Harlan P. Banks

2. THE EARLY HISTORY OF LAND PLANTS

Our predecessors painted successfully a broad and exciting picture of the origin and early evolution of land plants. Bower of Glasgow (1935), Zimmermann at Tübingen (1949), and Eames of Cornell (1936), to name but three, treated the Devonian psilophyte flora as a starting point in the comparative morphology of vascular plants. They made the evolution of psilophytes such an attractive concept that it is included in many introductory textbooks. Their achievements are remarkable because what few data were available to them were imprecise. Current research is filling in many gaps, correcting many misimpressions, and evolving new generalizations. My intent is to document some of the gaps in our knowledge, some means of filling them, some current data being obtained, and some of the fertile fields for future research.

Stratigraphy. The most serious drawback to accurate studies of evolution among the first land plants has been the lack of adequate data on the stratigraphic occurrence of the plants under consideration. Simply to label a plant as Devonian puts it in a time span of 60 million years (Table 1). If the data are more precise, Lower Devonian for example, the plant is included somewhere in a time span of 15 million years. Even in a general discussion, however, we can no longer rely solely on the words Lower, Middle, and Upper Devonian. In Table 2 the Devonian period is subdivided into six series. Even these are insufficient. Wherever possible

Table 1. Geologic Periods Involved in Origin of Land Plants

From Kulp, 1961.

Period		*Time period began*	*Duration of period* (millions)
Mississippian		345	
Devonian	Upper	365	20
	Middle	390	25
	Lower	405	15
Silurian	Middle	415	10
	Lower	425	10

Fig. 1. Rhyniophytina. A, *Rhynia*. B, *Cooksonia*. C, *Eogaspesiea*. D, *Hostimella*. E, *Hicklingia*. F, *Taeniocrada*. G, *Yarravia*. H, *Hedeia*. (A, After Kidston and Lang, 1921; B, from Andrews, 1959; C, after Daber, 1960; D, from a specimen; E, based on Kidston and Lang, 1923; F, from Kräusel and Weyland, 1930; G, from Andrews, 1959; H, from Andrews, 1959.)

one must pinpoint a lesser subdivision from which a given taxon is derived. It must be recognized also that for a variety of good reasons precise boundaries between certain horizons cannot always be drawn by stratigraphers. Thus such an assertion as "an abundance of vascular plants appears in Lower Devonian strata" must be challenged. Are the strata proved to be Lower Devonian? If true, exactly where in Lower Devonian time? These and other questions must be asked and re-asked as new data pour in.

The more precise stratigraphic approach changes some earlier impressions. We shall assume here without discussion that nearly all reports of pre-Devonian plants are ill-founded either because the plants have not been proved to be vascular or because the strata have been determined incorrectly. For example, the well-known *Baragwanathia* flora of Australia which was regarded as of Silurian age is now interpreted as Devonian (Jaeger, 1962). The one Upper Silurian plant

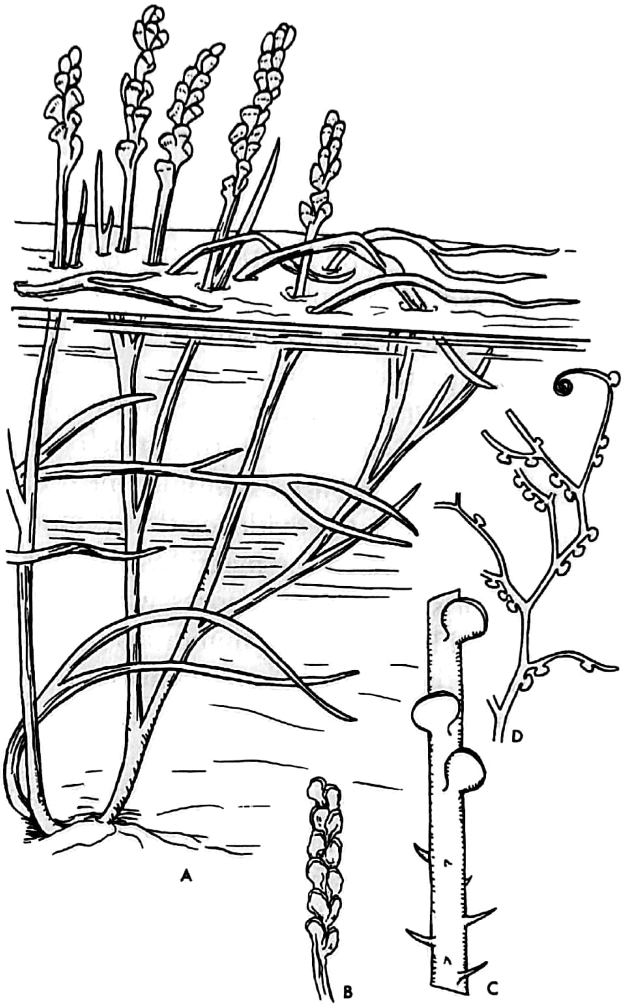


Fig. 2. Zosterophyllophytina. A, *Zosterophyllum*. B, *Bucheria*. C, *Psilophyton ornatum*. D, *Gosslingia*. (A, From Kräusel and Weyland, 1936; B, from Dorf, 1934; C, from Hueber, 1964; D, from Andrews, 1959.)

that seems to be indisputable is *Cooksonia* (Obrhel, 1962). At the moment it appears to be the oldest known vascular plant. More important, *Cooksonia* (Fig. 1B) is a simple plant in the original sense of a naked, dichotomizing axis bearing terminal sporangia. It was in this sense that *Rhynia* (Fig. 1A) was considered a starting point in the evolution of land plants.

After this late Silurian appearance, *Cooksonia* occurs again in the basal Lower Devonian Downtonian (Gedinnian) of Wales where it is represented by two species (Lang, 1937). There it is accompanied by another plant, *Zosterophyllum* (Fig. 2A), with naked stems on which sporangia are borne laterally rather than terminally. These two genera may be the extent of the flora of Gedinnian time. The next strata in which plants are found are either clearly Siegenian or are continental strata whose position with respect to the Gedinnian–Siegenian boundary is still in doubt. Several new taxa appear. Some of them (Figs. 1, 2, 4, 5) are *Taeniocrada*, *Psilophyton*, *Gosslingia*, *Hedeia*, and *Yarravia* in the psilophytes; ***Drepanophycus***, *Protolepidodendron*, and *Baragwanathia* among the lycopods; and ***Dawsonites***, a pre-fern.

In brief there is probably only one taxon that can be called a Silurian vascular plant, and there are but two in the early part of Gedinnian time. These are psilophytes. By Upper Gedinnian or Lower Siegenian time several additional taxa appear, and the psilophytes are joined by lycopods and possibly pre-coenopterids. This amount of change occurred in the span of 15 million years (Table 1) and it is the kind of change envisioned by Bower, Zimmermann, and Eames but is based entirely on data accumulated since they wrote.

Time and space do not permit a continued elaboration of stratigraphic data throughout the Devonian period, but without this much or more detail many generalizations about the Devonian flora are essentially meaningless. Of particular interest here is the parallelism between the evidence that is emerging from palynological studies and that presented above for macrofossils. Richardson (1964 and personal communication) reports that simple spores with trilete marks appear in Wenlockian time (Table 2) and become more numerous in Ludlovian and Gedinnian time. By Siegenian time the spore flora is considerably more diverse. Of course it is possible that some of these earliest spores represent bryophytes or algae, but the agreement between studies of micro- and macrofossils supports the concept that land plants may have arisen in uppermost Silurian or lowermost Devonian time after all. It does not support the hypothesis of a long antecedent history (e.g. Axelrod, 1959; Leclercq, 1956) for vascular plants. We seem to be back where we were in 1940, believing that simple land plants evolved into more complex land plants during Devonian time. Now, however, we have more evidence to support the hypothesis.

Psilophytales. Much has been said in the last decade about the use of this order as a catchall for plants whose affinities are unknown. However, current discoveries are refining our knowledge of individual taxa (Banks, 1965) and are adding intriguing new taxa. I venture therefore a reclassification of the psilophytes (Table 3) solely to emphasize the new information and to postulate some evolutionary developments that result. It will be noted that some categories included among the psilophytes—for example Psilophytidae, Asteroxylidae, and Pseudosporochnidae of Pichi-Sermolli (1958)—are now excluded for reasons given below.

Tentatively I propose two new subdivisions, Rhyniophytina and Zosterophyllophytina (Figs. 1, 2; Table 3). Rhyniophytina *subdiv. nov.* Type: *Rhynia* Kidston and Lang 1917, includes those genera whose sporangia are terminal in the sense employed originally by Kidston and Lang (1917) when they proposed the new category Psilophytales. Their stems are naked and, as pointed out by Hueber (1964), their sporangia are usually fusiform and may dehisce longitudinally. Sporangia of *Cooksonia* are globose. Therefore *Cooksonia* is maintained in a family by itself. In *Rhynia* and *Horneophyton* the xylem strand is terete in cross section and the protoxylem is central (Fig. 3A). I have recently found (1966) a similar strand in the form genus *Hostimella* (Fig. 1D), a genus for naked axes that dichoto-

Table 2. Subdivisions of Devonian Time and the First Appearance of Some Vascular Plants.

Period	*Series*	*Stage*	*First occurrences*
Mississippian	Tournaisian		
Devonian	Famennian		
	Frasnian		
	Givetian		*Colpodexylon, Archaeosigillaria,* other lycopods
	Eifelian (or Emsian)		*Asteroxylon, Rhynia, Horneophyton*
	Coblencian	Emsian	*Trimerophyton, Eogaspesiea*
		Siegenian	*Protolepidodendron, Cooksonia* *Taeniocrada* spp., *Gosslingia* *Psilophyton ornatum, Hedeia,* *Zosterophyllum, Dawsonites* *Drepanophycus, Baragwanathia, Yarravia*
	Gedinnian		cf. *Zosterophyllum myretonianum* *Cooksonia hemisphaerica* *Cooksonia pertonii*
Silurian	Ludlovian	Upper	*Cooksonia* sp.
		Middle	*Taeniocrada* sp. *Cooksonia* cf. *hemisphaerica* *C.* sp.
		Lower	
	Wenlockian		
	Llandovery		

Table 3. Reclassification of Psilophytes

- Rhyniophytina (psilophytes)
  - Rhyniales
    - Rhyniaceae
      - *Rhynia*
      - *Horneophyton*
      - *Hicklingia*
      - *Eogaspesiea*
      - *Taeniocrada*
      - *Hedeia*
      - *Yarravia*
      - *Hostimella*
    - Cooksoniaceae
      - *Cooksonia*
- Zosterophyllophytina (not psilophytes)
  - Zosterophyllales
    - Zosterophyllaceae
      - *Zosterophyllum*
      - *Bucheria*
    - Gosslingiaceae
      - *Gosslingia*
      - *Psilophyton* (non-Dawson, new name required)
      - *"Serrulacaulis"*
      - New genus of Lyon

Table 4. Classification Used in this Paper, with New Proposals

Division	Tracheophyta
Subdivision	Rhyniophytina
	Type *Rhynia* Kidston and Lang 1917
Order	Rhyniales
Family	Rhyniaceae
	Type: *Rhynia* Kidston and Lang
Family	Cooksoniaceae
	Type: *Cooksonia* Lang 1937
Subdivision subdiv. nov.	Zosterophyllophytina
	Type: *Zosterophyllum* Penhallow 1892
Order	Zosterophyllales
Family	Zosterophyllaceae
	Type: *Zosterophyllum* Penhallow 1892
	Gosslingiaceae
	Type: *Gosslingia* Heard 1927
Subdivision	Psilophytina–Psilotales
	Lycophytina
	Sphenophytina
Subdivision subdiv. nov.	Trimerophytina
	Type: *Trimerophyton* Hopping 1956
Subdivision	Pterophytina
Class	Cladoxylopsida
Class	Coenopteridopsida
Class	Filicopsida
Class	Progymnospermopsida
Class	Cycadopsida
Class	Coniferopsida
Class	Gnetopsida
Class	Angiospermopsida

mize. In the remaining Rhyniales the shape of the xylem strand is unknown. The genera here included in Rhyniaceae are fairly well established despite the paucity of good specimens and of morphological detail for several of them. Until these deficiencies are corrected, I am inclined to retain them in one family. Within this family the tendency toward more frequent branching and toward an aggregation of sporangia is clear (Fig. 1).

