TRACHEARY ELEMENTS OF THE FERNS.
II. MORPHOLOGY OF TRACHEARY ELEMENTS; CONCLUSIONS[1]

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ABSTRACT

WHITE, R. A. (U. Michigan, Ann Arbor.) Tracheary elements of the ferns. II. Morphology of tracheary elements; conclusions. Amer. Jour. Bot. 50(6): 514–522. Illus. 1963.—With an increase in evolutionary divergence there is an increase in the frequency of occurrence within each family of alternate and opposite pits. Although typical fern tracheids are long, slender, tapered and scalariformly pitted, those located in the roots of ferns become modified with regard to lateral pitting, presence of end plates and the occurrence of perforations. Although end plates most frequently occur in root tracheids, they occur also in the petiole and infrequently in the rhizome tracheids. The large scalariform pits on shortened, oblique end plates contrast sharply with the small alternate and opposite pits of the lateral walls. Such tracheary cells often have the aspect of true vessel members. *Marsilea* possesses perforate end plates, thus true vessel members, in the root. *Woodsia ilvensis* and *Notholaena sinuata* both have root tracheary elements which appear to be vessel members, but because true perforations in the end plates have not been experimentally demonstrated, they are referred to as "presumptive vessel members." The following morphological changes, (1) shortening of the tracheary elements; (2) increase in the occurrence of modified (alternate and opposite) pits on the lateral walls; (3) increase in the occurrence of end plates; and (4) a sporadic occurrence of true (*Pteridium aquilinum*, *Marsilea quadrifolia*) or presumptive vessel members (*Woodsia ilvensis* and *Notholaena sinuata*), all appear to be related to an increase in evolutionary divergence.

AMONG the angiosperms, the morphological characters of tracheary elements in the secondary xylem for which evolutionary trends have been determined are pitting patterns, the size of the pits, the presence or absence of an end plate, the difference between end plate and lateral wall pitting, and whether or not the tracheary cells were tracheids or vessel members (Bailey and Tupper, 1918; Bailey, 1949; Frost, 1930a, b; 1931). In the course of surveying tracheid lengths (White, 1963), numerous variations in some of these other characters were noted, and an attempt was made to determine the patterns of variation in fern tracheid morphology and whether or not there are any noticeable trends of evolutionary significance.

Scalariform lateral pitting is recognized as the most common type in the ferns (Bancroft, 1911; Bliss, 1939; Duerden, 1940; Eames, 1936; Esau, 1953, and others). There are perhaps 2 major exceptions to this: the Ophioglossaceae typically have circular bordered pits (Wright, 1920; Loughridge, 1932; Eames, 1936), and circular bordered pits have also been reported in the Marattiaceae (Bierhorst, 1960).

Numerous variations of the basic scalariform pattern have been noted in the literature (Bailey, 1919, 1925). Bierhorst (1960) has reviewed the standard literature on the subject and has added considerable information on the relationship between the pits on adjacent walls of the elements.

Since the beginning of the 20th century, the problem of whether the tracheary cells of certain ferns are tracheids or vessels has arisen in 4 major surveys of selected species of ferns (Gwynne-Vaughan, 1908; Bancroft, 1911; Bliss, 1939; Duerden, 1940). It is on the basis of these rather broad surveys that, except for *Pteridium*, the typical tracheary cell in the ferns is considered to be a tracheid (Esau, 1953). The primary concern of all these investigators was the presence or absence of a middle lamella and primary walls between the pits of adjacent tracheids.

METHODS—The slide preparation technique used was the standard one for macerated material (Johansen, 1940). In the study of lateral pitting patterns which follows, an analysis was made of tracheids of all 221 species included in the survey. Two slides of tracheids from each organ of each species were chosen at random, and 50 tracheids were examined for the presence of the 3 most common pitting patterns: typical scalariform, those which appeared alternate and those which appeared opposite.

RESULTS—*Pitting*—The present survey of the fern families reveals that scalariform pitting is most common in the metaxylem. Variations of the scalariform pattern occur in all the families of

TABLE 1. *Percentage of species in which lateral pitting patterns (scalariform, alternate, opposite or lacking) are present and the percent occurrence of species in each family with tracheids having end plates*

| Family	% Pred. scalariform	% Pred. alternate	% Alternate present	% Opposite present	End area	0
(0) Marattiales	89	22[a]	33			
(1) Ophioglossales						
Ophioglossum	50	20[a]				
Botrychium	50	60[a]				
(1.5) Gleicheniaceae	88		56			
(2) Osmundaceae	75		33			
(2) Schizaeaceae	100		50			50
(3.5) Cyatheaceae	83	17	100			
(4) Hymenophyllaceae	88	12	44			
(4.5) Pteridaceae	41	55	84	23	15	
(5) Aspidiaceae	37	67	100	11	18	
(5) Aspleniaceae	33	67	100	33		
(5.5) Parkeriaceae	67	33	100			
(5.5) Grammitidaceae	40	60			100	100
(6) Blechnaceae	33	67	100		13	
(6) Davalliaceae	46	50	67	8		
(6) Marsileaceae	16	50		83	16	
(6) Polypodiaceae	44	50		25	6	31
(7) Vittariaceae			100		100	100
(7) Salviniaceae	100% helical-reticulate					

