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## WOOD ANATOMY OF *CASSIOPE* (ERICACEAE)

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### ABSTRACT

Wood anatomical characteristics for 21 taxa of *Cassiope* are reported. Qualitative features differ somewhat from the general pattern of the Ericaceae. However, considerable deviation is found in the quantitative aspects of the wood features. The stems are very slender with narrow growth rings evident in all but one species. Vessel elements are very small and usually have scalariform perforation plates with several bars. Vessels are extremely abundant in transection. Vascular rays are mostly uniseriate with a few biseriate and all are composed exclusively of erect cells. The imperforate elements are tracheids which are the only conductive elements in the late wood. *Calluna*-type pith is found in most of the taxa while homogeneous pith is found in two species. The recognition of these in the separate genus *Harrimanella* is supported. *Cassiope* plants are often found in moist, protected microenvironments in arctic and alpine areas of extreme cold and desiccating winds. Short growing seasons and low mean temperatures probably contribute in large part to the dwarf stature of the plants, which in turn accommodates the reduced vascular system. The tracheids provide a safe conductive system in the late wood which is less susceptible to loss of function due to air embolisms. The vessel elements with scalariform perforation plates accommodate the presumably slow conductive rates in the earlier part of the growing season. The vessel elements of *Cassiope* are considerably smaller than most others known to have scalariform perforation plates. The values for vulnerability, an indicator of the degree of vessel redundancy and hence safety, are much lower than any yet calculated for any group. The same is true for figures for mesomorphy, which introduces vessel element length as an independent measure of degree of xeromorphy.

Key words: alpine ecology, arctic ecology, *Cassiope*, dwarf shrubs, ecological wood anatomy, Ericaceae, wood anatomy.

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### INTRODUCTION

While wood anatomy of trees and many larger shrubs has been studied, little is known about the wood anatomy of small shrubs. Even less is known about woods of arctic-alpine shrubs which often would be classed as dwarf shrubs. The reduced stature of the plants contributes to the general lack of adequate material for study in wood collections. The species affected by the climatic extremes offer unusually interesting material for the study of ecological wood anatomy. The harsh conditions belie the fact that some of the taxa that occur in these areas are members of groups which would be considered to have unspecialized woods.

*Cassiope* D. Don is a small genus of dwarf, evergreen shrubs in the Ericaceae. It is generally placed in the tribe Cassiopeae Stevens of the Vaccinioideae Endl. (Stevens 1971). *Cassiope* is restricted to the Northern Hemisphere. The plants often occupy moist sites near those exposed to cold desiccating winds and winter snow abrasion. Most often *Cassiope* forms patches varying in size and density depending upon the species and environmental conditions of the site. Not uncommonly two species may be sympatric. Many of the Asiatic taxa are sparsely represented in herbaria and label data are often scanty. Ranges for most of these taxa are poorly understood.

Few anatomical treatments have included more than a few species in any one

genus. The following general description of the woods of Ericaceae, including the Vacciniaceae, is taken from Metcalfe and Chalk (1950). Vessels extremely small, less than 25  $\mu\text{m}$  in diameter, to moderately small, 50–100  $\mu\text{m}$  in diameter, exclusively solitary except for incidental overlapping of tapering end walls. Perforation plates scalariform, simple, or foraminate. Spiral thickenings sometimes present in the vessel elements. Vessel density rarely less than 40 per  $\text{mm}^2$  and as high as 400 per  $\text{mm}^2$  in *Vaccinium*. Lateral wall pitting scalariform to opposite. Axial parenchyma scanty to absent. Rays typically of two sizes, the heterogeneous often lack procumbent cells. The imperforate elements tracheids, vasicentric tracheids (Carlquist 1985*b*), libriform fibers, or septate fibers.

#### MATERIALS AND METHODS

Liquid-preserved samples were stored in 50% ethyl alcohol prior to further preparation. Dry specimens were boiled to remove air and restore the tissues, then stored in 50% ethyl alcohol. Macerations were prepared using Jeffrey's solution (Johansen 1940) and stained in safranin. Woody stems of small proportions do not lend themselves to standard preparation using a sliding microtome. Softening of the wood samples prior to paraffin embedding and sectioning made this study possible. The stems were softened in a 4% solution of ethylene diamine and subsequently embedded in paraffin according to procedures outlined by Carlquist (1982*a*). Sections were cut at 15  $\mu\text{m}$  and stained with safranin. Some were counterstained with fast green. Table 1 lists some pertinent information on the collections used in this study. Table 2 summarizes the quantitative and qualitative data for all samples studied. Means are based on 25 measurements unless otherwise indicated. Multiseriate rays were rare if present at all. Stem and pith diameters (Table 2) were measured with the ocular micrometer.

*Cassiope abbreviata* Hand.-Maz. and three recently described taxa *C. pulvinalis* T. Z. Hsu, *C. nana* T. Z. Hsu, *C. argyrotiricha* T. Z. Hsu were not available at the time for inclusion in this study. Vouchers of my collections are deposited at LAM.

The kindness of the curators of BM, CAL, CAS, DS, E, KUN, L, LIV, and UC for the loan and use of herbarium specimens is greatly appreciated. The author is deeply indebted to Dr. Sherwin Carlquist for the use of space and materials as well as photographic assistance.

#### ANATOMICAL DESCRIPTION

Woods of *Cassiope* are generally ring porous (Fig. 1, 6, 10, 15). The growth rings possess vessels in the earlywood, whereas vessels are almost entirely lacking in the latewood. Vessels are variously present after the earliest-formed wood (Fig. 2, 7, 10, 22). Tracheids, the imperforate elements, comprise the bulk of the latewood in all of the taxa (Fig. 15, 22). The vessel diameters decrease generally from earlywood to later wood. The average width of the growth rings ranges from 34  $\mu\text{m}$  in *Cassiope hypnoides* to 105.6  $\mu\text{m}$  in *C. tetragona* ssp. *tetragona*. One species, *C. ericoides*, lacks growth rings (Fig. 13). Stem and pith diameters are listed in Table 2.

The pith of *Cassiope* conforms to two different patterns. Most of the taxa have a central pith region composed of thin-walled, irregularly shaped parenchyma

Table 1. Wood collections of *Cassiope*.

Taxon	Collection	Provenance
<i>C. dendrotricha</i> Hand.-Mazz.	Rock 22970 (UC)	China, Yunna, ca. 28°N lat., 4421 m.
<i>C. ericoides</i> (Pall.) D. Don	Bardunov & Kaplin 3094 (E)	USSR, Lake Baikal, 55°47'N lat., ca. 2134 m.
<i>C. fastigiata</i> (Wall.) D. Don	Duthie s.n. (CAS)	Kashmir, Pir Penjal, 33°38'N lat.
<i>C. hypnoides</i> (L.) D. Don	Forbes s.n. (UC)	USA, NH, Mt. Washington, 44°15'10"N lat., 1676 m.
<i>C. hypnoides</i>	Wallace 2122 (LAM)	USA, NH, Mt. Washington, 44°15'30"N lat., 1539 m.
<i>C. lycopodioides</i> (Pall.) D. Don ssp. <i>crispipilosa</i> Cald. & Tayl.	Calder, Savile & Taylor 22825 (DS)	Canada, BC, Morsby I., 53°03'N lat., 365 m.
<i>C. lycopodioides</i> ssp. <i>lycopodioides</i>	Wallace 2139 (LAM)	Canada, BC, Smithers, 54°46'N lat., 610 m.
<i>C. macrantha</i> Hand.-Mazz.	Handel-Mazzetti 8767 (E)	China, Yunnan, Se La, 27°40'N lat.
<i>C. mairei</i> Léveillé	Maire s.n. (E)	China, Yunnan, Io-Chan, ca. 26°N lat., 3200 m.
<i>C. mertensiana</i> (Bong.) G. Don ssp. <i>californica</i> Piper	Hansen 795 (DS)	USA, CA, Amador Co., 38°42'N lat., 2550 m.
<i>C. mertensiana</i> ssp. <i>ciliolata</i> Piper	Copeland 3898 (UC)	USA, CA, Siskiyou Co., 41°20'N lat., 2591 m.
<i>C. mertensiana</i> ssp. <i>gracilis</i> Piper	Cussick 3337 (DS)	USA, OR, Wallowa Co., ca. 45°N lat., 2650 m.
<i>C. mertensiana</i> ssp. <i>mertensiana</i>	Mr. & Mrs. E. Walker 966 (UC)	USA, AK, Ketchikan, 55°20'N lat., ca. sea level.
<i>C. mertensiana</i> ssp. <i>mertensiana</i>	Wallace 2153 (LAM)	Canada, BC, Manning Park, 49°05'N lat., 2063 m.
<i>C. myosuroides</i> W. W. Smith	Rock 25016 (UC)	China, Yunnan, SW of Lichiang, 26°51'N lat.
<i>C. palpebracta</i> W. W. Smith	Ward 583 (E)	China, Yunnan, Mekong-Yangtze div., 26°N lat., 4116 m.
<i>C. pectinata</i> Stapf	Forrest 13944 (E)	China, Yunnan, Bei-ma-shan, 28°N lat., 3658 m.
<i>C. redowskii</i> (Cham. & Schlecht.) G. Don	Kuznetsov s.n. (E)	USSR, Primorsky Dist., Mt. Setko, 52°14'N lat., 1475 m.
<i>C. selaginoides</i> Hook. f. & Thoms.	Wilson 3910 (BM)	China, western, 3911 m.
<i>C. stelleriana</i> (Pall.) DC.	Wallace 2150 (LAM)	Canada, BC, Smithers, 54°46'N lat., 610 m.
<i>C. tetragona</i> (L.) D. Don ssp. <i>saximontana</i> (Small) A. E. Porsild	Calder, Parmelee, Taylor 19673 (CAS)	Canada, BC, Quiniscoe Lake, 49°04'N lat.
<i>C. tetragona</i> ssp. <i>tetragona</i>	Nygaard s.n. (DS)	Greenland, Thule, 76°33'N lat., ca. sea level.
<i>C. wardii</i> Marquand	Ward 5752 (E)	Tibet, Temo-la, 29°30'N lat., 4350 m.



