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SYSTEMATIC CHARACTERS OF DEVONIAN FERNS¹

STEPHEN E. SCHECKLER²

ABSTRACT

Several groups of fern-like plants occur in the Middle and Upper Devonian and are probably evolved from the Trimerophytina of Banks. The branching systems of these plants are predominantly three-dimensional and are deceptively similar. All the plants are characterized by mesarch development of their primary xylem, but certain histological details permit their separation into at least three major groups—Progymnospermopsida, Cladoxylopsida, and Coenopteridopsida. The first group is somewhat better known anatomically than the others and is the least fern-like, probably evolving towards the gymnosperms. The second class is anatomically distinct from most other plant groups. The Devonian plants placed in Coenopteridopsida, with the exception of *Rhacophyton*, are mostly problematic. Utilizing data from these plants, several criteria are suggested as having value in the determination of the relationships of Devonian fern-like plants. In order of increasing value they are: cortical and epidermal histology, form of the primary xylem, presence (or absence) of secondary wood, and the structure of the protoxylem strands. The application of these criteria suggests that some, but not all, Devonian plants placed in Cladoxylopsida and Coenopteridopsida find their closest relationship with Carboniferous coenopterid ferns. No Devonian plant seems to be more closely related to modern ferns.

At present no Devonian plant is recognized as unequivocally related to the modern ferns. A number of Middle and Upper Devonian plants seem to be related to some Carboniferous coenopterid ferns, however. Our understanding of the relationships of the Devonian fern-like plants has been greatly aided by Banks' (1968) reclassification of Psilophytales into three new subdivisions: Zosterophyllophytina, Rhyniophytina, and Trimerophytina. The zosterophyll group is probably related to younger lycopods and is of no concern to a discussion of Devonian ferns. Trimerophytina is thought to have evolved from the more ancient and simple plants placed by Banks in Rhyniophytina. Plants at the trimerophyte level of organization are assumed to be the evolutionary source of the fern-like plants which radiated during Mid to Late Devonian time.

Trimerophytina currently includes four Lower Devonian genera: *Trimerophyton*, *Psilophyton*, *Pertica*, and *Dawsonites* (Banks, 1968; Kasper & Andrews, 1972). *Dawsonites* is a form genus for detached sporangia of the type borne by *Psilophyton*. Branching from the main axes of *Trimerophyton*, *Psilophyton*, and *Pertica* is pseudomonopodial, but the laterals divide isotomously, *i.e.* dichotomously or trichotomously, and form "tufts" of branchlets (Hopping, 1956; Hueber, 1968; Andrews, Kasper & Mencher, 1968; Kasper & Andrews, 1972). Some laterals of *Pertica* and *Psilophyton forbesii* (Fig. 13) terminate in pairs of sporangia. Other laterals are sterile and still others seem to be "mixed." Judging from morphology, fertile and sterile branches are homologous. Anatomy is known for *Psilophyton* (Fig. 1) and consists of an elliptical primary xylem strand and