Cronquist et al. (1966) have proposed the divisional name Rhyniophyta with *Rhynia* as the type. I agree in all respects with their argument but am retaining the divisional name Tracheophyta (Table 4) and the recommended subdivisional ending -phytina for the *Rhynia*-type plants. I am going farther than they by removing those former psilophytes whose sporangia are lateral. They are no longer to be considered psilophytes.

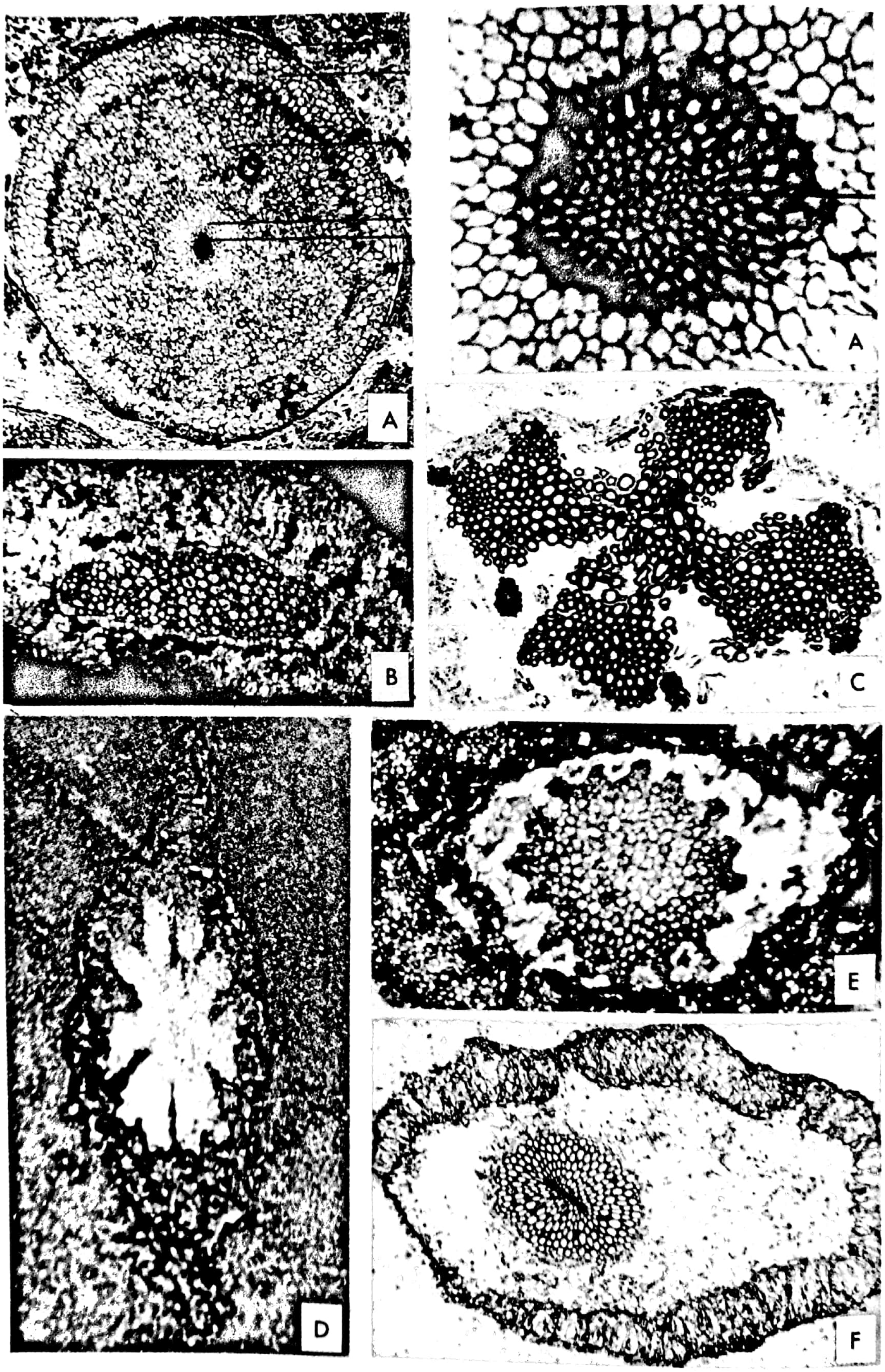
The second subdivision proposed, Zosterophyllophytina, is more diverse and is distinct from the original concept of Psilophytales. ZOSTEROPHYLLOPHYTINA *subdiv. nov.* Type: *Zosterophyllum* Penhallow 1892, includes those taxa (Fig. 2) whose sporangia are borne laterally, are globose or reniform in shape, and dehisce along the distal edge (Hueber, 1964). Where the xylem has been petrified (Fig. 3B) it appears in cross section as an elliptical, exarch strand (Heard, 1927; Hueber, work in progress). It is a relatively massive strand, at least as compared to those psilophytes whose anatomy is known. So far we do not know whether the sporangia are supplied by vascular traces. If they were, one would interpret them as terminal on short branches as in Psilotales. The question remains open pending the discovery of better-preserved axes.

Diversity in Zosterophyllophytina (Fig. 2) is apparent both between the two families (Table 3) and within each. Zosterophyllaceae have naked stems; Gosslingiaceae have naked, spiny, or toothed stems. In Zosterophyllaceae, *Zosterophyllum* and *Bucheria* have sporangia aggregated into spikes whereas in Gosslingiaceae they are scattered along the axis. In Gosslingiaceae, *Psilophyton* (non Dawson, new name required) (Hueber, 1964) has multicellular spines and Lyon (personal communication) has found a new taxon in the Rhynie chert that bears lateral, reniform, or globose sporangia and unicellular spines. *Gosslingia* and *Nothia* are naked. *"Serrulacaulis"* (Hueber, 1961) has teeth along the stem. All genera have sporangia scattered variously along the stem.

Certain genera (cf. Andrews, 1961) sometimes included among the psilophytes are omitted here. For example I now treat *Asteroxylon* as a lycopod. Other genera are omitted because they do not fit naturally into the present redefinition of psilophytes and do not contribute to the evolutionary series proposed here.

LYCOPHYTINA. Zosterophyllophytina appear first in rocks of late Gedinnian age (Table 2) followed soon by several Lycophytina such as *Drepanophycus* and *Baragwanathia.* Characters common to the two groups are lateral sporangia, exarch protostele (Fig. 3C,D,E), and small appendages. Lyon's (1964) discovery that *Asteroxylon* bore lateral sporangia strengthens the argument that it is a lycopod, not a psilophyte. In addition, its stelar anatomy agrees with that of several Devonian lycopods (Grierson and Banks, 1963). I have studied Lyon's preparations at Cardiff and am convinced that he has the true fertile region of *Asteroxylon* with its typical stele and leaves. If, as some geologists suspect, the Rhynie chert is Lower Devonian (Siegenian or Emsian) the possibility that *Asteroxylon* represents an intermediate stage in evolution of lycopods is markedly increased (Fig. 4). Its leaf traces extend only to the base of its leaves, but they are typical leaf traces and, morphogenetically, the stimulus to cause differentiation of vascular tissue in the leaves need be only slight. By contrast, the outgrowths on stems of Gosslingiaceae are clearly only multicellular (or unicellular) emergences.

It has been suggested that the three-forked leaves of *Colpodexylon* and bifid leaves of *Protolepidodendron* originated from a branch system. We do not have fossil evidence for branching systems that might have been reduced to produce


A
A
B
C
D
E
F

the abundance of leaves found characteristically on lycopod stems. On the contrary, the fossil evidence that we do have reveals axes liberally supplied with outgrowths (enations). Modern experimental studies demonstrate morphogenetic relationships between outgrowths and stems. I find it more in keeping with these studies to believe that the enations observed on stems that bear lateral sporangia might evolve into leaves interspersed between sporangia (*Asteroxylon* level) and then into leaves with axillary or adaxial sporangia (*Baragwanathia–Protolepidodendron*). This hypothesis (Table 5), starting with sporangia that are already lateral, also avoids the necessity of reducing terminal fertile telomes to produce the adaxial sporangia (Zimmermann, 1949, p. 70). Thus I am inclined toward the view that lycopod leaves arose as enations rather than as modified branch systems.

Again we are led back to the early ideas of Bower. We can speculate that he would be impressed by the new fossil evidence that supports more firmly his concept of origin of small leaves from enations than did the evidence available to him. We need not be disturbed by the appearance of *Baragwanathia, Protolepidodendron,* and *Drepanophycus* in the fossil record slightly earlier than *Asteroxylon,* for many reasons. Chief among these are the possibility that the Rhynie chert may ultimately be proved to be Lower Devonian or that *Asteroxylon* may have existed elsewhere in Lower Devonian time without being preserved in a form we can recognize. Hence, although stratigraphic data must be sought with care and with vigor, they must be used as guidelines rather than hindrances.

TRIMEROPHYTINA. In the Senni beds of early Siegenian age in Wales (Table 2) Croft and Lang (1942) found *Zosterophyllum, Psilophyton* (non Dawson, new name required) with lateral sporangia, and *Gosslingia.* Along with these genera they obtained a few small specimens of *Dawsonites* (Fig. 5A). This is the genus to which Halle assigned Dawson's supposed terminal sporangia of *Psilophyton* (Hueber, 1964). *Dawsonites* is abundant in strata of Emsian age at Gaspé, James Bay, and in Belgium. I am suggesting that it and *Trimerophyton* Hopping (1956), also from the Emsian, be included in a new subdivision for which I propose the name TRIMEROPHYTINA *subdiv. nov.* Type: *Trimerophyton* Hopping 1956. This subdivision includes plants with a main axis that branches pseudomonopodially. Each lateral branches a number of times, either trichotomously or dichotomously and finally terminates in a mass of fusiform sporangia (Fig. 5, A and B). Anatomy is known only for *Dawsonites* (Hueber, 1964; Banks, 1964; Fig. 3F). Its vascular strand is massive in comparison to that of *Rhynia.* These genera, branching freely and producing large sporangial trusses, seem a natural outgrowth of Rhyniophytina and simultaneously foreshadow the still more complex branching pattern

Fig. 3. Anatomy of some early Devonian plants, from specimens. A, *Rhynia* with small central, centrarch protostele. To the right, xylem enlarged. B, *Gosslingia* with large, exarch, elliptic protostele; cortical area of thick-walled cells. C, *Asteroxylon* with lobed protostele and leaf traces (small circles). D, *Colpodexylon* with lobed protostele. E, *Protolepidodendron* with ridged, exarch protostele. F, *Dawsonites.*

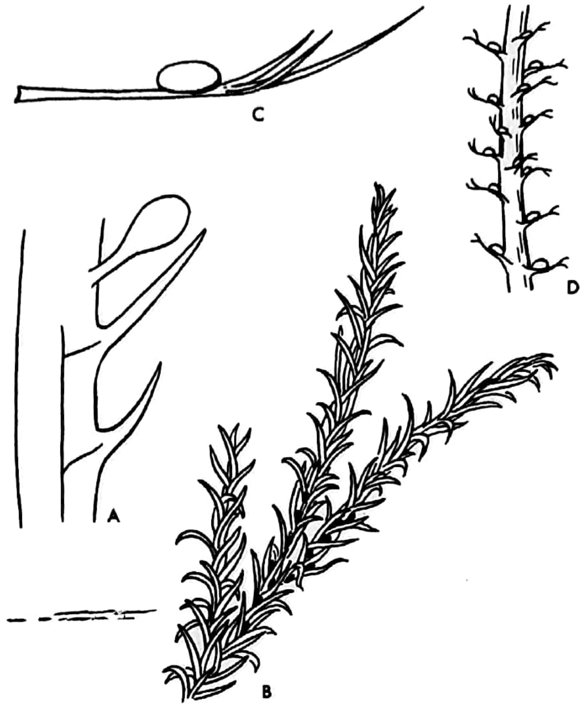


Fig. 4. *Asteroxylon* and the lycopods. A, *Asteroxylon* with leaf trace, appendages, and one lateral sporangium. B, *Baragwanathia* with sporangia (black) either cauline or axillary. C, *Colpodexylon,* one three-forked leaf with adaxial sporangium. D, *Protolepidodendron,* bifurcate leaves and adaxial sporangia. (A, Based on Lyon, 1964; B, based on Lang and Cookson, 1935; C, based on specimen; D, modified from Kräusel and Weyland, 1932.)

found among Cladoxylopsida, Coenopteridopsida and Progymnospermopsida toward which I suggest they evolved (Table 6).