[a] Circular bordered.

ferns. The most common change from the basic pattern is one which results in pits which are alternate in arrangement (Fig. 14, 16) and frequently approach the circular bordered condition (Fig. 13). It is probable that some of this alternate pitting is similar to that described by Bierhorst (1960), in which the pits are actually located in a valley or depression on the wall, which may be continuous across adjacent facets. In such a case, the pits which appear alternate should be referred to as opposite.[3] In numerous species, however (e.g. *Thelypteris dentata, Acrostichum aureum* and *Polystichum acrostichoides*), there are alternate pits on the lateral walls and no indications of valleys. This latter type as well as the former is referred to here as alternate, since the distinction is difficult if not impossible to determine in macerated material. Another variation from scalariform, namely opposite pits (Fig. 15, 20), occurs in certain species of Aspidiaceae, Aspleniaceae, Pteridaceae, Polypodiaceae and Marsileaceae.

In my survey (Table 1), scalariform pits were found to be present in all families. The occurrence of scalariform pitting is generally more common in the primitive families (Column 1) Ophioglossaceae, Marattiaceae, Osmundaceae, Schizaeaceae, Gleicheniaceae, Hymenophyllaceae and Cyathea-

ceae than in the more advanced families. Circular bordered pits occur in the Ophioglossaceae and Marattiaceae. In the species surveyed of the former family, no alternate pits occurred, while in the latter, alternate pits are present but not predominant. Also, among the more primitive families (Osmundaceae, Schizaeaceae, Gleicheniaceae, Hymenophyllaceae, Cyatheaceae) scalariform pitting is predominant while alternate lateral pits occur but do not predominate.

At the level of Cyatheaceae (i.e., 3.5 on the divergence index, Table 1), some of the species have tracheids in which pits are predominantly alternately arranged rather than scalariform. Above this level the percentage of predominantly alternate pits increases and maintains a high frequency among advanced families of ferns. With the increase of predominantly alternate pits, the percentage of predominantly scalariform pitted tracheids decreases. On this basis, it may be concluded that the scalariform pattern tends to be replaced by the alternate pattern. In tracheids of families of moderate to advanced taxonomic position (Fig. 15, 20), as alternate pits become more common, and eventually become dominant over the scalariform pattern, opposite pits occur. Although the frequency with which opposite pits occur is variable among these families (Table 1, Col. 3), a general increase is noted in each successively more advanced family, until in the Marsileaceae, 83% of the tracheids surveyed were observed to have opposite pits on their lateral walls. In no case, however, did opposite pits compose the predominant pitting pattern in the fam-