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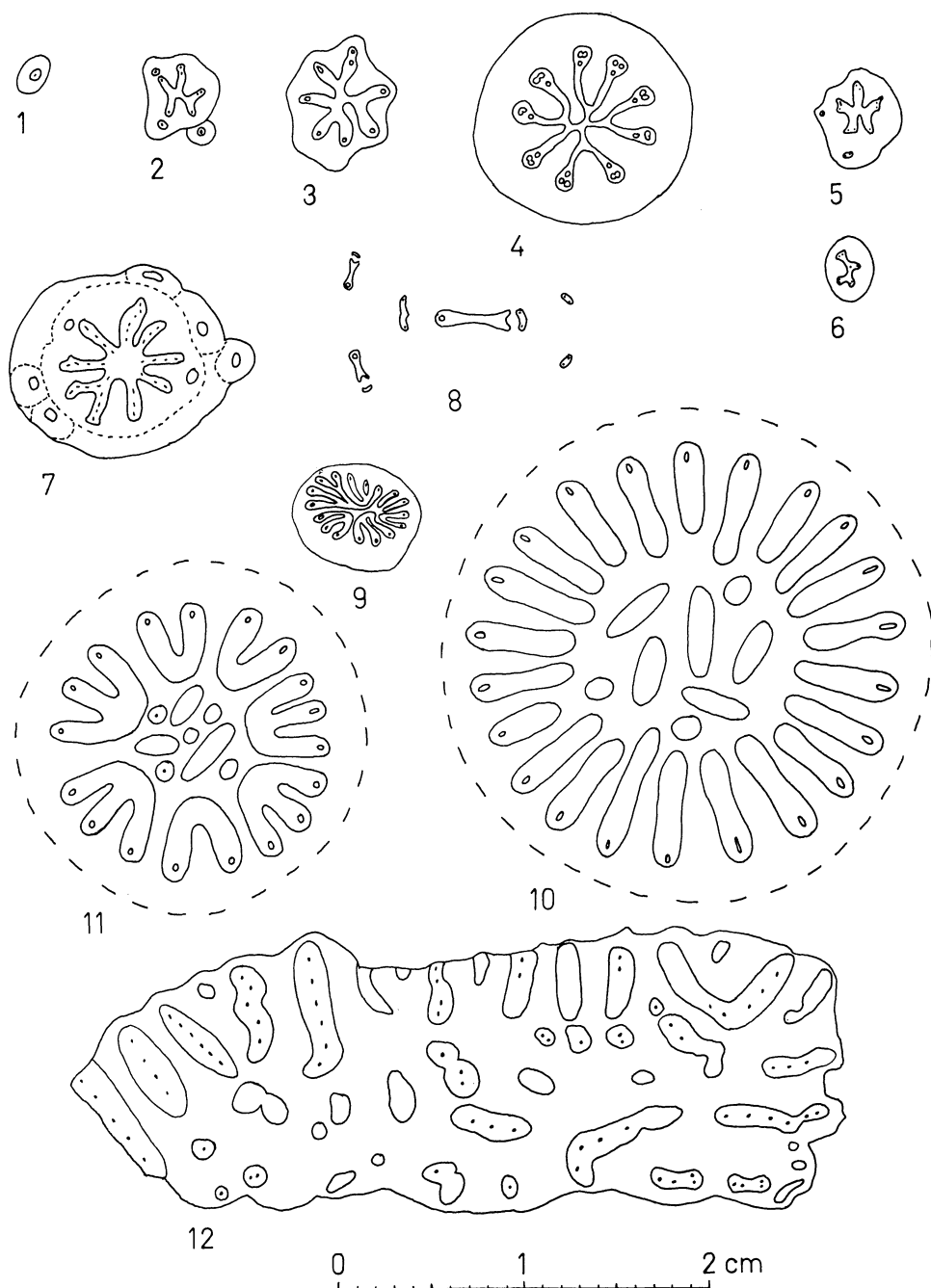
a well preserved outer cortex (Hueber & Banks, 1967; Hueber, 1968). Maturation of the xylem strand was mesarch to centrarch. From a plexus of Lower Devonian plants at the trimerophyte level of evolution it is suggested that the progymnosperms, cladoxylaleans, "coenopterids," and possibly some presphenopsids evolved (Banks, 1968; Skog & Banks, 1973). Each of these groups has similar morphology, but differences in their anatomy permit identification. Illustrations of many of these plants are found in Boureau (1970).

Progymnospermopsida was erected by Beck (1960a) for plants with fern-like reproduction but gymnospermous secondary tissues. Two groups of progymnosperms occur in the Middle and Upper Devonian, Aneurophytales and Archaeopteridales. The aneurophyte-type is the older and includes plants with the simplest morphology. Branching is helical or decussate except for the ultimate appendages, which dichotomize. One species, *Protopteridium minutum*, seems quite fern-like and had once been classified here. It has since been transferred to another genus, *Cathaiopteridium*, by Orléan (1966) and is no longer considered a progymnosperm. Branching in some of the younger archaeopterid-type plants is two-ranked, and the ultimate appendages are webbed and more obviously leaf-like. Sporangia are borne on some leaves in Archaeopteridales and on larger portions of the branching system in Aneurophytales. Despite the morphological resemblance of some progymnosperms to ferns, their vascular anatomy is distinctly that of a gymnosperm. This, along with some other features, has led to the conclusion that progymnosperms are neither ferns nor related to them, but are ancestral to younger gymnosperms (Beck, 1964, 1970, 1971; Namboodiri & Beck, 1968; Scheckler & Banks, 1971a).

