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Diversification of early ferns

Jean Galtier

Laboratoire de Paléobotanique, Institut des Sciences de l'Evolution,
L.A. 327 C.N.R.S., U.S.T.L., 34060 Montpellier, France

and

Andrew C. Scott

Geology Department, Chelsea College (University of London), 552 Kings Road,
London SW10 0UA, U.K.

Synopsis

A review of current knowledge of early fern evolution is presented including new data on age, morphology and anatomy with two diagrams summarising the early diversification of cauline and foliar anatomy and of the reproductive structures. The relationships and even the attribution of some Devonian taxa to the ferns is questioned whilst most of the Carboniferous coenopterids are considered indisputable ferns, some of them being related to modern filicaleans. The discovery, in the Lower Carboniferous of Scotland, of diverse annulate filicalean sporangia suggests an earlier (Tournaisian) radiation of true ferns than was previously assumed.

Introduction

It is now generally assumed that early Devonian Trimerophytina (Banks 1968, 1975) are the evolutionary source of several groups of fern-like plants which radiated during Mid to Late Devonian time (Gensel 1977; Chaloner and Sheerin 1979). There were apparently no 'true ferns' in the Devonian but there were a large number of extinct groups of 'so-called ferns' in the Carboniferous (Mickel 1974). A major difficulty is thus to distinguish what is really a fern amongst such Devonian and Carboniferous plants because they generally show a small number of characters, either vegetative anatomy or reproducive structures, but rarely both together. Traditionally, the ferns are defined as megaphyllous plants reproducing by spores but many Carboniferous members have not phylogenetically acquired all the fern characteristics (e.g. planated fronds) and such plants are commonly designated as 'fern-like' whilst they are indisputably ferns.

This review includes new information on the age, anatomy and morphology of early ferns. It is presented with the intention of providing an up-to-date summary emphasising evolution of these plants.

The early diversification of cauline and foliar anatomy

Phillips (1974) presented an excellent analysis of the vegetative anatomy and morphology of coenopterid ferns to which the reader is referred for detailed information. In the present paper, we discuss the evidence of early (i.e. Lower Carboniferous) phylogenetic trends in both cauline and foliar anatomy of coenopterids and Cladoxylales. The other palaeozoic groups, only known from Upper Carboniferous or younger strata (Marattiales, Osmundales), are not considered here.

The Devonian and Lower Carboniferous Cladoxylales have dissected or very deeply lobed stem xylem often designated as 'polystelic'. There were at least two kinds of appendages: either supplied by one small terete bundle or by several xylem strands originating simultaneously from different lobes of the stele (Fig. 1). The nature of these appendages (leaf or branch) is unclear (Leclercq *in* Andrews *et al.* 1970; Scheckler 1974).

Some members of the Zygopteridaceae such as the Tournaisian *Protoclepsydropsis* (Long 1967) had stems with a lobed stele but the bipolar (clepsydroid) trace of the appendage is detached from one arm only of the stem stele (Fig. 1). This broadly similar anatomy has sometimes been interpreted as the proof of relationship of the zygopterids with the Cladoxylales and with plants now included within the Iridopteridales. This trend (deeply marked actinostelic anatomy) persisted in some zygopterids (*Asterochlaena*) until the Permian.

Most of the zygopterids, however, show small solid or mixed protosteles. The maximum specialisation is exhibited in Upper Carboniferous time by the pentarch vitalised actinostele of *Ankyropteris* and by the highly parenchymatised stele of *Zygopteris* (Dennis 1974). Leclercq (1951) mentioned a poorly preserved actinostele in the Devonian *Rhacophyton* whiles Hueber (1983) described small solid protosteles in large stem-bearing *Clepsydropsis* petioles from the Tournaisian. Thus, the Visean *Metaclepsydropsis* (Fig. 1) remains the best evidence of early evolution of a mixed protostele in the Zygopteridaceae.

In the other coenopterids of the botryo-anachoropterid complex, a solid protostele is known in all phyletic lines until the Upper Carboniferous Westphalian where vitalisation of the protostele occurs in *Anachoropteris-Tubicaulis* and later a siphonostele evolved in *Botryopteris tridentata* and then in *Anachoropteris* and *Apotropteris* (Phillips 1974).

In conclusion, the stelar morphology in coenopterids is typically protostelic with an earlier vitalisation in the Zygopteridaceae. This very simple xylem anatomy is in fact similar or evolved just above the level of their presumed Devonian trimerophytic ancestors. In some phyletic lines which achieved filicalean characteristics in their leaf and sporangial morphology such as *Psalixochlaena* (Holmes 1977, 1981), the stem retained a 'primitive' protostelic mesarch anatomy that is identical to that of the early Devonian *Psilophyton*.

