mississippian age (Read & Campbell, 1939). In these species, all vascular strands tend to be circular in transverse section; they vary little in size and shape and they are evenly distributed within the pith, a set of features that distinguishes them from the Moroccan specimen.

Vascular tissues in *Polypetalophyton* are organized in one ring of radially elongated strands enclosing very few circular vascular segments (Hilton, Geng & Kenrick, 2003). Another difference from the Moroccan specimen is the lack of rays in the secondary xylem, a character that made the authors doubt the secondary nature of this tissue.

In both *Völkelia*, from the Mississippian of Silesia, and the *Cladoxylon* species with secondary xylem recorded from the Tournaisian of Germany and France (Bertrand, 1935; Galtier, 1970), the number of vascular strands is reduced compared to that of specimen GA5, and the strands are arranged differently. Other characters that distinguish these Mississippian taxa are: (1) protoxylem poles located in one single area, in the external part of the primary xylem; (2) their association with thin-walled elements in *Cladoxylon*; and (3) secondary xylem unevenly developed around the primary xylem, with more cells differentiated on the inner side of the stem.

The most similar taxon to the Moroccan specimen is *Xenocladia*, a monospecific genus of Middle Devonian age first described from New York State, then recognized in Germany and Kazakhstan (Arnold, 1940, 1952; Lemoigne & Iurina, 1983; Mustafa, 1980). In transverse section, the vascular system in *X. medullosina* consists of radially elongated strands arranged in a peripheral ring enclosing a number of variously shaped inner strands embedded in a ground tissue; this central part resembles the preserved portion of axis in GA5. Depending on the level of the plant, the vascular strands in *X. medullosina* comprise a variable amount of secondary xylem which surrounds the primary xylem evenly. Other characters shared with the Moroccan specimens include: a number of protoxylem poles that varies from one centrarch in the smallest primary xylem strands to several mesarch in the largest ones; and lack of parenchyma, or any other type of thin-walled elements, associated with the protoxylem. Several differences, however, make the assignation of the Moroccan specimen to *X. medullosina* uncertain. These are the absence of rays reported in the secondary xylem of the latter species, and absence of scalariform tracheids in the xylem of the Moroccan specimen.

Vascular strand shape in specimen GA5 is either circular or elongated. It may be more variable in *X. medullosina*, with the occurrence of trilobed strands in the Kazakhstan specimens; specimen GA5 is referred to as cf. *Xenocladia*.

7. Discussion

Despite uncertainties concerning the dating of the layer that yielded specimen GA5, the age of the fossil assemblage is very well constrained compared with the generally low level of stratigraphic resolution usually obtained for Palaeozoic plant remains in Gondwana. The plant remains found at El Gara, however, do not represent an *in situ* natural assemblage but material that was supplied from a land area and transported in the sea prior to burial. There is, however, no specific information to constrain precisely the position of the source area where the *Archaeopteris* trees grew. Unfortunately, no data on the seawater circulation during early Frasnian times are available for the Anti-Atlas shelf area. Moreover, the palaeogeographical position of Gondwana is uncertain. Several different palaeogeographical reconstructions for the Late Devonian have been presented in the last two decades (see J. Dopieralska, unpub. Ph.D. thesis, Univ. Giessen, 2003, for review). Reconstructions based on palaeomagnetic data (e.g. Stampfli & Borel, 2002; Tait *et al*. 2000) favour the position of the North African margin of Gondwana at a high southern latitude of ∼50–60° S and the existence of a 3000 km wide ocean between Gondwana and Euramerica. Biogeographic data (Janvier & Villarroel, 2000; McKerrow *et al*. 2000; Young, 2003; Young, Moody & Casas, 2000), however, suggest a much closer position of Gondwana to Euramerica, with the North African margin at about 20–40° S.

