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WOOD AND BARK ANATOMY OF EMPETRACEAE; COMMENTS ON
PAEDOMORPHOSIS IN WOODS OF CERTAIN SMALL SHRUBS

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ABSTRACT

Wood and bark of 12 collections of Empetraceae representing three genera containing seven species (one with two subspecies) are analyzed with respect to quantitative and qualitative features. Empetraceae have vessels somewhat angular in transection, with scalariform perforation plates and scalariform to opposite vessel-ray pitting. Imperforate tracheary elements are all tracheids. Axial parenchyma is sparse and not subdivided. Rays are characteristically uniseriate and composed of upright cells (older stems have rays with both upright and procumbent cells). These features ally Empetraceae closely to Ericaceae and Epacridaceae. The narrow vessels, quite numerous per mm², denote a high degree of wood xeromorphy; growth rings and tracheid presence also may be indicative of adaptation to drought or physiological drought due to cold. Rays composed of upright cells, nonconversion of the uniseriate rays to multiseriate or heterocellular rays, and decrease in vessel element and tracheid length with age are generally accepted criteria for paedomorphosis in dicotyledonous woods, and these apparently apply to *Corema* and *Empetrum* as well as small shrubs similar to them: *Cassiope* (Ericaceae), *Empleuridium* (Celastraceae), *Myrothamnus* (Myrothamnaceae), and *Tetratea* (Tremandraceae). Data on bark are presented for all taxa of Empetraceae.

Key words: ecological wood anatomy, Empetraceae, Ericaceae, Ericales, paedomorphosis, wood anatomy.

INTRODUCTION

A synoptic study of wood anatomy of all generally recognized taxa of Empetraceae can be offered here because of the materials available to me. Empetraceae encompass a curious series of disjunct distributions (data from Fernald 1950 and Webb 1972). *Ceratiola ericoides* Michaux occurs in sandhills of the southeastern United States as far north as South Carolina. *Corema album* D. Don occurs on coastal sandhills of the western half of the Iberian peninsula, whereas *C. conradii* Torr. may be found in coastal sandhills and pine barrens of northeastern North America. The genus *Empetrum* is bipolar: *E. rubrum* Vahl ex Willd. occurs in southern Chile and Argentina, whereas the remaining species are boreal. One can include all of the boreal species in *E. nigrum* L., or recognize several segregate taxa. Webb (1972) in the *Flora Europaea* claims *E. nigrum* subsp. *nigrum* plus a polyploid high-latitude or high-elevation subspecies, *E. nigrum* subsp. *hermaphroditum* (Hagerup) Bocher, for the Old World. In the New World, Fernald and Wiegand (1913) made a case for recognition of *E. atropurpureum* Fernald & Wiegand (higher elevations near timberline) and *E. eamesii* Fernald & Wiegand (Labrador and Newfoundland), whereas *E. nigrum* is coastal. Recently, the Old World high-latitude and high-elevation subspecies has been transferred from *E. nigrum* to *E. eamesii* as *E. eamesii* subsp. *hermaphroditum* (Hagerup) D. Love. This transfer is accepted here; other populations segregated from the *E. nigrum* complex have fewer distinctions than this polyploid, and are not recognized here.

The wood anatomy of Empetraceae proves to be of special interest with respect to ecology. The extreme habitats cited above prove to be matched by wood adaptations. The significance of scalariform perforation plates in regard to ecology can be examined in Empetraceae, because both simple and scalariform plates coexist in the family, and populations of a single species differ in this respect. Empetraceae have cells that must be termed tracheids according to the usage of Bailey (1936) or the IAWA Committee on Nomenclature (1964). Tracheids by this definition deter the grouping of vessels, so that vessel grouping, characteristic of xeromorphic woods with fiber-tracheids and libriform fibers (Carlquist 1984) is not to be expected in Empetraceae. Moderate degrees of vessel grouping do occur in Empetraceae; these are analyzed with respect to growth ring and packing considerations because large numbers of vessels per mm² appear to result in elevation of numbers of contacts among vessels (Carlquist, Eckhart, and Michener 1984).

The uniseriate rays of Empetraceae, composed characteristically of upright cells, suggest a kind of paedomorphosis. I cited such rays as Paedomorphic Type III in my analysis of ray types (Carlquist 1988). Do other features of the wood of Empetraceae suggest juvenilism, or paedomorphosis, in woods of Empetraceae and similar shrubs? Barghoorn (1941*b*) figured wood of *Corema conradii* and cited it as an example of loss of rays. Is that interpretation valid, or is a kind of paedomorphosis involved?

The data of Metcalfe and Chalk (1950), Greguss (1959), and Miller (1975) on wood anatomy of Empetraceae appear accurate in most respects. The present account provides more information because all taxa of the family are examined. Availability of this material induced me to study bark anatomy as well as wood anatomy for the family.

MATERIALS AND METHODS

The geographical sources of the specimens studied (Table 1) are as follows: *Ceratiola ericoides* (Carlquist s. n.), sandhills near Appalachicola, Florida; *C. ericoides* (Carlquist 8037 RSA), Ordway-Swisher Reserve near Gainesville, Florida; *Corema album* (Pedro 13-III-1938 NY), coastal sands, Portugal; *C. conradii* (Churchill 7571762 POM), Five Islands, Sagadahoc Co., Maine; *C. conradii* (MacKeener 249 NY), Nantucket, Massachusetts; *Empetrum atropurpureum* (McKelvey 26-VII-1922 POM), Mt. Washington, New Hampshire; *E. eamesii* subsp. *eamesii* (MacKenzie 16-VII-1921 NY), Newfoundland, Canada; *E. eamesii* subsp. *hermaphroditum* (Abbe 517 NY), Long Island, Minnesota; *E. eamesii* subsp. *hermaphroditum* (Astru 10-VII-1970 NY), southern Greenland; *E. nigrum* (Fosberg 36536 RSA), Bois Bubert Island, Washington Co., Maine; *E. rubrum* (Carlquist 7288 RSA), Antillanca, Puyehue National Park, Chile; *E. rubrum* (Goodall 923 RSA), near sealevel, Punta Maria, Tierra del Fuego, Argentina. For aid in collection of or permission to use these materials, I am grateful to C. Ritchie Bell, Dana Griffin III, Richard Franz, Patricia Holmgren, Stephen Morgan, William L. Stern, and Robert F. Thorne. Specimens have been determined or redetermined in accordance with the nomenclatural sources cited above.

Wood of *Ceratiola ericoides* (Carlquist 8037) was preserved in aqueous 50% ethyl alcohol. All of the remaining specimens were available in dried form, and these were boiled in water and stored in aqueous 50% ethyl alcohol. All specimens

Table 1. Wood characteristics of Empetraceae.