In contrast to this slow early evolution of stem anatomy through Lower Carboniferous time, it is evident from Figure 1 that diversification quickly affected the foliar anatomy of the coenopterids. This is particularly true in the zygopterid petiole or phyllophore. Apparently, both types of fronds (bi- and quadriseriate arrangement of pinnae quickly evolved an elliptical to hour-glass-shaped (clepsydroid) xylem in cross-section. Through Visean time, *Metaclepsydropsis, Diplolabis* and *Etapteris* (Etapteroideae) exhibit different geometrical transformation of the primitive ellipsoid shape. Interestingly, the biseriate Clepsydroideae evolved later a similar H-shaped xylem in *Ankyropteris* phyllophores, but the Lower Carboniferous

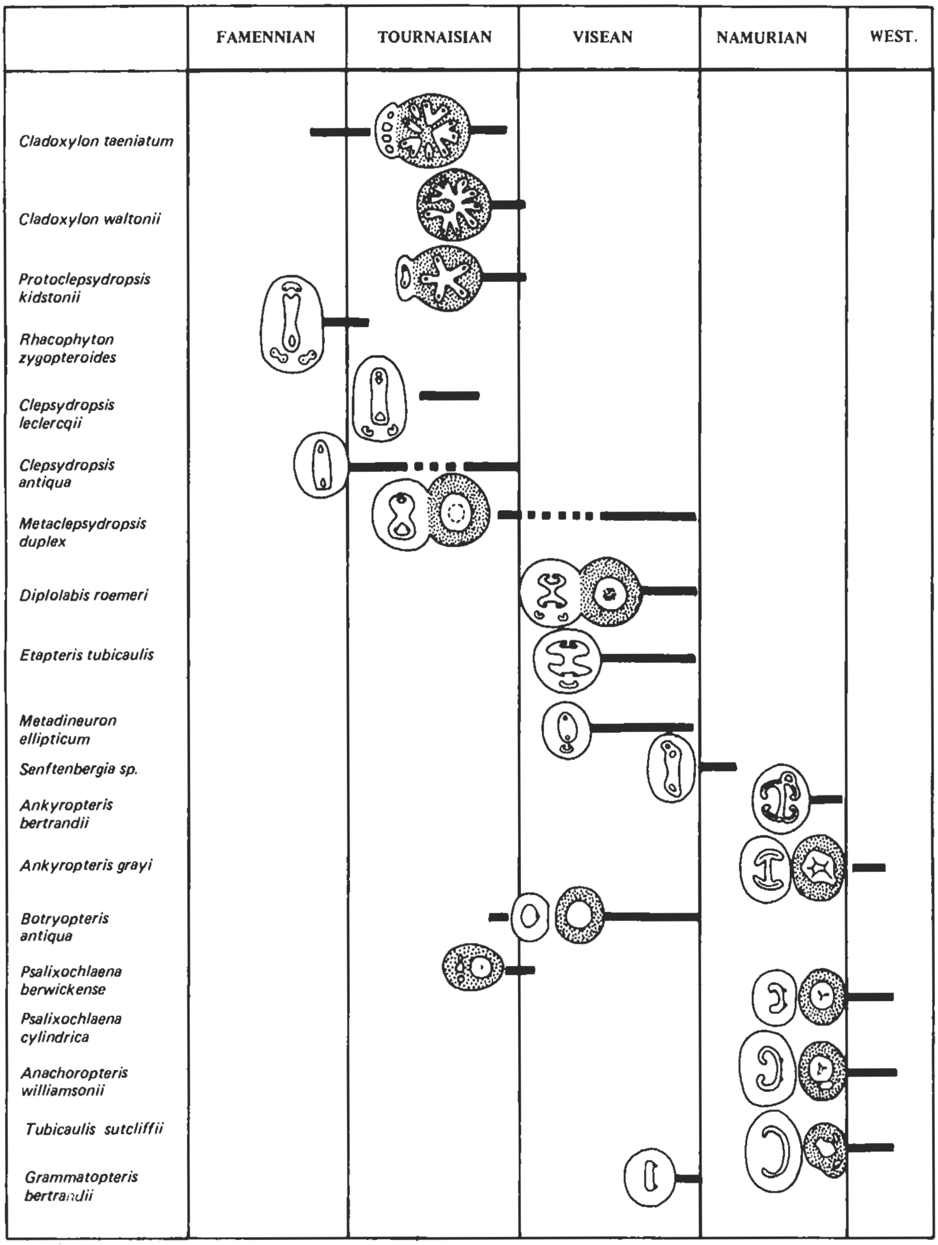

Figure 1. Early diversification of cauline (stippled) and foliar anatomy in ferns. The Cladoxylales have dissected stem xylem that may be compared to the lobed xylem of *Protoclepsydropsis*—whilst most of the Carboniferous coenopterids have simple protostelic mesarch cauline anatomy similar to their presumed trimerophytic ancestors. In contrast, evolutionary diversification quickly affected the foliar anatomy, particularly in zygopterid phyllophores and later in anachoropterids and botryopterids.

representatives (*Clepsydropsis* and *Senftenbergia* sp., Fig. 1) still have a simple clepsydroid anatomy.

Early botryopterids and anachoropterids are represented in the Lower Carboniferous by *Botryopteris antiqua* and *Grammatopteris bertrandi* (Fig. 1) which have simple oval foliar bundles while the evidence of leaves is missing in *Psalixochalaena berwickense* (Long 1976). In these groups, the diversification of foliar anatomy is delayed until late Carboniferous times as was observed in the cauline anatomy. Anachoropterids evolved various configurations and size of the inverted C-shaped xylem in cross-section. Very distinct types became established by the early Westphalian (Fig. 1) suggesting an important Namurian radiation which is not documented in the fossil record. In botryopterids, several phyletic lines have been suggested by Phillips (1974). From the primitive oval-shaped foliar xylem of *Botryopteris antiqua*, they evolved tridentate and omega cross-sectional shapes later in the Upper Carboniferous (not included in Fig. 1).