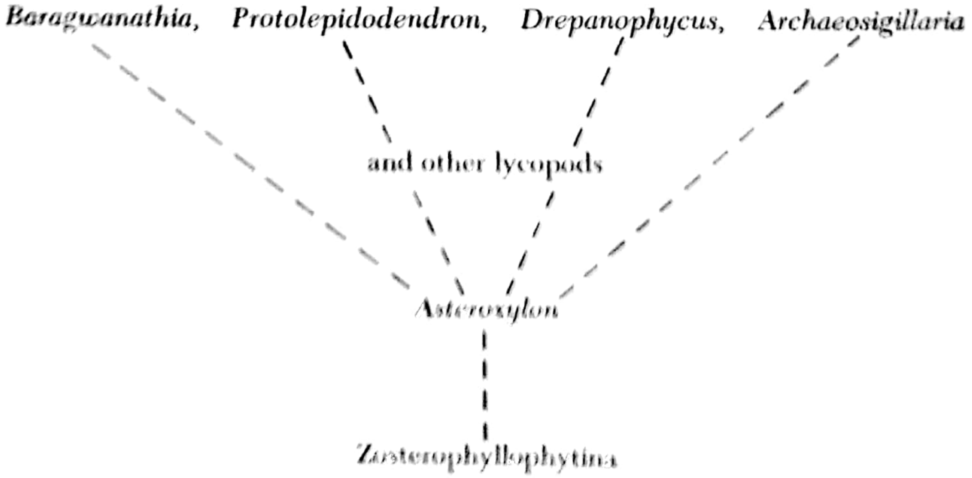
My suggested new subdivision Trimerophytina was actually foreseen many years ago by Halle (1916) when he described a Lower Devonian flora from Röragen in Norway. It included *Hostimella, Aphyllopteris, Drepanophycus* (*Arthrostigma*), *Psilophyton, Sporogonites, Pachytheca,* and groups of sporangia that he considered similar to those Dawson had assigned to *Psilophyton.* Halle pointed out that neither Dawson nor any subsequent author had found these paired, terminal sporangia attached to *Psilophyton.* He gave them a new name, *Dawsonites arcuatus,* to emphasize this point. I have studied Halle's types in Stockholm and find them similar to those from Gaspé being studied by Hueber, Leclercq, and me (Fig. 5A). Halle's comments on morphology (1916, p. 39) are significant here. He referred to *D. arcuatus* as the "best evidence of the beginnings of the filicinean phylum in the Older Devonian." He further stated that "the sporangia of *Dawsonites* recall those of certain Upper Devonian and Carboniferous ferns generally considered to be primitive as for instance *Dimeripteris* and perhaps *Stauropteris.*" Clearly Halle felt that the lateral, fertile branch systems of *Dawsonites* could become planated and ultimately webbed to make fronds such as those characteristic of Carboniferous strata.

Andrews (1961) has made the point in another way. He discusses the psilophytes in one chapter and then, in order to show the "broad stream of evolution with many specialized side branches," discusses in successive chapters the "pre-ferns," the true ferns, and finally seed-ferns. Among the pre-ferns he includes the plants I refer to Cladoxylopsida, Coenopteridopsida, and Progymnospermopsida. In separate chapters he writes later about lyocopods and horsetails as distinct groups that pursued paths independent of the "main stream." It is also noteworthy that Andrews treats *Trimerophyton* as a plant included in the psilophytes only with doubt. I have simply gone farther in separating it and *Dawsonites* taxonomically from other psilophytes.

CLADOXYLOPSIDA. Devonian Cladoxylopsida, once rare, are proving to be more abundant than was expected. Genera whose stratigraphic position is based on reliable evidence appear in Givetian time and continue into the Frasnian (Table 6). Only *Cladoxylon* (Fig. 5C,H) is known from younger rocks, and the group as a whole lasts only through Carboniferous time. *Schizopodium* (Fig. 5G) and *Xenocladia* (Fig. 5F) are known only from petrifactions. The former was first reported by Harris (1929) from the Middle Devonian of Australia. Subsequently it has been found in the Middle Devonian (Read, 1938) and Upper Devonian (Hueber, 1959) of New York. One of its major features is the radially seriated tracheids that surround the apices of the xylem arms. The problem is whether to call them secondary xylem or simply radially seriated primary xylem. *Xenocladia* was first reported from the Middle Devonian by Arnold in 1940 and by him again in 1952 on the basis of better material. I have found it in rocks of Upper Devonian age (Banks, 1961). It compares favorably with the Carboniferous plants assigned to Cladoxylales by Bertrand (1935).

Pseudosporochnus (Fig. 5D,E) has long been held to be a bushy psilophyte. Leclercq and Banks (1962) showed that it had a typical cladoxylalean stele and

Table 5. Relationship of Devonian Lycopods to Zosterophyllophytina



was much more complex in its branching pattern than had been assumed previously. Its ultimate appendages, borne spirally, forked trichotomously once or oftener. Every fork then dichotomized three times, resulting in a much-branched, planated, but not webbed, frond. Some fronds bore sporangia terminally. *Cladoxylon scoparium* Kräusel and Weyland (1926) (Fig. 5C) branched as profusely as *Pseudosporochnus* but more irregularly. Its ultimate appendages were much smaller and less branched and its fertile appendages were fan-shaped, bearing sporangia terminally. These genera are related on the basis of their gross morphological structure and their multifasciculate xylem. In fact the order *Cladoxy-*

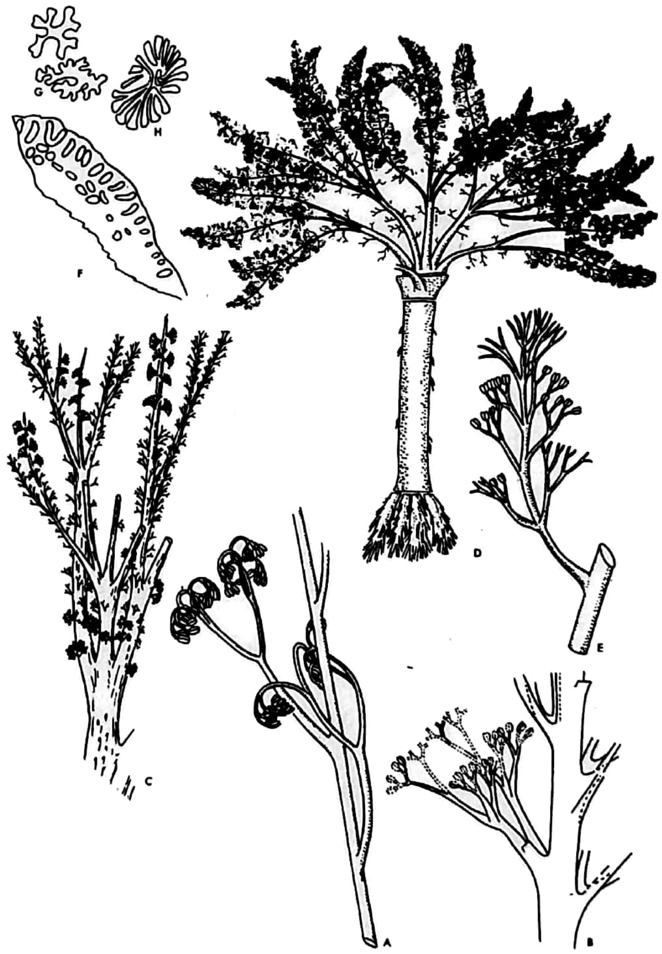


Fig. 5. Trimerophytina and Cladoxylopsida. A, *Dawsonites*. B, *Trimerophyton*. C, *Cladoxylon scoparium*. D, *Pseudosporochnus*. E, One of the spirally arranged fronds of *Pseudosporochnus*. F, *Xenocladia* with radially aligned peripheral xylem strands and some of the more circular central strands. G, *Schizopodium*, two variations of the much-lobed xylem strand. H, *Cladoxylon* with xylem strand similar to that found in *Pseudosporochnus*. (A, From Hueber, 1964; B, from Hopping, 1956; C, from Kräusel and Weyland, 1926; D, and E, from Leclercq and Banks, 1962; F, from specimen; G, from Hueber, 1960; H, from Hueber, 1960.)

lales was founded on petrified specimens of Mississippian age whose xylem was much divided; it is only the Devonian representatives for which external morphology is known.

There are two recent additions to the Devonian cladoxylaleans. Ananviev (1957) found a *Hyenia*-like axis and a *Pseudosporochnus*-like fertile branch system. He concluded the two were probably parts of one plant and erected a new Lower Devonian taxon *Protohyenia* for them. He chose this name because the sporangia were upright, not recurved. In 1964 he reported finding a cladoxylalean type of multifasciculate vascular system in the fertile branch system. Bonamo and Banks (1966b) suggest that the fertile branch system is therefore a *Pseudosporochnus* as Ananiev thought originally (it is not listed here on Table 6 because I am unconvinced that it is really of Lower Devonian age). The remaining piece of Ananviev's *Protohyenia* is probably *Hyenia*. Thus the new sphenopsid *Protohyenia* that was thought to be the earliest representative of that group no longer exists.

Table 6. Possible Evolutionary Trends from Rhyniophytina–Trimerophytina

	Cladoxylopsida	*Coenopteridopsida*	*Progymnospermopsida*
Tournaisian	Several genera and species	Several genera and species	*Callixylon* *Siderella* *Protopitys*
Famennian	*Pietzschia*	*Rhacophyton*	*Callixylon* *Archaeopteris* *Aneurophyton*
Frasnian	*Pietzschia* *Pseudosporochnus* *Xenocladia* *Cladoxylon* *Schizopodium*	*Rhacophyton* *Asteropteris* *Reimannia* *Arachnoxylon*	*Ginkgophyton* *Callixylon* *Archaeopteris* *Sphenoxylon* *Tetraxylopteris* *Aneurophyton*
Givetian	*Pseudosporochnus* *Cladoxylon scoparium* *Calamophyton* *Xenocladia* *Schizopodium*	*Asteropteris* *Iridopteris* *Reimannia* *Arachnoxylon*	*Actinopodium* *Svalbardia* *Sphenoxylon* *Protopteridium* *Aneurophyton*
Eifelian			*Aneurophyton*
Emsian	Trimerophytina	*Dawsonites* *Trimerophyton*	
	Rhyniophytina	*Eogaspesiea* *?Rhynia, ?Horneophyton*	
Siegenian	Trimerophytina Rhyniophytina	*Dawsonites* *Taeniocrada, Yarravia* *Hedeia, Cooksonia*	
Gedinnian	*Cooksonia*		

Leclercq and Schweitzer (1965) have just reported the discovery of typical cladoxylalean anatomy in *Calamophyton bicephalum.* They are convinced therefore that *Calamophyton* is not a sphenopsid. It agrees with other Devonian cladoxylaleans in the branching of its main axis. (Leclercq and Andrews, 1960) and its numerous terminal sporangia. It agrees too in the morphology of its sterile appendages which are more like those of *Cladoxylon scoparium* than like those of *Pseudosporochnus.* However, the sporangia of *Calamophyton* are borne on recurved branches of sporangiophores whose morphology is more complex than the equivalent fertile leaves of *Pseudosporochnus* and *Cladoxylon scoparium.* This of course raises doubt about the systematic position of *Hyenia,* which shares many characteristics with *Calamophyton* (Bonamo and Banks, 1966b). It will be a matter of no small interest to learn whether *Hyenia* remains in Sphenopsida or must also be transferred. It will be equally interesting to see if the new anatomical information from *Calamophyton* that seems to make it a cladoxylalean continues to outweigh the morphological evidence that *Calamophyton* does have a primitive sphenopsid sporangiophore.

Trimerophytina seems a natural group to serve as a precursor of Cladoxylopsida, both anatomically and morphologically. Its stratigraphic occurrence is significant. Trimerophytina appear earlier in geologic time, at least so far as we can tell from present knowledge (Table 6). For the future, many details remain to be cleared up. Spores are known for *Dawsonites* (Hueber, 1964), *Calamophyton* (Bonamo and Banks, 1966b), and *Trimerophyton* only. Structure of sporangia is known only for *Dawsonites* (work in progress, Banks, Hueber and Leclercq) where their walls are several layers thick and are composed of cells similar to the cortex of the branches. They are supplied by large vascular strands and probably possessed stomates. Thus sporangia of *Dawsonites* fit the usual criteria for primitive organs. It is essential to find spores and sporangial structure for the other genera, to find external morphology for *Xenocladia* and *Schizopodium,* and to find anatomical structure and better-preserved spores for *Trimerophyton.* If ever all these data are forthcoming, we may have some exact knowledge of the role played by Cladoxylopsida in evolution. At present they are most commonly regarded as a plexus that might have had some connection to the medullosan pteridosperms or as an independent line that ended blindly. It seems just as likely to me that they represent one of several experimental lines developing during late Middle and Upper Devonian time. Each of the newly developing lines may have undergone the several possible changes such as lobing and dissection of the stele, aggregation or reduction in number of sporangia, and specialization of sporangia and their position. Certain individuals from each of the several lines may then have evolved in the direction of pteridosperms. In the present state of our knowledge I see no reason to single out one group (plexus or line) as the only one that was capable of evolving into pteridosperms, especially as continuing research enlarges each group in turn and shows it to be relatively specialized.