Taxon	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Ceratola ericoides</i>	Carlquist s.n.	15	12	1.10	26	489	354	0	Sv	1.2	448	2.5	329	Usp	19
<i>C. ericoides</i>	Carlquist 8037	7	5	1.03	22	709	303	0	Sv	1.0	423	2.3	204	U	9.4
<i>Corema album</i>	Pedro 13-III-1938	9	10	1.08	22	319	230	10.2	sCv	1.8	347	2.8	203	Usp	16
<i>C. conradii</i>	Churchhill 7571762	3	15	1.27	18	1017	274	0-4	Scv	1.6	356	1.8	188	U	4.8
<i>C. conradii</i>	MacKeener 249	4	19	1.23	19	1132	221	0	S	1.2	291	2.3	203	Us	3.7
<i>Empetrum atropurpureum</i>	McKelvey 26-VII-1922	6	20	1.16	29	546	267	0-10	SCV	0.7	325	1.6	145	Us	14
<i>E. eamesii</i> subsp. <i>eamesii</i>	MacKenzie 16-VII-1921	8	61	1.56	22	1181	158	0-8	ScV	0.7	226	1.4	99	Us	2.9
<i>E. eamesii</i> subsp. <i>hermaphroditum</i>	Abbe 517	5	34	1.20	21	1017	199	9.5	S	0.7	264	1.6	89	Us	4.1
<i>E. eamesii</i> subsp. <i>hermaphroditum</i>	Astru 10-VII-1970	3	18	1.32	24	815	208	10.7	S	0.7	256	1.6	110	U	6.1
<i>E. nigrum</i>	Fosberg 36536	6	23	1.48	19	897	256	12.0	S	0.7	352	2.1	211	Us	5.4
<i>E. rubrum</i>	Carlquist 7288	12	20	1.07	20	887	260	8.9	S	0.7	355	1.6	173	Usp	5.9
<i>E. rubrum</i>	Goodall 923	5	25	1.16	15	1418	227	0-6	ScV	0.7	303	2.1	101	Us	2.4

Key to columns: 1, diameter of wood cylinder of stem, mm; 2, age of stem, number of annual rings; 3, mean number of vessels per group as seen in transection; 4, mean vessel diameter, μm ; 5, mean number of vessels per mm^2 of transection; 6, mean vessel element length, μm ; 7, mean number of bars per perforation plate (range from 0 given if simple plates common but scalariform also present); 8, perforation types—S (simple), C (scalariform), V (vestigial bars at margins), upper case indicates most common condition; 9, mean vessel wall thickness, μm ; 10, mean tracheid length, μm ; 11, mean tracheid wall thickness, μm ; 12, mean height of uniseriate rays, μm ; 13, ray cell types—U (upright), S (square), P (procumbent), lower case indicates type is quite uncommon; 14, Mesomorphy index (vessel diameter times vessel element length divided by number of vessels per mm^2).

were sectioned on a sliding microtome; where possible, sections 14 μm thick were prepared; thicker sections were cut only in order to reduce tearing. Sections were stained in safranin; some were counterstained with fast green. Macerations were prepared with Jeffrey's fluid and stained in safranin. Many stems of Empetraceae, especially those of smaller shrubs, are contorted and fissured; the specimens selected represent straighter wood grain. All of the means calculated in Table 1 are based upon 25 measurements except for vessel wall thickness and tracheid wall thickness, for which typical conditions were selected for measurement. Nomenclature is according to the IAWA Committee on Nomenclature (1964). Vessel diameter is measured as lumen diameter at the widest point (regardless of whether that widest diameter tended to be tangential or radial in direction). "Ring porous" is defined here as a condition in which earlywood vessels (first quarter of the growth ring) average twice or more the diameter of vessels in the last quarter of the growth ring. "Semi-ring porous" thereby can be used for all growth rings in which growth-ring demarcation evident is present, but in which vessel diameter contrast is less marked. Some will prefer a definition of "ring porous" that involves an abrupt change in diameter from earlywood to latewood, but that definition is difficult to apply because it is not quantified.

WOOD ANATOMY

Most features are summarized in Table 1. Those for which condensed tabular summary is inconvenient are described in the running text below.

Growth Rings

Growth rings are present in all Empetraceae. Growth rings are demarcated in *Ceratiola* not by markedly wider vessels in the earlywood or narrower vessels in latewood, but by radially narrow tracheids that terminate growth rings (Fig. 1). *Corema album* (Fig. 9) is similar to *Ceratiola ericoides* in this respect. *Corema conradii* has more marked contrast of vessel diameter between earlywood and latewood (Fig. 8). All collections of *Empetrum* show a sharper contrast between earlywood and latewood, and are best termed semi-ring porous because the earlywood vessels are appreciably greater in diameter, but not so strongly as in hardwoods typically called ring porous. A case could be made for terming growth rings in woods such as Figure 11 as ring porous. "Ring porous" has been typically defined in terms of temperate hardwoods with extremely large earlywood vessels, but attention has not been paid to demarcating "ring porous" from "semi-ring porous" in a quantified way. At low magnification the wide earlywood vessels appear in concentric rings (Fig. 14, 15, 17). The earlywood vessels are often wider radially than tangentially (Fig. 15), and are often so dense that tracheids among them are very few in number (Fig. 14, 16, 17, 19). *Empetrum* also shows differentiation in diameter of earlywood tracheids (wider radially) as opposed to the last several layers of latewood tracheids (radially narrow, appearing flattened in transection). *Corema* and *Empetrum* have slightly thicker-walled tracheids at the termini of growth rings. The growth rings of *Ceratiola* (Fig. 1) and *Corema album* (Fig. 9) are wider than those of *Corema conradii* and *Empetrum* (Fig. 14, 15, 17). To be sure, growth rings tend to become narrower with age in a stem, and less vigorous stems have narrower growth rings.