The wood fragments found at El Gara do not show any growth rings. This indicates that the *Archaeopteris* trees that produced such wood grew under equable conditions, in warm and wet habitats. If they inhabited shorelines on the North African margin of Gondwana, this shoreline must have been located more or less in a similar position as suggested by faunistic data (see McKerrow *et al*. 2000). In a palaeogeographical scenario with Gondwana and Euramerica close together, transport of wood from Euramerica towards the Moroccan shelf would easily be possible. Pedder (1999) showed that coral larvae migrated during Middle Devonian times from the southeastern margin of Euramerica, across the Variscan terranes, to the Anti-Atlas area. Although we cannot exclude the possibility that the plant fragments were transported over a long distance from growing sites, the occurrence of wood material in the Anti-Atlas, which is derived from wet and warm climatic conditions, does not support the position of the North African margin of

Gondwana at high southern latitudes as suggested by Tait *et al.* (2000) and Stampfli & Borel (2002).

The plant remains described here consist of anatomically preserved fragments of axes that belong to the progymnosperm group Archaeopteridales (*Callixylon henkei*) and of one specimen affiliated to the Cladoxylopsida (cf. *Xenocladia*). A *Callixylon henkei*-type of wood has already been found in the eastern Anti-Atlas but in younger, early Famennian deposits. Similarly, most other records of this species or other related taxa were also from the Famennian (*C. clevelandensis* and *C. huronensis*) (Chitaley, 1988; Chitaley & Cai, 2001; Lemoigne, Iurina & Snigirevskaya, 1983). The Gondwanan record of cladoxylopsids (Iridopteridales excluded) has been hitherto very limited and has not included any *Xenocladia*-type remains until this work (Berry *et al.* 2000; Chambers & Regan, 1986; Soria, Meyer-Berthaud & Scheckler, 2001). Contrary to *C. henkei*, all other reports of *Xenocladia*, in Euramerica and Kazakhstan, are older, of Middle Devonian age (Arnold, 1952; Lemoigne & Iurina, 1983; Mustafa, 1980). Studies made on assemblages from the Frasnian of New York State demonstrate the increasing abundance of *Archaeopteris* through this period and the decline of other groups such as the Aneurophytalean progymnosperms and the Cladoxylopsida (Scheckler, 1986). No aneurophytes were collected at El Gara despite the fact that they were woody and potentially capable of preservation. Interestingly, the record of aneurophytes in the Middle and Upper Devonian of Gondwana is remarkably poor, although some evidence indicates that they once colonized this palaeocontinent (Berry *et al.* 2000; Gerrienne *et al.* 2001).

Palaeobotanical research in the Devonian of the Anti-Atlas is new and still in progress, yet some patterns are emerging concerning the composition of plant assemblages deposited on the North African margin of Gondwana during the Late Devonian. (1) Most plant remains reported to date from the Upper Devonian of the Anti-Atlas were found in black shale deposits corresponding to poorly oxygenated waters. (2) Most plant remains described from the Frasnian and Famennian localities of the Anti-Atlas are derived from large plants, possibly trees, but not necessarily woody. The 16 cm wide trunk of *Pietzschia schülleri* and the lycopsid branches that are currently being investigated from early Famennian deposits possess little lignous structures, the former comprising large amounts of well-preserved delicate parenchymatous tissues. This suggests that transport of cladoxylopsids and lycopsids prior to burial and fossilization might have been short. (3) The two groups of plants found in the Frasnian beds of El Gara, the Archaeopteridales and the Cladoxylopsida, are also the best represented groups in the early Famennian plant localities of Mader and Tafilalt. *Callixylon henkei*-type axes occur both in the Frasnian and in the Famennian deposits of the Anti-Atlas and they are all devoid of growth rings. The

cladoxylopsid axes described from the Famennian of eastern Anti-Atlas differ from the genus *Xenocladia* by the absence of secondary tissues. They belong to two species of *Pietzschia*, a genus long considered as the closest related taxon to *Xenocladia*.