A last important aspect of foliar and cauline anatomy concerns the thickening of metaxylem tracheids. In the coenopterids, this ranges from scalariform to elliptical and circular bordered pitting. This feature contrasts with the simple scalariform pitting of modern ferns and it has been taken in account for the traditional concept of coenopterids as a specialised group of ferns without any relationship to living forms. Amongst the Zygopteridaceae a differentiation has been recognised which may be phylogenetic. Earliest forms show scalariform metaxylem, a feature maintained in the younger biseriate Clepsydroideae and *Ankyropteris*. In contrast, the quadriseriate Etapteroideae including simple Lower Carboniferous forms like *Dineuron* evolved multiseriate to circular bordered pitting in their tracheids (Galtier 1970). In the botryopterids and anachoropterids, multiseriate scalariform pitting (as in *Botryopteris antiqua* stem) is regarded as primitive and circular bordered pitting occurs first in the leaves.

In this discussion, the Marattiales and Osmundales have not been mentioned because ancestors of these groups are not known in the Lower Carboniferous. We must recall that a fundamental difference exists in the anatomy of these living ferns where the C-shaped foliar xylem has its concavity oriented towards the stem axis while it is the reverse in the anachoropterids (Fig. 1). However, some Palaeozoic forms with an oval to bar-shaped foliar xylem strand as *Grammatopteris* or *Catenopteris* (Phillips and Andrews 1966) have been suggested as possible ancestors of the Osmundales (Miller 1971).

The early diversification of vegetative morphology

In addition to anatomical features discussed above, information on vegetative morphology includes cauline branching, occurrence of shoots on fronds, habit, frond morphology with development of lamina and root structure.

The morphological interpretation of fragmentary remains of plants which are partly indeterminate in growth is of course difficult. However, modern 'whole plant' studies, sometimes including an ontogenetical approach, result in a very well documented knowledge of some early ferns. Thus *Tedelea* (*Ankyropteris*) *glabra* (Eggert 1959, 1963; Eggert and Taylor 1966) and *Psalixochlaena cylindrica* (Holmes

1977, 1981) are amongst the best understood and fully reconstructed Palaeozoic plants with detailed information on all parts of their sporophyte (stem, leaf, root, sporangium), and on their ontogeny, branching and general habit.

Amongst the groups of ferns and fern-like plants considered in this account, knowledge of the general morphology of the Iridopteridales is rather poor due to the fragmentary nature of the fossils; no reconstruction has been attempted and nothing is known of their habit.