Cladoxylopsida forms a distinctive group of Middle Devonian to Lower Carboniferous plants. The group is characterized by dissected xylem and is well summarized by Leclercq (1970). Only the Devonian plants are known morphologically. The Middle Devonian genus *Pseudosporochnus* is the most completely known. Leclercq and Banks (1962) demonstrated the probability that at least one species, *P. nodosus*, was a small tree which bore a crown of branches at its summit (Fig. 18). Major branches divided equally into a number of lesser branches and all bore helically arranged leaves. The leaves divided in one plane and were either sterile or bore pairs of sporangia at their tips. The anatomy of the branches (Figs. 10–11) consists of an outer system of radially oriented bundles and an inner system of elliptical or terete strands (Leclercq & Lele, 1968). Protoxylem strands are mesarch, and those near the periphery of the outer xylem bundles developed cavities called peripheral loops.

Branches of the Middle Devonian *Cladoxylon scoparium* also divided equally and bore helically arranged ultimate appendages (Kräusel & Weyland, 1926). Fan-shaped organs (Fig. 17) replaced some ultimate appendages and bore terminal sporangia. Although the precise morphology of the fan-shaped fertile organs and the ultimate appendages is still not well understood, the two types of organs seem to be homologous (Leclercq, 1970). The xylem of *C. scoparium* consists of numerous interconnected strands much like that of *C. dawsonii* (Fig. 9).

Calamophyton had long been thought of as a pre-sphenopsid but was shown



FIGURES 1-12. Outlines of typical cross sections of some Devonian fern-like plants. Where known, the positions of protoxylem strands are indicated by dots or small circles.—1. *Psilophyton* sp. (from Hueber & Banks, 1967).—2. *Ibyka amphikoma* (from Skog & Banks, 1973).—3. *Arachnoxylon kopfii* (from Read, 1938).—4. *Asteropteris noveboracensis* (modified from Dawson, 1881).—5. *Iridopteris eriensis* (from Arnold, 1940).—6. *Stenokoleos bifidus* (from Matten & Banks, 1969).—7. *Langoxylon asterochlaenoideum* (from Stockmans, 1968).—8.

to have cladoxylalean anatomy (Leclercq & Schweitzer, 1965). Morphologically, this Middle Devonian plant is similar to *Pseudosporochnus* and *Cladoxylon scoparium* but differs by having recurved fertile organs which recall the sporangiophores of younger sphenopsids. Banks (1968) questioned whether anatomy would outweigh the morphology of the fertile organs, and *Calamophyton* continues to be treated as an early sphenopsid (Bierhorst, 1971; Skog & Banks, 1973).

Two other cladoxylaleans, both Upper Devonian, are also known from morphology. One has been referred to the genus *Cladoxylon* and branched dichotomously (Leclercq, 1970; 139). The other is a new plant discovered by me. A detailed description will be published elsewhere, but the new plant differs from other Devonian Cladoxylales by branching pseudomonopodially and by possessing an actinostele in proximal branches.

All other Devonian cladoxylaleans are known only from petrifications. Two are described here. *Xenocladia* is known only from fragments. Evidently this Middle Devonian plant represented a portion of a large trunk like that possessed by *Pseudosporochnus* (Arnold, 1952). *Xenocladia* (Fig. 12) differs from other Cladoxylales by its size and the large number of protoxylem strands found in some bundles. Many of the xylem strands of the Upper Devonian *Cladoxylon dawsonii* (Fig. 9) are connected at the center of the axis. Protoxylem strands are found only at the tips of the strands (Read, 1935).

Astralocaulis (= *Schizopodium* Harris) is often compared with Cladoxylales. The genus may have been misinterpreted, however, and is currently under investigation (Hueber, 1971). For this reason it will not be described here.