8. Conclusions

This work documents the discovery of Frasnian plant remains in the Anti-Atlas of southern Morocco. The anatomically preserved plant fragments found in black shales of El Gara in the Dra Valley represent the first assemblage of plants of this age recorded in Africa. Plants belong to two major groups, the progymnosperm Archaeopteridales and the Cladoxylopsida, and are referred to two taxa, *Callixylon henkei* and *Xenocladia*, all well represented in Euramerica or elsewhere. Comparisons with younger, early Famennian assemblages of the Anti-Atlas do not show any significant changes in terms of broad taxonomic composition nor of ecologically meaningful features (absence of growth rings) during Late Devonian times.

References

ANDERSON, H. M., HILLER, N. & GESS, R. W. 1995. *Archaeopteris* (Progymnospermopsida) from the Devonian of southern Africa. *Botanical Journal of the Linnean Society* **117**, 305–20.

ANDERSON, J. M., ANDERSON, H. M., ARCHANGELSKY, S., BAMFORD, M., CHANDRA, S., DETTMANN, M., HILL, R., MCLOUGHLIN, S. & RÖSLER, O. 1999. Patterns of Gondwana plant colonisation and diversification. *Journal of Australian Earth Sciences* **28**, 145–67.

ARNOLD, C. A. 1934. *Callixylon whiteanum* sp. nov., from the Woodford chert of Oklahoma. *Botanical Gazette* **96**, 180–5.

ARNOLD, C. A. 1940. Structure and relationships of some Middle Devonian plants from Western New York. *American Journal of Botany* **27**, 57–63.

ARNOLD, C. A. 1952. Observations on fossil plants from the Devonian of eastern North America. VI. *Xenocladia medullosina* Arnold. *Contributions from the Museum of Paleontology University of Michigan* **IX**, 297–309.

BELKA, Z., KAZMIERCZAK, M. & KAUFMANN, B. 1997. Tectonic control on the sedimentation, volcanic activity and the growth of mud mounds in the Palaeozoic of the eastern Anti-Atlas, Morocco. *First International Conference on North Gondwanan Mid-Palaeozoic Biodynamics (IGCP Project 421), Vienna, 1997, Abstracts*, 9.

BELKA, Z., KLUG, C., KAUFMANN, B., KORN, D., DÖRING, S., FEIST, R. & WENDT, J. 1999. Devonian conodont and ammonoid succession of the eastern Tafilalt (Ouidane Chebbi section), Anti-Atlas, Morocco. *Acta Geologica Polonica* **49**, 1–23.

BERRY, C. M. 2000. A reconsideration of *Wattieza* Stockmans (here attributed to Cladoxylopsida) based on a new species from the Devonian of Venezuela. *Review of Palaeobotany and Palynology* **112**, 125–46.

BERRY, C. M. & FAIRON-DEMARET, M. 2002. The architecture of *Pseudosporochnus nodosus* Leclercq et Banks: a Middle Devonian cladoxylopsid from Belgium. *International Journal of Plant Sciences* **163**, 699–713.

BERRY, C. M., MOREL, E., MOJICA, J. & VILLARROEL, C. 2000. Devonian plants from Colombia, with discussion of their geological and palaeogeographical context. *Geological Magazine* **137**, 257–68.

BERRY, C. M. & STEIN, W. 2000. A new iridopteridalean from the Devonian of Venezuela. *International Journal of Plant Sciences* **161**, 807–27.

BERTRAND, P. 1935. Contribution à l'étude des Cladoxylées de Saalfeld. *Palaeontographica* **80B**, 101–70.

BRIGGS, J. C. 1995. *Global biogeography*. Developments in Palaeontology and Stratigraphy, 14. Amsterdam: Elsevier, 452 pp.

CAI, C.-Y. 1989. Two *Callixylon* species from Upper Devonian of Junggar Basin, Xinjiang. *Acta Palaeontologica Sinica* **20**, 75–8.

CAI, C.-Y. & WANG, Y. 1995. Devonian floras. In *Fossil floras of China through the geological age*s (eds X. Li *et al*.), pp. 28–77. Guangzhou: Guangdong Science and Technology Press.

CHAMBERS, T. C. & REGAN, M. A. 1986. *Polyxylon australe* – a new cladoxylalean axis from the Devonian of Australia. *Australian Journal of Botany* **34**, 675–89.