The contemporaneous Devonian Cladoxylales are better known. A characteristic 'digitate' branching has been described and a semi-arborescent habit was proposed for *Calamophyton* and *Pseudosporochnus* with well documented reconstructions (Leclercq and Banks 1962; Schweitzer 1973). In these two genera, small dichotomising ultimate appendages are interpreted as leaves. In all these morphological features, the Devonian Cladoxylales differ markedly from the younger coenopterid ferns where semi-arborescent forms are very rare but where large megaphylls are present.

Detailed information on vegetative morphology of coenopterids will be found in Phillips (1974) and Taylor (1981).

Knowledge of the roots is rather poor: they are diarch and generally adventitious, being borne more or less densely along stems.

Cauline dichotomous branching occurs in the Zygopteridaceae (*Diplolabis*, *Metaclepsydropsis*, *Zygopteris*) but also in *Psalixochlaena*, *Rhabdoxylon*, *Botryopteris* which are relatively small ferns with a probably creeping rhizome. An exception is the zygopterid *Austroclepsis* (Sahni 1928) which was a small arborescent fern with a trunk of *Tempskya* type composed of several dichotomising stems surrounded with petioles and root mantle.

Lateral or axillary branching is rare but occurrs in some species of *Ankyropteris*, *Psalixochlaena* and *Tubicaulis* (Galtier and Holmes 1982) that were relatively small and scrambling plants.

Shoots occur on fronds in many species of *Botryopteris* and *Anachoropteris*. They are borne either laterally or adaxially and in position varying from proximal to distal (Phillips 1970, 1974; Holmes 1984). These generally short cauline units are interpreted as a means of vegetative propagation and have been compared to epipetiolar and epiphyllous buds in modern dennstaedtioid and dipterid ferns (Mickel 1974).

An erect habit has been attributed to some species of *Zygopteris*, *Ankyropteris*, *Tubicaulis*, *Grammatopteris* where large unbranched stems are only known. The contemporaneous Marattiales are represented by the tree-fern *Psaronius* with unbranched trunks up to 8 m high.

It is significant that different types of habit have evolved in ferns through the Carboniferous and sometimes in the same genus (*Zygopteris*, *Ankyropteris*, *Botryopteris*). This early diversification of overall morphology parallels, in these groups, the major acquisition of the megaphyll by planation of a lateral branch system.

In most of the coenopterids, the frond is biseriate and pinnate but the zygopterid Etapteroideae have quadriseriate fronds with primary pinnae borne in pairs on the phyllophore. This unique morphology is related to the peculiar anatomy of the phyllophore, intermediate between a dorsiventral petiole and a radially symmetrical axis. In all groups, the distal frond members tend to be planated and laminate pinnules are present from early Upper Carboniferous; they correspond mainly to *Pecopteris*, *Sphenopteris* and *Alloiopteris* compression foliage. In contrast, evidence of laminate pinnules is lacking in earliest (*Rhacophyton*) and in the Lower Carboniferous ferns *Musatea globata* and *Botryopteris antiqua*. These two Upper Visean ferns represent distinct evolutionary trends and possess partly three-dimensional distal frond units. They exhibit slight webbing but only *Musatea* possesses a lamina 1 mm wide with a specialised mesophyll (Galtier 1981). Present data suggest that in several groups of early filicalean ferns, the frond evolved increasingly laminate pinnules from the late Lower Carboniferous.

The Marattiales, only known from Upper Carboniferous, also exhibit large fronds with *Pecopteris*-type pinnules.

It is important to emphasise that the filicalean fern pinnules that evolved by Upper Carboniferous time are characterised by their modest size and monopodial nervation. In both time of the appearance of lamina and in the size of pinnules, the ferns contrast with the pteridosperms which also possess fern-like leaves. Fossil evidence suggests that the pteridosperm leaves, which are partly dichotomous and pinnately branched, developed broader laminate pinnules with mainly dichotomous nervation as early as late Devonian and Tournaisian. It is significant that pteridosperm foliage with undissected pinnules several centimetres wide, like the Visean *Cardiopteridium*, were contemporaneous with ferns practically devoid of laminate pinnules. There is a strong probability that the evolution of the pteridosperm frond, including dorsiventral anatomy and webbing, was completed in the late Devonian and thus preceded the evolution of the fern leaf (Galtier 1981). This feature must be interpreted as confirmation that ferns and pteridosperms orginated and evolved independently during Devonian time and that ferns cannot be the ancestors of pteridosperms.

The early diversification of reproductive structures

Information on the fertile parts of Palaeozoic ferns will be found in Eggert (1964), Andrews *et al.* (1970) and Taylor (1981). In this paper, additional data from recent studies are presented with the objective of summarising the salient features and possible evolutionary trends in fertile morphology from Lower Carboniferous time.