Table 2. Wood characteristics of *Cassiope* (Eriacaceae).

Taxon	Collection	1	2	3	4	5	6	7	8
<i>C. dendrotricha</i>	Rock 22970	E	1.76	0.36	8	87.5	9	2290	272
<i>C. ericoides</i>	Bardunov & Kaplin 3094	E	2.23	0.23	—	—	15	2002	217
<i>C. fastigiata</i>	Duthie s.n.	E	1.22	0.22	12	41.6	10	2673	215
<i>C. hypnoides</i>	Forbes s.n. Wallace 2122	C	0.70	0.05	7	46.4	13	1901	180
		C	0.77	0.08	10	34.5	14	2047	210
<i>C. lycopodioides</i> ssp. <i>lycopodioides</i>	Wallace 2139	C	1.21	0.13	12	45.0	13	2466	208
<i>C. lycopodioides</i> ssp. <i>crispilosa</i>	Calder, Savile, Taylor 22825	C	1.65	0.16	15	49.6	15	1942	278
<i>C. macrantha</i>	Handel-Mazzetti 8767	E	0.90	0.22	5	68.0	13	2549	328
<i>C. mairei</i>	Maire s.n.	E	1.54	0.22	16	41.2	15	2022	306
<i>C. mertensiana</i> ssp. <i>californica</i>	Hansen 795	C	1.98	0.55	12	59.5	18	1731	195
<i>C. mertensiana</i> ssp. <i>ciliolata</i>	Copeland 3898	C	1.48	0.20	11	58.1	16	1671	234
<i>C. mertensiana</i> ssp. <i>gracilis</i>	Cussick 3337	C	2.77	0.27	16	78.1	17	1590	194
<i>C. mertensiana</i> ssp. <i>mertensiana</i>	Walker 966 Wallace 2153	C	2.90	0.47	16	75.9	25	1299	299
		C	3.63	—	37	49.0	22	1049	176
<i>C. myosuroides</i>	Rock 25016	C	1.04	0.19	6	70.8	14	2448	247
<i>C. palpebracta</i>	Ward 583	P	1.01	0.16	8	53.1	16	1856	237
<i>C. pectinata</i>	Forrest 13944	E	2.11	0.34	11	80.4	13	1977	300
<i>C. redowskii</i>	Kuznetsov s.n.	E	2.25	0.26	10	99.5	17	1811	241
<i>C. selaginoides</i>	Wilson 3910	E	1.35	0.24	9	61.6	14	1741	258
<i>C. stelleriana</i>	Wallace 2150	P	1.62	0.27	10	67.5	20	1686	196
<i>C. tetragona</i> ssp. <i>saximontana</i>	Calder, Parmelee, Taylor 19673	E	2.31	0.50	19	47.6	19	1696	196
<i>C. tetragona</i> ssp. <i>tetragona</i>	Nygaard s.n.	E	3.79	0.41	16	106	14	1149	148
<i>C. wardii</i>	Ward 5752	E	2.42	0.51	12	79.5	14	2193	251
Mean for all samples			1.85	0.27		63.6	15	1904	234

Key to numbered columns: 1. leaf type (E = ericoid with revolute margins forming abaxial groove; C = concave but no abaxial groove; P = planar).—2. Stem diameter, mm.—3. Pith diameter, mm.—4. Mean number of growth rings.—5. Mean width of growth rings,  $\mu\text{m}$ .—6. Mean vessel diameter,  $\mu\text{m}$ .—7. Mean number of vessels per  $\text{mm}^2$  of transection.—8. Mean vessel element length,  $\mu\text{m}$ .—9. Mean vessel wall thickness,  $\mu\text{m}$ .—10. Mean number of bars per perforation plate.—11. Percent simple perforation plates.—12. Mean number of vessels per group.—13. Mean tracheid diameter,  $\mu\text{m}$ .—14.

cells surrounded by a cylinder of longitudinally elongate, thick-walled cells (Fig. 1, 18, 22–23). This type of pith has been called the *Calluna*-type (Watson 1964). The pith of *C. hypnoides* and *C. stelleriana* lacks the central region composed of thin-walled irregularly shaped parenchyma cells (Fig. 6, 9, 20–21). This corresponds to the homogeneous type (Watson 1964). All cells of the pith in these two taxa are square to vertically elongate and thick walled.

Vessel elements of *Cassiope* are thin walled compared to tracheids of the same wood (Fig. 2, 7, 13, 19). Mean vessel diameters range from only 9  $\mu\text{m}$  in *C.*

Table 2. Continued.

9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
0.8	9.4	0	1.9	5.0	311	2.5	409 (6)	15	228	1.14	s-o	0.0039	1.06	0.9
0.8	6.8	0	1.5	5.0	246	2.5	— —	—	121	1.14	o-a	0.0075	1.63	6.3
0.8	9.7	0	1.6	5.0	285	2.5	510 (4)	20	326	1.32	s-o	0.0039	0.84	2.0
1.2	14.2	0	1.5	7.5	216	2.5	236 (7)	11	177	1.20	s-o	0.0068	1.22	3.4
0.8	11.6	0	1.2	7.5	236	2.5	258 (5)	11	157	1.12	s-o	0.0066	1.38	4.2
0.6	6.8	0	2.1	7.5	242	2.5	237 (1)	17	147	1.16	s-o	0.0053	1.10	4.4
1.2	8.1	0	2.3	6.2	303	2.5	187 (1)	25	180	1.09	s-o	0.0077	2.14	6.1
1.2	16.0	0	2.0	7.5	367	2.5	— —	—	199	1.19	s-o	0.0051	1.67	4.5
0.8	17.1	0	1.1	8.7	350	3.0	— —	—	182	1.14	s	0.0074	2.26	6.4
1.2	2.3	48	1.6	7.5	268	2.5	238 (1)	12	142	1.37	s-o	0.0104	2.03	11.4
0.8	4.2	20	1.6	7.5	284	2.5	— —	—	207	1.21	o	0.0096	2.24	6.6
1.2	1.7	64	1.3	7.5	253	1.8	258 (1)	12	150	1.30	o-a	0.0107	2.07	8.3
1.2	3.1	8	1.3	10.0	313	2.5	375 (3)	22	202	1.05	o-a	0.0192	5.74	31.7
1.2	0.6	76	1.2	10.0	223	2.5	174 (6)	15	95	1.27	o-a	0.0209	3.69	15.4
1.2	9.3	0	1.8	10.0	322	2.5	— —	—	139	1.30	s	0.0057	1.41	5.8
1.2	13.2	0	1.4	7.5	293	2.5	— —	—	146	1.24	s-o	0.0086	2.04	7.6
1.2	10.8	0	1.5	7.5	325	2.5	425 (1)	17	332	1.08	s-o	0.0066	1.98	3.5
0.8	13.1	0	1.8	7.5	267	2.5	— —	—	188	1.11	o-a	0.0094	2.26	9.4
1.2	10.1	0	1.4	10.0	281	2.5	148 (1)	20	166	1.09	s-o	0.0080	2.07	4.2
1.2	10.1	0	1.4	8.7	253	1.8	187 (1)	20	121	1.29	s	0.0118	2.31	16.9
0.8	11.2	0	1.3	7.5	243	2.5	520 (1)	17	164	1.24	o	0.0112	2.19	13.8
0.8	3.1	4	1.4	7.5	179	2.5	121 (7)	22	110	1.21	o	0.0122	1.80	2.8
0.8	7.7	0	1.5	7.5	288	2.5	225 (1)	17	189	1.15	o	0.0064	1.61	5.3
1.0	8.7	9.6	1.5	7.65	276	2.5	282	17	177	1.17		0.0081	1.89	7.8

Mean tracheid length,  $\mu\text{m}$ .—15. Mean tracheid wall thickness,  $\mu\text{m}$ .—16. Mean multiseriate ray height,  $\mu\text{m}$ ; number of rays encountered given in parentheses.—17. Mean multiseriate ray width,  $\mu\text{m}$ ; based on same number of rays in column 16.—18. Mean uniseriate ray height,  $\mu\text{m}$ .—19. Ratio of imperforate element length to vessel element length.—20. Type of lateral wall pitting on vessels (s = scalariform; o = opposite; a = alternate).—21. Vulnerability Index (see text).—22. Mesomorphy Index (see text).—23. Conductivity (see text).