CHITALEY, S. 1988. The wood *Callixylon* from the Late Devonian of Ohio, USA. *Review of Palaeobotany and Palynology* **53**, 349–57.

CHITALEY, S. & CAI, C. 2001. Permineralized *Callixylon* woods from the Late Devonian Cleveland Shale of Ohio, U.S.A. and that of Kettle Point, Ontario, Canada. *Review of Palaeobotany and Palynology* **114**, 127–44.

CINGOLANI, C. A., BERRY, C. M., MOREL, E. & TOMEZZOLI, R. 2002. Middle Devonian lycopsids from high southern palaeolatitudes of Gondwana (Argentina). *Geological Magazine* **139**, 641–9.

DIMICHELE, W. A. & HOOK, R. W. 1992. Paleozoic terrestrial ecosytems. In *Terrestrial ecosystems through time* (eds A. K. Behrensmeyer *et al*.), pp. 205–325. Chicago: The University of Chicago Press.

GALTIER, J. 1970. Recherches sur les végétaux à structure conservée du Carbonifère inférieur français. *Paléobiologie Continentale* **I**, 1–221.

GALTIER, J., PARIS, F. & EL AOUAD-DEBBAJ, Z. 1996. La présence de *Callixylon* dans le Dévonien supérieur du Maroc et sa signification paléogéographique. *Comptes Rendus de l'Académie des Sciences Paris Série IIa* **322**, 893–900.

GERRIENNE, P., MEYER-BERTHAUD, B., REGNAULT, S., MORENO SANCHEZ, M. 2001. First record of the plant *Rellimia* Leclercq & Bonamo (Aneurophytales) from Africa: paleogeographic implications. *15th International Senckenberg Conference, Frankfürt*, *Abstracts*, 41.

HILL, R. S., TRUSWELL, E., MCLOUGHLIN, S. & DETTMANN, M. E. 2000. Evolution of the Australian flora: fossil evidence. In *Flora of Australia* (ed. A. E. Orchard), pp. 251–320. Canberra: Australian Government Publishing Service.

HILTON, J., GENG, B. & KENRICK, P. 2003. A novel Late Devonian (Frasnian) woody cladoxylopsid from China. *International Journal of Plant Sciences* **164**, 793–805.

Hollard, H. 1967. Le Dévonien du Maroc et du Sahara nord-occidental. In *International Symposium on the Devonian System, Volume 1* (ed. D. H. Oswald), pp. 203–44. Calgary: Alberta Society of Petroleum Geology 1.

HOSKINS, J. H. & CROSS, A. T. 1951. The structure and classification of four plants from the New Albany Shale. *American Midland Naturalist* **46**, 684–716.

IURINA, A. 1988. The Middle and Late Devonian floras of northern Eurasia. USSR Academy of Sciences. *Transactions of the Palaeontological Institute* **227**, 1–175.

JANVIER, PH. & VILLARROEL, C. 2000. Devonian vertebrates from Colombia. *Palaeontology* **43**, 729–64.

KLAPPER, G. 1997. Graphic correlation of Frasnian (Upper Devonian) sequences in Montagne Noire, France, and Western Canada. In *Paleozoic sequence stratigraphy, biostratigraphy, and biogeography; studies in honor of J. Granville ('Jess') Johnson* (eds G. Klapper, M. A. Murphy and J. A. Talent), pp. 113–29. Geological Society of America, Special Paper no. 321.

KLAPPER, G. 2000. Species of *Spathognathidae* and *Polygnathidae* (Cononta) in the recognition of Upper Devonian stage boundaries. *Courier Forschungsinstitut Senckenberg* **220**, 153–9.

KRÄUSEL, R. & WEYLAND, H. 1929. Beiträge zur Kenntnis der Devonflora, III. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **41**, 315–60.

LARDEUX, H. 1969. *Les Tentaculites d'Europe occidentale et d'Afrique du Nord*. Cahiers de Paléontologie du C.N.R.S., Paris, 260 pp.