Many distinctive types of fertile fern structures have been recorded from the early Upper Carboniferous; some of them are shown on the upper part of Figure 2.

Sori and synangia of exannulate sporangia borne on foliage of the *Pecopteris* type are related to the Marattiales. The oldest genera are the Westphalian *Scolecopteris* (11, Fig. 2) and *Cyathotrachus*. Their spores are either large, trilete forms of the *Cyclogranisporites* type or small, monolete forms of *Punctatosporites* type (Laveine 1970; Millay 1979). The most abundant fossil record of Marattiales is in the Upper Carboniferous and Permian where the tree-fern *Psaronius* became the dominant coal swamp plant. At present nothing is known of the orgin of the group before Westphalian time but it is very unlikely that this sudden appearance is real (Millay 1979).

Musatea (2, Fig. 2) from the Upper Visean of France and Scotland (Galtier 1968, 1981) resembles the marattialean *Scolecopteris* with radially arranged sessile sori of elongated sorangia lacking an annulus and with dehiscence facing inward. Connection of this fertile structure with the zygopterid fern *Metaclepsydropsis* has been

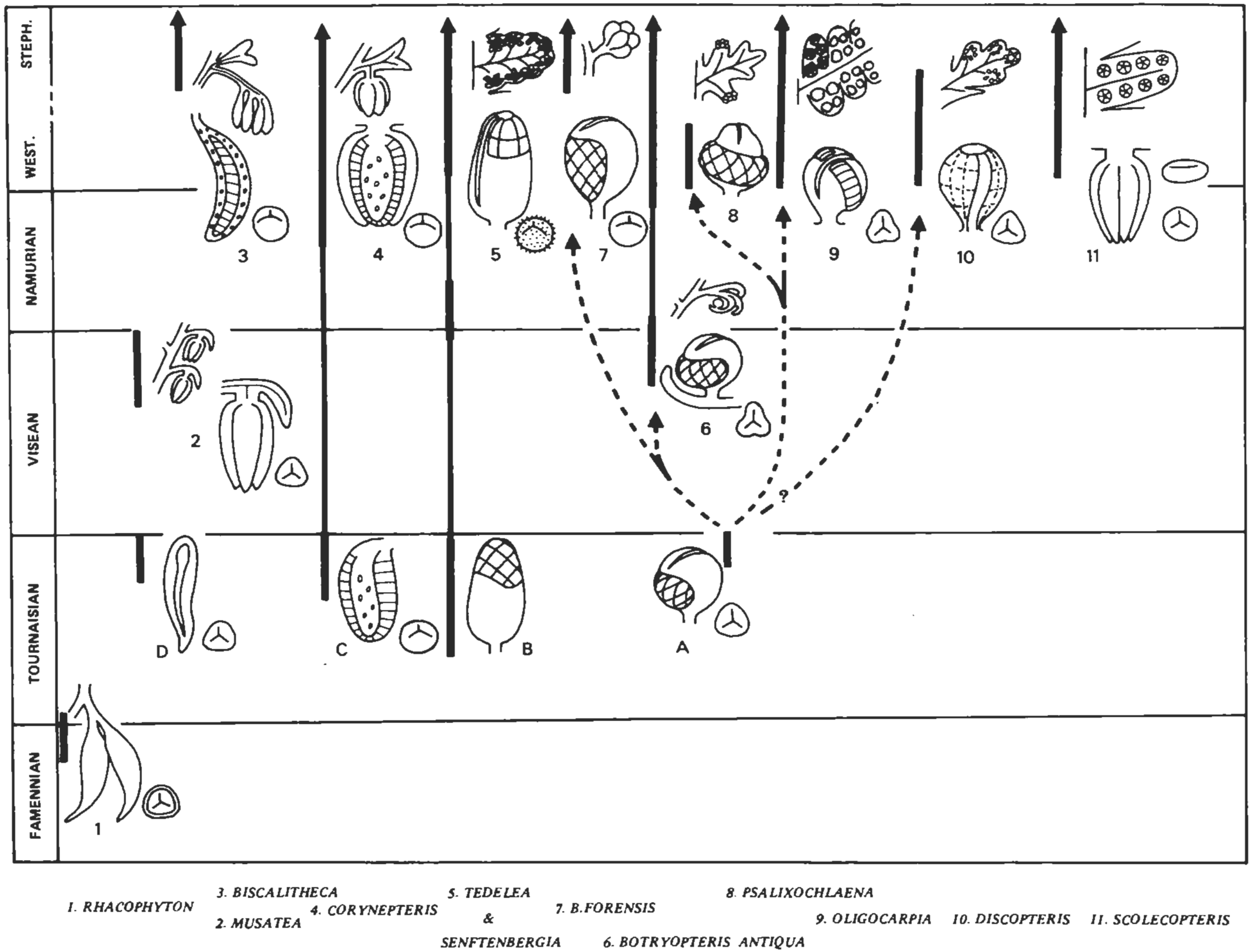

Figure 2. Early diversification of reproductive structures in ferns. From Visean to Westphalian time, very different types of fertile fern structures have been recorded. Some shown here include synangia of exannulate sporangia as in the Marattiales (*Scolecopteris*) or the Zygopteridaceae (*Musatea*) and diverse types of annulate sporangia. Some of these later types are very specialised (*Corynepteris, Biscalitheca*) whilst others are nearly identical to those of living Filicales and Osmundales. This similarity also exists in the arrangement of the sporangia on laminate pinnules. New data from the Lower Carboniferous of Scotland and France (types labelled A–D, see text for further explanation) have extended the range of annulate and exannulate fern sporangia back to the Tournaisian. The Devonian *Rhacophyton* is distinct in sporangium and spore morphology. All early ferns have trilete spores but the Marattiales also possess monolete forms.

demonstrated by Chaphekar and Alvin (1972) so this plant cannot be considered an ancestor of the Marattiales.

Other zygopterids show the same tendency towards sporangial aggregation, particularly *Corynepteris* (4, Fig. 2) where sessile sori of elongate sporangia occur on the abaxial surface of reduced pinnules. However, the sporangia have a prominent U-shape annulus and their double dehiscence area is facing outward. Galtier and Scott (1979) discussed the relationships of *Corynepteris* with *Biscalitheca* (3, Fig. 2). These two genera possess very specialised annulate sporangia without equivalent amongst extant ferns.