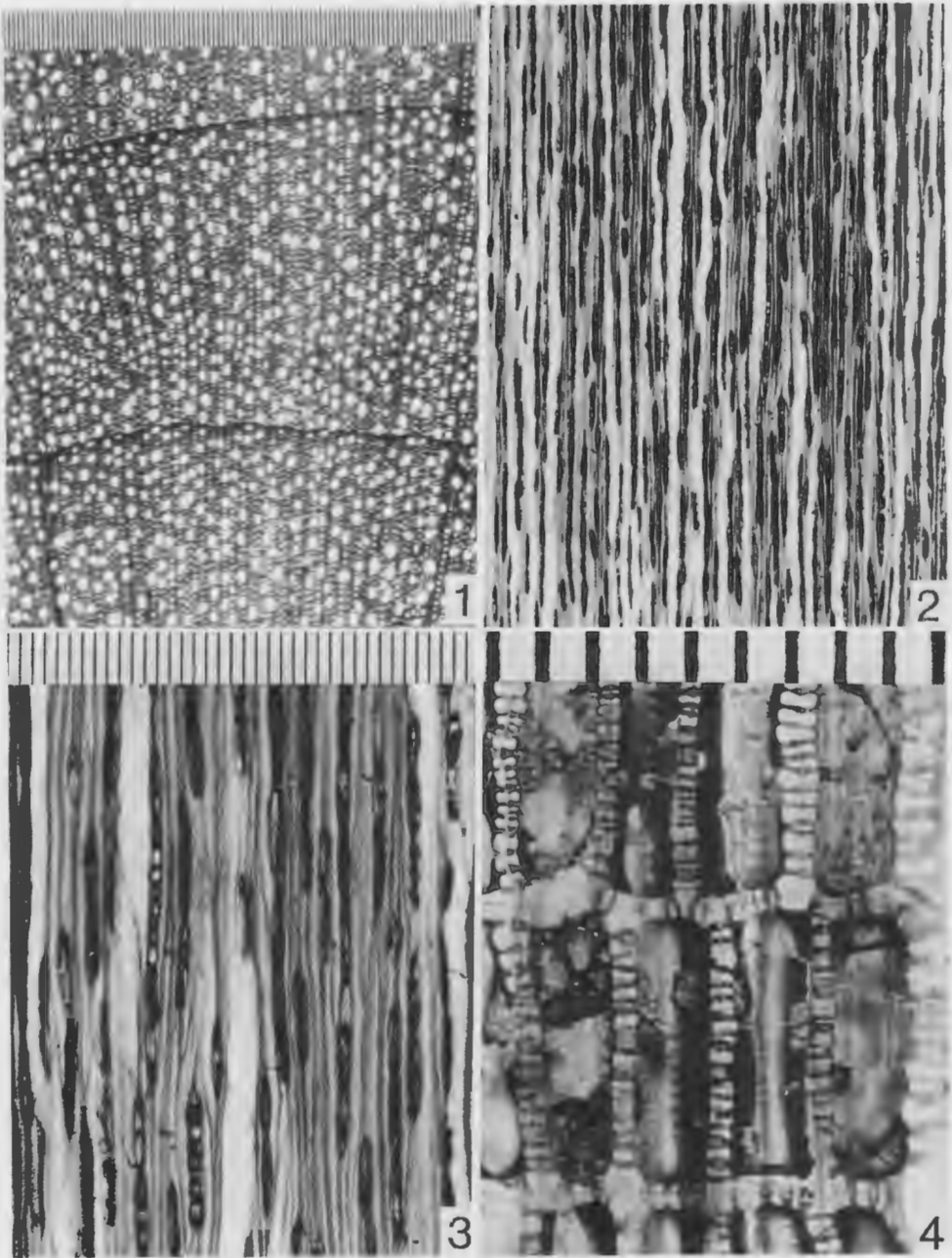


Fig. 1-4. Wood sections of *Ceratiola ericoides* (Carlquist s. n.).—1. Transection; growth rings are wide and semi-ring porous.—2. Tangential section; uniseriate rays are abundant.—3. Portion of tangential section to show that in some rays, vertically short cells that are square or even procumbent (as seen in radial section) are present.—4. Radial section; pits on ray cells are mostly bordered; cells contain dark-staining deposits. (Fig. 1, 2, magnification scale above Fig. 1 [finest divisions = 10 μ m]; Fig. 3, scale above Fig. 3 [divisions = 10 μ m]; Fig. 4, scale above Fig. 4 [divisions = 10 μ m].)

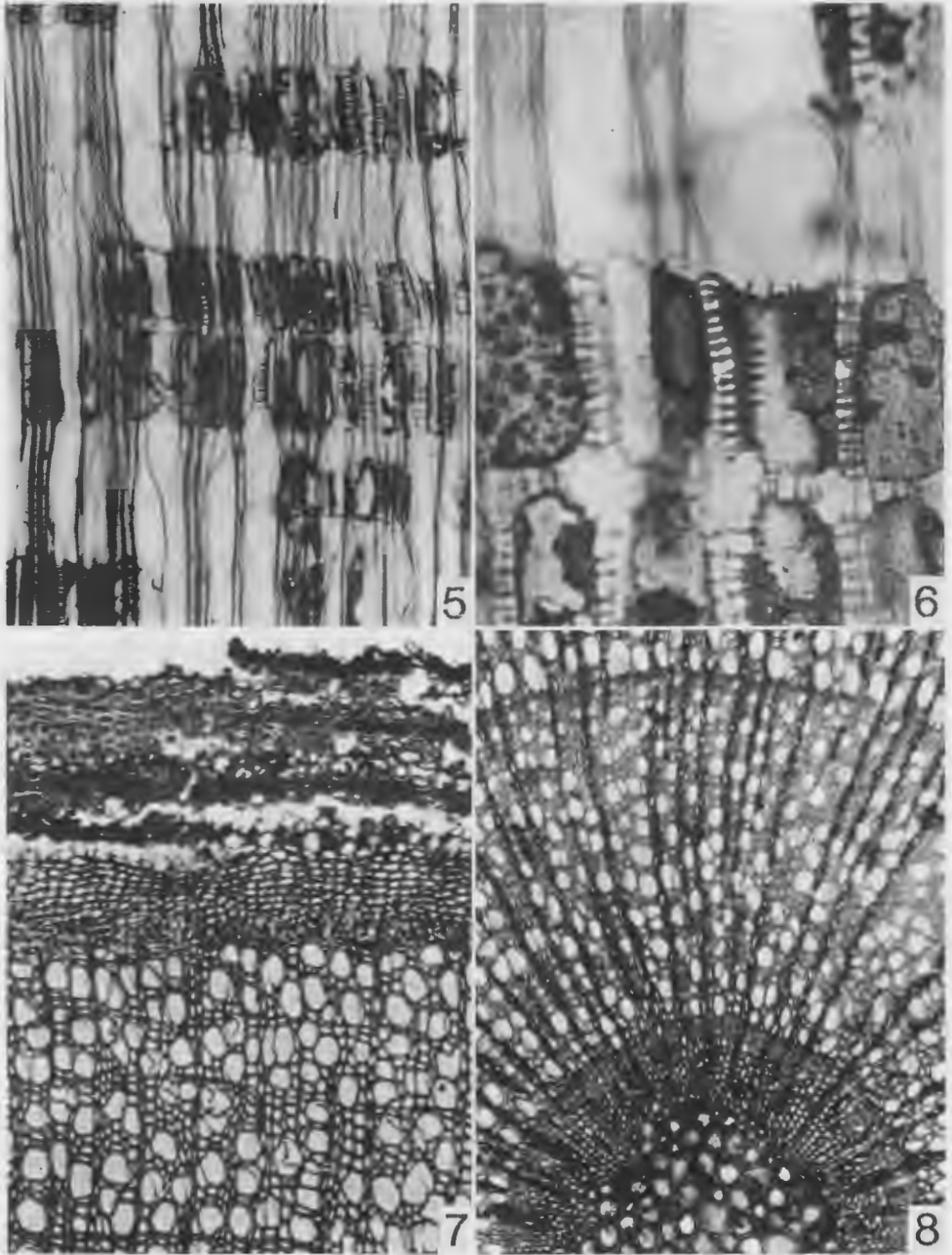


Fig. 5-8. Wood sections of *Ceratiola* and *Corema*.—Fig. 5-7. *Ceratiola ericoides* (Carlquist s. n.).—5. Radial section, to show upright ray cells.—6. Portion of radial section; perforation plate, above, has irregular margins due to presence of vestigial bars.—7. Transection of outer portion of stem; bark, above, is composed of successive periderms, phellem composed of sclereids.—8. *Corema conradii* (MacKeener 249), transection of center of stem to show growth rings; first growth ring composed mostly of thick-walled tracheids. (Fig. 5, 7, 8, scale above Fig. 3; Fig. 6, scale above Fig. 4.)