Several Devonian plants (*Arachnoxylon*, *Reimannia*, *Iridopteris*, and *Asteropteris*) with lobed xylem strands have been placed into Coenopteridopsida (Banks, 1968). To this list might be added *Ibyka*, *Langoxylon*, and *Stenokoleos*. The chief feature relating these plants to the Carboniferous coenopterid ferns is the resemblance of some of their protoxylem strands to peripheral loops. Noteworthy also, however, is the similarity of some to the Lower Carboniferous genus *Protoclepsydraxis* (Long, 1967). The value of *Reimannia* has been greatly diminished by the findings that similar three-lobed xylem strands occur in several other Devonian plants (e.g. *Stenokoleos*, *Triloboxylon*, *Proteokalon*, and *Actinoxylon*). The existence of *Reimannia* as a natural taxon is seriously in doubt, and it will not be considered any further here.

Ibyka has been recently described from petrifications and compressions as a possible Middle Devonian precursor to sphenopsids (Skog & Banks, 1973). I include this plant here because of its anatomical similarity to the others. *Ibyka* branched helically except for its ultimate appendages and fertile organs, which dichotomized (Fig. 14). The fertile organs were not well preserved but

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Rhacophyton zygopteroides primary xylem of fertile frond (from Leclercq, 1951).—9. *Cladoxylon dawsonii* (from Read, 1935).—10. *Pseudosporochnus nodosus* first order branch (from Leclercq & Lele, 1968).—11. *Pseudosporochnus nodosus* third order branch (from Leclercq & Lele, 1968).—12. *Xenocladia medullosina* (from Arnold, 1952).

seem to be homologous to ultimate appendages. A typical cross section (Fig. 2) shows a five- or six-armed actinostele from which traces depart helically.

Arachnoxylon (Fig. 3) is known only from Middle and Upper Devonian petrifications (Arnold, 1935; Read, 1938; Banks, 1964, 1968). It differs from the petrified axes of *Ibyka* by its larger size and greater number of arms. Traces have not been described for *Arachnoxylon*, but from the protoxylem arrangement of Read's specimen (Fig. 3) one can guess that they were helical.