[3] The concepts of "opposite" and "alternate" pits are in need of review and developmental study. For the present, I have interpreted "opposite" pits to mean those which are arranged in a line perpendicular to the long axis of the cell, and "alternate" to mean those which are disposed in a line oblique to the axis. It is possible (Bierhorst, 1960) that the 2 conditions are variations of one basic pattern.
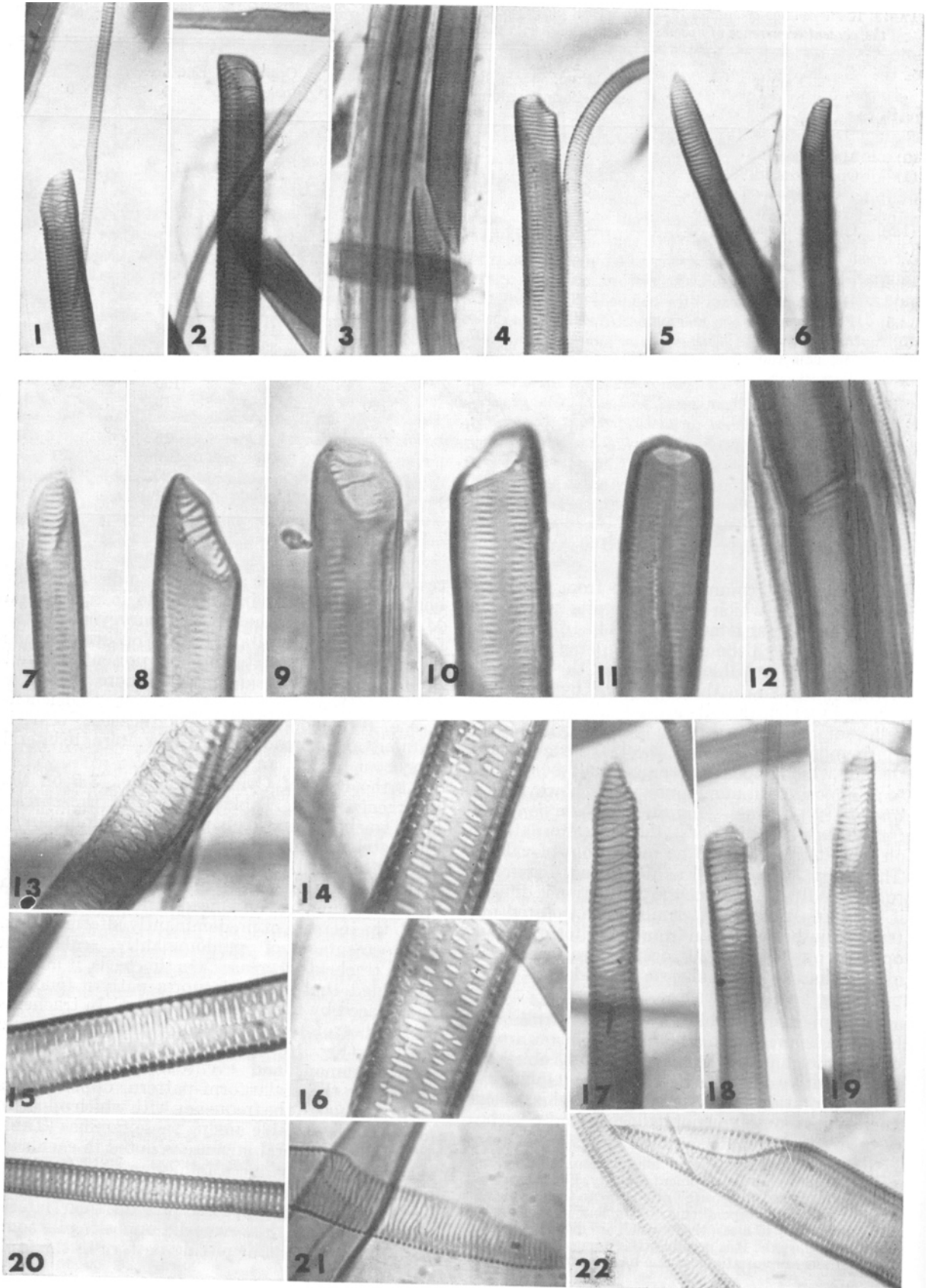
ily. The lack of any lateral pitting was characteristic of all the tracheids of the Vittariaceae and Grammitidaceae and in approximately 25% of the tracheids surveyed in the Polypodiaceae.

In summary, a comparison of the 3 pitting patterns (Table 1, Cols. 1–3) reveals a consistent change from tracheids in families on the lower taxonomic levels to those in families of higher taxonomic position. Scalariform pits are predominant to a lesser degree in successively more advanced families. As the predominance of scalariform pits declines, in addition to the increase in *occurrence* of alternate pits, there is a concomitant increase in the percentage of cases where alternate pits are predominant. Opposite pits occur (Table 1, Col. 3) only in families where alternate pits are of frequent occurrence, and where they are the predominant pattern of pitting in better than 50% of the tracheids observed in each family. The aquatic Salviniaceae appears to be different from other families of ferns, in the occurrence of only helical, reticulate and very loosely scalariform pits on the walls of much reduced tracheids (Table 1).

The data obtained from this survey of patterns of pits on the lateral tracheid walls indicate that taking living ferns at large, the trend in pitting appears to be from primitively scalariformly pitted tracheids, to alternately to oppositely pitted tracheids.

This trend in lateral pitting from scalariform, to alternate, to opposite is different from the typical trend described for the higher seed plants: viz; scalariform to opposite to alternate (Bailey and Tupper, 1918; Frost, 1930a, b; Tippo, 1946, and others).

According to Zimmerman (1959), in angiosperms, the formation of a perpendicular bar across the scalariform pit results in the formation of opposite pits. The alternate position comes about by a positional change of the opposite pits. In many ferns, however, there is an oblique, rather than a perpendicular, bar which traverses the scalariform pits.

Opposite pits, which occur on tracheids which also have alternate pits in abundance (Table 1), may originate in 2 different ways: (1) directly from the "typical" scalariform pit (as in angiosperms); and (2) by a positional rearrangement of the alternate pits. The first kind of modification

is seen clearly in the Pteridaceae, Polypodiaceae, and in the Marsileaceae.

Additional work will be necessary before a complete picture of how opposite pits originate can be drawn.