*dendrotricha* to 25  $\mu\text{m}$  in *C. mertensiana* ssp. *mertensiana*. The length of vessel elements ranges from 148  $\mu\text{m}$  in *C. tetragona* ssp. *tetragona* to 328  $\mu\text{m}$  in *C. macrantha*. Transections of woods show that most species have less than two vessels per group. *Cassiope macrantha*, *C. lycopodioides* ssp. *lycopodioides*, and *C. lycopodioides* ssp. *crispilosa* are the only taxa with more than two vessels per group (Fig. 14, 18, 23). No spiral thickenings were observed in the vessel elements.

Scalariform perforation plates predominate in the genus (Table 2). The mean number of bars per perforation plate is 17 in *C. mairei* and only 3.1 in *C. tetragona*

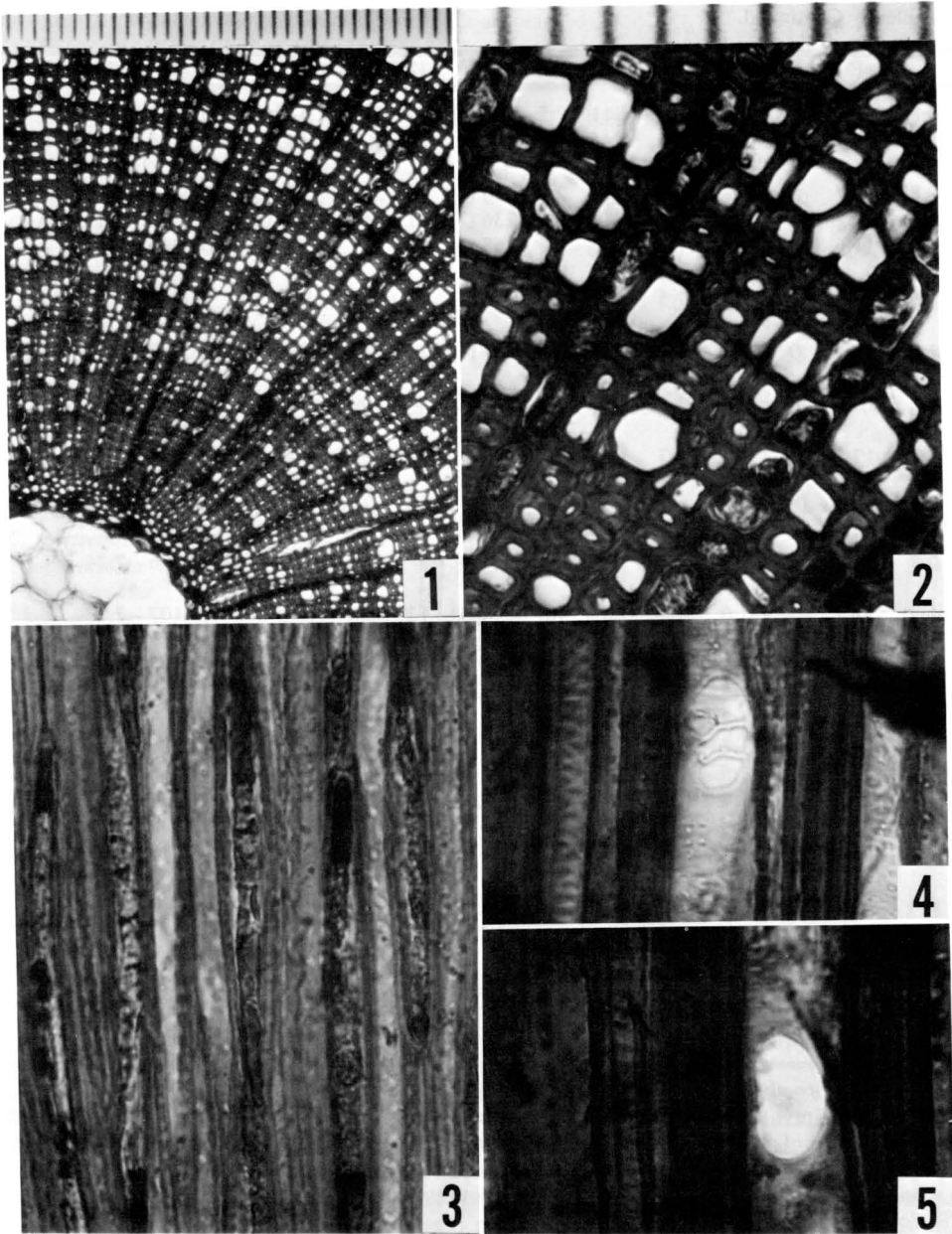


Fig. 1-5. Wood sections of *Cassiope mertensiana* ssp. *ciliolata* (Copeland 3898).—1. Transection of stem showing growth rings; vessels lacking in latewood; uniseriate rays predominate; pith at lower left.—2. Transection of stem, vessels solitary and vessel overlap areas; thick-walled tracheids predominate in latewood; pith toward lower left.—3. Tangential section showing erect cells of uniseriate rays with dark contents.—4. Perforation plate from radial section with irregular bars.—5. Simple perforation plate from radial section. (Fig. 1, magnification scale above Fig. 1 [finest divisions = 10  $\mu$ m]; Fig. 2-5, magnification scale above Fig. 2 [divisions = 10  $\mu$ m].)

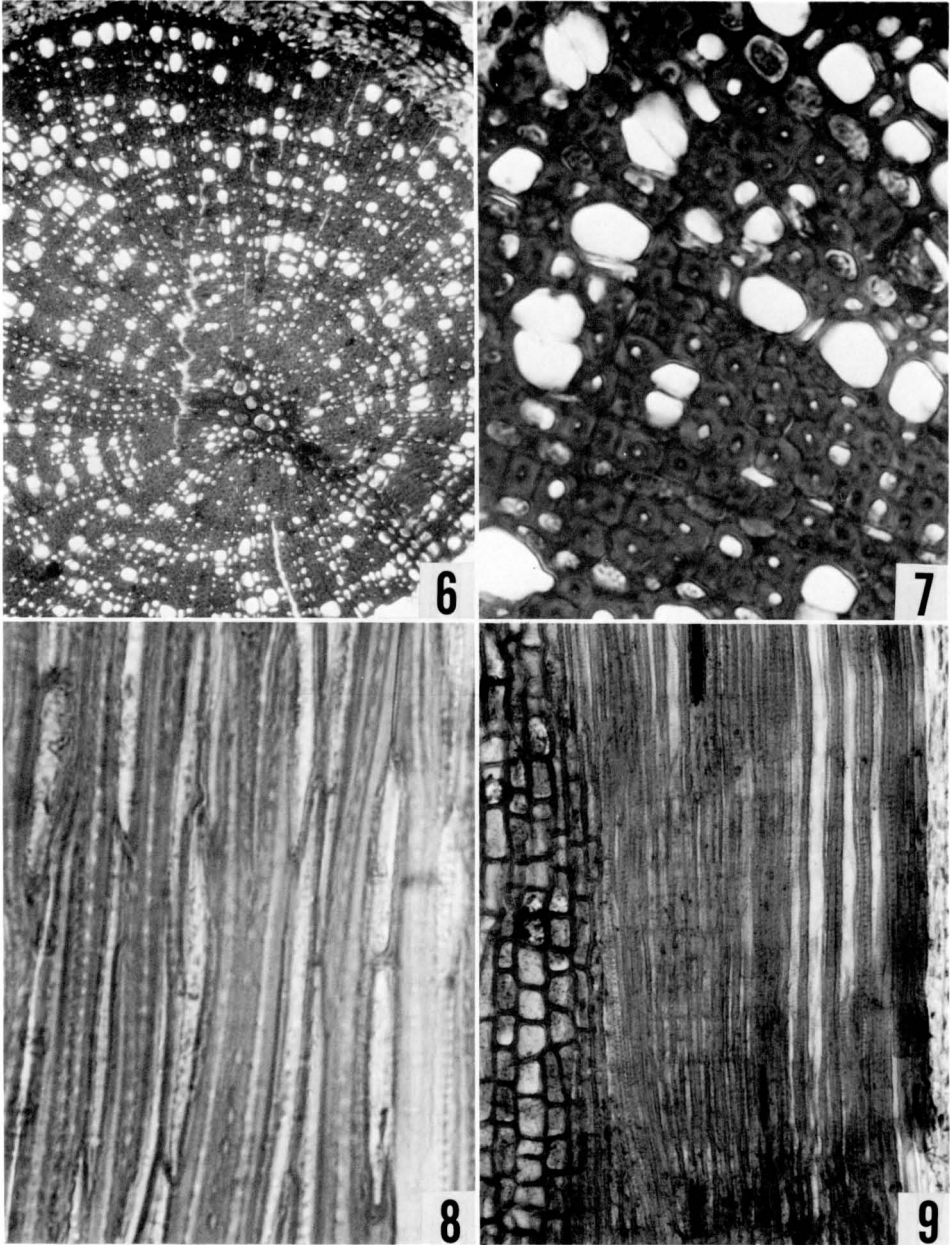


Fig. 6-9. Wood sections of stem of *Cassiopia hypnoides* (Forbes s.n.).—6. Transection, large earlywood vessels evident; thick-walled tracheids in latewood.—7. Transection showing parenchyma between vessels middle right; uniseriate ray upper right.—8. Tangential section, uniseriate rays; two-celled uniseriate ray at right.—9. Radial section showing thick-walled pith cells at left; bark area at right. (Fig. 6, 9, scale above Fig. 1; Fig. 7, 8, scale above Fig. 2.)