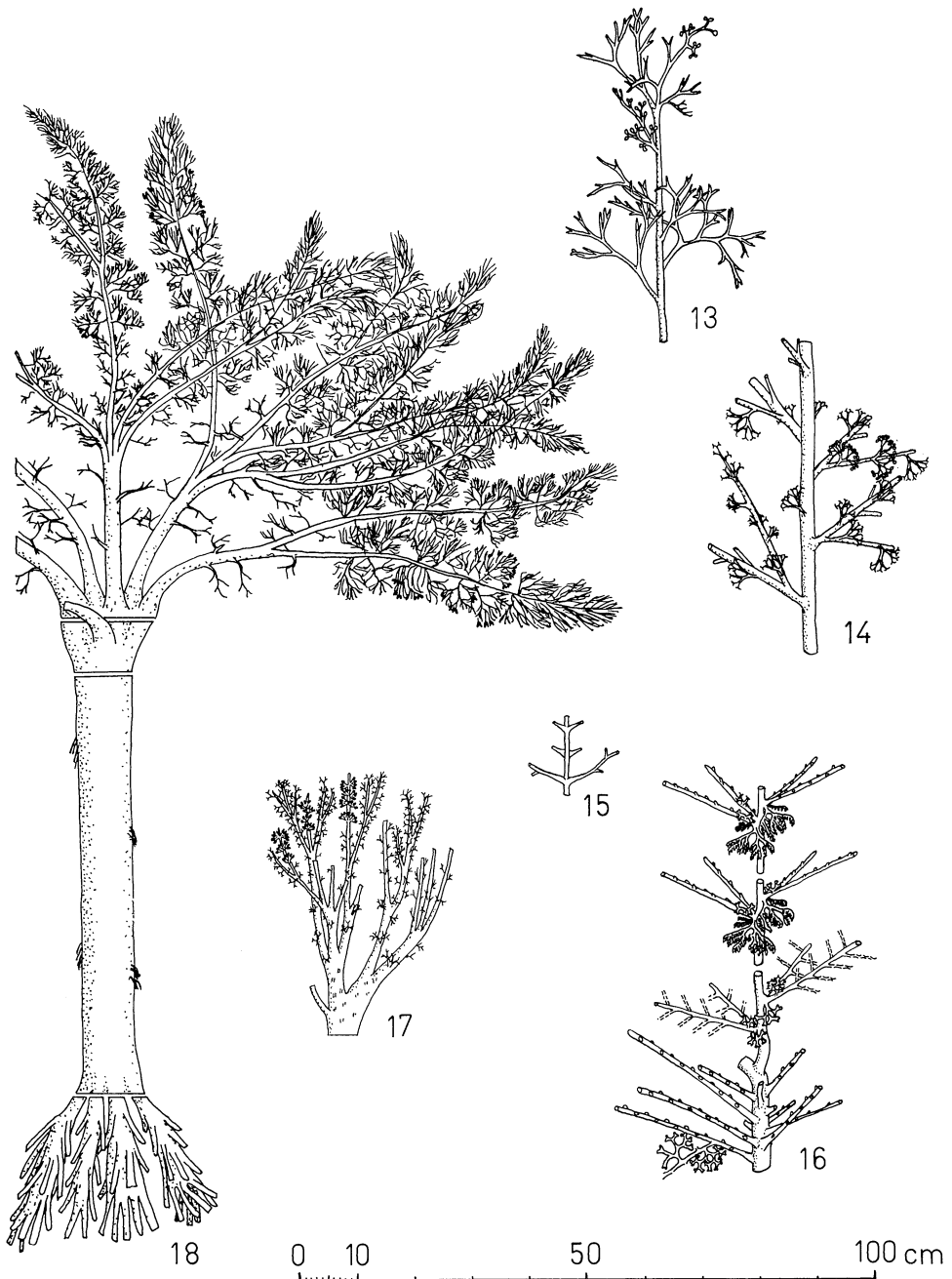
Asteropteris (Fig. 4) is also known from Middle and Upper Devonian petrifications (Banks, 1964). Its xylem strand is similar to those of *Arachnoxylon* and *Ibyka* but is larger, has more lobes, and bears whorled traces to appendages. The traces are bilobed at first but develop four protoxylem poles distally (Bertand, 1913; Dawson, 1881).

Langoxylon (Fig. 7) occurs in the Middle Devonian and has a large actinostele. Appendages are numerous and probably depart helically (Stockmans, 1968). *Langoxylon* differs from the previous genera by having many protoxylem strands in the arms of the actinostele.

Iridopteris (Fig. 5) is a poorly known Middle Devonian petrification genus (Arnold, 1940). Its xylem strand is bilaterally symmetrical unlike the others and it seems to bear two sizes of appendages. The larger is supplied by an elliptical trace with two peripheral protoxylem strands. The other type of appendage is supplied with a small centrarch trace. Protoxylem strands are located at the margins of the actinostele and differences in their arrangement suggest a helical departure of the smaller appendages. Frequently the protoxylem strands are paired and aligned tangentially.

Stenokoleos was first described from rocks thought to be Mississippian, but the genus is known also from the Upper and possibly Middle Devonian (Matten, 1968; Matten & Banks, 1969). The Upper Devonian species, *S. bifidus*, bears distichous pairs of appendages, which bear two-ranked laterals (Fig. 15). The xylem strand of the main axis is highly variable, and one of several possible shapes is shown in Figure 6. Traces to the appendages are three-lobed at first. The protoxylem strands of *Stenokoleos* are paired and tangentially aligned at the tips of the arms supplying appendage traces. Matten and Banks (1969) drew attention to the similar departure of traces in *Stenokoleos*, *Tristichia*, and *Tetrastichia*. The latter two genera are presumed to be pteridosperms, but seeds have not been found attached. The departure of traces of the three genera is also remarkably similar to some parts of the Carboniferous coenopterid *Stauropteris* (Surange, 1952; Emberger, 1968).