Further studies are obviously necessary to determine whether or not the alternate pits in fern tracheids are comparable to those in seed plants, especially in view of the possible difference in origin of alternate pits in the 2 groups. When these differences are resolved, a better comparison between the trends in the ferns and those in seed plants may be possible.

In addition to the changes in lateral pitting from scalariform to alternate to opposite, which appear to be correlated with evolutionary level in the ferns (and, therefore, with a decrease in average tracheid length), another character, that of the occurrence of a clearly distinct terminal overlap area between adjacent tracheids, appears to be correlated with the more advanced pitting patterns.

Nature and significance of the terminal overlap area—Typical fern tracheids are elongate, tapered at both ends and have scalariform pits on all walls. In the rhizome and petiole, these cells typically overlap along the greater proportion of their length, rather than having relatively short oblique terminal overlaps like those of vessel members. As a consequence, it is not usually possible to distinguish an "overlap" area between 2 tracheids from the lateral walls of the tracheids.

Tracheids are traditionally considered to differ from vessel members in at least 2 ways: (1) in vessel members, there is a distinct end plate present which represents the area of articulation between vertically contiguous cells; no such specialization occurs in typical tracheids; (2) there are true perforations in the end plates of vessel members which allow for direct and uninterrupted vertical flow of water between cells; in tracheids the middle lamella and primary wall constitute a barrier through which water must pass when flowing from one tracheid to the next. The first change apparently is prerequisite to the second and may be considered intermediate.

The first characteristic is frequently overlooked when differentiating between the 2 cell types, but its importance as one of the characteristics of vessel elements has been emphasized by Frost

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Fig. 1–22.—Fig. 1–6. Selected examples of presumptive vessel members from roots of *Woodsia ilvensis*. ×200.—Fig. 1, 2. Tracheary elements which most closely resemble true vessel members.—Fig. 3. Articulation between tracheary cells superposed in a vertical column.—Fig. 4–6. Examples of the variation found in the morphology of the end plant.—Fig. 7–12. Examples of true vessel members in the roots of *Marsilea quadrifolia*. ×480.—Fig. 7, 8, 9. Oblique, scalariform perforation plate.—Fig. 10, 11. Perforation plate transverse and simple perforate.—Fig. 12. Articulation between 2 vessel members with simple perforate transverse end plates.—Fig. 13. Circular bordered pits in a petiolar tracheid of *Asplenium bulbiferum*. ×400.—Fig. 14. Opposite and alternate pits on petiolar tracheid of *Acrostichum aureum*. ×350.—Fig. 15. Opposite arrangement of pits on petiolar tracheid of *Pteris serrulata*. ×550.—Fig. 16. Alternate arrangement of pits on petiolar tracheid of *Thelypteris dentatus*. ×700.—Fig. 17–19. Presumptive vessel members from the roots of *Notholaena sinuata*. ×200.—Fig. 20. Opposite pits on root tracheid of *Polystichum acrostichoides*. ×150.—Fig. 21. Petiolar tracheid of *Dryopteris thelypteris*, with vessel-like end plate. ×300.—Fig. 22. Vessel member of *Pteridium aquilinum*. ×375.

TABLE 2. *Widths of scalariform bars and pits on overlap areas and lateral walls, of tracheids in rhizomes, roots and petioles of ferns. Measurements are in microns*

Family	Rhizome				Root				Petiole			
	Overlap[a]		Lateral[a]		Overlap		Lateral		Overlap		Lateral	
	Bar	Pit	Bar	Pit	Bar	Pit	Bar	Pit	Bar	Pit	Bar	Pit
Marattiaceae	2.80	1.68	2.80	1.57	2.97	1.85	2.80	4.09	3.14	3.02	5.04	5.60
Ophioglossaceae	3.08	1.79										
Gleicheniaceae	2.91	1.57	5.15	1.29	3.42	3.10	3.47	1.79	3.30	1.51	3.98	1.01
Osmundaceae	2.74	1.29		1.12	1.96	2.13	2.80	1.12	3.02	1.40	2.80	1.12
Schizaeaceae	1.74	1.12	1.68	1.12	2.69	2.02						
Cyatheaceae	4.09	2.18	4.20	1.85	2.80	2.07	3.47	1.57	4.76	1.96	5.43	1.17
Hymenophyllaceae	2.86	1.29	5.49	1.51	3.02	1.12	5.26	0.67	3.25	1.12	3.36	1.46
Pteridaceae	2.52	1.23	2.63	1.12	2.08	1.79	4.65	0.78	3.36	2.18	4.37	1.46
Aspidiaceae	2.41	1.23	3.08	1.12	2.58	1.96	3.81	1.06	2.63	1.51	3.25	1.40
Aspleniaceae	2.07	0.67										
Parkeriaceae	1.90	1.51	2.24	1.12	2.24	2.29	2.69	2.24	1.85	2.07	2.02	1.85
Blechnaceae	3.25	1.85	2.86	1.68	3.02	2.86	4.76	3.08	2.63	1.40	3.98	1.12
Polypodiaceae	2.69	1.68	2.69	1.12	2.13	1.79	2.80	1.29	2.69	1.12	2.74	0.56
Grammitidaceae	2.24	1.12	2.80	1.12	2.24	1.57	2.24	1.68	3.08	1.68	3.36	1.12
Marsileaceae	2.24	0.62							2.24	1.40		
Vittariaceae	2.52	1.57			2.63	1.85			2.50	1.12		

[a] Area of tracheid.