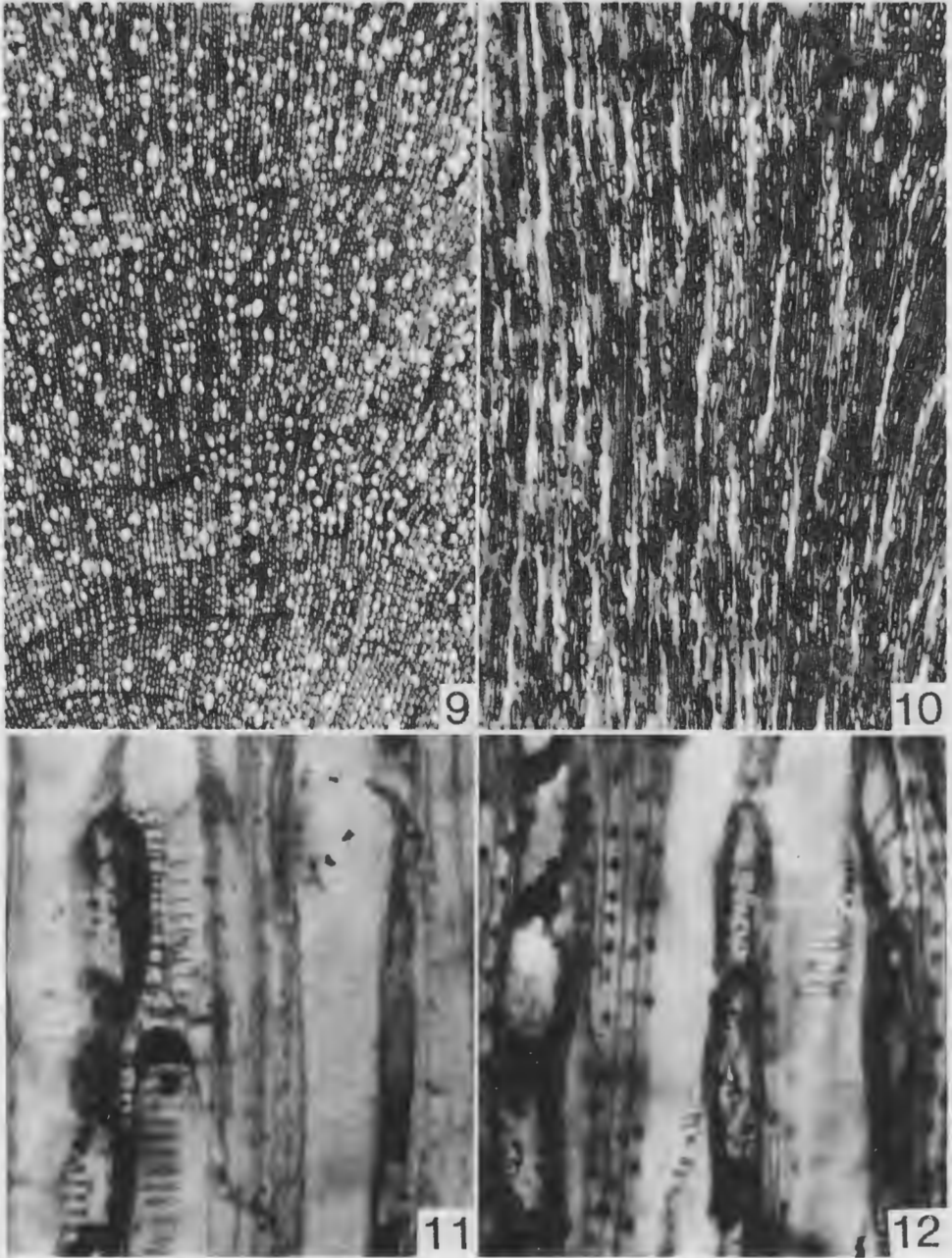


Fig. 9-12. Wood sections of *Corema album* (Pedro 13-III-1938).—9. Transection; growth rings are wide, semi-ring porous.—10. Tangential section; ray cells are relatively large.—11. Portion of radial section; ray cells, left; lateral wall pitting on vessel at right.—12. Portion of radial section; perforation plates in two vessels; dark-staining compounds outline pit cavities of tracheids. (Fig. 9, 10, scale above Fig. 1; Fig. 11, 12, scale above Fig. 4.)

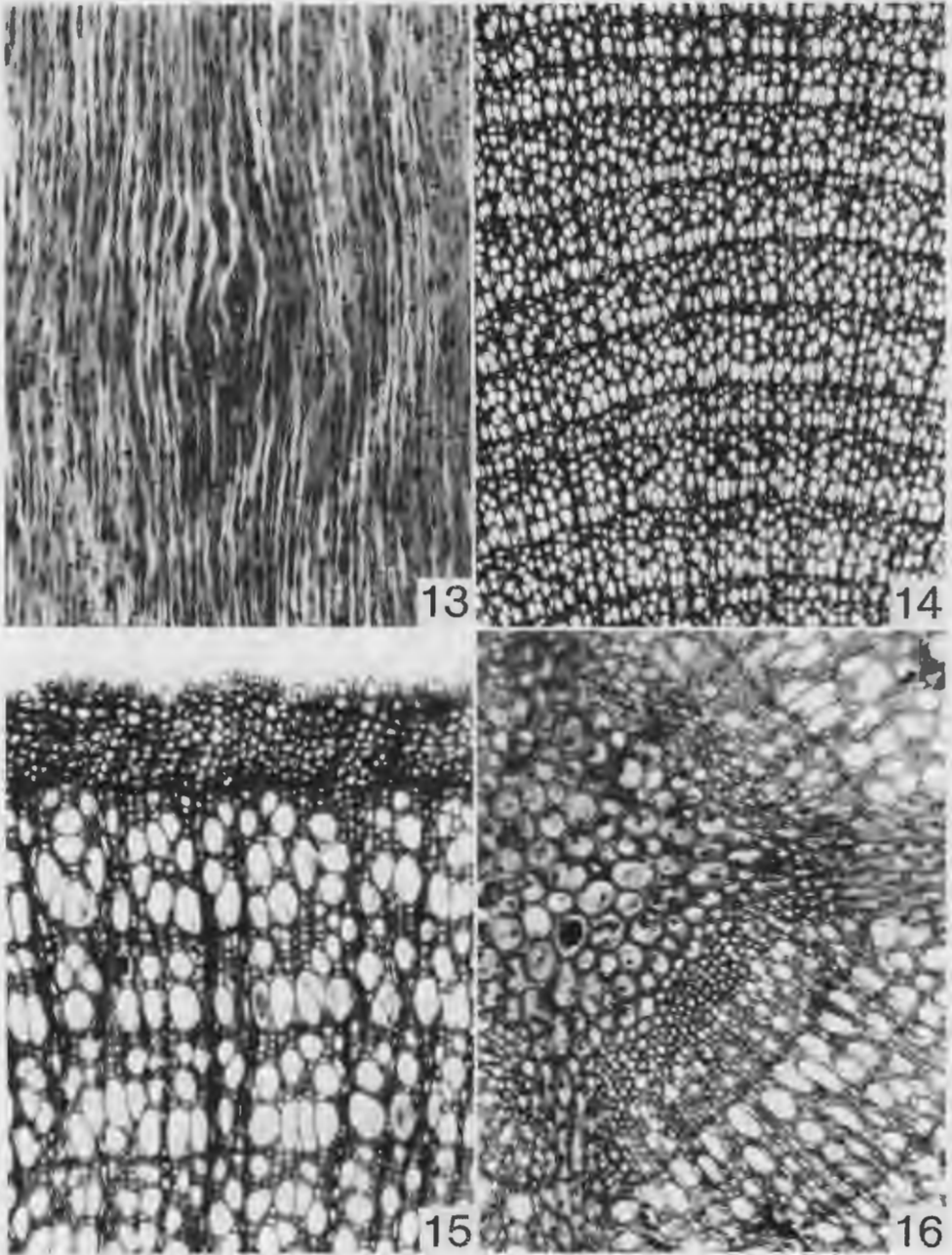


Fig. 13-16. Wood sections of *Empetrum eamesii*.—13. Tangential section of *E. eamesii* subsp. *hermaphroditum* (Abbe 517) in center, several multiseriate rays produced by breakup of a primary ray.—14-15. Transections of *E. eamesii* subsp. *eamesii* (MacKenzie 16-VII-1921).—14. Ten growth rings, showing ring porous condition.—15. Outer portion of stem, showing secondary phloem from which periderms have been lost; large vessels (below) are radially elongate.—16. Transection of center of stem, *E. eamesii* subsp. *hermaphroditum* (Astru 10-VII-1970); primary rays, right, below, extend outward toward cambium. (Fig. 13, 14, scale above Fig. 1; Fig. 15, 16, scale above Fig. 3.)