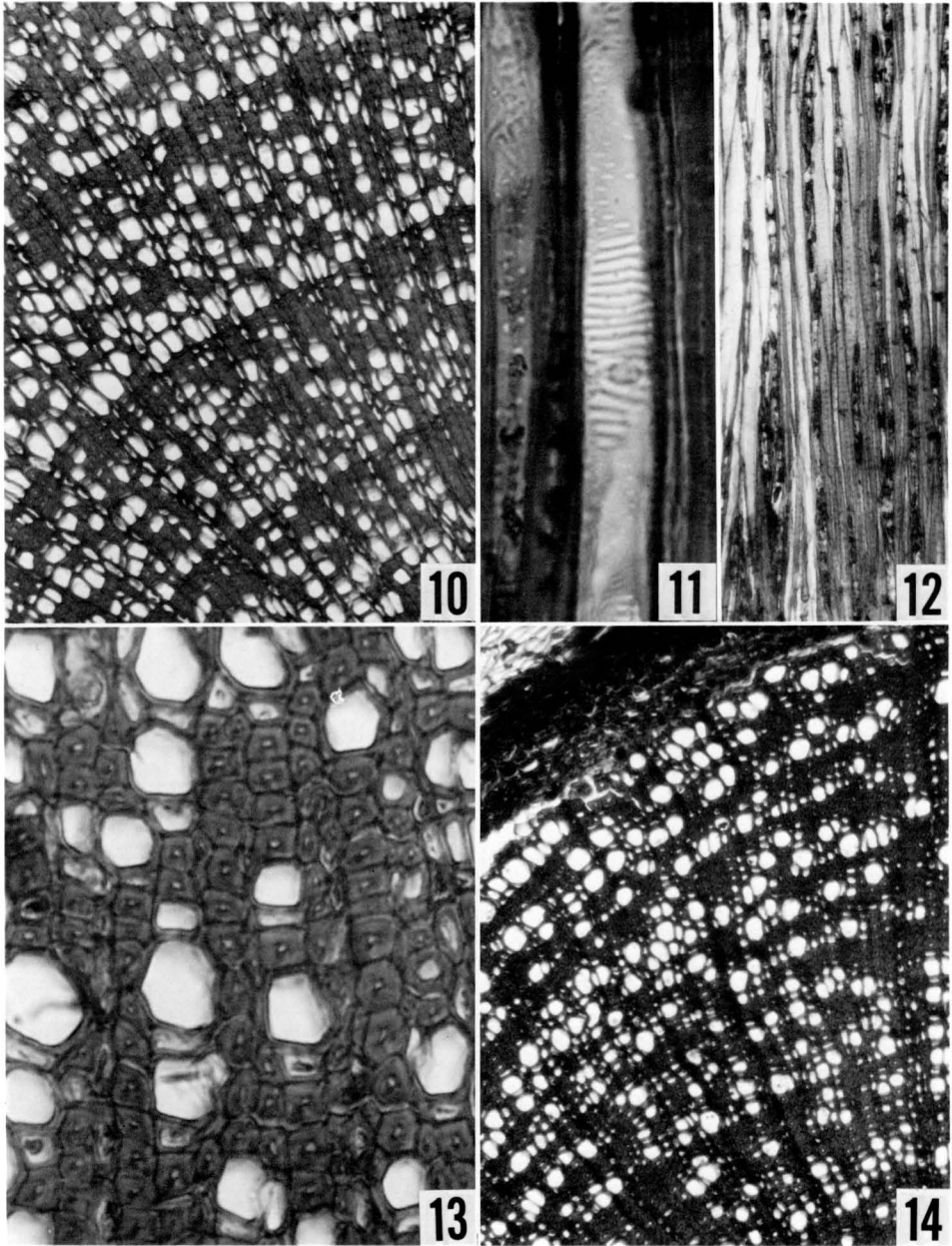


Fig. 10–14. Wood sections of stems of *Cassiopia*.—10–11. *C. redowskii* (Kuznetsov s.n.).—10. Transection showing growth rings; vessels lacking in latest wood; vessels decrease somewhat from earliest vessels formed then decrease little; pith toward lower right.—11. Perforation plate and lateral wall pitting from radial section.—12. *C. fastigiata* (Duthie s.n.). Tangential section showing uniseriate rays composed entirely of erect cells; portion of biseriate ray at upper middle.—13. *C. ericoides* (Bardunov & Kaplin 3094). Transection, no growth rings evident; vessels thin walled compared to tracheids; pith toward bottom.—14. *C. lycopodioides* ssp. *cristapilosa* (Calder, Savile, Taylor 22825). Transection, large vessels restricted to earlywood; vessels somewhat grouped; some paratracheal parenchyma evident. (Fig. 10, 14, scale above Fig. 1; Fig. 11, 12, 13, scale above Fig. 2.)



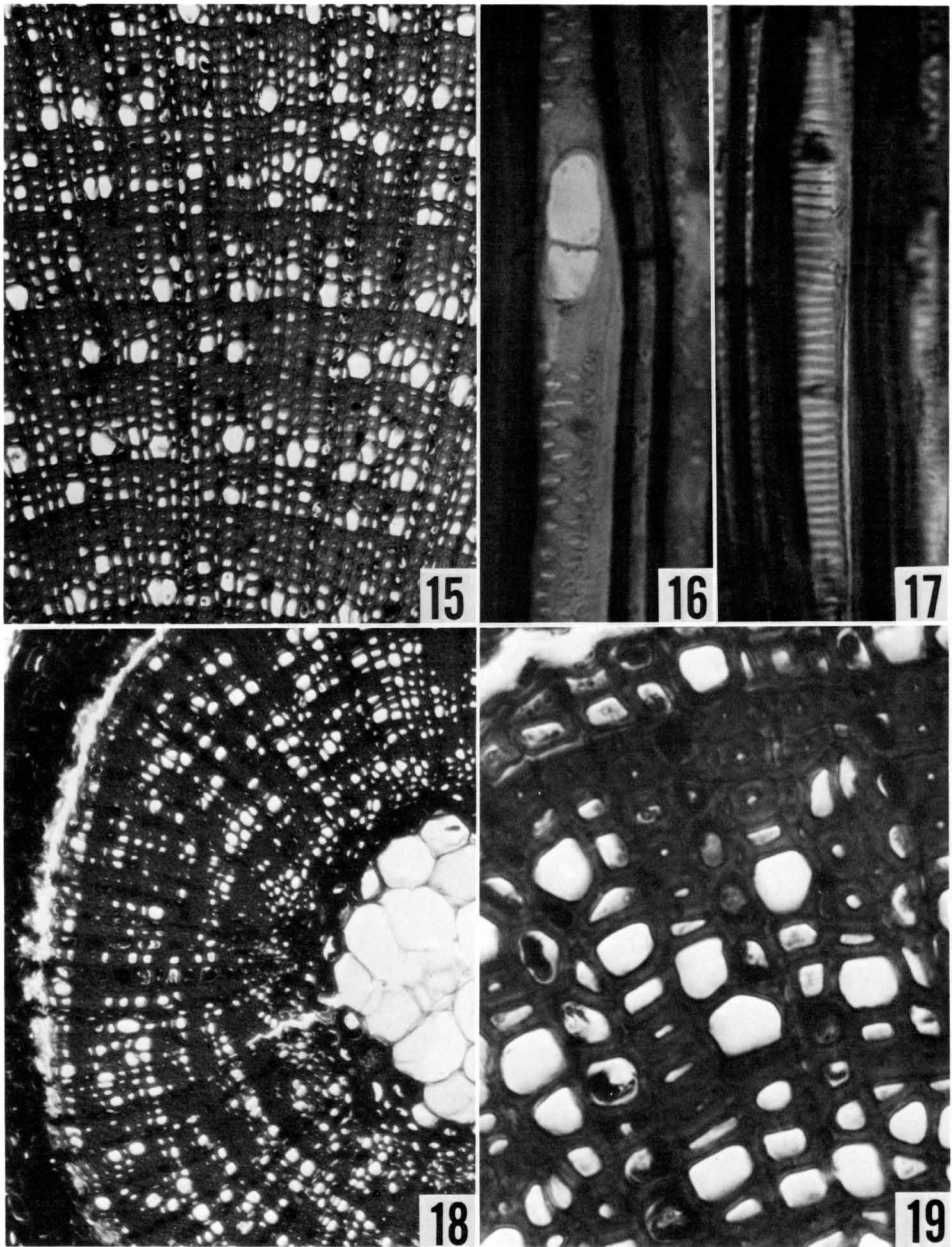


Fig. 15–19. Wood sections of stems of *Cassiope*.—15–16. *C. mertensiana* ssp. *mertensiana* (Mr & Mrs Walker 966).—15. Transection showing growth rings; tracheids in latewood; some paratracheal parenchyma present; uniseriate rays evident.—16. Radial section, vessel perforation plate with single bar, and lateral wall pitting.—17. *C. myosuroides* (Rock 25016). Radial section showing scalariform lateral wall pitting and perforation plate of vessel; bars bordered.—18–19. *C. macrantha* (Handel-Mazzetti 8767).—18. Transection showing growth rings; pith of thin-walled parenchyma cells; larger vessels in earlywood; uniseriate rays evident.—19. Transection showing thin-walled vessels, thick-walled tracheids; uniseriate ray with dark contents at lower left; pith toward lower right. (Fig. 15, 18, scale above Fig. 1; Fig. 16, 17, 19, scale above Fig. 2.)