(1930a, b) in his very complete study of trends in xylem of dicotyledons. True vessel members have been reported to occur in 2 fern genera, *Pteridium* (Fig. 22), and *Marsilea* (Fig. 7–12) (White, 1961). This study reveals several other genera with highly specialized terminal overlap areas which have the morphological characteristics of end plates. It is possible that the end plates in at least 2 of these genera are perforate, but experimental demonstration of perforation has not yet been made.

In the rhizome, such distinct areas of overlap between adjacent tracheids occur occasionally in species where opposite pits occur on the same tracheids. In this study such species include: *Woodsia montevidensis* (Aspidiaceae), *Pteridium aquilinium* (Pteridaceae), *Phlebodium aureum* and *Microgramma lycopodiodes* (Polypodiaceae). The overlap area is short with scalariform pitting that contrasts with the alternate or opposite pitting of the lateral walls. Thus a structure closely resembling a typical end plate of a vessel member results.

Somewhat surprisingly, in view of their more highly modified lateral pitting, fewer petiolar than root tracheids have these distinct short overlap areas. Such "end plates" do occur however, in petioles of species of Aspidiaceae, Davalliaceae, Pteridaceae, and Grammitidaceae (Fig. 21).

The presence of end plates occurs most frequently in tracheids of the root (Fig. 1–6, 7–12, 17–19). The combination of lateral pitting which is most often alternate or opposite with short scalariformly pitted overlap areas between the tracheids undoubtedly led to the description of true vessels in the root of *Nephrodium* (=*Dryopteris*) *filix-mas* (Russow, 1872).

In the Vittariaceae and Grammitidaceae it occurs because the overlap area of the short tracheids in these families is scalariformly pitted, while there are few, scattered, or no lateral pits. Occasionally, short overlap areas are also seen in root tracheids in the Blechnaceae, but these are not of common occurrence in that family. Certain species of the Pteridaceae (*Adiantum cuneatum, Notholaena sinuata* [Fig. 17–19]), Aspidiaceae (*Cystopteris fragilis, Thelypteris palustris, Woodsia obtusa*), Polypodiaceae (*Phlebodium aureum, Polystichum acrostichoides*), Grammitidaceae (*Adenophorus hillebrandii*), and Marsileaceae (*Marsilea quadrifolia* [Fig. 7–12]) have relatively short overlap areas between adjacent tracheary cells in the root, and also have lateral pits which differ from the pitting present on the overlap area. If these 2 characters (scalariform end plates and reduced lateral pits) were the only ones on which to base a judgment, these species, and those that have similar cell types, would have true "vessels," rather than tracheids. However, the characteristic of a vessel member which distinguishes it from a tracheid is the presence of true perforation.

Vessel and vessel-like cells—In a survey such as the present one, where emphasis was not on differentiating between vessel members and tracheids, sections were not made of all the species. In those cases where sections were made, however, the difficulty in determining whether the membrane was truly absent or merely absent as a result of sectioning technique made it impractical to draw conclusions concerning the nature of the element based solely on this evidence. Other characteristics, including the presence of a distinct overlap area or "end plate," the extent to which the pit-

ting of this overlap differed from lateral pitting, and the difference between the width of the pit and the secondary wall thickening on the overlap were taken into consideration.

In order to use comparative characteristics, such as difference between size of pits of the overlap area and lateral walls, it was necessary to determine what the typical conditions were in tracheids of each of the major organs of the plant. Any significant trends in pit sizes among the fern families would have to be taken into consideration before ascribing a "vessel-like" condition to tracheids in any particular species. Such a survey of pit sizes was made, using several representative species in each family (Table 2).

On the basis of these data, comparisons can be made between the average pit sizes in the 3 organs. In each organ, rhizome, root and petiole, the pits are smaller, and areas of secondary thickening between the pits are wider on the lateral walls than on the overlap areas.

In the rhizome elements, where there is little differentiation between lateral walls and areas of overlap, and where the pitting pattern is typically scalariform over the entire tracheid, the size of the pits on the tapered ends differs very little from those on the lateral walls and in most cases, the thickness of the scalariform bars is not much different between the 2 areas (Table 2). Clear exceptions to this are seen in Gleicheniaceae and Hymenophyllaceae, where the lateral scalariform bars are much wider than those of the overlap areas.