COENOPTERIDOPSIDA. A second plexus that might have evolved from Trimerophytina is Coenopteridopsida (Table 6). Arnold (1935, 1940) and Read (1938) described *Reimannia, Arachnoxylon,* and *Iridopteris* on the basis of small axes preserved only as petrifactions (Fig. 6). Xylem in *Reimannia* is three-lobed; in the other two it is five-lobed. The first collections of all three genera were made in rocks of Givetian age, but I have found *Reimannia* and *Arachnoxylon* in younger Frasnian rocks (Banks, 1961). Arnold (1940) erected Iridopteridineae, a suborder of Coenopteridales, for them and speculated about which part of a plant they might represent. We are really no better off today than when he wrote, as far as details of the three genera are concerned. All three are characterized by the production of simple, terete vascular strands. Nothing is known of the appendages supplied by the strands except that they are spirally arranged. Peripheral loops are found in the protoxylem areas, a characteristic associated with coenopterids.

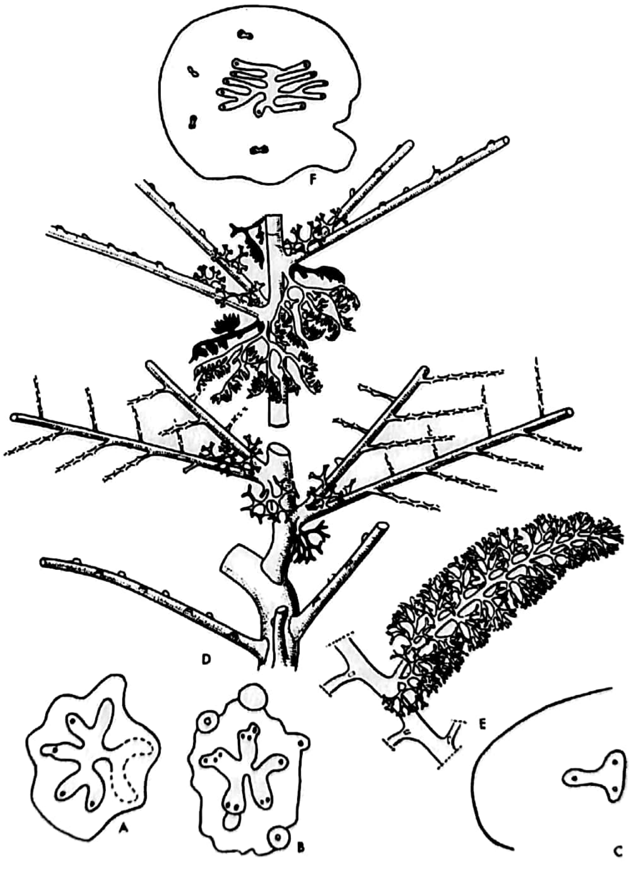


Fig. 6. Coenopteridopsida. A, *Arachnoxylon* with lobed, mesarch xylem strand. B, *Iridopteris,* lobed, mesarch xylem strand and circular, mesarch traces. C, *Reimannia* with lobed, mesarch xylem strand. D, *Rhacophyton,* three lowest pinnae unbranched and showing only bases of pinnules; four upper pinnae each showing the basal dichotomy, the catadromic pinnules (some fertile), and points of attachment of ultimate pinnules. E, One pinna of *Rhacophyton* enlarged to show the much-branched, unwebbed pinnules. F, *Asteropteris* with lobed, mesarch xylem strand and clepsydroid leaf traces. (A, From Read, 1938; B, from Arnold, 1940; C, from specimen; D and E, from Leclercq, 1951; F, from specimens.

Since Arnold's publication we have learned that some cladoxylaleans and some progymnosperms possess variously lobed or divided xylem strands from which arise simple terete strands (leaf traces?). Coenopterid ferns, on the other hand, often produce clepsydroid traces to their appendages. All three groups exhibit mesarchy. It seems perfectly possible therefore that Iridopteridineae may be related to cladoxylaleans or to progymnosperms just as easily as to Coenopteridales (Table 6). They may represent only plants that were at an evolutionary level just below that attained by cladoxylaleans, coenopteridaleans, and progymnosperms. Information is as yet too sparse to make a reassignment in the present classification system.

The Frasnian genus *Asteropteris* (Fig. 6F) has been called the oldest representative of coenopterid ferns. It possessed a much-lobed xylem strand off which leaf traces arose in a whorl. Peripheral loops are present in the tips of the arms of xylem, and they seem to remain closed as in the clepsydroid coenopterid ferns. The traces to the rachides have two peripheral loops even before they are free from the arms of xylem. They are typically clepsydroid in form. When seen farther out in the cortex, they have developed four peripheral loops, two at each end of the clepsydroid bundle. Bertrand (1914) confirmed Dawson's original interpretation that the many-rayed, central vascular strand is reminiscent of Cladoxylales. However, the appearance of four protoxylem strands in the leaf traces led him to conclude that its closest affinity lay with Coenopteridales, and he compared the xylem strand of the stem with that of *Asterochlaena.* If the peripheral loops in the clepsydroid traces are permanent and if they give rise to traces that are closed rings, then *Asteropteris* will be included among the clepsydroid coenopterids. To date, however, only short lengths of stem have been found petrified, and the leaf traces have never been seen outside the cortex. Dawson's single specimen came from marine rocks of Frasnian age in central New York, and Hueber (1960) collected several axes in continental deposits in eastern New York. Specimens showing external morphology have yet to be discovered. *Asteropteris* is one of the important plants badly in need of additional study.

Rhacophyton (Fig. 6D) is the one unquestioned member of Coenopteridales to be discovered in Devonian strata, and both its anatomy and morphology have been found. *R. zygopteroides* is the best-known species (Leclercq, 1951, 1954). The xylem strand of its stem is star-shaped, and its arms produce clepsydroid traces to the rachides. Both sterile and fertile fronds are borne spirally and are characterized by clepsydroid traces. Vegetative fronds bear pinnae in a distichous manner, and traces to the pinnae are small crescentic bundles whose departure leaves an open peripheral loop. Similar bundles supply the ultimate pinnules which are divided several times and are unwebbed (Fig. 6E). Fertile fronds, on the contrary, divide at their base into two primary pinnae whose xylem strand is again clepsydroid. Further branching of the fertile fronds resembles that of vegetative fronds. *Rhacophyton* has therefore certain features of both Clepsydropsidaceae and Etapteridaceae (Zygopterids). The four-ranked branching of fertile pinnae, the temporary peripheral loops, and the crescentic pinna bundles are similar to Etapteridaceae. The two-ranked branching of the vegetative fronds is a character of the Clepsydropsidaceae.

Sporangia of *Rhacophyton* are borne on a catadromic pinnule situated at the base of the paired pinnae. It is a dichotomously branched, concave cluster of fusiform sporangia that probably dehisced longitudinally and are reminiscent of sporangia of Trimerophytina and Rhyniophytina.

It must be admitted that Devonian representatives of the coenopterid lines are still sparse. Nevertheless, the distinctive anatomy and morphology of the Carboniferous coenopterids, which are rapidly becoming a large and diverse complex, make a search for Devonian precursors inevitable. Three characters that command attention are the tendency to produce leaves as modifications of large branch systems (Mamay and Andrews, 1950), the production of large masses of terminal sporangia, and the possession of a complex vascular system. All three characterize *Rhacophyton* as well as Carboniferous coenopterids. *Asteropteris* and the iridopterids are known only by their anatomy. The former is more coenopterid-like, whereas the latter are simpler and could be placed in any one of several groups. Most striking is the parallelism between the fronds of *Rhacophyton* and the large branch systems of progymnosperms, between the fertile pinnules of *Rhacophyton* and the fertile complexes of some progymnosperms, and between the sterile pinnules of *Rhacophyton* and those of Aneurophytales. In *Rhacophyton* the anatomy of the frond differs from that of the stem, whereas in progymnosperms a change in anatomical structure occurs only in the production of the ultimate appendages. Yet the ultimate appendages in most Devonian members of both groups are unwebbed telomic structures, whereas in both groups the lateral branch systems resemble large fronds. Clearly, parallel changes were occurring in the two groups. In the same way, the aggregation of numerous fusiform, terminal sporangia into complex fertile branch systems was advancing in parallel fashion in the two groups. Many gaps remain to be filled between Trimerophytina and *Rhacophyton*, but the outline of a series is evident.

X PROGYMNOSPERMOPSIDA. Progymnospermopsida (Beck, 1960) are a third group that may have evolved from Rhyniaceae by way of Trimerophytaceae. It is a group about which data are accumulating rapidly and about which considerable evolutionary speculation is bound to emerge as the plants become better known. The group is characterized by secondary xylem with circular bordered pitting, usually narrow vascular rays as in many coniferophytic gymnosperms, and by pteridophytic reproduction. Some taxa are so preserved that they show anatomical structure only, some show morphological features only, some show both. Some taxa are apparently homosporous, some heterosporous. A tentative classification of the group is given in Table 7 and an idea of their occurrence in time is given in Table 6.

It is reasonable to speculate that Aneurophytales (Fig. 7) is the most primitive order in the group. *Aneurophyton, Tetraxylopteris,* and *Protopteridium* are all protostelic. *Protopteridium* is included here on the basis of work reported (Bonamo and Banks, 1967). Specimens of the first two genera are mesarch, those of the third

Table 7. Tentative Classification of Progymnospermopsida

- Archaeopteridales
  - *Svalbardia*
  - *Actinopodium*
  - *Ginkgophyton* sensu Beck
  - *Archaeopteris*
  - *Callixylon*
  - *Siderella*
- Protopityales
  - *Protopitys*
- Aneurophytales
  - *Protopteridium*
  - *Aneurophyton*
  - *Tetraxylopteris*
  - *Sphenoxylon*

probably are. Axes of *Aneurophyton* have a three-lobed protostele whereas those of *Tetraxylopteris* have four-armed protosteles. In both genera the stele is the same in all orders of branching except the ultimate divisions. It consists of elongate tracheids with multiseriate bordered pits on all walls and of high, mostly uniseriate, rays. The xylem of *Protopteridium* is less well known, but its primary xylem is reported to be three- or four-lobed (Kräusel and Weyland, 1938). *Sphenoxylon* was erected (Read, 1937) for a single petrified stem that seemed to have a pith surrounded by four radiating arms of primary xylem. Beck (1957), Hueber (1960), and Matten (1965) have contributed to the strong probability that *Sphenoxylon* and *Textraxylopteris* are synonymous. The genus *Sphenoxylon*, however, must be retained as an organ genus for petrifactions for which external morphology is lacking.

Secondary xylem like that of many gymnosperms seems to have become well established in Aneurophytales, hence, by late Eifelian time. Secondary phloem consisting of phloem rays, various kinds of parenchyma cells, and fibers has been described for *Tetraxylopteris* (Beck, 1957). In spite of good preservation there is no indication that typical sieve cells have evolved.

Branching in *Aneurophyton* is spiral, in *Tetraxylopteris* it is opposite, decussate, and in *Protopteridium* it is probably spiral although the ultimate branches may be dichotomous. In both of the first two genera there are several orders of branching which have been regarded as primitive fronds. The branch systems terminate in dichotomized ultimate appendages that are not planated and not webbed. In *Aneurophyton* the appendages are said to be without vascular supply whereas in *Tetraxylopteris* they are supplied by a terete xylem strand. This latter character indicates that the ultimate appendages may be equivalent to leaves. *Protopteridium* lacks these regularly arranged, dichotomized ultimate appendages. It may possess pinnately lobed appendages, some of which are sterile and some of which are fertile. These pinnately lobed sterile appendages have long been regarded as the earliest evidence for the origin of fern-like leaves (Fig. 7A), but see Bonamo and Banks (1967).