The Upper Devonian genus *Rhacophyton* represents another type of coenopterid fern. In this type (etapteroid) the peripheral loop opens during the departure of a trace. The other Devonian plants thought to be coenopterids have a different type of peripheral loop (clepsydroid) which remains closed. Two species of *Rhacophyton* are well known from both compressions and petrifications, *R. zygopteroides* and *R. ceratangium* (Leclercq, 1951, 1954; Andrews & Phillips, 1968). The two differ mainly by the morphology of their pinnules and fertile appendages. *Rhacophyton* (Fig. 16) has a large stem which bears fronds in a crowded helix. Vegetative fronds are twice pinnate, and the pinnules



FIGURES 13-18. Reconstructions of the known branching of some Devonian fern-like plants.—13. *Psilophyton forbesii* (from Andrews, Kasper & Mencher, 1968).—14. *Ibyka amphikoma* (from Skog & Banks, 1973).—15. *Stenokoleos bifidus* (from Matten & Banks, 1969).—16. *Rhacophyton zygopteroides* (from Leclercq, 1951).—17. *Cladoxylon scoparium* (from Kräusel & Weyland, 1926).—18. *Pseudosporochnus nodosus* (from Leclercq & Banks, 1962).

are bifurcate. Fertile fronds are four-ranked and more complex. Their primary pinnae divide at the base and are subtended by a pair of pendulous organs, which bear the sporangia. The xylem of the stem of *R. zygopteroides* is stellate, that of the frond (Fig. 8) is bipolar. *Rhacophyton ceratangium* is said to have a bipolar xylem strand in all parts. Externally *Rhacophyton* resembles the branching systems of some progymnosperms placed in Aneurophytales (Andrews & Phillips, 1968; Bierhorst, 1971). The anatomy of the frond of *Rhacophyton* is so similar to some other coenopterid ferns, however, that it would be difficult to deny an affinity.

If it becomes better known, the Middle Devonian genus *Protocephalopteris* may prove to be related to *Rhacophyton*. Despite similarities in their reconstructions (Schweitzer, 1968), however, *Protocephalopteris* is based on only a few small fragments, while *Rhacophyton* is far better known.

The preceding descriptions show that a large number of Middle and Upper Devonian plants have some of the characters of primitive ferns, *i.e.* reproduction by spores, branching systems that resemble fronds, and mesarch xylem strands. Identification of the "true" affinities of these plants is difficult, but study of their anatomy suggests that it is possible. Several anatomical criteria are here suggested as useful in the determination of relationship of the Devonian fern-like plants. In order of increasing value they are: histology of the cortex and epidermis, form of the primary xylem, presence of a vascular cambium, and the structure of the protoxylem strand.

Cortical histology affects the appearance of some compressed axes. Specimens of *Pseudosporochnus nodosus* have a distinctive pattern of sculpturing. Leclercq and Banks (1962) attributed the sculpturing to the presence of "nests" of sclereids in the cortex. Tangential sections of the cortex of a newly collected petrification referable to *Pseudosporochnus* show that the "nests" of sclereids occur in the same pattern seen on compressions. Other compressed axes show a different type of pattern dominated by longitudinal ridges. The anatomy of these axes suggests that the ridges are due to the multi-stranded xylem rather than to the distribution of different types of cells in the cortex. Hairs are present on compressed axes of *Ibyka* and a petrified axis of *cf. Pseudosporochnus* and demonstrate that they can be recognized in either type of preservation. The features just described can be useful in separating specimens of a plant from others in the same collection (Leclercq & Banks, 1962; Skog & Banks, 1973).