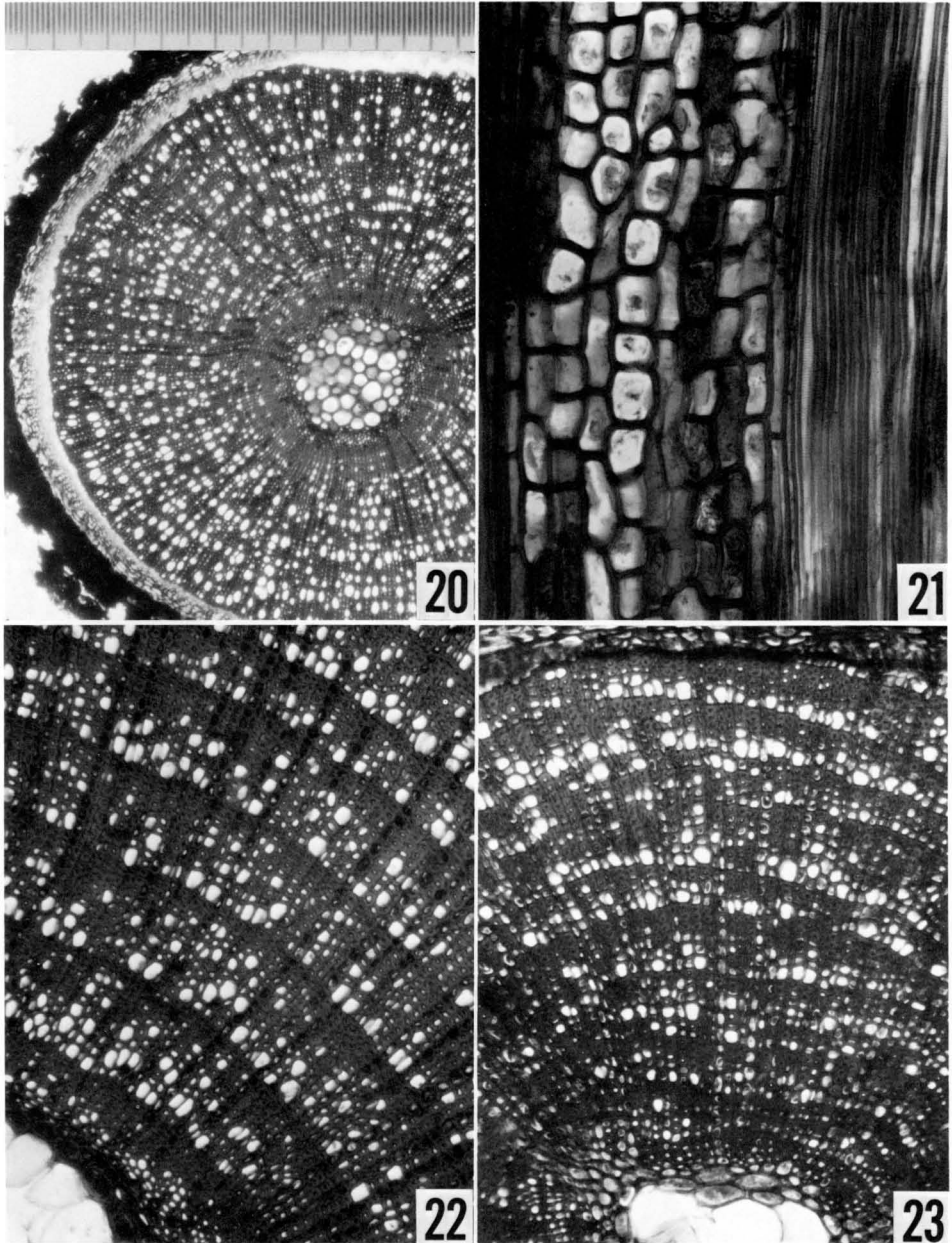


Fig. 20–23. Wood sections of stems of *Cassiopa*.—20–21. *C. stelleriana* (Wallace 2150).—20. Transverse section, thick-walled cells of homogeneous pith evident; vessels large in earlywood.—21. Radial section showing thick-walled pith on left; vessel element at right with scalariform lateral wall pitting.—22. *C. wardii* (Ward 5752). Transverse section showing growth rings lacking vessels in latewood; uniseriate rays evident; biseriate ray extends toward upper middle of section; thin-walled cells of pith at lower left.—23. *C. lycopodioides* ssp. *lycopodioides* (Wallace 2139). Transverse section, vessels grouped somewhat; growth rings evident; pith of thin-walled cells internal to layer of thick-walled cells. (Fig. 20, magnification scale above Fig. 20 [finest divisions = 10  $\mu\text{m}$ ]; Fig. 21, 22, 23, scale above Fig. 1.)

ssp. *tetragona*. Often some of the bars are forked (Fig. 11) or irregular (Fig. 4). Simple perforation plates were found only in *C. mertensiana* and *C. tetragona* (Fig. 5). Figures in Table 2 indicate the percentage of simple perforation plates found among the two species and their subspecific taxa.

Lateral wall pitting of vessel elements is scalariform to opposite (Fig. 11, 16–17). Some pitting approaching the alternate condition was observed in *C. mertensiana* ssp. *gracilis*. In some species such as *C. myosuroides*, vessel elements are so narrow that lateral wall pitting seems to merge with the perforation plate (Fig. 17). The pits are fully bordered (Fig. 16).

Tracheids constitute the imperforate elements in *Cassiope*. These elements have fully bordered pits and range in size from 179  $\mu\text{m}$  in *C. tetragona* ssp. *tetragona* to 367  $\mu\text{m}$  in *C. macrantha*. Tracheid wall thickness was similar for all the specimens studied (Table 2). The ratio of imperforate element length to vessel element length was low, ranging from 1.37 in *C. mertensiana* ssp. *californica* to 1.05 in *C. mertensiana* ssp. *mertensiana*.

Axial parenchyma was extremely scanty, occurring only as a few isolated cells if present at all (Fig. 7, 14).

The vascular rays of *Cassiope* are composed exclusively of erect cells. The multiseriate rays are merely biseriate, by virtue of having a single erect cell alongside an otherwise uniseriate ray. Very few multiseriate rays were seen; the numbers upon which the figures are based are given in parentheses in Table 2. The multiseriate rays range in height from 121  $\mu\text{m}$  in *C. tetragona* ssp. *tetragona* to 510  $\mu\text{m}$  in *C. fastigiata*. The width of the multiseriate rays is 11  $\mu\text{m}$  in *C. fastigiata* and ranges up to 25  $\mu\text{m}$  in *C. lycopodioides* ssp. *crispilosa*. Uniseriate rays predominate in *Cassiope* (Fig. 3, 8, 12, 15, 22). The height of the uniseriate rays ranges from 110  $\mu\text{m}$  in *C. tetragona* ssp. *tetragona* to 332  $\mu\text{m}$  in *C. pectinata*.

## DISCUSSION

### *Systematic Conclusions*

There have been few quantitative treatments of the wood anatomy of members of the Ericaceae. Some notable works include those of Cox (1948*a, b*). Metcalfe and Chalk (1950) provide a summary of the anatomical characteristics of the Ericaceae, although they separated the Vacciniaceae. The wood of the Ericaceae is considered to be relatively unspecialized, containing vessel elements, generally with scalariform perforation plates, and scalariform to opposite lateral wall pitting (Frost 1931). The woods of *Cassiope* differ only slightly from the qualitative features described by Metcalfe and Chalk (1950) for the Ericaceae and Vacciniaceae. Imperforate elements are tracheids and no spiral thickenings were observed in the vessels. The major features of deviation are the vascular rays. Multiseriate rays are rare and these are narrow biseriate rays. All of the ray cells are erect.

Coville (1901) proposed separation of *Cassiope hypnoides* and *C. stelleriana* into a new genus, *Harrimanella*. He based this, in part, on the presence of alternate, decurrent leaves; terminal, ebracteate flowers; short sepals; pleated corolla with erect lobes; filaments of two unequal lengths and enlarged at base; and short stout styles. Not all of the characters proposed by Coville are consistent in *Harrimanella*, but the two species have been found to have homogeneous pith. *Cassiope* has opposite leaves; axillary bracteate flowers; long sepals; nonpleated corolla with



reflexed lobes; filaments of a single length not enlarged at base; slender elongate cylindrical styles; and heterogeneous pith. The heterogeneous pith has been termed the *Calluna*-type by Watson (1964). This view has been supported by Stevens (1970, 1971).