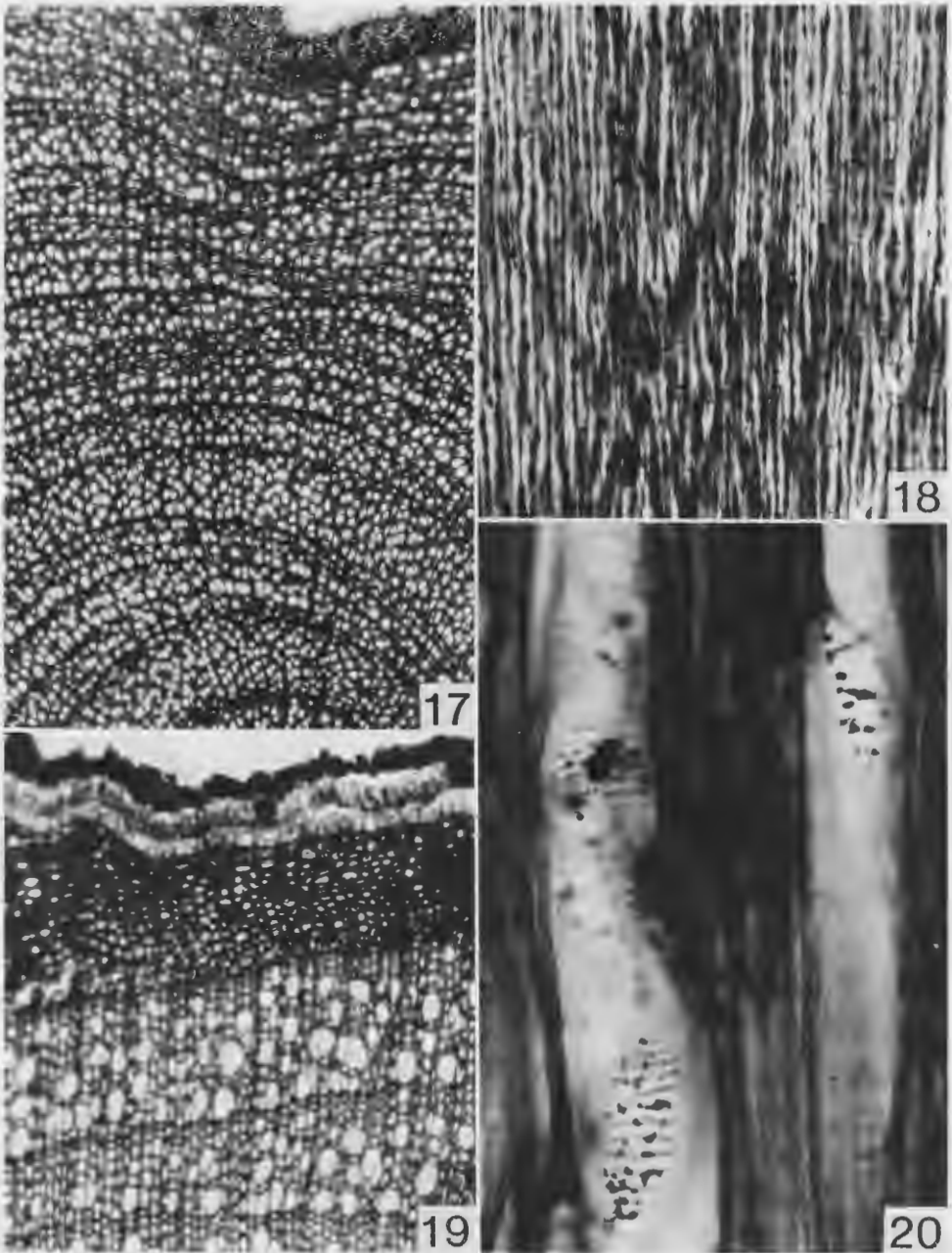


Fig. 17-20. Wood sections of *Empetrum*.—17-19. *E. rubrum* (Goodall 923).—17. Transection; secondary phloem at top; ring porous condition is present.—18. Tangential section; dark-staining compound present in rays.—19. Transection of outer portion of stem; layers of thin-walled sclereids composing phellem at top.—20. Portion of radial section; droplets of dark-staining material cling to perforation plates. (Fig. 17, 18, scale above Fig. 1; Fig. 19, scale above Fig. 3; Fig. 20, scale above Fig. 4.)

Vessel Elements

In transectional view, vessel elements are moderately angular in outline (Fig. 7, 8) or rounded (Fig. 15, 16, 19). They are certainly not as markedly angular as vessels of *Cercidiphyllum*, *Cornus*, or other genera cited for representing that characteristic. Vessels tend to be solitary, but are grouped to various extents (Table 1, column 3). Vessel grouping is low in *Ceratiola* (Fig. 1, 7) and *Corema* (Fig. 8, 9). The highest mean number of vessels per group calculated for the family, 1.56, was observed in a collection of *E. eamesii* subsp. *hermaphroditum* (Fig. 15), in which growth rings are narrow and in which earlywood vessels are crowded.

Mean vessel diameter fluctuates within a narrow range in the family (Table 1, column 4), although differences within a ring are dramatic (e.g., Fig. 15) and one may properly object that with marked ring porosity, mean vessel diameter is physiologically meaningless. Interestingly, mean diameter is relatively uniform for the family even despite various degrees of ring porosity. The mean vessel diameter in the family (between 15 μm and 29 μm) is notable because these vessel diameters are so low compared with that of dicotyledons as a whole (94 μm , Metcalfe and Chalk 1950). Vessel diameter is generally thought to be inversely proportional to vessel density, the number of vessels per mm^2 . In Empetraceae, vessel density (Table 1, column 5) deviates from inverse proportionality rather considerably. The sample with the narrowest vessels, 15 μm (Fig. 17), *E. rubrum* (Goodall 923), does have the highest mean vessel density (1418 vessels per mm^2). However, the lowest mean vessel density (319 vessels per mm^2) occurs in *Corema album* (Pedro 13-III-1938), in which mean vessel diameter is also relatively low, 22 μm (Fig. 9).

Mean vessel element length ranges from 158 μm to 354 μm in the family (Table 1, column 6). Comparison of mean vessel diameter and mean vessel element length in the family reveals that there is not a close correlation between these two dimensions. More significant correlations, which will be discussed below, may be found if one compares vessel element length with number of annual rings (Table 1, column 2).

Perforation plates in Empetraceae range greatly with respect to whether they are simple, scalariform, or with vestigial bars (Table 1, columns 7, 8). *Ceratiola* has simple perforation plates (Fig. 5, upper right), although some of these have vestigial or incomplete bars (Fig. 6). In *Corema*, *C. album* has mostly scalariform perforation plates whereas in *C. conradii* one collection has simple plates plus a few scalariform plates and the other collection has simple plates exclusively. *Empetrum* collections show marked differences with respect to presence of simple and scalariform perforation plates. In both *E. eamesii* subsp. *hermaphroditum* and *E. rubrum*, one collection proved to have scalariform perforation plates characteristically, whereas the other collection had simple plates (plus a very few scalariform plates). The collection of *E. atropurpureum* was notable in that simple, scalariform (Fig. 20), and irregularly margined plates were present in about equal numbers.

Bars on perforation plates of *Empetrum* tend to be slender (especially where more numerous), as shown in the earlywood plates of *E. nigrum* (Fig. 23), but in the same wood section, plates with thicker bars (Fig. 22) may be found in the latewood. The perforation plate of *E. rubrum* illustrated (Fig. 24) is shown at a higher scale than those of Figures 22 and 23, and corresponds in actual size with