Some progymnosperms (Aneurophytales) and the plants described earlier as Devonian coenopterids have lobed xylem strands. Other progymnosperms (Archaeopteridales) and Cladoxylales have primary xylems consisting of several discrete strands. The multi-stranded type of primary xylem has been suggested as evolving by dissection of an actinostele (Harris, 1929; Arnold, 1952; Namboodiri & Beck, 1968; Skog & Banks, 1973). If this evolutionary sequence is valid, it should be possible to cite examples of Devonian plants whose actinosteles contain abundant xylem parenchyma. Three plants with this type of primary xylem are listed here: my new plant with cladoxylalean anatomy, *Proteokalon* (Aneurophytales, see Scheckler & Banks, 1971*b*), and one presumed early coenopterid. This suggests that the dissection of an actinostele occurred several

times in Devonian plants. The parallel development of a multi-stranded xylem from an actinostele indicated by these plants suggests that classifications based solely on numbers of xylem strands in an axis are unrealistic.

Several Devonian Cladoxylales (*Xenocladia*, *Cladoxylon dawsonii*, and my new plant) have aligned cells that resemble secondary xylem at the margins of some xylem bundles. The only "cladoxylalean" in which vascular rays have been illustrated is *Cladoxylon kidstoni* (Solms-Laubach, 1910: Taf. 3, Fig. 13). The specimen upon which the species was based was only doubtfully referred to *Cladoxylon*, however (Seward, 1917: 205–207). Numerous tangential and radial sections of *Xenocladia*, an Upper Devonian *Cladoxylon*, and my new plant clearly demonstrate that vascular rays were absent from the aligned cells of these plants. In agreement with Leclercq (1970), I interpret the aligned cells to be metaxylem. Additional support for this interpretation comes from the structure of the walls of the outer cells of the xylem bundles of several Devonian Cladoxylales. Both the aligned cells of *Xenocladia* and the late metaxylem elements of other, smaller axes have thicker walls and fewer pits than the inner, early metaxylem tracheids. These cells appear fiber-like and may prove to be a distinctive anatomical character of Cladoxylales and related plants. Progymnosperms differ from the Devonian Cladoxylales by possessing a vigorous vascular cambium that produced remarkably gymnospermous secondary xylem and secondary phloem (Beck, 1970; Scheckler & Banks, 1971a, b). The aligned tracheids present in some axes of *Rhacophyton* (Leclercq, 1951; Andrews & Phillips, 1968) have not been shown to have vascular rays and may also be metaxylem.

Closed (clepsydropsoid) versus open (etapteroid) peripheral loops may be fundamental to the classification of Coenopteridopsida (Leclercq, 1954). The closed peripheral loop has been defined as a rod of parenchyma surrounded by tracheids of the protoxylem (Leclercq, 1970). This type of protoxylem structure has been illustrated for *Clepsydropsis* and for some of the Carboniferous Cladoxylales (Bertrand, 1935; Galtier, 1966). It occurs also in *Stenokoleos* (Beck, 1960b; Matten & Banks, 1969), *Cladoxylon dawsonii*, and another Devonian plant with an actinostele. The protoxylem tracheids of the peripheral loop are not disorganized. The lack of nearby xylem parenchyma cells outside of the peripheral loop suggests that the parenchyma of the loop should not be interpreted as cavity parenchyma or tyloses as Bierhorst (1971) has done. Parenchyma near the tip of a xylem arm of *Triloboxylon* (Aneurophytales, Scheckler & Banks, 1971a) is deceptively similar to a peripheral loop, but the protoxylem strands of the genus are independent of it. A different type of protoxylem structure occurs in some other Devonian plants and seems to have been confused with a peripheral loop. The protoxylem strands of *Ibyka*, a petrified specimen of *cf. Pseudosporochnus*, and my new cladoxylalean disintegrate and form lacunae that superficially resemble peripheral loops. The interiors of the lacunae differ by being filled with disorganized protoxylem tracheids instead of parenchyma (see Skog & Banks, 1973).

The peripheral loops of *Rhacophyton* and some other coenopterids (*e.g.* *Dineuron*, *Metaclepsydropsis* and others—see Boureau, 1970) differ from those

just described by opening during the departure of traces. Whether this type of loop was filled with parenchyma or some other cells, it forms an easily recognized structure that serves to relate these fern-like plants.