LEMOIGNE, Y. & IURINA, A. 1983. *Xenocladia medullosina* CH. A. Arnold 1940. 1952 du Dévonien moyen du Kazakhstan (URSS). *Geobios* **16**, 513–47.

LEMOIGNE, Y., IURINA, A. & SNIGIREVSKAYA, N. 1983. Révision du genre *Callixylon* Zalessky 1911 (*Archaeopteris*) du Dévonien. *Palaeontographica* **186B**, 81–120.

LJASCHENKO, G. P. 1959. *Coniconques dévoniens des régions centrale et orientale de la Plate-fome russe*. Gosgeoltekzhidat, Léningrad, 153 pp. (in Russian).

MARCELLE, H. 1951. *Callixylon velinense* nov. sp. Un bois à structure conservée du Dévonien de Belgique. *Bulletin de l'Académie Royale de Belgique, Sciences* **37**, 908–19.

MCKERROW, W. S., MACNIOCAILL, C., AHLBERG, P. E., CLAYTON, G., CLEAL, C. J. & EAGAR, R. M. C. 2000. The late Palaeozoic relations between Gondwana and Laurussia. In *Orogenic processes: quantification and modelling in the Variscan belt* (eds W. Franke, V. Haak, O. Oncken and D. Tanner), pp. 9–20. Geological Society of London, Special Publication no. 179.

MEYER-BERTHAUD, B., SCHECKLER, S. E. & WENDT, J. 1999. *Archaeopteris* is the earliest modern tree. *Nature* **398**, 700–1.

MEYER-BERTHAUD, B., WENDT, J. & GALTIER, J. 1997. First record of a diverse assemblage of *Callixylon* from the Upper Devonian of Gondwana. *American Journal of Botany* **84**, 139.

MUSTAFA, H. 1978. Beiträge zur Devonflora II. *Argumenta Palaeobotanica* **5**, 91–132.

MUSTAFA, H. 1980. Beiträge zur Devonflora IV. *Argumenta Palaeobotanica* **6**, 115–32.

PEDDER, A. E. H. 1999. Paleogeographic Implications of a Devonian (Givetian, Lower *Varcus* Subzone) Rugose Coral Fauna from the Mader Basin (Morocco). *Abhandlungen der geologischen Bundesanstalt* **54**, 385–434.

PRYER, K. M., SCHNEIDER, H., SMITH, A. R., CRANFILL, R., WOLF, P. G., HUNT, J. S. & SIPES, S. D. 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature* **409**, 618–22.

RAYMOND, A. & METZ, C. 1995. Laurussian land-plant diversity during the Silurian and Devonian: mass extinction, sampling bias, or both? *Paleobiology* **21**, 74–91.

READ, C. B. & CAMPBELL, G. 1939. Preliminary account of the New Albany Shale flora. *American Midland Naturalist* **21**, 435–48.

REMY, W. & REMY, R. 1977. *Die floren des erdaltertums*. Essen: Verlag Glückauf GMH, 468 pp.

RICHTER, R. H. 1854. Thuringische Tentaculiten. *Zeitschrift der deutschen geologischen Gesellschaft* **VI**, 275–90.

ROEMER, F. A. 1850. Beiträge zur geologischen Kenntniss des nordwestlichen Harzgebirges. *Palaeontographica* **3**, 1–67.

ROTHWELL, G. W. 1999. Fossils and ferns in the resolution of land plant phylogeny. *Botanical Review* **65**, 188–218.

SCHECKLER, S. E. 1986. Floras of the Devonian–Mississippian transition. *University of Tennessee, Department of Geological Sciences, Studies in Geology* **15**, 81–96.

SNIGIREVSKAYA, N. S. & SNIGIREVSKY, S. M. 2001. New locality of *Callixylon* (Archaeopteridaceae) in the Late Devonian of Andoma Mountain (Vologda Region, northwest Russia) and its importance for the reconstruction of archaeopterid distribution. *Acta Palaeobotanica* **41**, 97–105.