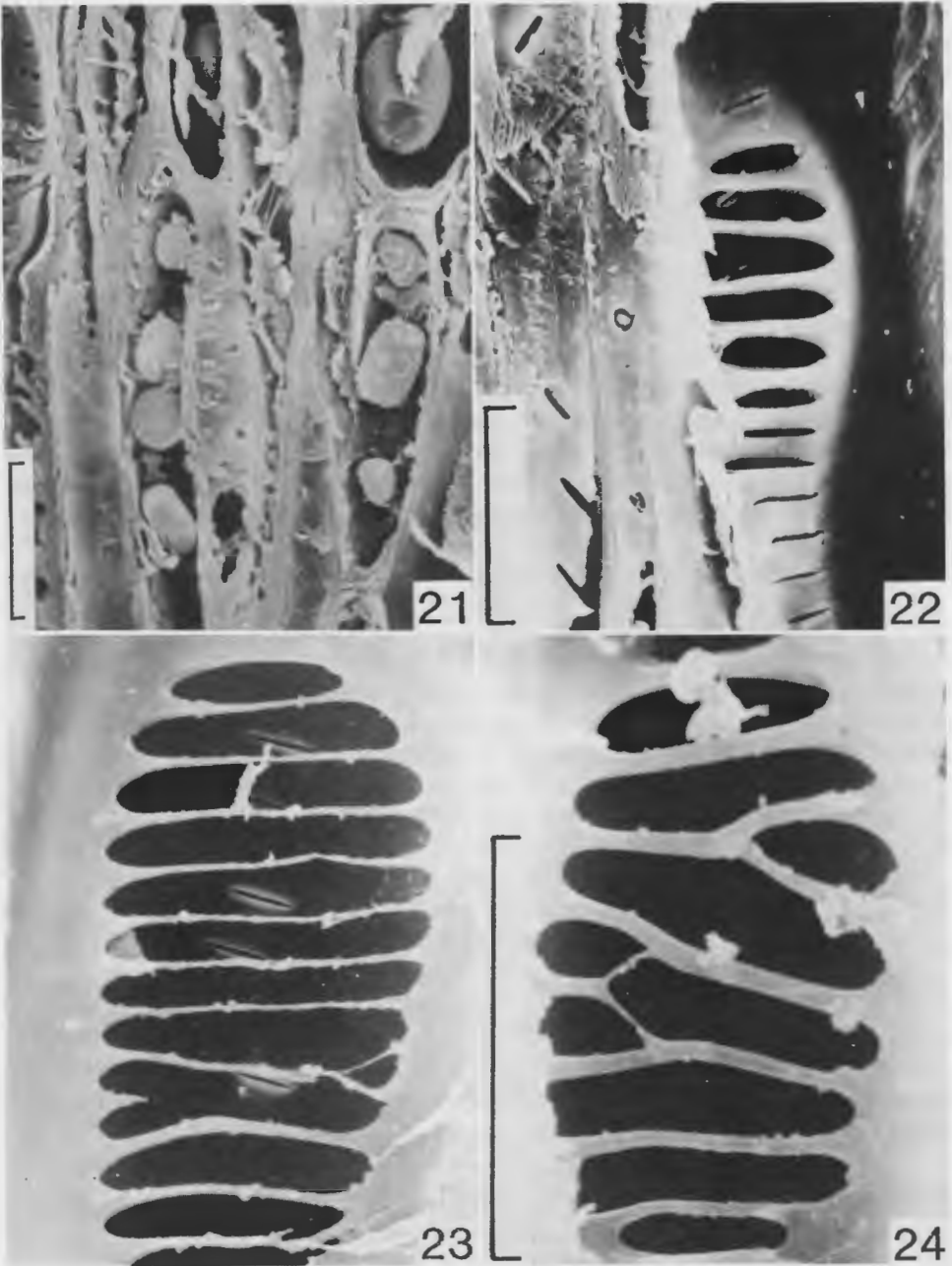


Fig. 21–24. SEM photographs of wood sections of *Empetrum*.—21–23. *E. nigrum* (Fosberg 36536).—21. Tangential section; droplets of dark-staining compounds present in ray cells.—22. Radial section; latewood perforation plate, and, left, tracheids with circular bordered pits.—23. Earlywood perforation plate with slender bars.—24. *E. rubrum* (Carlquist 7288), latewood perforation plate. (Fig. 21, scale shown by 10 μ m bracket at lower left; Fig. 22, 23, 10 μ m bracket at lower left in Fig. 22; Fig. 24, 10 μ m bracket at lower left in Fig. 24.)

the perforation plate of Figure 22; therefore the wide bars in Figure 23 are not an exception to the generalization that most latewood plates tend to be smaller and to have thicker bars than do the earlywood perforation plates. The most numerous bars per plate in the family (18) was recorded in *Corema album*.

Lateral wall pitting of vessels can be divided into vessel-ray pitting, vessel-tracheid pitting, and vessel-vessel pitting. In all Empetraceae, vessel-tracheid pitting consists of sparse circular bordered pits. Vessel-vessel pitting is mostly scalariform (Fig. 22), although identifying vessel-vessel interfaces with certainty is difficult. Vessel-ray pitting in *Ceratiola* is scalariform with some transitional pitting (vessel side). Vessel-ray pitting in *Corema* ranges between scalariform and transitional as shown in Figure 11, or (less commonly) opposite. In *Empetrum*, one finds the range from scalariform to opposite, but where opposite pitting appears present, often the two rows of pits are slightly vertically offset (e.g., in Fig. 11, the pits on the right side of the vessel are not exactly opposite those on the left side). Alternate pitting in the sense of equidistant circular bordered pits is not present. Vessel wall thickness (Table 1, column 9) is characteristically about $0.7 \mu\text{m}$ in *Empetrum*; vessel walls are appreciably thicker in *Ceratiola* and *Corema*.

Tracheids

Following the usages of terms by Bailey (1936) and the IAWA Committee on Nomenclature (1964), Empetraceae have tracheids as their imperforate tracheary element type. Tracheid walls are rather densely covered with pits the same diameter (usually $3\text{--}4 \mu\text{m}$) as those of vessels, as shown by the dark-staining compounds in the pit cavities in Figure 12. The circular nature of the pit cavities and the slitlike nature of pit apertures, are shown in the SEM photograph, Figure 22. Pit cavity diameter is slightly greater in *Ceratiola* (about $4.0 \mu\text{m}$), slightly smaller in *Empetrum* ($3.2\text{--}3.9 \mu\text{m}$) and intermediate in *Corema* ($3.7\text{--}4.0 \mu\text{m}$).

Mean tracheid length is shown in Table 1, column 10. The range for mean tracheid length within the family is $226 \mu\text{m}$ to $448 \mu\text{m}$, and this range tends to parallel closely that for vessel elements in the various collections.

Tracheid wall thickness (Table 1, column 11) is least in *Empetrum*, averaging $2.1 \mu\text{m}$ or less; it is intermediate in *Ceratiola* ($2.3 \mu\text{m}$ and $2.5 \mu\text{m}$ in the two collections) and *Corema conradii* ($1.8 \mu\text{m}\text{--}2.3 \mu\text{m}$), and greatest in *C. album* ($2.8 \mu\text{m}$). Tracheid diameter was not included in the tabulations because reliable mean figures could not, in my opinion, be obtained: tracheids vary too greatly in mean diameter.

Axial Parenchyma

As noted by Metcalfe and Chalk (1950), axial parenchyma in wood of Empetraceae is very sparse. Greguss (1959) failed to find axial parenchyma in *Empetrum nigrum*. My observations on the family showed that axial parenchyma cells are fusiform and never subdivided into strands. They have bordered pits with pit cavity diameter about half that of tracheids, are a little thinner walled than tracheids, and may have contents. Miller's (1975) description of axial parenchyma in "*Empetrum nigrum*" (*E. eamesii* subsp. *hermaphroditum* in the present paper) is in agreement with my findings. Axial parenchyma was recorded as moderately sparse in *Corema album*, *Empetrum atropurpureum* and *E. rubrum* (both collec-

tions). It is very sparse in the remaining collections studied. The distribution of axial parenchyma is difficult to determine: vessel density is so great that the possibility for axial parenchyma to occur surrounded by tracheids is very limited. Thus, axial parenchyma in the family must tentatively be termed scanty vasicentric. Metcalfe and Chalk (1950) make similar comments about axial parenchyma distribution in Ericaceae.

Rays

In almost half of the stems studied, a quadrangular pith with primary rays extending outward from the angles was seen (Fig. 16). Only in the collection shown in Figure 16 did the primary rays extend all the way to the cambium as multiseriate rays. In all of the other collections, fragmentation of these few primary rays into uniseriate rays occurred just outside the pith. Several such small multiseriate ray portions are seen in the center of Figure 13. With the exception of these few primary ray fragments, all rays of Empetraceae are uniseriate.