Pith structure has been recognized as a useful generic character (Fritsch 1903; Stevens 1971; Watson 1964). The results here do, in fact, show that *Cassiope sensu stricto* has the *Calluna*-type pith composed of a central area of thin-walled irregularly shaped to boxy parenchyma cells surrounded by a multiple-celled layer of erect, cylindrical, thick-walled parenchyma cells. The two species separated as *Harrimanella* have their entire pith composed of thick-walled cells. These results support the recognition of *Harrimanella hypnoides* (L.) Coville and *H. stelleriana* (Pall.) Coville. These two species have distinctive homogeneous pith (Fig. 9, 21). For comparison, however, in this paper both taxa will be listed as species of *Cassiope*. These two pith types do occur elsewhere in the Ericaceae (Stevens 1971). There do not seem to be any other subdivisions of *Cassiope* warranted on the basis of wood anatomical features.

#### *Evolution of Dwarf Habit and Significance to Wood Anatomy*

There is general difficulty in separating cause and effect relationships with respect to habit in dwarf shrubs. Most, if not all, species of *Cassiope* could be considered dwarf shrubs. The tiny, often appressed and abaxially grooved, evergreen leaves would seem adapted to conserve water. The stems are slender, forming a decumbent system on a layer of older larger decumbent branches. Roots form irregularly along many of the stems at the soil interface. *Cassiope hypnoides* is among the smallest, with its evergreen leafy stems seldom longer than 10 cm. Forsaith (1920) reported several differences between woods from the harsh slopes of Mt. Washington, New Hampshire, and different species from the same genera from lower more protected areas nearby. The most significant of these were the decreased size of vessels and their elimination in the outer portions of the growth rings in *Betula* from the alpine area, and the simplification of the rays in all of the taxa studied. In the alpine species *Betula glandulosa* Michx., *Alnus crispa* (Ait.) Pursh, and *Rhododendron lapponicum* (L.) Wahlenb., Forsaith found marked decrease in the width of the rays. Uniseriate rays predominated the material he studied. Miller (1975) described the wood anatomical characteristics of ten dwarf shrubs from southeastern Greenland. The species were *Juniperus communis* L. ssp. *nana* (Willd.) Syme, *Betula nana* L., *Empetrum nigrum* L. ssp. *hermaphroditum* (Lange) Bocher, *Cassiope tetragona* (L.) D. Don, *Loiseleuria procumbens* (L.) Desv., *Rhododendron lapponicum* (L.) Wahlenb., *Vaccinium uliginosum* L. ssp. *microphyllum* Lange, *Dryas integrifolia* M. Vahl, *Salix glauca* L., and *S. herbacea* L. Those for which Miller (1975) gave complete data are presented in Table 3. All of the taxa examined by Miller (1975) had predominately uniseriate rays except *Dryas integrifolia*. Here again is an indication of the decrease in ray complexity in dwarf shrubs. Only *Empetrum* and *Cassiope* were reported by Miller to have rays composed exclusively of erect cells.

More recently, Baas, Chenglee, Xinying, Keming, and Yuefen (1984) described some effects of dwarf growth on wood structure of taxa of normally taller stature. They studied conifers as well as hardwoods. Only their data on hardwood taxa will be considered here. Baas et al. (1984) reported a reduction in vessel element

Table 3. Wood anatomical comparisons of different taxa and ecological categories.

Taxon and/or ecological category	Reference	VD	V/MM	VL	IE	IEL	IE/VE	V	M
<i>Cassiope</i>		15.4	1904	234	T	276	1.17	0.008	1.9
Stem parasites									
<i>Misodendron</i>	Carlquist 1985a	17.3	692	60	L	191	3.19	0.025	1.5
Shrubs (Bruniaceae)	Carlquist 1978	28.0	255	777	T	859	1.10	0.109	85.2
Dwarfed trees	Baas et al. 1984	44.7	130	339	—	—	—	0.342	116.1
Normal trees of above	Baas et al. 1984	67.8	93	465	—	—	—	0.729	339.0
Rock-crevice species									
<i>Linconia cuspidata</i> Swartz	Carlquist 1978	20.0	182	546	T	706	1.29	0.109	60.0
<i>Staavia pinifolia</i> Willd.	Carlquist 1978	29.0	450	548	T	655	1.20	0.06	35.3
<i>Brachysiphon ruprestris</i> Sonder	Carlquist and DeBuhr 1977	23.0	336	427	T	613	1.44	0.068	29.2
<i>Sonderothamnus petraeus</i> (Barker) R. Dahlgren	Carlquist and DeBuhr 1977	23.0	231	456	T	547	1.20	0.099	45.4
Arctic shrubs	Miller 1975	25.1	509	250	F	318	1.27	0.049	12.3
Arctic Ericaceae	Miller 1975	21.0	688	216	F	249	1.16	0.030	6.6
Coastal shrubs	Carlquist 1977b	41.0	118	349	—	—	—	0.347	121.2
Desert shrubs	Carlquist 1977b	29.0	353	218	—	—	—	0.082	17.9

Key to columns: VD = mean vessel diameter,  $\mu\text{m}$ ; V/MM = vessels per  $\text{mm}^2$ ; VL = mean vessel element length,  $\mu\text{m}$ ; IE = imperforate element type (T = tracheid; F = fiber tracheid; L = libriform fiber); IEL = mean length of imperforate element,  $\mu\text{m}$ ; IE/VE = ratio of imperforate element length to vessel element length; V = vulnerability; M = mesomorphy.

lengths, and diameters, as well as an increase in the number of vessels per mm<sup>2</sup> in natural and artificially dwarfed plants as compared to normal sized plants of the same species from similar provenance. Only those species with complete data from Baas et al. (1984) are presented in Table 3 for comparison. From these data it may be seen that there is some correlation between decreased size of the plant and decreases in vessel element length, vessel diameter, and an increase in the number of vessels per unit area. Baas et al. (1984) attribute most of the differences to phenotypic plasticity rather than the selection of favorable genotypes. They consider these effects of dwarf growth the result of stress rather than functional adaptations. Experimental data would be required to substantiate this claim; however, in some cases this is undoubtedly the source of some of the observed anatomical differences between plants of one species of two habit types.

The basis of observed structure in dwarf shrubs and dwarfed specimens of normally larger shrubs or trees is not completely known although some evidence may be discussed here. Coe (1967) noted that elongation of internodes, normal for alpine plants transplanted to lower elevations in Kenya, could be averted by subjecting plants to nighttime low temperatures approximating typical diurnal fluctuations experienced in the native habitat. There is a tendency at low temperatures for photosynthates to be converted to storage products rather than cellulose for cell growth (Tranquillini 1979). Tranquillini cited this as a major factor in the decreased diameter of stems at high altitudes and latitudes. Increasing altitude delays the onset of the growing season which is then shortened, even though growing seasons may end at approximately the same time (Tranquillini 1979). This, coupled with the fact that growth rate decreases with increasing altitude, is responsible for a reduction in shoot increment at high altitudes (Tranquillini 1979). Tranquillini described some basic differences found between the deciduous larch and the evergreen spruce in their response to the delayed start of the growth period at higher altitudes. Larch extends new leaves which photosynthesize for up to two months prior to the period of vigorous shoot extension. The sudden occurrence of killing frosts in the latter part of the season would tend to eliminate the leaves after they had been functional for some period of time and eliminate that year's shoot formation at no loss to the plant. Spruce rapidly completes shoot growth in the early summer, which is followed by the completion of needle growth. Sudden killing frosts in the latter part of the season would kill off the newer unhardened leaves but this would not be detrimental to growth since photosynthetic activity is carried on throughout much of the year. Roots along the branches where they contact the substrate may provide a water source close to areas of active growth early in the growing season. They may also alleviate the need for large stems and favor numerous smaller stems instead.

The wood anatomical characteristics of dwarfed plants of normally full sized species are not, of course, comparable to those of normally dwarf species. This is evident by noting the figures given in Table 3. The woods of *Cassiope*, *Misodendron*, and those arctic plants studied by Miller (1975) would qualify as normally dwarf shrubs. These three groups have vessels that are narrower, shorter, and much more abundant than those in the group studied by Baas et al. (1984). Data on rock-crevice species are also given in Table 3. These compare in general to the figures given for desert shrubs.

*Ecological Discussion and Conclusions*

Some workers have attributed many trends in wood anatomical features to changes in latitude (Baas 1973; Graaff and Baas 1974). Generally these include shorter, narrower vessel elements, lower rays, stronger expression of growth rings, and higher vessel frequency at higher latitudes. Mesic and xeric habitats at the same latitude would not, however, be expected to support species with the same anatomical features. This was found to be the case by Forsaith (1920). He noted a decrease in vessel and ray sizes in plants from the alpine summit of Mt. Washington, New Hampshire, as compared to those from lower elevations on the same mountain. Vliet (1979) showed a decrease in vessel element length in *Terminalia* to be associated with decreased water availability. Dickison and Phend (1985) also note that mesic-xeric trends can override latitudinal trends in *Styrax*. Data presented in Table 2 show no consistent correlations with latitude.

The general ecological conditions under which *Cassiope* grows are xeric. Microenvironmental conditions are, however, often more moderate. *Cassiope hypnoides*, for example, at Mt. Washington, New Hampshire, occurs in the Snowbank Community protected from the cold, abrasive, high-velocity winds of the summit (Hadley and Bliss 1964). The mean summer temperatures are about 12 C, and the highest wind velocity recorded was 231 mph. Even though the woods of *Cassiope* are relatively unspecialized, they reflect some remarkable adaptations to their harsh arctic and alpine habitats. These are described in the following paragraphs. It is important to remember that an entire series of xerophytic adaptations occurs in these plants, especially in their leaves. All of the species are evergreen. The plants may experience severe low temperatures at any time of the year. During winter these plants are often covered to a considerable depth by snow. Under the snow, however, no water is lost due to transpiration in the saturated atmosphere (Tranquillini 1979).