In the petiolar tracheids, the pits are separated by scalariform bars which are generally wider than those found in the rhizome tracheids of the same species. The petiolar pit sizes may be the same (Osmundaceae, Gleicheniaceae, Hymenophyllaceae), wider (Marattiaceae, Pteridaceae, Aspidiaceae, Parkeriaceae, Marsileaceae), or narrower (Blechnaceae, Polypodiaceae) than the pits in the rhizome. In contrast to the lack of difference in width of scalariform bars and size of pit in the lateral wall and overlap areas in the rhizome tracheids, there is considerable difference between the 2 regions in petiolar tracheids. In general, the lateral pits are much smaller and the bars between the pits much wider than those of the overlap area (Table 2).

The pits on the overlap areas of the tracheids in the roots tend to be the widest in the plant. Frequently, these pits are equal to or wider than the bars separating them. As in the petiole, pits of the lateral walls are characterized by a considerable reduction in size and an increase in the width of the scalariform bars separating them.

There appears to be no correlation between pit size and relative evolutionary advancement in the ferns. The pits in the advanced families Polypodiaceae and Vittariaceae are not much different from those commonly found in the relatively primitive families, Marattiaceae and Gleicheniaceae. Pit sizes appear to be variable within and

between families of ferns and show no clear evolutionary trends.

Modification of the terminal overlap areas between the tracheids is correlated with the occurrence of opposite pits or the complete absence of lateral pits. Pitting of the overlap areas between vertically contiguous tracheids is typically scalariform, even when the lateral wall pits may be alternate or opposite. When such cells are separated by maceration technique, the overlap areas, particularly in the root, but also in the petiole and very infrequently in the rhizome, result in tracheids which have the aspect of vessel members. The presence of vessel-like overlap areas appears to be correlated with both short tracheid length and the occurrence of opposite lateral pits, which in turn seem to be correlated with level of evolutionary divergence.

The results of pit-size measurements indicate that the greater majority of the tracheary cells which have "vessel-like" tendencies, including very distinct oblique overlap areas in the roots, are nevertheless still tracheids because they lack the second criterion of perforations. Throughout this survey of tracheids, however, special efforts were made to uncover those tracheary cells which might differ enough from the normal condition to warrant consideration as possible vessel members. There were strong indications that vessel members rather than tracheids are present in roots of Woodsia ilvensis (Fig. 1–6) and Notholaena sinuata (Fig. 17–19), in addition to the previously known occurrence of vessels in Pteridium and Marsilea.

In both Pteridium and Marsilea, true perforation of the end plate has been proven either by detailed observation of sections as in Pteridium (Bliss, 1939; Duerden, 1940), or by passage of ink particles through several articulated cells (White, 1961). Unfortunately such tests were not possible in Woodsia and Notholaena.

In Woodsia, the root tracheids are short ($\overline{X} = 0.91$ mm) and the suspected vessel members are very small in contrast to those in Marsilea ($\overline{X} = 3.6$ mm) or Pteridium ($\overline{X} = 1.56$ mm). A complete range of end plates intermediate between the short oblique condition (Fig. 1–6) and a very long tracheid-like scalariform overlap area are present in this species. There is a reduction in the number of scalariform bars on the end plate, concomitant with a decrease in its angle of inclination and length. In every instance, however, the cells have scalariform end plates. This is similar to the situation in Pteridium but contrasts with the condition in Marsilea, where a complete spectrum from oblique scalariform to transverse simple perforate end plates are present (Fig. 7–12). Four replications of verified material from several different sources all revealed tracheary elements which appear to be vessel members by virtue of their short length, short overlap area, reduced scalariform perforations on their ends and the very diminished width of the scalariform bars of the end plate.

With the discovery of vessel-like cells in the roots of *Woodsia ilvensis*, a survey was made of root tracheids of 16 other species of *Woodsia*. In no other species was the situation as extreme as that found in *W. ilvensis*. There were indications, however, of a strong tendency toward the vessel-like condition in several other species, namely: *W. mexicana, W. polystichoides* and *W. scopulina*. The species *W. alpina, W. oregana, W. glabella, W. montevedensis, W. obtusa* and *W. subcordata* showed this tendency to a lesser extent. No indications at all of a vessel-like condition were present in my samples of *W. machrochlaena, W. manchuriensis, W. rosthorniana* and *W. mollis*. Of special interest are the presumed hybrids between species having tendencies toward the vessel condition and *Woodsia ilvensis*, in which apparently true vessel members are present. In both presumed hybrids, *Woodsia glabella* × *ilvensis* and *W. oregana* × *ilvensis* (Brown, 1958), the condition was closer to the more generalized character (i.e., slight vessel-like tendency) than the more specialized vessel-like character present in *W. ilvensis*. A similar situation where the unusual character of one of the parents is mainly not expressed in the hybrid has also been described by Wagner (1962) for free (i.e., generalized) vs. reticulate (specialized) venation in Applachian *Asplenium*. Also of some interest is the fact that the species showing the clearest approach to the vessel condition have an average tracheary element length which is shorter than that determined for the species where no vessel-like specialization of the tracheids was in evidence.