Mean uniseriate ray height (Table 1, column 12) ranges from 89 to 329 μm . The figures for mean height of uniseriate rays bear a close proportionality to figures for mean vessel element length (and thus presumably the mean length of fusiform cambial initials) in the various collections. Very likely most rays originate as a result of subdivision of fusiform cambial initials rather than from breakup of initials in the primary ray zones, explaining this close proportionality.

With respect to ray histology, rays of Empetraceae consist wholly or predominantly of upright cells (Table 1, column 13, Fig. 10). Square cells are infrequent, procumbent cells even more infrequent. The frequency of these latter types increase (albeit only to a small degree) with age of stem, in accordance with the findings of Barghoorn (1941a). Ray cell wall thickness is unusual in that as seen in tangential sections of wood, ray cell walls appear very thin: usually about 1 μm in thickness. In radial sections, on the other hand, all collections showed ray cell wall thickness in excess of 2 μm (Fig. 6); thus, tangentially oriented and horizontally oriented walls are much thicker than radially oriented walls. The walls seen in sectional view in radial sections mostly bear bordered pits (Fig. 6), a fact clearly evident where dark-staining compounds fill the pit cavities.

Cell Contents

The deposits of dark-staining compounds in woods of Empetraceae are evident in all collections, and may be seen most abundantly in rays (Fig. 2-6, 8, 11, 12, 18). These compounds may also be seen in pit cavities of the tracheids (Fig. 12) and clinging to the bars of scalariform perforation plates (Fig. 20). In some portions of older stems in a few collections, large numbers of vessels are filled with the dark-staining compounds. Such exceptional abundance of the dark-staining compounds seems related to trauma, but the less excessive deposits in most wood samples of Empetraceae must be considered normal and characteristic of the family. The spherical objects shown in Figure 21 are not starch grains, but large droplets of the dark-staining compounds, as comparison with slides viewed with light microscopy demonstrated. Use of polarizing equipment did not reveal either starch or crystals in the wood of the collections studied.

BARK ANATOMY

Empetraceae have thin bark that tends to be papery or, in *Ceratiola*, somewhat shaggy. In transections of stems, one sees a relatively thin zone of secondary phloem, overlain by one or more of the successive periderms (Fig. 7). If the periderms are removed by sectioning, one sees only the secondary phloem (Fig. 15). The liquid-preserved stems of *Ceratiola ericoides* (Carlquist 8037) permitted me to observe that adjacent to the cambium there are a few layers of sieve tube elements with associated companion cells. Evidently production of secondary phloem is slow and collapse of sieve tube elements and companion cells more than a year old is rapid, because by far most of the secondary phloem in the stems sectioned consists of phloem parenchyma, with sieve tube elements and companion cells quite crushed and no longer evident.

In examining periderm formation of Empetraceae, I noted that a number of layers of phellem are produced by each periderm. If one looks for phellogen and phelloderm, one finds a single layer of cells in which wall thickenings (such as one would expect in phellem) are absent or present only in the distal portions of cells. This layer may be tangentially subdivided; the inner, and radially flatter of the two layers is arguably phelloderm. Lacking material that clearly shows initiation of a periderm, I am entertaining the possibility that the inner layer is, rather, an active phellogen and the outer layer of cells is the most recently derived phellem. This interpretation is enhanced by the fact that where the two layers without marked wall thickenings can be observed, the tangential wall between the two layers is contained within the spherical shape of the parent cell, indicating recency of division that one would not expect of phelloderm. If periderm is stripped away, as in Figure 15, the outermost layer of cells is such a layer, with wall thickenings on the distal portions of cells.

The collections of Empetraceae differ somewhat with respect to phellem composition. *Ceratiola* bark is composed of up to seven layers of sclereids (Fig. 7), and several of the successive periderms remain attached to the stem in patches separated by grooves in the bark; in this way, the shaggy appearance of bark in *Ceratiola* is achieved. *Corema album* has phellem composed of flattened suberized cells, whereas that of *C. conradii* is composed of cells that I term sclereids because their walls are rigid and do not collapse with age. The phellem of *Empetrum atropurpureum* is composed of several layers of sclereids, whereas that of *E. eamesii* and *E. nigrum* is apparently thinner walled and nonsclerified. Phellem of *E. rubrum* is composed of thin-walled sclereids (Fig. 19, above). Accumulations of the dark-staining materials (which probably give the bark of *Corema* and *Empetrum* a reddish-brown color in gross aspect) may be seen in phellem cells. Although only one or two periderms adhere to sections in my slides of *Corema* and *Empetrum* stems, examination of herbarium specimens reveals several papery periderms adherent to older stems, so that evidently some of the successive periderms in these two genera are easily broken away during the sectioning process.

CONCLUSIONS

Ecological Wood Anatomy

The vessel features of Empetraceae suggest a high degree of adaptation to drought, either because of soil dryness (the sandy habitats of *Ceratiola* and *Corema* may

be dry seasonally) or physiological drought (extreme cold in *Empetrum* environments must result in freezing of soil and very likely of water in the vessels on occasion). Narrow vessels embolize less readily than wide ones (Ellmore and Ewers 1985; Ewers 1985). Consequently, the narrow mean vessel diameter characteristic of *Empetrum* can be regarded as a primary form of adaptation to resistance to embolism formation. If a high number of vessels per mm^2 of transection confers redundancy and therefore conductive safety of the vessel system (see Carlquist 1975), large numbers of vessels per mm^2 must be indicative of wood xeromorphy. The way in which shortness of vessel elements relates to wood xeromorphy is less clear at the present time, but patterns of evolution in dicotyledon woods do suggest a relationship, perhaps the confinement of air bubbles within individual vessel elements (Carlquist 1988). The three quantitative features of vessels just mentioned were combined into a formula called "Mesomorphy": vessel diameter times vessel element length divided by number of vessels per mm^2 (Carlquist 1977). Although an arbitrary formula, this index has the advantage of demonstrating both conductive efficiency and conductive safety. The latter is obviously very important in plants of extreme environments such as those occupied by many Empetraceae; the Hagen-Poiseuille equation, which expresses only conductive efficiency, does not really demonstrate the ecological adaptation of such woods. The values for Mesomorphy in Empetraceae (Table 1, column 14) are notably low: 2.4 to 19. Lower values are very rare, but have been reported for *Cassiope* (Ericaceae), which occupies cold and windblown boreal sites much like those of *Empetrum* (Wallace 1986). Interestingly, the highest values for Mesomorphy in Empetraceae are in the two species from relatively low latitudes where frost is minimal: *Ceratiola ericoides* (19, 9.4) and *Corema album* (16). This suggests that in alpine or high latitude sites, wood of a maximally xeromorphic formulation is to be expected. The southern California survey of Carlquist and Hoekman (1985) exemplifies this; in this survey, the alpine shrubs have an average Mesomorphy figure (27) lower than that of any other major plant association except desert shrubs (20.9). Woods of Empetraceae qualify as highly xeromorphic by any standards.

Another feature that relates to conductive safety is the presence of tracheids (rather than fiber-tracheids or libriform fibers) as the imperforate tracheary element type. The relative abundance in woods of dry habitats of woods with tracheids (either true tracheids or vasicentric tracheids) has been noted earlier (Carlquist 1985; Carlquist and Hoekman 1985). Tracheids are theoretically safer than vessel elements because the presence of pit membranes in pits of tracheids prevents spread of bubbles from one tracheid into a neighboring tracheid, whereas the absence of a pit membrane in a perforation plate permits spread of bubbles from one vessel element to the next with greater ease.

A wood in which tracheids occur as the background imperforate tracheary element type has a kind of potential conductive safety with regard to growth ring phenomena. The earlywood contains conductively more efficient wider vessels, but the latewood contains not only fewer and narrower vessels (which are safer than wider vessels, as noted above), but also a greater area devoted to tracheids than earlywood. This phenomenon was noted in the recognition of the Type 5 growth ring (Carlquist 1988). Although vessel density in Empetraceae is greater than in the examples of Type 5 illustrated in that source, all species of Empetraceae fall into Type 5, as do all species of *Cassiope* (Wallace 1986).