Growth rings in high altitude or latitude species probably represent annual rings due to the brevity and abrupt termination of the growing season. The growth rings of *Cassiope* may be classified as Type V (Carlquist 1980). This type of growth ring combines greater flow rates in the early part of the growing season with greater safety in the latter part of the season. Under severe water stress from freezing, tracheids are less susceptible to incapacitation from air embolisms than are vessel elements. Air embolisms may be localized and reabsorbed more readily in tracheids than in vessels. Type V growth rings here may accommodate moderate flow rates associated with a primitive type of wood, one having tracheids as the imperforate elements and few vessels after earlywood vessels and microphylls as suggested by Carlquist (1980). This is possible, in part, because of the xeromorphic leaf modifications in most of the species of *Cassiope*. The absence of growth rings in *C. ericoides* may indicate a constant low availability of water coupled with the apparent xeromorphic leaf adaptations (Carlquist 1978). Persistence of relatively large vessels after the earliest wood in *C. redowskii* (Fig. 10) may reflect a habitat where the growing season is longer and water more abundant, coupled with a harsh cold season.

The vessels of *Cassiope* are all very narrow as may be seen from Table 2. Vessels with narrow diameters are less susceptible to incapacitation from air embolisms than are wide vessels (Zimmermann and Brown 1971). Carlquist (1975) cites

short, narrow vessel elements as indicative of xeromorphy in woods. The narrow vessels of *Cassiope* would be better able to remain functional under severe water stress than wide vessels. The number of vessels per group is low in *Cassiope* and for most taxa the vessels are effectively solitary. This is usually the case for woods in which tracheids represent a subsidiary conducting system (Carlquist 1984). Figures for the mean numbers of vessels per group are given in Table 2. Numbers just above 1.0 indicate that solitary vessels predominate but that some grouped vessels are also present. The explanation for figures higher than 1.0 may lie in two factors. The stems of *Cassiope* are very narrow and the growth rings are very narrow so that vessels would be more likely to be grouped incidentally than in plants with wider stems and growth rings. There does not seem to be such a correlation from the data in Table 2. A second possibility seems more likely. Vessels occur mostly in the earlywood while the tracheids occur to the exclusion of the vessels in the latewood. The occasional grouping of vessels in the earlywood may possibly increase conductivity. Solitary vessels are usually interspersed among tracheids in the earlywood but are effectively absent from the latewood.

The abundance of vessels in the woods of *Cassiope* reflects the safety emphasized by Carlquist (1977a) in his index of vulnerability. Baas et al. (1984) attributed this feature as well as others found in dwarf trees to stress. Aloni and Zimmermann (1983) ascribe increases in vessel diameter and decreases in vessel density to decreasing auxin concentration. This they could control by the exogenous application of lanolin containing naphthaleneacetic acid. Small vessel diameters and high vessel densities in *Cassiope* could be the result of a decrease in auxin concentration, due to the late development of new leaves each season (Tranquillini 1979). Graaff and Baas (1974), Oever, Baas, and Zandee (1981), and Dickison and Phend (1985) have attributed increases in vessel frequency to increasing latitude. This is obviously not the case in *Cassiope*.

Perforation plates in *Cassiope* are predominately scalariform, although simple perforation plates are found mixed among vessels in two species. Scalariform perforation plates are the primitive condition (Frost 1930; Carlquist 1975). Carlquist (1975) stated that groups of dicotyledons with scalariform perforation plates seem to be those with an unbroken history of occupation of mesic habitats. Zimmermann (1978) claimed that phylogenetic retention of scalariform perforation plates facilitated the breakup of air bubbles formed as a result of thawing of woods in the spring. The vessels of *Cassiope* have presumably low conductivity rates since all of the plants have tiny xeromorphic leaves, are covered by winter snows, and have tracheids to perform conductive functions in the latter part of the growing season. Scalariform perforation plates are not a selective disadvantage under these conditions as noted by Carlquist (1980). The evergreen *Cassiope* may likewise experience a decreased demand for water in the spring as leaves develop later in the season as described for spruce by Tranquillini (1979). The decreased demand for rapid conduction of water would accommodate the retention of scalariform perforation plates in *Cassiope*. *Salix herbacea* and *S. glauca* both have simple perforation plates typical of this deciduous genus (Miller 1975). This observation coupled with the low conductivity rates noted above do not support Zimmermann's theory as to the reasons for phylogenetic retention of scalariform perforation plates. There is a great and immediate demand for water in the early spring to facilitate expansion of new leaves. This would be accentuated by the



delayed onset of the growth period due to the increased latitude as noted for altitude by Tranquillini (1979). Fortunately, spring in these regions is also the season of greatest abundance of water. Simple perforation plates accommodate this situation. However, this is not the situation found in the evergreen genus *Cassiope*. In fact the only occurrences of simple perforation plates are in taxa from more mesic environments and may have evolved in response to an earlier seasonal need and availability of water rather than a shorter growth season. Perforation plate morphology is simplified with increasing xeromorphy according to Carlquist (1975). Bissing (1982) noted a lower stability of the ratio of simple perforation plates in plate-dimorphic woods correlated with decreasing moisture availability. Bissing (1976) noted in the plate-dimorphic woods he studied, *Myrica californica* Cham. & Schlecht., *Rhododendron occidentale* (T. & G.) Gray, and *Platanus racemosa* Nutt., that the scalariform perforation plates were found principally in the latewood. The same positioning was found in the plate-dimorphic taxa of *Cassiope*. These findings would accommodate consideration of the presence of scalariform perforation plates in narrower elements in the latewood as a xeromorphic adaptation. Carlquist (1975) delineated the probable minimal vessel element length and diameter for vessels with scalariform perforation plates. The data for *Cassiope* in Table 2 greatly decrease the vessel element length and diameter possible for elements with scalariform perforation plates. Scalariform perforation plates were associated with vessel elements at least 30  $\mu\text{m}$  in diameter and at least 600  $\mu\text{m}$  long by Carlquist (1975). Frost (1930) gave the average vessel element length 0.41 mm as indicative of vessels with simple transverse perforation plates. Vessel elements with entirely scalariform plates were found on elements whose average length was 1.09 mm. The mean vessel element lengths for all taxa of *Cassiope* with scalariform perforation plates are 0.328 mm or less. The bars on the perforation plates of *Cassiope* are thin, although on some of the perforation plates with few bars, a few bars are thicker. The success of plants with scalariform perforation plates in the harsh arctic-alpine habitats may be due in part to the fact that water is relatively plentiful early in the growing season when the vessels are the functional conductive system. Later in the season tracheids are the only functional conductive elements in *Cassiope*. This possibility is generally supported by Miller (1975). His data on nine dicotyledons show the presence of scalariform perforation plates to be correlated with the occurrence of what he called fiber-tracheids in six of seven taxa having scalariform perforation plates. The libriform fibers he noted for *Betula* are probably in error (Metcalf and Chalk 1950). The presence of tracheids as a backup conductive system may relieve selective pressure for simplification of the scalariform perforation plate. The only two plants in Miller's (1975) study with simple perforation plates are *Salix glauca* L. and *S. herbacea* L. Both are deciduous, and both have libriform fibers as the imperforate elements. There is no backup conductive system in the form of tracheids which requires some sacrifice, in this case the leaves. The lack of leaves in the early spring, in turn, requires large vessels in the earlywood to facilitate rapid growth. In fact, *Salix glauca* was noted as having vessels of greater diameter than all other arctic species he studied except *Vaccinium uliginosum* L. ssp. *microphyllum* Lange.

Scalariform to opposite lateral wall pitting on the vessel elements predominates in *Cassiope*. Frost (1931) associated this type of lateral wall pitting with elements 1.13 mm long, on the average. Vessel elements of *Cassiope* are 0.328 mm or less

in length. One would expect all lateral wall pitting to be alternate according to the categories delineated by Frost (1931). Opposite lateral wall pitting predominates in *Cassiope*. A condition approaching alternate occurs rarely and characterizes taxa from areas which are presumably more mesic, and/or have a longer growing season.

The presence of helical thickenings has been considered to be possibly related to increasing xeromorphy (Baas 1973; Carlquist 1975, 1978). Carlquist (1975) noted previous citations of correlations with latitude. *Cassiope* lacks helical thickenings and consequently is not accommodated by either of the above explanations. The elements in *Cassiope* may be too narrow to have helical thickenings or they may not have evolved in this phyllad. There is no correlation to the occurrence of frosts as noted for Staphyleaceae (Carlquist and Hoekman 1985a).

Tracheids provide greater safety under conditions of high water stress due to lack of water or due to freezing. The numerous narrow vessel elements in the earlywood are sufficient for conducting water available in greater quantity in the early part of the season. The conductive function is taken over by the tracheids in the latewood. Water is less abundant in the latter part of the season due in part to rapid runoff and evaporation in the dry atmosphere. The retention of tracheids in *Cassiope* is undoubtedly an ancestral condition.