SOLMS-LAUBACH, H. 1910. Ueber die in den Kalksteinen des Culm von Glätzisch-Falkenberg in Schlesien erhaltenen strukturbietenden Pflanzenreste. IV. *Völkelia refracta, Steloxylon ludwigii. Zeitschrift für Botanik* **2**, 529–54.

SORIA, A. & MEYER-BERTHAUD, B. 2004. Tree fern growth strategy in the Late Devonian cladoxylopsid species *Pietzchia levis* from the study of its stem and root system. *American Journal of Botany* **91**, 10–23.

SORIA, A., MEYER-BERTHAUD, B. & SCHECKLER, S. E. 2001. Reconstructing the architecture and growth habit of *Pietzchia levis* sp. nov. (Cladoxylopsida) from the Late Devonian of southeastern Morocco. *International Journal of Plant Sciences* **162**, 911–26.

STAMPFLI, G. M. & BOREL, G. D. 2002. A plate tectonic model for the Paleozoic and Mesozoic constrained by dynamic plate boundaries and restored synthetic oceanic isochrones. *Earth and Planetary Science Letters* **196**, 17–33.

TAIT, J., SCHÄTZ, M., BACHTADSE, V. & SOFFEL, H. 2000. Paleomagnetism and Palaezoic palaeogeography of Gondwana and European terranes. In *Orogenic processes: quantification and modelling in the Variscan belt* (eds W. Franke, V. Haak, O. Oncken and D. Tanner), pp. 21–34. Geological Society of London, Special Publication no. 179.

TALENT, J. A., MAWSON, R., AITCHISON, J. C., BECKER, R. T., BELL, K. N., BRADSHAW, M. A., BURROW, C. J., COOK, A. G., DARGAN, G. M., DOUGLAS, J. G., EDGECOMBE, G. D., FEIST, M., JONES, P. J., LONG, J. A., PHILIPS-ROSS, J. R., PICKETT, J. W., PLAYFORD, G., RICKARDS, R. B., WEBBY, B. D., WINCHESTER-SEETO, A. J., WRIGHT, A. J., YOUNG, G. C. & ZHEN, Y.-Y. 2000. Devonian palaeobiogeography of Australia and adjoining regions. *Memoir of the Association of Australasian Palaeontologists* **23**, 167–257.

WENDT, J. 1988. Facies pattern and paleogeography of the Middle and Late Devonian in the eastern Anti-Atlas (Morocco). In *Devonian of the World, Volume I: Regional Synthesis* (eds N. J. McMillan, A. F. Embry and D. J. Glass), pp. 467–80. Canadian Society of Petroleum Geologists, Memoir no. 14.

WENDT, J. & BELKA, Z. 1991. Age and depositional environment of Upper Devonian (early Frasnian to early Famennian) black shales and limestones (Kellwasser facies) in the eastern Anti-Atlas, Morocco. *Facies* **25**, 51–90.

WNUK, C. 1996. The development of floristic provinciality during the Middle and Late Paleozoic. *Review of Palaeobotany and Palynology* **90**, 5–40.

YOUNG, G. C. 2003. North Gondwana mid-Palaeozoic connections with Euramerica and Asia: Devonian vertebrate evidence. *Courier Forschunginstitut Senckenberg* **242**, 169–85.

YOUNG, G. C., MOODY, J. M. & CASAS, J. E. 2000. New discoveries of Devonian vertebrates from South America, and implications for Gondwana-Euramerica contact. *Comptes Rendus de l'Académie des Sciences, Séries IIA* **331**, 755–61.

ZALESSKY, M. D. 1909. Communication préliminaire sur un nouveau *Dadoxylonà* faisceaux de bois primaire autour de la moëlle, provenant du Dévonien supérieur du bassin du Donetz. *Bulletin de l'Académie des Sciences de Saint Petersbourg* **IV**, 1175–8.

ZALESSKY, M. D. 1911. Etude sur l'anatomie du *Dadoxylon tchihatcheffi* Goeppert. *Mémoire du Comité Géologique de Russie N. S.* **68**, 18–29.