Other Carboniferous ferns however possess annulate sporangia nearly identical to those of certain living Filicales and Osmundales. An excellent example is *Senftenbergia*, a fructification corresponding to some *Pecopteris* frond compressions. The sporangia, isolated or in groups, are arranged in two rows along the pinnule margins; each sporangium is ovoid with a prominent apical annulus and longitudinal dehiscence. The spores conform either to *Convolutispora* or to *Raistrickia* types (Laveine 1969; Grauvogel-Stamm and Doubinger 1975). For a long time, *Senftenbergia* has been regarded as the oldest representative of the family Schizaeaceae (Radforth 1939). Recently, Jennings and Eggert (1977) described a partially petrified specimen of *Senftenbergia* of late Mississipian age showing a vascular trace resembling *Clepsydropsis* and *Ankyropteris*. This could be indicative of closer affinities to the Tedeleaceae, a new family based on the previous zygopterid species *Tedelea* (*Ankyropteris*) *glabra* (5, Fig. 2) (Eggert and Taylor 1966). *Tedelea* and *Senftenbergia* are similar in sporangial morphology (including distal annulus of at least two tiers of cells instead of only one in the living Schizaeaceae) and in the possession of *Raistrickia* spores. On the basis of anatomical features, they do not appear directly related to the extant Schizaeaceae.

The Upper Carboniferous *Oligocarpia* (9, Fig. 2) is generally considered as the earliest representative of the family Gleicheniaceae (Abbott 1954). The sporangia, with an equatorial transverse–oblique uniseriate annulus, are grouped into circular sori on *Sphenopteris*-like pinnules. Spores are triangular, trilete and correspond to *Granulatisporites* (Grauvogel-Stamm and Doubinger 1975).

The permineralised *Sermaya* (Eggert and Delevoryas 1967) with an anatomy of *Anachoropteris* also has pinnules bearing radial sori of annulate sessile sporangia with spores attributed to *Granulatisporites* or *Leiotriletes*. Sermaya has been proposed the type of the Sermayaceae, a new family of the Filicales which now includes another genus, *Doneggia* (Rothwell 1978). It was suggested that *Oligocarpia* might be the compressed form of *Sermaya* but the annulus is uniseriate in *Oligocarpia* while it is biseriate in the Sermayaceae.