The occurrence in woods of Empetraceae of both scalariform and simple perforation plates is worth examining with respect to conductive characteristics. While a traditional view is that disappearance of bars represents a shift to conductive efficiency, Zimmermann (1983) offers an alternative interpretation. Zimmermann's hypothesis claims that scalariform perforation plates are potentially advantageous when frozen water in vessels thaws; the bars in the perforation plates are thought to sieve out water bubbles, preventing their spread into the vessel and hastening the resorption of bubbles. Scalariform perforation plates are quite common in tropical uplands where frost is unknown (Carlquist 1988). However, in the case of Empetraceae, the distribution of simple versus scalariform perforation plates tends not to reinforce Zimmermann's hypothesis. The *Empetrum* collections from Greenland and Newfoundland have simple perforation plates; the Greenland *Empetrum* studied by Miller (1975), however, did have scalariform perforation plates. Of the two species of *Corema*, *C. conradii* (New England and adjacent regions) is from a colder area than *C. album* (western shores of the Iberian peninsula), but *C. conradii* has predominantly simple plates, whereas those in *C. album* are scalariform. One can conclude that little selection for simplification of the perforation plate is evident. The relatively wide perforations, coupled with small number of bars per perforation plate in Empetraceae, offer minimal impedance to flow in vessels of Empetraceae. In addition, the earlywood perforation plates have very slender bars, whereas wide bars persist in the latewood plates (this would accord with the hypothesis that higher flow rates produce selective pressure for greater perforation areas). In assessing this situation, one should note that the small ericoid leaves of Empetraceae have minimal transpiration, so water flow in vessels of Empetraceae is likely slower than it is in broadleaved dicotyledons, and thus the selective pressure for perforation plate simplification is not very great at most.

Paedomorphosis in Rays and Other Features

The rays of Empetraceae are unusual among dicotyledons at large in being uniseriate and in being composed characteristically of upright cells. A few square and erect cells do appear in older stems, as one would expect in view of the findings of Barghoorn (1941a). Uniseriate rays composed characteristically of upright ray cells are cited by Barghoorn (1941b) as indicating a stage in development of raylessness, but is this true? Barghoorn uses *Corema conradii*, *Tetra-theca ciliata* Lindl. (Tremandraceae), and *Staavia glutinosa* (L.) Thunb. (Bruniaceae) as examples in this connection. Other genera with this type of ray, including *Dracophyllum* (Epacridaceae), *Empleuridium* (Celastraceae), *Myrothamnus* (Myrothamnaceae), and *Setchellanthus* (Capparaceae), can be added (Carlquist 1988: 195). Interestingly, many of these are relatively small shrubs of finite size, which may correlate with the predominance of upright cells characteristic of paedomorphosis in woods (Carlquist 1962). This interpretation is reinforced by the fact that in younger stems of Empetraceae, square and procumbent cells are lacking, and they are very few even in older stems (Table 1, column 13). Because Paedomorphic Type III rays are defined as characteristically being composed of upright cells (Carlquist 1988), and presence of appreciable numbers of procumbent

cells in such uniseriate rays would transfer them into the Heterogeneous Type III of Kribs (1935), the rays of Empetraceae can be considered as paedomorphic to the extent they lack procumbent cells (as is mostly true of them).

A number of genera of dicotyledons (probably many more than have presently been reported) have uniseriate rays exclusively at the onset of secondary growth, but show ontogenetic change of many of these into multiseriate rays, as in *Schisan-dra* (Carlquist 1988:346). By virtue of not showing this progression, rays of Empetraceae can be regarded as paedomorphic.

In woods that exemplify paedomorphosis, the age-on-length curve for vessel elements (and imperforate tracheary elements) is not obtained. Rather, vessel elements and imperforate tracheary elements become shorter, instead of longer, as growth progresses (Carlquist 1962). Do Empetraceae fulfill this criterion? If one compares ages of stems to vessel element lengths (Table 1, columns 2 and 6), one finds that older stems of *Corema* and *Empetrum* do indeed have shorter vessel elements and tracheids (although not markedly so). The older stem of *Ceratiola* has longer vessel elements and tracheids, but one must note that *Ceratiola* forms much larger shrubs than do *Corema* and *Empetrum*, so that one might have expected *Ceratiola* to have escaped from juvenilism. Interestingly, the shortest mean vessel element lengths in *Cassiope* were reported in those specimens for which largest (and presumably oldest) stems were available: *C. mertensiana* (Bong.) G. Don subsp. *mertensiana* and *C. tetragona* (L.) D. Don subsp. *tetragona* (Wallace 1986). This example appears to confirm the interpretation given for wood in Empetraceae, as does the predominance of upright ray cells in *Cassiope*. *Cassiope* forms diminutive sprawling shrubs, much as does *Empetrum*, in high-latitude and high-elevation sites.

Paedomorphosis is usually found in wood of rosette trees belonging to predominantly herbaceous groups (e.g., Campanulaceae), "woody herbs" such as *Penstemon* of the Scrophulariaceae (Michener 1986), shrubby and arboreal succulents, and even annuals (Carlquist and Eckhart 1984). The small but woody shrubs represented by *Empetrum*, *Empleuridium*, *Myrothamnus*, and *Tetrateca* represent a category not originally included in my exposition of paedomorphosis in dicotyledonous woods (Carlquist 1962). However, these small shrubs satisfy criteria for paedomorphosis and undoubtedly exemplify the phenomenon. Barghoorn's concept that *Corema* and the other small shrubs with uniseriate rays represent stages in evolution of raylessness does not appear to be validated. In this connection, one should note that in none of the Empetraceae studied (or in the other shrubs cited) do rays appear to be scarce; by contrast, they are abundant (e.g., Fig. 2).

Systematic Considerations

With respect to wood features indicative of generic delimitation, one may cite the thick, sclerenchymatous periderms and rather wide growth rings, with little difference in diameter between latewood and earlywood and latewood vessels, of *Ceratiola* (although the nature of growth rings can justly be cited as having an ecological basis). *Corema* has ray cells that are notably wide tangentially compared to those of the other two genera. *Empetrum* differs from *Corema* and *Ceratiola*

in its offset ("alternate") files of elliptical pits on vessel-ray interfaces. The growth rings of *Empetrum* are much more markedly ring porous than those of *Corema* or *Ceratiola*, but again this may be primarily an ecological distinction.

Scalariform versus simple perforation plates does not seem a distinction by which genera or even species differ, because in *E. eamesii* and *E. rubrum*, either scalariform perforation plates or simple perforation plates are present, depending on the population (a variation pattern that does not correspond, apparently, to ecology).

With respect to systematic affinity of Empetraceae, the most recent (e.g., Cronquist 1988) as well as the older phylogenetic systems are almost uniform in claiming the family as a member of Ericales. Dissenting views are few; one such is the opinion of Fernald (1950) who claimed a sapindalean affinity for Empetraceae.

Wood features of Empetraceae that are common also in Epacridaceae and Ericaceae (data from Metcalfe and Chalk 1950 and Wallace 1986) include: vessels angular to rounded in outline; vessels with scalariform to simple perforation plates; vessel-ray pitting scalariform, transitional, and opposite; tracheids present as the basic imperforate tracheary element type; axial parenchyma very sparsely vasicentric if only by virtue of vessel abundance; uniseriate rays commonly present (multiseriate rays if present not wide but commonly biseriate), the uniseriate rays characteristically composed of upright cells. Although some of these features can be cited as indicating a similar degree of phyletic advancement for the three families, there is a range within each of the families and the similarities, rather, are probably indicative of close relationship.

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