Sporangia of *Aneurophyton* are borne in clusters on small, recurved branches. Available evidence indicates that they are homosporous. Sporangia of *Protopteridium* are believed to be borne on the upper side of large, lateral, upcurved branch systems (Fig. 9C). These systems bear pairs of short pinnae whose branches carry large numbers of slender, pedicellate sporangia. In *Tetraxylopteris* (Fig. 9D), large sporangial complexes consist of dichotomously and pinnately branched appendages (Bonamo and Banks, 1966a). In all three genera the sporangia are elongate and fusiform, and they probably dehisce longitudinally. They seem clearly to be an extension of the evolutionary series initiated by *Rhyniophytina* that bore terminal sporangia and that was continued by *Trimerophytina.*

Spores referable to *Aneurospora* have been found in sporangia of *Aneurophyton* (Streel, 1964); *Rhabdosporites langi* has been isolated from sporangia of *Tetraxylopteris* (Bonamo and Banks, 1966a) and has been found in association with *Protopteridium* as well (Lang, 1926; Richardson, 1960).

Protopitys, a Mississippian genus, was long regarded as related to conifers or to pteridosperms because of its abundant secondary wood characterized by bordered pits on the walls of the tracheids. When its primary xylem was found, some placed the genus among the ferns, perhaps because of its predominantly

Fig. 7. Progymnospermopsida. A, *Protopteridium hostimense,* main branches attached spirally, lesser branches dichotomous; toward the apex there are sterile and then fertile pinnae. B, *Aneurophyton* showing forked, ultimate appendages. C, *Svalbardia,* fertile pinnules. D, *Svalbardia,* sterile pinnules. E, *Tetraxylopteris* fronds, arranged spirally on main axis; subsequent branching is opposite decussate. (A, Kräusel and Weyland, 1933; B, from specimens; C and D, from Høeg, 1942; E, from Beck, 1957.)

scalariform tracheids. No foliage has been observed, but leaf traces originate as crescent-shaped collateral bundles at either end of the elliptical pith. Arrangement of appendages is therefore distichous. Walton (1957) reported a new species of *Protopitys* that bears fertile branches in distichous fashion. Each fertile branch of *Protopitys* dichotomizes several times and then forks pinnately. The resemblance of these branches to the sporangial complexes of *Protopteridium* and *Tetraxylopteris* (Fig. 9) is striking.

The ultimate divisions in *Protopitys* terminate in sporangia, and a vascular strand extends to the base of the sporangium as in *Dawsonites.* Sporangia are elongate-fusiform, their walls are two to three cells in thickness, and stomates apparently were present as in *Archaeopteris* (Carluccio et al., 1966) and in *Dawsonites.* Dehiscence is longitudinal as in *Tetraxylopteris, Dawsonites,* and other genera. The sporangia are unique in having radially elongate epidermal cells when viewed in a transverse section of a sporangium. In surface view they are longitudinally elongate as in several other genera. Spores range from 82 to 163 μ in diameter, and Walton suggested incipient heterospory as one interpretation of this wide range in size. However, Richardson (1965) finds numerous genera of isolated spores in which the range in size is as great or greater.

The entire fertile branch system is recurved as it is in *Protopteridium* and *Tetraxylopteris* (Fig. 9). The tendency toward pinnate branching also recalls these two genera, and the position, shape, structure, and dehiscence of the sporangia can clearly be regarded as derived from such progenitors as Trimerophytaceae. Anatomically the fertile branch system is more highly evolved than in any of the genera mentioned. It is supplied by one large crescent-shaped leaf trace that is almost endarch (Walton, 1957). This trace dichotomizes in the proximal portion of the fertile branch, and thenceforth only more or less circular traces have been seen in the other divisions of the fertile branch. This suggests that the fertile branch is equivalent to a leaf or frond. Walton referred to it as a sporophyll. Whatever it is called, it is somewhat more highly evolved than fertile branches of Aneurophytaceae and Trimerophytaceae. In addition, the stem of *Protopitys* with its pith, almost endarch primary xylem bundles, and crescent-shaped leaf trace is more highly evolved than that of either of the two families named. Yet the inclusion of *Protopitys* in Protopityales in the Progymnospermopsida (Table 7) is justified by its combination of characters.

Archaeopteridales are known best for the two genera *Callixylon* Zalessky 1911 and *Archaeopteris* (Dawson) Stur 1875. Both occur in Frasnian and Famennian time, both have been found in strata that may prove to be uppermost Givetian, and *Callixylon* occurs also in Tournaisian. If *Siderella* proves to be synonymous with *Archaeopteris,* as suggested by Carluccio et al. (1966), then both *Callixylon* and *Archaeopteris* continue into Tournaisian. Beck (1960) was the first to find a branch determined as *Archaeopteris* attached to a stem assignable to *Callixylon.* As a result of this connection of a presumed gymnosperm and a presumed fern, Beck suggested the name Progymnospermopsida for plants whose reproduction is pteridophytic and whose secondary xylem is gymnospermous.

Archaeopteris (Fig. 8) has been regarded as a bipinnate frond of a fern to which the terms rachis, pinna, and pinnule were applied. On the basis of the newly discovered anatomy of this "frond," Carluccio et al. (1966) suggest that it is in fact a branching system whose ultimate appendages should be called leaves rather than pinnules. *Callixylon is* known from petrified axes up to 28 ft in length and 5 ft in diameter. Its pith is surrounded by discrete mesarch bundles that produce branch traces in spiral sequence. Each bundle divides tangentially, producing one trace and one reparatory strand so that the trace leaves no gap in the stele. The resulting branches may be rachides assignable to *Archaeopteris.* Proximally their anatomy in transverse section resembles that of *Callixylon* (Carluccio et al., 1966) the stem to which they are attached. More distally, their primary xylem is siphonostelic (Fig. 9A) with ten to twelve lobes. From the main axis (rachis) opposite lobes give rise to branch traces (pinna traces) that, in fertile *A. macilenta,* become siphonostelic like the main branch. The other lobes produce smaller

Fig. 8. *Archaeopteris* (modified from Beck, 1962). Branching system arranged spirally on stem (*Callixylon*); stipules clasping base of branch, rachial pinnules on main branch between laterals; laterals bear sterile and fertile leaves; sporangia in two rows on laminar, forked leaf. Anatomy of main axis (rachis): pith (lined), lobed siphonostele, bundles of sclerenchymatous cells (dotted), mesarch traces with two protoxylem strands, and divided traces.

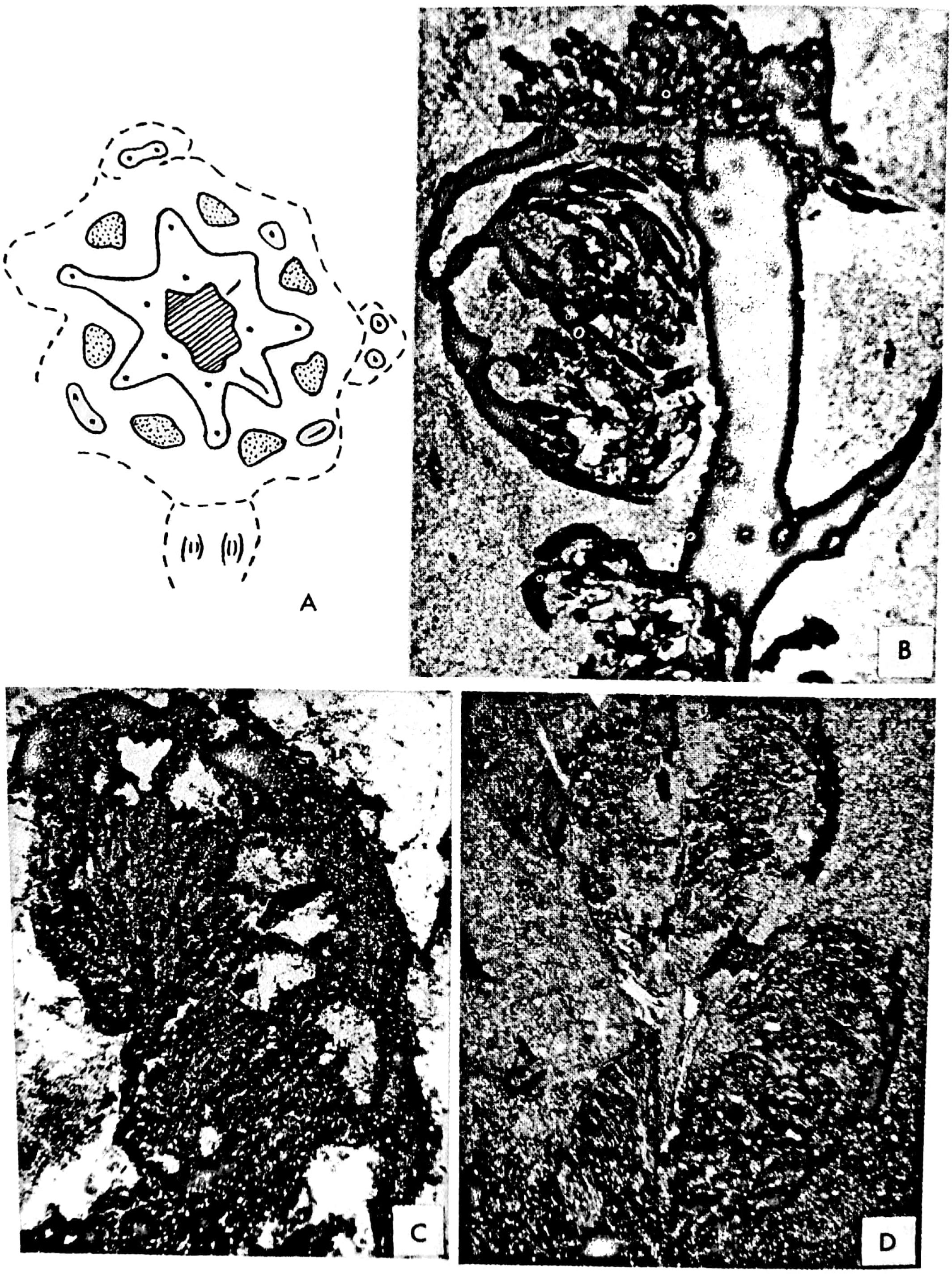


Fig. 9. Progymnospermopsida. A, Anatomy of *Archaeopteris*. B, Sporophyll of *Protopitys*. C, Sporangial complex of *Protopteridium*. D, Sporangial complexes of *Tetraxylopteris*. (A, From Carluccio et al., 1966; B, from Walton, 1957; C, from Kräusel and Weyland, 1938; D, from specimen.)

traces in spiral order. These traces appear to supply leaves (rachial pinnules) along the main axis. From the fertile lateral axes (branches or pinnae), small traces are produced in spiral order. They supply the leaves (pinnules) which therefore are spirally arranged despite their apparently bilateral symmetry.

The ultimate branches (pinnules) of fertile axes are spirally arranged. They are often several times dichotomized and bear two rows of sporangia on their adaxial surface. The epidermis of both fertile leaves and sporangia is composed of elongate cells and stomates (Carluccio et al., 1966). The fertile leaves are laminar, and the sporangia are probably primitive in construction. No sporangia have been found petrified, but the presence of stomates suggests that they had a wall several cells in thickness. Dehiscence was longitudinal (Andrews et al., 1965). Heterospory has been proved in some species (Arnold, 1939; Pettitt, 1965) and has been suggested in others (Kräusel and Weyland, 1941). Pettitt (1965) reported megaspores similar to the dispersed spore genus *Biharisporites* and microspores like *Cyclogranisporites.*

Svalbardia Høeg (1942) and *Actinopodiopsis* Høeg (1942) were described from Middle Devonian strata in Spitzbergen. The former (Fig. 7, C and D) has been regarded as a precursor of *Archaeopteris.* Carluccio et al. (1966) have suggested that *Actinopodiopsis* might represent petrified axes of *Svalbardia* although the two have not been found attached. The ultimate branches (pinnules) of *Svalbardia* are forked several times into filiform segments. In contrast to *Archaeopteris* they are unwebbed as in the Aneurophytales. This character along with the somewhat less regular arrangement of sporangia on the ultimate fertile branches may support the concept of *Svalbardia* as a Middle Devonian precursor of the predominantly Upper Devonian *Archaeopteris.* If axes assignable to *Actinopodiopsis* prove to be parts of the plant called *Svalbardia,* the difference between *Svalbardia* and *Archaeopteris* will be little more than the webbing of the leaves (pinnules) of the latter.