The Psalixochlaenaceae constitute another new family of Filicales (Holmes 1981). In the permineralised *Psalixochlaena cylindrica* (8, Fig. 2) the sporangia, with a biseriate oblique annulus, are borne on the concave end of truncated pinnule lobes. Holmes emphasised the possession of gradate marginal sori as opposed to simple sori borne in a superficial position in the Sermayaceae.

Other contemporaneous ferns have annulate sporangia and may be considered also as filicaleans; *Boweria* or *Grambastia* (Brousmiche 1978) are *Sphenopteris*-like compression foliages with isolated or grouped annulate sporangia and trilete spores referred to *Leiotriletes* but their affinities remain unclear.

Amongst permineralised ferns, the Botryopteridaceae exhibit another type of anatomy. The sporangia of *Botryopteris antiqua* (6, Fig. 2) are similar in size to those of the above mentioned genera, with a short pedicel and a horizontal annulus; spores are triangular, trilete and referred to *Granulatisporites* (Galtier 1967). Clusters of up to 3 sporangia occur but they do not constitute sori as each sporangium is on a lobe with an independent vascular supply (Galtier 1970, 1981). This organisation is related to the absence of flat lamina; it is significant that in younger representatives of *Botryopteris* where fronds have evolved laminate pinnules, sporangia of similar size and morphology are found attached in superficial position beneath a pinnule vein (Good 1979). In the Upper Carboniferous species *B. cratis* (Millay and Taylor 1980), the sporangial morphology is like that of *B. antiqua* but the sporangium is twice as large and the spores are oval, trilete, of the *Verrucosisporites* type. Other Upper Carboniferous species such as *B. forensis* (7, Fig. 2) have fertile pinnae in the form of spherical sporangial aggregations exceeding 5 cm in diameter. The sporangia are terminal with a broad lateral plate of thickened cells (Phillips and Andrews 1965); this annulus is less prominent than in *B. antiqua* or *B. cratis* but the spores are similar to those of *B. cratis.*

The genus *Botryopteris* is an excellent example of a taxon where the 'whole plant' systematics will result in a more natural classification. Several phyletic lines relying on vegetative plant morphology including branching have been suggested (Phillips 1974; Galtier and Phillips 1977) but only the continued discovery of the corresponding fertile parts will allow recognition of the value of these phyla and a decision to be made as to whether major changes, such as the creation of new genera, are necessary or not.

Continuous search in older strata will also contribute to a better knowledge of the early history of the group; our current work on Lower Carboniferous floras of Europe now extends the range of *Botryopteris.* It is significant that foliar members with a *Botryopteris antiqua*-type of anatomy are associated with a large number of small spherical annulate sporangia (Fig. 2 A) in the late Tournaisian of Loch Humphrey Burn, Scotland (Scott *et al.* 1983). Their size and general organisation is similar to *B. antiqua* (6, Fig. 2) but these sporangia correspond to a more primitive type from which several sporangial morphologies may be *hypothetically* derived as we suggest by dotted lines in Figure 2. These theoretical derivations must not be misinterpreted as a suggestion of a unique Tournaisian common ancestor to these different fern lineages!

Possible relationship is indicated with *Discopteris* (10, Fig. 2), an Upper Carboniferous fern compression sometimes referred to the Osmundales. Pfefferkorn (1978) rather suggests affinities with the coenopterids on considering the sporangial structure with a very wide annulus but Brousmische (1977) does not support this interpretation. Assignment to the Osmundales was based on the interpretation of a distal plate of cells as a rudimentary annulus. In fact in the Osmundales this plate is rather lateral and resembles the new Tournaisian sporangia (Fig. 2 A) and some *Botryopteris*; similarity in the sporangial organisation of the living Osmundales to *Botryopteris antiqua* or *B. cratis* has been noted (Galtier 1967; Millay and Taylor 1980) but anatomical evidence supporting a possible ancestry of the Botryopteridaceae with regard to the Osmundales is lacking.

The other three reproductive structures that we recently recognised in the Upper

Tournaisian of Scotland (Fig. 2 B-C-D) are rare in comparison to the *Botryopteris*-like sporangia (Fig. 2 A).

The *Senftenbergia*-like sporangium (Fig. 2 B) is elongated, with an apical annulus made of several tiers of cells. Interestingly an anatomically preserved sporangium also showing an apical annulus has been reported from the Mid-Upper Tournaisian of France (Galtier 1981). The Scottish specimen thus confirms the extension of this phyletic group of ferns back to the Tournaisian. Prior to these two records, the earliest representatives of the group were of uppermost Visean-Namurian age from Scotland and America (Radforth 1939; Jennings and Eggert 1977).