With the presence of vessel members in *Pteridium aquilinum* and, possibly, in *Woodsia ilvensis*, both dry habitat species, it seemed reasonable that this character might be related to xerophytic habitat. Even *Marsilea* in many of its ecological niches is a functional xerophyte for long periods during each year. In view of this, species typical of dry areas were checked, including *Pellaea, Cheilanthes, Ceterach,* and *Notholaena,* and of these vessel-like elements were uncovered only in the roots of *Notholaena sinuata*. The end plates in this species are highly specialized in comparison with the lateral walls, and the pits are greatly widened in contrast to the much reduced width of the scalariform bars. Again, as in *Woodsia*, there is a complete spectrum of end plate types ranging from long and very tracheid-like to shorter, more oblique end plates, and all of the end plates appear to be scalariform perforate.

In view of the taxonomic position of these species, plus the fact that other species of their genera and closely related genera do not have tracheary elements of this character, the presence of apparent vessel members in *Notholaena sinuata* and *Woodsia ilvensis* points to the possible sporadic occurrence of this cell type still to be found in other species, genera, and perhaps even families of ferns. In view of the infrequent occurrence in a survey of over 200 species, however, it is not probable that vessel members will ever be found as commonplace structures.

The proven occurrence of vessels in *Pteridium* and *Marsilea* (White, 1961), and their probable occurrence in the roots of *Woodsia ilvensis* and *Notholaena sinuata* are evidence of parallel development in widely different and separate families of ferns. *Pteridium* is a ubiquitous species of the Pteridaceae, and *Marsilea* is a very highly specialized species of "aquatic" fern in the Marsileaceae. Their occurrence in relatively unspecialized genera such as *Woodsia* (Aspidiaceae) and *Notholaena* (Adiantaceae) is notable because it takes away the uniqueness of this cell type in the ferns. Occurrence of vessel members in all these species suggests the probable parallel and independent development of these cells at least several times in the ferns. The evolutionary correlation of the vessel member in the ferns is unclear, for there are numerous species more highly evolved in other respects than *Woodsia* and *Notholaena* which lack any evidence of this cell type. It thus appears to be a character which occurs more or less at random among the species of ferns, and before any pattern can be described, more species will have to be surveyed.

DISCUSSION—Investigation of comparative lengths of tracheary cells led to a broad survey of other morphological characters of fern tracheids. A study of the pitting patterns on lateral walls of tracheids tends to indicate that scalariformly pitted tracheids are primitive. In families of somewhat more specialized taxonomic levels there is an increase in the frequency of alternate and opposite pitting. The latter pattern occurs only in families of the highest levels of evolutionary divergence. In the ferns, both alternate and opposite pits appear to be derived from scalariform pits. In higher seed plants within the secondary xylem, opposite pits are thought to be derived from scalariform pits, and alternate pits are thought to be derived through a positional rearrangement of the opposite pits.

Indications were found that opposite pits in ferns may have 2 separate origins: one from scalariform which appears most common, and another by modification of the position of alternate pits. Further investigation is necessary to determine whether they are fundamentally different, or whether they are brought about by developmentally similar processes. This latter possibility remains, since Bierhorst (1960) refers to pits which appear alternate, but which should be classified as opposite because of the way they develop. Correlations were noted between opposite pits, relatively short cell length and the occurrence of modified overlap areas which gave the tracheids a vessel-member aspect. Since sections were not made of each species that was macerated, and since those that were made were inconclusive as to the presence or absence of a membrane between

the cells, other characters were used to suggest the presence of vessel members. In order to use pit size and width of scalariform bars for this purpose, it was necessary to know the normal values for these characters in the tracheids of species from families of varying taxonomic levels. A survey was made of selected species, and although no trends which correlated with taxonomic advancement of the families were noted, several comparisons were noted between pits in tracheids of different organs of the same plant. Interestingly, petiolar tracheids, although most modified with regard to lateral wall pitting, had fewer specialized overlap areas, and the pits were not much larger in these areas than those on overlap areas of the much less specialized rhizome tracheids. The pits on the end plates of the root tracheids, by contrast, were the widest in the plant. There are at least 2 ways that structural modifications of the tracheary cells may improve the efficiency of water conduction. First, in order to reduce obstruction of water flow, the individual cells making up the column can become very long. In view of the lack of specialization of ends in petiolar tracheids, and their great lengths, it appears that increase in tracheid length may be one modification found in this organ. Although sclerenchyma is common in the cross section of the petiole, the tracheids undoubtedly also play a part in the support of this organ and this might explain the reduction in pit size on the lateral walls, with a concomitant increase in secondary wall area.