Ginkgophyton sensu Beck (1963) is an axis bearing spirally arranged, wedge-shaped, sterile leaves. Little is known of its gross morphology. Internally it resembles *Callixylon* except that it lacks banded pitting on the radial walls of the tracheids. The discovery that leaves (pinnules) of *Archaeopteris* are borne spirally suggests that Beck's *Ginkgophyton* is an oversized *Archaeopteris obtusa. A. macilenta* is borne on a stem (*Callixylon*) that has banded pitting (Beck, 1960, 1962). *A. macilenta* itself has banded pitting (Carluccio et al., 1966). All known species of *Callixylon* show banded pitting. However, it is unknown whether all fronds of *Archaeopteris* show this character. Thus only future discoveries can answer such questions as: Does the frond of *A. obtusa* show grouped pitting? Can the *Ginkgophyton* of Beck be synonymous with *Archaeopteris*? Are there two closely related genera that differ only in the arrangement of their pits on tracheid walls?

Progymnosperms are a group with considerable morphological significance regardless of whether they gave rise directly to gymnosperms (Beck, 1962; Meeuse, 1963) or merely paralleled the evolution of gymnosperms and ferns (Leclercq, 1962). The origin of the pteropsid leaf is one of the most significant questions to which progymnosperms contribute. It is unnecessary here to repeat all that has been written (e.g. Andrews, 1961, p. 84–87) about the origin of pteropsid leaves from branch systems, but it is important to point out that Aneurophytales exemplify this concept. Their anatomy is the same in all orders of branching except in the ultimate divisions, and their branching is three-dimensional. Nevertheless, the systems of lateral branches simulate fronds. Planation of these three-dimensional structures would produce even more obvious fronds, and webbing of the ultimate divisions would produce pinnule-like structures. In Archaeopteridales the result of planation and webbing can be seen. The "frond" of *Archaeopteris* bears "pinnae" in two rows (planated), but the ultimate leafy divisions (pinnules), though webbed, are still borne in a spiral sequence. Presumably descendants produced leaves (pinnules) in distichous fashion. Thus in the Archeopteridales (Pityales), just as in the Aneurophytales, leaves may have been evolving simultaneously in two ways, lateral branch systems were becoming fronds, and ultimate branchlets were becoming leaves. From Archaeopteridales (Pityales), Meeuse (1963, p. 157–64) has speculated that further evolution resulted in the cycadophyte leaf on the one hand and the coniferophyte leaf on the other. In the former case, the entire branch system (frond) of *Archaeopteris* became the large compound leaf of the cycadophytes, whereas only the ultimate pinnules (leaves) of *Archaeopteris* evolved into the coniferophyte leaf such as the sword-shaped leaf of *Cordaites*. All we have learned about progymnosperms to date supports this interpretation. In fact the discovery (Carluccio et al., 1966) that the leaves (pinnules) of *Archaeopteris* are borne spirally removes the one difficulty mentioned by Meeuse (1963, p. 159). He wrote of the "alternate or subopposite dictichous arrangement" in *Archaeopteris* changing to the helical arrangement in *Cordaites*. No such change was necessary.

Sporangia of progymnosperms are elongate cylindrical organs similar to those of Trimerophytaceae. Often they had a long attenuated apex. Where known, they had stomates on their surface and dehisced by a single longitudinal slit. Their wall probably consisted of several layers of cells, one of which broke down or sometimes separated from the others to form a sac-like structure in which the spores escaped as a mass (Pettitt, 1965). Only *Archaeopteris* is known to have been heterosporous.

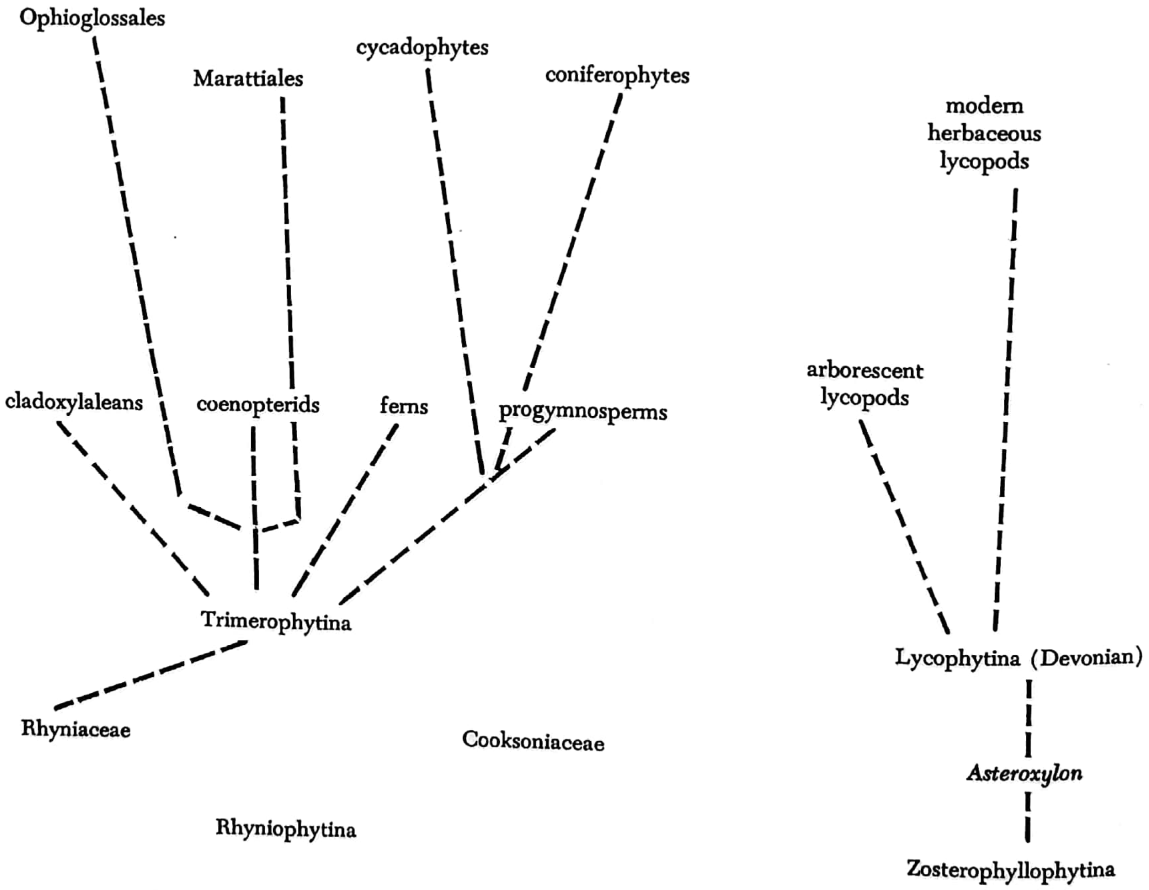
Archaeopteris has been used by Meeuse (1963, p. 142ff.) as the starting point in the evolution of both pteridosperm and cordaite reproductive organs. His Figure 5 illustrates the possibility that some individual fertile pinnules of *Archaeopteris* evolved into pteridosperm male synangia such as those of *Crossotheca*, others into seeds. In the evolution of the integument, he assumes, with Benson (1935), that it was produced by sterile megasporangia enclosing one fertile one. It seems to me that an alternative, and equally unproved, hypothesis is that fertile pinnules lost all but one megasporangium which then became surrounded by the numerous dichotomized tips of the fertile pinnule. This suggestion follows more closely the evidence from other sources (e.g. Andrews, 1963) that integuments were formed by the fusion of sterile telomes around a megasporangium. Because the sterile leaf of *Archaeopteris* appears to have evolved from webbed, ultimate branchlets (telomes), it is reasonable to consider the much-divided fertile leaf to be the same. Thus if it were reduced to bearing only a single megasporangium, its divisions might well envelop that megasporangium after the fashion of the origin of integument postulated by Andrews (1961, Fig. 13–4).

Meeuse also derives coniferophyte reproductive organs from progymnosperms like *Archaeopteris*. He assumes (his Fig. 4) that each pinna becomes one male or one female short shoot (cone) of *Cordaites*. This involves the migration of one sterile pinnule to the axis (rachis) below the insertion of the pinna (short shoot) to form a subtending bract. It seems to me that a rachial pinnule of *Archaeopteris* (Fig. 8) might serve this function equally well. It involves also the reduction of the remaining sterile pinnules to scale-like structures aggregated closely (cone-fashion) around one or a few fertile pinnules. He derives other coniferophytes from the cordaite type.

In discussing the evolutionary significance of the progymnosperms and their role in the various hypotheses of origin of more highly evolved plant groups one important point stands out: our ignorance of the exact limits of axis and leaf. At least some of the controversy over the axial or appendicular nature of an organ is the result of a failure to look at the evolutionary origins of the organ. *Archaeopteris* is a case in point. Prior to learning its anatomical structure the custom was to speak of its frond, its pinnae, and its pinnules, either sterile or fertile, because those are the terms that would be applied to a living plant of similar appearance. On this premise one would call the sporangia foliar. Anatomy has shown (Carluccio et al., 1966) that this apparently flattened frond is a branch system whose penultimate branches (pinnae) are distichous but whose ultimate divisions are still spirally arranged. Only the ultimate divisions differ anatomically from the rest of the branch system and they can be called leaves. Some species of *Archaeopteris* have unwebbed leaves (*A. fissilis*) and related genera (*Svalbardia*) are similarly unwebbed. The leaves of the more primitive progymnosperms (e.g. *Aneurophyton* and *Tetraxylopteris*) are homologous. If we go back slightly farther to *Dawsonites* there is no particular organ that can be called leaf, and its sporangia, the apparent precursors of those of progymnosperms, are considered stem borne. It is clear that leaves of progymnosperms are merely slightly modified branches and that the distinction between leaf and branch (stem) is difficult to draw. Thus if one chose to regard the ultimate, sporangium-bearing branches of progymnosperms as axial rather than appendicular organs, he would call the sporangia axial or the plants stachyosporous. I would prefer to regard the ultimate appendages as appendicular and to call the progymnosperms phyllosporous, because I interpret the ultimate appendages as prototypes of leaves. I consider the fertile pinnules of *Archaeopteris* as homologues of the sterile pinnules. Thus no matter how modified these pinnules might become (e.g. reduced to bearing a single terminal sporangium) their sporangia (or seeds if *Cordaites* were derived from them) would be leaf-borne.

Sphenophytina and Filicopsida. The origin of these two groups is speculative. The sphenophytes may have been derived from Rhyniophytina. The ferns may have had a similar origin by way of Trimerophytina. Some characters associated with Filicopsida evolved in each of the three groups, Cladoxylopsida, Coenopteridopsida, and Progymnospermopsida, and the various evolutionary series seen among them could equally well have led to ferns. Beck (1962) has cited several reasons for believing that progymnosperms are neither ferns nor progenitors of ferns. Similar reasoning applies to cladoxylaleans and coenopterids, e.g. Delevoryas (1962, p. 79–80). Yet the existence of these three groups and the characters they share indicate that true ferns may be only one more expression of the morphological variation that produced these groups. It is from the early, plastic members that other

Table 8. Summary of Evolutionary Concepts



groups evolved, not from the easily recognized, obvious, highly evolved forms. The derivation of Ophioglossales and Marattiales from coenopterids has been argued pro and con, but it is more likely that early coenopterids, rather than those with fixed and definitive characters, were the progenitors (Table 8).

Speed of evolution of land plants. Banks (1965) has suggested that new habitats on the land and limited competition permitted rapid colonization and the development of variation. Further, it is possible that in Silurian–early Devonian time, slight genetic changes effected more pronounced morphological changes than is true today. On this basis some of the types reviewed here, plus others that are omitted, might easily have evolved in the relatively short time that was available.

Palynology. The study of spores found in Devonian strata is proceeding rapidly. In the area of stratigraphy the results will facilitate the correlation of marine and continental strata so that the latter can be placed more accurately than at present. They may improve interregional stratigraphic correlations, as Richardson (1965) has shown in his comparison of the microfloras of Scotland and Russia. The following publications are examples of the kind of extensive studies that will be needed to accomplish these results: Allen, 1965; Kedo, 1955; McGregor, 1964; Richardson, 1965; Streel, 1964; Tchibrickova, 1962; Vigran, 1964.