The occurrence of *Corynepteris*-like sporangia in the same Scottish late Tournaisian deposits (Fig. 2 C) is documented both from macerations and serial sections of sporangia with a very distinctive U-shaped annulus. *In situ* spores are of the *Apiculatisporites* or *Acanthotriletes* type. Even found detached, there is strong evidence in favour of a close relationship of these sporangia with the *Corynepteris* group of which this discovery significantly extends the range; till now, the oldest known *Corynepteris-Alloiopteris* were of Namurian age.

The fourth category of fern-like sporangia (Fig. 2 D) from the Tournaisian of Scotland are always found dehiscent and apparently broken as if resulting from the disorganisation of a mature synangium. They are comparable to *Musatea* (2, Fig. 2). However, the possibility exists that they belong to an early marattialean that one may expect possibly to have the same sporangial organisation.

Amongst the late Devonian fern-like plants, the Cladoxylales have primitive fertile structures with terminal exannulate sporangia. In *Rhacophyton* (1, Fig. 2), specialised fertile pinnae borne in the aphlebia position, sporangial morphology and spores of *Perotriletes* type (Andrews and Phillips 1968) differ from anything known in the supposed related younger zygopterids.

In conclusion, this review indicates that the range of fertile fern structures extends back to the Tournaisian. This is suggestive of an earlier first diversification of ferns still not documented in the fossil record. It will be noted that, with the exception of the Upper Carboniferous Marattiales which have both monolate and trilete spores, all the other early ferns have trilete (subtriangular to spherical) spores.

Conclusions

Recent studies on late Palaeozoic ferns have significantly increased our knowledge of their anatomy, morphology and ontogeny, and have led to a more natural approach to the systematics based on both vegetative and reproductive features.

For some groups, the knowledge of fertile parts is rather poor (Cladoxylales) or non-existent (Iridopteridales). Thus the relationships of these plants and even their attribution to the ferns remains an open question.

The other plants, previously referred to as Coenopteridales, are considered as unquestionable ferns with only some reservation for *Rhacophyton* and *Stauropteris* which stand apart with an unusual combination of vegetative and reproductive characteristics.

In future work on coenopterid ferns, new data on sporangial distribution and structure and on spore morphology will be decisive for the elucidation of a phylogeny up until now based on vegetative morphology. Information on fertile morphology alone is, however, also difficult to interpret. It is becoming evident that one type of sporangial morphology may have evolved more than once. For example, the *Senftenbergia*-type with an apical annulus cannot be used as a definitive character for the Schizaeaceae. But as stated by Mickel (1974) 'this does not mean that the modern members of the family are unrelated but rather that we must use caution is ascribing schizaeaceous affinities to all fossil ferns bearing sporangia with apical annuli'. The same is true for possible gleicheniaceous affinities of *Oligocarpia* mentioned above.

Future investigations will also result in a better understanding of the relationships of the ferns with the ancestral Trimerophytina and with their contemporaneous progymnosperms and pteridosperms.

The discovery in the late Tournaisian of Scotland of abundant and diverse fern sporangia, including annulate filicalean types, is of interest regarding an early diversification of the group that took place at least by Tournaisian time.

The origin of ferns from the Trimerophytina remains to be documented by the discovery of intermediate forms of Emasian to Famennian age. It is significant that many Lower and even Upper Carboniferous ferns exhibit protostelic stem anatomy, unplanated leaves devoid of or with reduced laminate pinnules and terminal sporangia, all features reminiscent of or just evolved above the trimerophyte level.

Future investigation of fern-like foliage and fertile parts of Famennian to Tournaisian age should lead to a better definition of the concept of fern, if attention is focused on the search for distinctive characters of fern leaves and sporangia, compared with progymnosperm and pteridosperm leaves and sporangia. In this context, the suggestion that the pteridosperm frond evolved earlier than the fern leaf is of importance. Also of great interest would be a critical re-evaluation of fertile parts showing similar trends in ferns and pteridosperms as for example the grouping (sori or synangia) of elongate exannulate sporangia.

For the moment, the Palaeozoic ferns include some specialised groups, such as the Zygopteridaceae that originated in the Devonian and disappeared in the Permian, that cannot be related to modern ferns. Other contemporaneous coenopterids possess a 'generalised' type of anatomy and sporangium from which any type of modern structure can be theoretically derived. The present tendency is to include these ferns within the Filicales whilst waiting for the discovery in Triassic and Jurassic deposits of intermediate forms linking them to extant families.

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