The condition in the root may be an example of a second method by which water movement may be facilitated, namely an enlargement of the pits between contiguous cells. The larger the pits, the less the total resistance that would be offered to flow of water. Numerous species of ferns have root tracheids which are modified in this manner, resulting in cells which are similar in appearance to vessel members. The end result of this trend would be the complete loss of membranes from the pits resulting in vessel members. Vessel members have been known in *Pteridium* for a long time, and have recently been shown to occur in the roots of *Marsilea*. As a result of this survey, 2 other species, *Woodsia ilvensis* and *Notholaena sinuata*, which possess presumptive vessel members are reported. A change in tracheary elements from tracheids to vessels may be an ecological response to increased water efficiency, for the species with vessels are either typical of dry habitats (*Pteridium*, *Woodsia*, *Notholaena*) or functionally xerophytic at certain times of the year (*Marsilea*). Ecological adaptation is not the sole explanation for the tracheary modifications discussed here, however, for numerous xerophytic fern species very closely related to those which have vessel members have no indication of this cell type.

There is evidence that vessels may have arisen first in the roots of ferns as well as of monocotyledons (Cheadle, 1943). The evidence is (1) that tracheids approaching in morphology the vessel member occur primarily in roots; and (2) that in 3 species, true or presumptive vessel members are found only in the roots.

Characters such as opposite pits, terminal overlap areas which resemble end plates, and the presence of true vessel members are all characteristics found only in families of medium to advanced taxonomic levels of Filicales. The very primitive and more distantly related species of the Ophioglossales and Marattiales have few specializations in tracheid morphology other than the circular bordered pits which are characteristic of both groups. The primitive families of the Filicales also show very few specializations of the "typical fern tracheid" character: alternate pits occur, but in low percentages, and never as the dominant pitting pattern. No specializations of overlap areas occur among the most primitive families: Osmundaceae, Schizaeaceae, Gleicheniaceae, Cyatheaceae, Parkeriaceae or Hymenophyllaceae. In contrast, correlated with taxonomic advancement, alternate pits, opposite pits and specialization of the overlap areas occur in medium to advanced families. The occurrence of vessel members, although not restricted to advanced families such as the Marsileaceae, is in families which are also characterized by other advanced morphological characters.

The purpose of the present paper and the previous one in this series (White, 1963) was to determine the evolutionary trends in the xylem elements of the ferns. Factors which were found to affect tracheid length significantly were taken into consideration when samples were chosen for a statistical analysis of the relationship between tracheid length and taxonomic divergence in the ferns. Even when careful techniques were applied, there was no significant correlation between the 2 factors for tracheids in the rhizome and petiole. Internode length is considered to be of importance in the lack of positive results in the rhizome, but no similar reasons can be found for the petiolar material. In the root, there was a significant correlation between length and divergence at the 5% level.

With a lack of correlation in 2 of the 3 organs tested, and the number of exceptions to the pattern in the root, although the correlation was significant, it is impossible to state categorically that a relationship exists between tracheid lengths and evolutionary divergence similar to that thought to obtain in the angiosperms. Additional information, along with a sampling technique to remove some of the remaining variables in tracheid selection, might improve the correlation in the other organs. At present, there are indications that an improvement in technique and a more refined index of taxonomic divergence would further substantiate the trends outlined above.

On the basis of this study, I have concluded that the following morphological changes are related to an increase in evolutionary divergence in

the ferns: (1) a shortening of the tracheary elements; (2) an increase in the occurrence of modified lateral pitting; (3) an increase in the occurrence of end plates (terminal overlap areas), especially in the root tracheids; and (4) a sporadic occurrence of true vessel members (in *Marsilea* and *Pteridium*) and presumptive vessel members (in *Woodsia ilvensis* and *Notholaena sinuata*).

There are several evolutionary trends in the tracheary elements of the ferns which are similar to those in the angiosperms: the shortening of tracheary elements with evolutionary divergence (at least in the root), the origin of vessel members from scalariformly pitted tracheids and the comparative shortness of vessel members when compared with tracheids in the same or closely related species. Vessel members and presumptive vessel members are, however, of rather sporadic occurrence in the ferns among families of intermediate and advanced levels of evolutionary divergence and therefore do not necessarily indicate a high level of advancement.

On the basis of the available information, I am inclined to believe, in conclusion, that the similarities in evolution of tracheary cells in the Filicineae and the Angiospermae result from parallel evolution.

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