Some spores have been found in situ and described in full detail. This detail has permitted the application to them of names used in palynological nomenclature (Table 9). In many cases, e.g. *Calamophyton,* the spore has proved to belong to an existing taxon for sporae dispersae. Other spores have been found in situ in Devonian plants, but either their descriptions have been too meager or their preservation too poor to correlate them with names used in palynological nomenclature (Table 10).

Table 9. Devonian Plants Bearing Named Spores in Situ

Plant	*Spore*	*Reference*
Archaeopteris cf. *jacksonii*	*Cyclogranisporites* *Biharisporites*	Pettitt, 1965
Svalbardia polymorpha	*Lycospora*	Vigran, 1964
Tetraxylopteris schmidtii	*Rhabdosporites*	Bonamo & Banks, 1966a
Aneurophyton germanicum	*Aneurospora*	Streel, 1964
Dawsonites sp.	*Retusotriletes*	Hueber, 1964
Barinophyton richardsonii	*Calamospora*	Pettitt, 1965
Enigmophyton superbum	*Phyllothecatriletes* *Enigmophytospora*	Vigran, 1964
Calamophyton bicephalum	*Dibolisporites*	Bonamo & Banks, 1966b
Eviostachya høegii	*Acanthotriletes*	Leclercq, 1957

Table 10. Some Devonian Plants with Spores in Situ but Unnamed

Plant	*Reference*
Pseudosporochnus krejcii	Leclercq, 1940
Protopteridium spp.	Lang, 1926; Obrhel, 1961; Halle, 1936.
Hyenia elegans	Leclercq, 1940
Trimerophyton robustius	Hopping, 1956
Barrandeina dusliana	Obrhel, 1961
Zosterophyllum llanoveranum	Croft & Lang, 1942
Psilophyton ornatum	Hueber, 1964
Nothia aphylla (Asteroxylon)	Kidston & Lang, 1920b
Horneophyton Lignieri	Kidston & Lang, 1920a
Rhynia gwynne-vaughanii	Kidston & Lang, 1917
Cooksonia sp.	Croft & Lang, 1942
Sporogonites exuberans	Croft & Lang, 1942

Isolated spores whose parent plants are known will serve to predict the megafossils that may be found in nearby deposits. Spores, like megafossils, will contribute to our understanding of the time of origin of land plants and of the origin of various groups of land plants. Even now some generalizations are possible (Richardson, 1964). Lower Devonian spores are simple, trilete, and azonate with smooth, apiculate, or spinose exines. Examples are *Retusotriletes, Calamospora, Lophotriletes, Acanthotriletes, Punctatisporites, Apiculatisporites, Leiotriletes,* and *Emphanisporites.* Younger Devonian spores show more diversity of ornament, structure and size. *Archaeotriletes, Hystrichosporites,* and *Ancyrospora* possess bifurcate spines. *Hymenozonotriletes* sensu Naumova is a zonate spore. *Rhabdosporites, Auroraspora, Calyptosporites,* and *Endosporites* are "cavate" spores. *Biharisporites* is an example of an Upper Devonian megaspore, and the first monolete spore appears in upper Eifelian in Russia. It is of particular interest to note that the appearance of simple spores probably belonging to land plants coincides fairly well with the appearance of simple vascular plants. This adds to the confidence with which one can think of late Silurian and early Devonian as the time of origin of vascular plants.

Seeds have not been demonstrated in Devonian strata, but heterospory may have appeared as early as Givetian time, with the spores associated with *Enigmophyton* in Spitsbergen. Heterospory is known in several plants in Frasnian time (e.g. Pettitt, 1965), and numerous isolated megaspores have been reported from Upper Devonian strata (Chaloner, 1959). The closest approach to the seed condition is demonstrated by *Cystosporites devonicus* (Chaloner and Pettitt, 1964) from the Frasnian of Quebec. This fossil is a megaspore tetrad in which one spore enlarges and three abort. *Cystosporites* is a Carboniferous genus and it has been found only in the genus *Lepidocarpon*. Thus the tetrads described by Chaloner and Pettitt may indicate an early form of the seed habit, the lycopod type. Because they found no associated fructifications, the authors speculate that *Cystosporites* could represent a species of *Archaeopteris* in which the number of megaspores was much reduced. In view of the relative abundance and variety of lycopods in Upper Devonian and of our present knowledge of heterospory in *Archaeopteris,* I prefer to agree with the authors that this find is the beginning of the lycopod type of seed habit.

In summary, the importance of careful stratigraphic records of proved vascular plants is stressed. *Cooksonia,* a simple, leafless plant with terminal sporangia appears in late Silurian time as the first representative of Tracheophyta. Additional simple plants appear in lowest Devonian time, and the number and diversity of land plants increase markedly in succeeding deposits. The appearance of simple spores at first, and more complex ones subsequently, substantiates the results from megafossils, although vascular plant spores appear somewhat earlier in Silurian time than present records of megafossils indicate. Evolutionary series are becoming clearer as the morphology–anatomy of the plants is clarified. Psilophytales are distributed between two new subdivisions: Rhyniophytina with terminal sporangia and Zosterophyllophytina with lateral sporangia. The latter may have given rise to lycopods with *Asteroxylon* as an intermediate type. Rhyniophytina, on the other hand, seems to have evolved through Trimerophytina, a new subdivision, toward four groups—the cladoxylaleans, the coenopteridaleans, the true ferns, and the progymnosperms. The last may have given rise to both cycadophyte and coniferophyte lines. The importance of knowing whole plants is demonstrated by the changes in classification that are being effected, e.g. *Asteroxylon* is a lycopod, not a psilophyte; *Pseudosporochnus* is a cladoxylalean rather than a psilophyte; and *Archaeopteris* and *Callixylon* are names applied to different parts of one plant, neither a fern nor a gymnosperm. There is stronger support for the evolution of some leaves as enations, some as webbed, planated terminal branches, and some as entire, large branch systems. The evolution of branch systems found in Devonian progymnosperms into fronds found in Mississippian strata should be studied carefully by means of anatomical data. Heterospory is becoming better known in Devonian plants, and definitive descriptions of spores in situ are increasing in number. Isolated spores (sporae dispersae) promise to add precision to age determinations in continental strata and to facilitate interregional correlation of strata. Although Devonian seeds are still unknown, an approach to the seed habit is seen in the discovery of *Cystosporites,* heretofore found only within *Lepidocarpon* in Carboniferous rocks. The floras of oldest Devonian (Gedinnian) and youngest Devonian (Famennian) are the least well known. Both are extremely important. The older is significant because we are still groping for an understanding of the reasons for the abrupt and rapid increase in new kinds of plants after the earliest and simplest *Cooksonia.* The other is important because of the probable gradual transition from Devonian into Mississippian floras with the development of the seed habit, the true ferns, and several new subdivisions of Tracheophyta. Extensions in the stratigraphic range of Devonian plants are increasing in number and will lead to more detailed thinking about paleoecology. Gradually, as the flora is revealed in increasing detail, speculation about rates of evolution can go beyond the suggestion that early evolution could be rapid because the plants were invading a new area with an abundance of niches, because there was little competition, and because small genetic changes produced marked changes in morphology.

Acknowledgments. I wish to thank Miss Elfriede Abbe for her skillful preparation of the illustrations, and I am grateful for the opportunity to discuss this paper with Dr. Patricia Bonamo. This work was supported by a John Simon Guggenheim Memorial Fellowship and by National Science Foundation Grant GB 4493.

ADDENDUM

Since this manuscript was submitted in July 1966, new data have clarified and extended some of the tentative suggestions made originally. Foremost among these is the work on *Psilophyton.* Hueber and Banks (1967) selected a neotype for *P. princeps* Dawson 1859. It has spines and large clusters of terminal sporangia similar to those illustrated here as Figure 5A. Additional details are given in Hueber (in press). *Psilophyton princeps* should be added to the plants included in Trimerophytina. Other species of the genus undoubtedly will be added soon (e.g. *P. krauselii* Obrhel). *Dawsonites* can remain in Trimerophytina as a form genus for sporangia that are unconnected to an identifiable axis or that are not shown to occur in large clusters. Hueber and Banks (1967) showed also that *Psilophyton princeps* var. *ornatum* Dawson 1871 differs anatomically from *Psilophyton princeps.* Its lateral sporangia and its elliptic, exarch protostele relate it clearly to Zosterophyllophytina. In the present paper this variety has been referred to as *Psilophyton ornatum* or as *Psilophyton* (non Dawson, new name needed). Specifically this means that a new generic name should be erected for the variety *ornatum.*

Banks and Davis (1967) have extended the concept of Zosterophyllophytina by reporting a new genus with lateral sporangia.

Banks (in press) described the anatomy of *Hostinella* collected at Röragen in Norway. He accepted Obrhel's (1961) suggestion that this generic name be spelled with an *n* instead of an *m.* Its structure resembles that of a *Psilophyton,* thus reinforcing Halle's (1916) suggestion that his *Hostinella* might be part of his *Psilophyton goldschmidtii.* This raises the question whether *Hostinella* should remain in Rhyniophytina, as in the present paper, or should be transferred to Trimerophytina. No answer is possible until other specimens yield anatomical data.

Bonamo and Banks (1967) have now completed the description of fertile branches of *Tetraxylopteris,* comparing them in detail with those of *Protopteridium.* Their results bear directly on the problem of origin of megaphyllous leaves.

Matten and Banks (1967) have documented the evidence that the progymnosperm genera *Sphenoxylon* and *Tetraxylopteris* are synonymous.

Chaloner (1967) has contributed a well-documented account of the early occurrences of the spores of vascular plants. He reached conclusions on the origin of land plants that are similar to the views presented here. Banks (in press) has added details to the time of occurrence of the first macrofossils of land plants.

Pettitt and Beck (1967) reported the existence of seeds in Upper Devonian time, a step in advance of the *Cystosporites* mentioned in the present paper.

REFERENCES

Allen, K. C., 1965. Lower and Middle Devonian spores of North and Central Vestspitsbergen. *Palaeontology, 8:* 687–748.

Ananiev, A. R., 1957. New fossil plants from the Lower Devonian deposits of the village of Torgashino, south-eastern zone of western Siberia. (Transl., Geol. Surv. Canada, 64104), *Bot. Zhur., 42:* 691–702.

———, 1964. Recent studies on the Devonian floras of Siberia. Tenth Int. Bot. Congr., Edinburgh, p. 17–18 (abstr.).

Andrews, H. N., Jr., 1961. *Studies in Paleobotany.* Wiley, New York and London, 487 p.

———, 1963. Early seed plants. *Science, 142:* 925–31.

Andrews, H. N., Jr., T. L. Phillips, and N. W. Radforth, 1965. Paleobotanical studies in Arctic Canada. I. *Archaeopteris* from Ellesmere Island. *Canad. J. Bot., 43:* 545–56.

Arnold, C. A., 1935. Some new forms and new occurrences of fossil plants from the Middle and Upper Devonian of New York State. *Buffalo Soc. Natur. Sci., Bull., 17:* 1–12.

———, 1939. Observations on fossil plants from the Devonian of eastern North America. IV. Plant remains from the Catskill Delta deposits of northern Pennsylvania and southern New York. *Univ. Michigan, Mus. Paleont. Contrib., 5:* 271–314.

———, 1940. Structure and relationships of some Middle Devonian plants from western New York. *Am. J. Bot., 27:* 57–63.

———, 1952. Observations on fossil plants from the Devonian of eastern North America. VI. *Xenocladia medullosina* Arnold. *Univ. Michigan, Mus. Paleontol. Contrib., 9:* 297–309.

Axelrod, D. I., 1959. Evolution of the psilophyte paleoflora. *Evolution 13:* 264–75.

Banks, H. P., 1961. The stratigraphic occurrence of Devonian plants with applications to phylogeny, p. 963–68, in *Recent Advances in Botany,* v. 2. Univ. Toronto Press.

———, 1964. Putative Devonian ferns. *Torrey Bot. Club Mem. 21:* 10–25.

———, 1965. Some recent additions to the knowledge of the early land flora. *Phytomorphology, 15:* 235–45.

———, 1966. Anatomy of a *Hostimella, Am. J. Bot.,* 53 (6/2): 628.

———, in press. The stratigraphic occurrence of early land plants and its bearing on their origin. Vol. II, *Proc. Int. Symposium on the Devonian System.* D. H. Oswald, ed., Calgary, Canada.

———, in press. Anatomy and affinities of a Devonian *Hostinella. Phytomorphology.*

Banks, H. P., and M. R. Davis, 1967. A new genus of Devonian zosterophylloids. *Am. J. Bot., 54:* 650.