Utilizing the criteria outlined above, a number of observations and interpretations can be made regarding Devonian "ferns." The presence of a well developed vascular cambium in Devonian progymnosperms relates them with younger gymnosperms, but not with ferns. The inability to demonstrate vascular rays in *Rhacophyton* and Cladoxylopsida suggests that the aligned cells present on some axes of each should not be used as evidence against their affinity to other fern-like plants.

The presence of two distinct types of protoxylem structure in some members of both Cladoxylales and the Devonian coenopterid-like plants suggests that each assemblage may contain unrelated plants. Skog and Banks (1973) suggested that *Ibyka* and some of the Middle Devonian Cladoxylales formed a plexus from which evolved sphenopsids. The presence of protoxylem lacunae in *Ibyka* and many sphenopsids was viewed by them as significant to their argument. Protoxylem lacunae, however, are not unique to Sphenopsida and are found in representatives of the ferns, gymnosperms, and angiosperms (Boureau, 1970; Bierhorst, 1971). The closed parenchymatous peripheral loop, on the other hand, does seem to be unique to some cladoxylalean plants and some Devonian and Carboniferous coenopterid-like plants.

The demonstration that at least three fern-like plants which had abundant xylem parenchyma in their primary xylem strands existed in the Devonian suggests that dissected xylem may have arisen in several groups of early plants. If so, this might mean that not all plants with cladoxylalean anatomy were necessarily related. Nor were they necessarily unrelated to other plants with actinosteles. Although the data are premature, I make the tentative suggestion that the Devonian and Carboniferous plants with closed, parenchymatous peripheral loops will ultimately be found to be related. The other plants, with protoxylem lacunae, are possibly parallel in their anatomy and some, as Skog and Banks (1973) suggest, may be related to the sphenopsids.

The points raised in the preceding discussion of Devonian "ferns" are summarized as follows:

1. Trimerophytina of Banks, from the Lower Devonian, is the most likely source for the fern-like plants found in younger strata. Trimerophytes and their presumed derivatives, Progymnospermopsida, Cladoxylopsida, Coenopteridopsida, have mesarch xylem strands and many branch pseudomonopodially.
2. Some progymnosperms have simply organized branching systems that resemble those of other fern-like plants. Anatomy, however, suggests that they were ancestral to younger gymnosperms.
3. Plants with cladoxylalean anatomy form a distinct group from the Middle Devonian to Lower Carboniferous. Their relationships with other groups of plants are obscure.
4. Some of the Middle and Upper Devonian plants with lobed xylem strands

may be related to Carboniferous coenopterid ferns. Many have protoxylem strands that resemble peripheral loops.

5. *Rhacophyton* has similar morphology to some progymnosperms but its anatomy demonstrates its affinity with Zygopteridaceae.

6. Cortical histology and the presence of hairs can sometimes be determined from either compressed or petrified axes and offer valuable clues to the identity of specimens.

7. The possibility that multi-stranded vascular systems could have evolved by dissection of actinosteles is supported by the presence of xylem parenchyma in the primary xylem strands of three, apparently unrelated, Devonian plants.

8. Longitudinal sections of *Xenocladia*, *Cladoxylon* sp., and a new plant show that vascular rays are absent from the aligned cells of these Devonian plants. The aligned elements are interpreted as metaxylem. They and the late metaxylem elements of other cladoxylalean axes have thicker walls and fewer pits than early metaxylem tracheids and are fiber-like. In contrast, vascular rays are obvious in the wood of progymnosperms. The aligned tracheids of *Rhacophyton* have not been demonstrated to have vascular rays and might also be metaxylem.

9. The peripheral loops of *Clepsydropsis* and related coenopterids remain closed during the departure of traces and consist of a rod of parenchyma surrounded by protoxylem tracheids. This type of protoxylem structure occurs also in some Devonian and Carboniferous Cladoxylales and in some Devonian plants with actinosteles. Other Cladoxylales and actinostelic plants have a different type of protoxylem structure which resembles a peripheral loop. In these plants, however, the protoxylem strands distintegrate and form lacunae.

10. Those Devonian and Carboniferous plants with parenchyma-filled peripheral loops may be related to some coenopterid ferns. The other plants, with protoxylem lacunae, may be related to Sphenopsida or other groups.

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