The ratio of tracheid length to vessel element length is quite low for *Cassiope*. Comparison of figures in Table 3 shows Bruniaceae to be similar in this regard as are the rock-crevice species and those taxa studied by Miller (1975). These data generally agree with comments by Carlquist (1986) for woods in which the imperforate elements are tracheids. Carlquist and Hoekman (1985b) show that vessel elements longer than might be expected in their "alpine" category are associated with the presence of tracheids. *Misodendron* differs considerably because the figure for imperforate element length is based on the lengths of the libriform fibers. *Misodendron* lacks a supplementary conductive system in the form of tracheids. One can readily appreciate the release from selective pressure to form shorter though fewer vessel elements with simple perforation plates afforded by the presence of tracheids by comparing figures for *Cassiope* and *Misodendron* in Table 3. *Misodendron* lacks tracheids so the vessel elements, which must sustain the plant throughout the season, are much shorter, although not much wider than those of *Cassiope*. Presumably, the shorter vessel elements are better able to withstand the water stress.

The rare occurrence or absence of axial parenchyma is not surprising in *Cassiope*. It is generally considered to be a storage site for photosynthates. There is little storage required in these evergreen dwarf plants. Axial parenchyma is scanty or absent in the Ericaceae as a whole (Metcalf and Chalk 1950).

The predominance of erect-celled uniseriate rays is one of the more striking features of the woods of *Cassiope*. Biseriate rays are rare and are evidenced only by the presence of single cells along an otherwise uniseriate ray. Kribs (1935) described the structure of his primitive ray type (Heterogeneous I). In this type the uniseriate rays are high, numerous, and composed of vertically elongate cells. The multiseriate rays in this type are composed of interior portions with radially or vertically elongate cells with elongate uniseriate wings. Barghoorn (1941a) noted a phylogenetic trend in elimination of the multiseriate rays. He further agreed with Kribs that the exclusive presence of uniseriate rays was highly specialized.

Barghoorn (1941a) stated that many species of highly modified shrubs and semi-shrubs possess exclusively uniseriate, vertically elongate rays. Uniseriate rays have been noted in the early secondary xylem of *Illicium* (Bailey and Nast 1948; Carlquist 1982c), *Sarcococca* (Carlquist 1982b) and *Bursera* (Barghoorn 1941a), although those in *Bursera* are heterogeneous. There is no apparent correlation between stem diameter and multiseriate rays (Table 2). Forsaith (1920) found a preponderance of uniseriate rays among alpine plants from Mt. Washington, New Hampshire, and related this to the lack of nutritive substances for storage. Carlquist, Eckhart, and Michener (1984) note exclusively erect cells in the rays of smaller stems while procumbent cells predominate in the larger stems in *Acanthogilia gloriosa* (Bde.) Day & Moran, a subshrub of the Polemoniaceae. These authors noted the prevalence of exclusively erect ray cells in the Polemoniaceae. The authors consider this to indicate a potential derivation of *Acanthogilia* from an herbaceous group in the Polemoniaceae. Carlquist et al. (1984) point out that only minor modification is required to convert ray areas to zones of fibers in woods with exclusively erect ray cells and short cambial initials. This is not the case in *Cassiope* since the Ericaceae are a primarily woody group.

Barghoorn (1941b) noted that a reduction in rays by suppression of ray initials was the condition found chiefly in dwarf plants or plants growing in unfavorable environments. He illustrated *Corema conradii* Torr. (Empetraceae), *Staavia glutinosa* (L.) Thbg. (Bruniaceae), and *Tetratheca ciliata* Lindl. (Tremandraceae) as all having exclusively uniseriate rays composed of erect cells. Carlquist (1976) suggested that erect-celled uniseriate rays represented a mechanism for vertical transport in small stems, not over 5 cm in diameter, in *Roridula*.

The very slender stems of *Cassiope* have little requirement for storage or lateral transport of materials, so reduction in the ray tissue is not at all unexpected. Vertical transport is a more serious constant need. Uniseriate, erect-celled rays probably function quite well in this regard with the similar safety built in that would be found in the tracheids.

Carlquist (1977a) noted the value of redundancy of vessels in xeromorphic woods of Tremandraceae. Where vessels are numerous and narrow, air embolisms formed under conditions of water stress or freezing would have a lesser overall effect on the conductive capacity of the wood. Woods with fewer, wider vessels would be at greater risk of severe incapacitation under similar water stress. In the former instance there are more vessels, so the loss of conductive capacity in some has a lesser effect. Carlquist (1977a) formulated a ratio called vulnerability, dividing mean vessel diameter in  $\mu\text{m}$  by number of vessel elements per  $\text{mm}^2$ . He considered species with ratios below 0.30 to have exceptionally numerous narrow vessels. This indicates low vulnerability to incapacitation from air embolisms and consequently high xeromorphy. Carlquist (1977a) also formulated another index, using the independently controlled vessel element length, by multiplying the vulnerability index by the mean vessel element length. This index he termed mesomorphy (Carlquist 1977a). In his interpretation of the values for these two indices Carlquist (1977c) considered vulnerability values below 1.0 to be indicative of a high degree of xeromorphy and a figure around 3.0 to mark the lower limit for true mesomorphy. Mesomorphy values below 30.0 probably indicate true xeromorphy. Low mesomorphy values have been attributed to the occurrence of frosts in *Illicium* (Carlquist 1982c). The length of vessel elements is dictated



by the length of the fusiform cambial initials and consequently not readily modified compared to the diameter of the vessel elements, which often differ across a single annual growth ring. This indicates that the mesomorphy index is a more conservative indicator of basic mesomorphy in a group and that the vulnerability index is a sensitive indicator of xeromorphic structure.

Carlquist (1977b) provided some very interesting data regarding the floristic distributions of wood anatomical features for which he calculated values for vulnerability and mesomorphy. Values for vulnerability and mesomorphy for all specimens of *Cassiope* examined for this study reflect the considerable degree of xeromorphy of the woods (Table 2). The occurrence of xeromorphic adaptations in the woods of *Cassiope* is not surprising considering the harsh environmental conditions under which the plants exist. The plants occupy microenvironments in many cases that are close to the surface and have temperatures higher than ambient air temperatures (Bliss 1962). Nearby sites are often exposed to high-velocity, cold, dry winds. The habitats are subject to abrupt cessation of growing season and to drought caused by freezing even on a diurnal basis. Water is available slowly in spring at shallow depths. The microphyllous, overlapping, appressed nature of the leaves, the occurrence of stomata often in abaxial grooves, and low appressed habit of most of the species reflect the xeric conditions under which these plants exist. The abundant, narrow vessel elements, reduced rays, and particularly the exclusive occurrence of tracheids in the latewood of *Cassiope* all point to extreme xeromorphy in a primitive wood type.

Comparison of the values for vulnerability and mesomorphy for all of the material reflects extreme xeromorphy in *Cassiope*. The figures for vulnerability are among the lowest known to date as are those for mesomorphy. If one compares these figures with those of some of the groups listed in Table 3, *Cassiope* is the most xeromorphic group of woods or wood flora. One of the most similar groups, as far as the extreme xeromorphy of the woods, is *Misodendron* (Carlquist 1985a). *Misodendron*, a group of stem parasites with simple perforation plates, may be so adapted to maintain sufficiently high transpiration rates to obtain nitrogen from the xylem of the host as was suggested for the mistletoes (Bloom, Chapin, and Mooney 1985). The data from taxa studied by Miller (1975) are summarized in Table 3. His data would have lower vulnerability and mesomorphy values if the data for the deciduous *Salix glauca* were deleted. Figures extracted from Miller (1975) for the Ericaceae result in a lower vulnerability and a mesomorphy index that is cut nearly in half. The effect of dwarf habit on woody plants is apparent from data in Table 3 extracted from Baas et al. (1984). There is a decrease in vessel diameter and length of vessel elements as well as an increase in vessels per mm<sup>2</sup>. However, the figures for vulnerability and mesomorphy are indicative of more mesomorphic woods. This is not unexpected since the plants studied by Baas et al. (1984) were not taxa evolutionarily adapted to a dwarf habit but rather dwarf specimens of normally larger mesomorphic taxa from Japan. The remaining figures in Table 3 are derived from normally small plants, from their native habitats. Figures for coastal shrubs of Western Australia are included for comparison as are those for desert shrubs (Carlquist 1977b).

Data for four rock-crevice species from relatively primitive Bruniaceae and Penaeaceae are included in Table 3 for comparison. Additionally, members of both of these families have tracheids as the imperforate element type which makes

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figures can be predictive of vegetative adaptations if, for instance, the mesomorphy index is higher than the vulnerability index otherwise indicates (Carlquist and Hoekman 1985a). Oever et al. (1981) presented data on relative conductivity ( $C = \text{radius of vessel to the fourth power times vessel frequency}$ ) for *Symplocos*. They expected to find relationships between vessel diameter and frequency that would result in equally efficient water transport systems for *Symplocos* throughout its range. This is not possible since the taxa have different foliage systems, different habits, and undoubtedly different microenvironmental requirements. Figures for conductance are included for information in Table 2. They are based on the dimensions as applied to uniform unobstructed tubes which is not the case in vessel elements. There is also no consideration given to liabilities of woods adapted for rapid conductive capacity during periods of water stress.

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