Beck, C. B., 1957. *Tetraxylopteris schmidtii* gen. et sp. nov., a probable pteridosperm precursor from the Devonian of New York. *Am. J. Bot., 44:* 350–67.

——, 1960. The identity of *Archaeopteris* and *Callixylon. Brittonia, 12:* 351–68.

——, 1962. Reconstructions of *Archaeopteris* and further consideration of its phylogenetic position. *Am. J. Bot., 49:* 373–82.

——, 1963. *Ginkgophyton* (*Psygmophyllum*) with a stem of gymnospermic structure. *Science, 141:* 431–33.

Benson, M., 1935. The fructification, *Calathiops Bernhardti,* n. sp. *Ann. Bot., 49:* 155–60.

Bertrand, P., (1913) 1914. Étude du stipe de l'*Asteropteris noveboracensis.* Twelfth Congr. Geol. Int., Canada, Compt. Rend., p. 909–24.

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

Bonamo, P. M., and H. P. Banks, 1966a. A study of the fertile branches of *Tetraxylopteris. Am. J. Bot.,* 53 (6/2): 628.

——, 1966b. *Calamophyton* in the Middle Devonian of New York State. *Am. J. Bot.,* 53: 778–91.

——, 1967. *Tetraxylopteris schmidtii:* Its fertile parts and its relationships within the Aneurophytales. *Am. J. Bot., 54:* 755–68.

Bower, F. O., 1935. *Primitive Land Plants.* Macmillan, London.

Carluccio, L. M., F. M. Hueber, and H. P. Banks, 1966. *Archaeopteris macilenta,* anatomy and morphology of its frond. *Am. J. Bot. 53:* 719–30.

Chaloner, W. G., 1959. Devonian megaspores from arctic Canada. *Palaeontology, 1:* 321–32.

——, 1967. Spores and land plant evolution. *Review Paleobotany and Palynology, 1.*

Chaloner, W. G., and J. M. Pettitt, 1964. A seed megaspore from the Devonian of Canada. *Palaeontology, 7:* 29–36.

Croft, W. N., and W. H. Lang, 1942. The Lower Devonian flora of the Senni beds of Monmouthshire and Breconshire. *Phil. Trans. Roy. Soc., 231B:* 131–63.

Cronquist, A., A. Takhtajan, and W. Zimmermann, 1966. On the higher taxa of Embryobionta. *Taxon, 15:* 129–34.

Delevoryas, T., 1962. *Morphology and evolution of fossil plants.* Holt, Rinehart & Winston, New York, 189 p.

Eames, A. J., 1936. *Morphology of Vascular Plants, Lower Groups.* McGraw-Hill, New York.

Grierson, J. D., and H. P. Banks, 1963. Lycopods of the Devonian of New York State. *Palaeontographica America, 4:* 219–95.

Halle, T. G., 1916. Lower Devonian plants from Röragen in Norway. *Kungl. Svenska Vetenskapsakad. Handl., 57:* 1–46.

——, 1936. On *Drepanophycus, Protolepidodendron* and *Protopteridium,* with notes on the Palaeozoic flora of Yunnan. *Palaeontologia Sinica A., 1:* 1–38.

Harris, T. M., 1929. *Schizopodium Davidi* gen. et. sp. nov., a new type of stem from the Devonian rocks of Australia. *Phil. Trans. Roy. Soc., 217B:* 395–410.

Heard, A., 1927. On Old Red Sandstone plants showing structure from Brecon (South Wales). *Geol. Soc.* (*London*) *Quart. J., 88:* 195–208.

Høeg, O. A., 1942. The Downtonian and Devonian flora of Spitzbergen. *Norges Svalbard-Og Ishavs–Undersøkelser Skr., 83:* 1–228.

Hopping, C. A., 1956. On a specimen of *"Psilophyton robustius"* Dawson, from the Lower Devonian of Canada. *Proc. Roy. Soc. Edinb., 66B:* 10–28.

Hueber, F. M., 1959. "Fossil flora of the *Onteora* 'red beds' (Upper Devonian) in New York State, a preliminary survey." M.S. thesis, Cornell Univ., 55 p.

——, 1960. "Contributions to the fossil flora of the *Onteora* 'red beds' (Upper Devonian) in New York State." Ph.D. thesis, Cornell Univ. (Libr. Congr. Card No. Mic. 61–1432) 212 p., Univ. Microfilms, Ann Arbor, Mich. (*Diss. Abstr., 22:* 405–06).

——, 1961. Psilophytes in the Upper Devonian of New York. *Am. J. Bot., 48:* 541 (abstr.).

——, 1964. The psilophytes and their relationship to the origin of ferns. *Torrey Bot. Club Mem., 21:* 5–9.

——, in press. *Psilophyton:* The genus and the concept. Vol. II, *Proc. Int. Symposium on the Devonian System,* D. H. Oswald, ed., Calgary, Canada.

Hueber, F. M., and H. P. Banks, 1967. *Psilophyton princeps:* The search for organic connection, *Taxon, 16:* 81–85.

Jaeger, H., 1962. Das Alter der ältesten bekannten Landpflanzen (*Baragwanathia*-flora) in Australien auf Grund der begleitenden Graptolithen. *Paläont. Z., 36:* 7.

Kedo, G. I., 1955. Middle Devonian spores from north-east Belorussiya SSR. *Palaeont. i. stratig. BSSR, 1:* 5–47 (in Russian).

Kidston, R., and W. H. Lang, 1917. On Old Red Sandstone plants showing structure from the Rhynie chert bed, Aberdeenshire. Part I. *Rhynia Gwynne-Vaughani,* Kidston and Lang. *Trans. Roy. Soc. Edinb., 51:* 761–84.

——, 1920a. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part II. Additional notes on *Rhynia Gwynne-Vaughani,* Kidston and Lang; with descriptions of *Rhynia major* n. sp. and *Hornea Lignieri,* n. g., n. sp. *Trans. Roy. Soc. Edinb., 52:* 603–27.

——, 1920b. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part III. *Asteroxylon Mackiei* Kidston & Lang. *Trans. Roy. Soc. Edinb., 52:* 643–80.

Kräusel, R., and H. Weyland, 1926. Beiträge zur Kenntnis der Devonflora II. *Abhandl. Senckenberg. Naturforsch. Ges., 40:* 115–55.

——, 1938. Neue Pflanzenfunde im Mitteldevon von Elberfeld. *Palaeontographica, 83B:* 172–95.

——, 1941. Pflanzenreste aus dem Devon von Nord-Amerika. *Palaeontographica, 86B:* 1–78.

Kulp, J. L., 1961. Geologic time scale. *Science, 133:* 1105–14.

Lang, W. H., 1926. Contributions to the study of the Old Red Sandstone flora of Scotland, III. On *Hostimella (Ptilophyton) thomsoni* and its inclusion in a new genus, *Milleria. Trans. Roy. Soc. Edinb., 54:* 785–90.

——, 1937. On the plant-remains from the Downtonian of England and Wales. *Phil. Trans. Roy. Soc. B, 227:* 245–91.

Leclercq, S., 1940. Contribution à l'étude de la flore du Dévonien de Belgique. *Mém. Acad. Roy. Belg., 12:* 3–65.

——, 1951. Étude morphologique et anatomique d'une fougère du Dévonien Supérieur, le *Racophyton zygopteroides* nov. sp. *Ann. Soc. Géol. Belg., 9:* 1–58.

——, 1954. An Upper Devonian Zygopterid showing clepsydropsoid and etapteroid features. *Am. J. Bot., 41:* 488–92.

———, 1956. Evidence of vascular plants in the Cambrian. *Evolution, 10:* 109–14.

———, 1957. Étude d'une fructification de Sphenopside à structure conservée du Dévonien Supérieur. *Mém. Acad. Roy. Belg., 14:* 1–39.

———, 1962. Deux plantes du Dévonien. *Bull. Soc. Roy. Bot. Belg., 95:* 51–59.

Leclercq, S., and H. N. Andrews, Jr., 1960. *Calamophyton bicephalum,* a new species from the Middle Devonian of Belgium. *Ann. Missouri Bot. Gard., 47:* 1–23.

Leclercq, S., and H. P. Banks, 1962. *Pseudosporochnus nodosus* sp. nov., a Middle Devonian plant with cladoxylalean affinities. *Palaeontographica, 110B:* 1–34.

Leclercq, S., and H. J. Schweitzer, 1965. *Calamophyton* is not a sphenopsid. *Bull. Acad. Roy. Belg., 11:* 1394–1402.

Lyon, A. G., 1964. The probable fertile region of *Asteroxylon Mackiei* K. and L. *Nature, 203:* 1082–83.

Mamay, S. H., and H. N. Andrews, Jr., 1950. A contribution to our knowledge of the anatomy of *Botryopteris. Torrey Bot. Club Bull., 77:* 462–94.

Matten, L. C., 1965. "Contributions to the Upper Devonian flora of New York." Ph.D. thesis, Cornell Univ. (Libr. Congr. Card No. Mic. 65–14, 701) 141 p., Univ. Microfilms, Ann Arbor, Mich. (*Diss. Abstr., 26:* 2999–3000).

Matten, L. C., and H. P. Banks, 1967. Relationship between the Devonian progymnosperm genera *Sphenoxylon* and *Tetraxylopteris. Bull. Torrey Bot. Club, 94:* 321–33.

McGregor, D. C., 1964. Devonian miospores from the Ghost River Formation, Alberta. *Geol. Surv. Canada, Bull., 109:* 1–31.

Meeuse, A. D. J., 1963. From ovule to ovary: A contribution to the phylogeny of the megasporangium. *Acta Biotheoret., 16:* 127–82.

Nikitin, P. A., 1934. Fossil plants of the Petino horizon of the Devonian of the Voronezh region I. *Kryshtofovichia africani* nov. gen. et. sp. *Akad. Nauk SSSR, Izv., Ser. 7:* 1079–92 (in Russian).

Obrhel, J., 1961. Die Flora der Srbsko-Schichten (Givet) des mittelböhmischen Devons. *Sbornik Ustředniko Ústavu, Geologického, 26:* 7–44.

———, 1962. Die Flora der Pridolí-Schichten (Budňany-Stufe) des mittelböhmischen Silurs. *Geologie, 11:* 83–97.

Pettitt, J. M., 1965. Two heterosporous plants from the Upper Devonian of North America. *Brit. Mus. (Nat. Hist.) Geol. Bull., 10:* 83–92.

Pettitt, J. M., and C. B. Beck, 1967. Seed from Upper Devonian. *Science, 156:* 1727–29.

Pichi-Sermolli, R. E. G., 1958. The higher taxa of the Pteridophyta and their classification. *In* "Systematics of today," *Uppsala Universitets Årsskrift, 6:* 70–90.

Read, C. B., 1937. The flora of the New Albany shale. Part 2. The Calamopityeae and their relationships. *U.S. Geol. Surv. Prof. Paper, 186E:* 81–104.

———, 1938. Some Psilophytales from the Hamilton group in western New York. *Torrey Bot. Club Bull., 65:* 599–606.

Richardson, J. B., 1960. Spores from the Middle Old Red Sandstone of Cromarty, Scotland. *Palaeontology, 3:* 45–63.

———, 1964. Stratigraphical distribution of some Devonian and Lower Carboniferous spores, *Cinquième Congr. Int. Stratigr. Géol. Carbonifère, 13B:* 1111–14.

———, 1965. Middle Old Red Sandstone spore assemblages from the Orcadian basin north-east Scotland. *Palaeontology, 7:* 559–605.

Streel, M., 1964. Une association de spores du Givétian Inférieur de la Vesdre, à Goé (Belgique). *Ann. Soc. Géol. Belg., 87:* 1–30.

Tchibrickova, E. V., 1962. Spores from Devonian terrigenous deposits of the Bashkir region and the southern slopes of the Urals. *Akad. Nauk. Bashkir. SSR* 353–476. (in Russian).

Vigran, J. O., 1964. Spores from Devonian deposits, Mimerdalen, Spitsbergen. *Norsk Polarinstitutt Skr.*, *132:* 5–32.

Walton, J., 1957. On *Protopitys* (Göppert): With a description of a fertile specimen "*Protopitys scotica*" sp. nov. from the calciferous sandstone series of Dunbartonshire. *Trans. Roy. Soc. Edinb.*, *63:* 333–40.

Zimmermann, W., 1949. Geschichte der Pflanzen. Thieme, Stuttgart, 111 p.