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Sherwin Carlquist

Pomona College; Rancho Santa Ana Botanic Garden

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WOOD AND BARK ANATOMY OF THE NEW WORLD
SPECIES OF *EPHEDRA*

SHERWIN CARLQUIST

Rancho Santa Ana Botanic Garden
and
Department of Biology, Pomona College,
Claremont, California 91711

ABSTRACT

Quantitative and qualitative data are presented for wood of 42 collections of 23 species of *Ephedra* from North and South America; data on bark anatomy are offered for most of these. For five collections, root as well as stem wood is analyzed, and for two collections, anatomy of horizontal underground stems is compared to that of upright stems. Vessel diameter, vessel element length, fiber-tracheid length, and tracheid length increase with age. Vessels and tracheids bear helical thickenings in 10 North American species (first report); thickenings are absent in Mexican and South American species. Mean total area of perforations per mm² of transection is more reliable as an indicator of conductive demands than mean vessel diameter or vessel area per mm² of transection. Perforation area per mm² is greatest in lianoid shrubs and tree-like shrubs, less in large shrubs, and least in small shrubs. Plant size is roughly proportional to ecology, and thus perforation area per mm² is indicative also of ecology. Growth rings are not marked in lianoid or tropical or subtropical species. Latewood has few or no vessels (and thus offers maximal conductive safety) in species from colder and drier habitats. The ecology of the species range from dry to extremely dry habitats. Rays are mostly wide multiseriate, but three tropical or subtropical species have uniseriate rays plus narrow multiseriate rays—possibly a primitive condition. The fiber-tracheids (parenchyma of other authors) are nucleated, and are considered a result of tracheid dimorphism phylogenetically. Tracheids are vaguely storied in a few species. Minute calcium oxalate crystals cover outer surfaces of wood ray cells, phloem ray cells, sieve cells, and phloem parenchyma abundantly in most species; the crystals are slightly less abundant on vessel, tracheid, and fiber-tracheid surfaces (first report of these crystals on these cell types). Crystals, tannins, and five types of sclerenchyma in bark are considered types of herbivore deterrents. Bark of some species is richer in these features; other species are poor in sclerenchyma or tannins or both. Independent evolution of vessels in Gnetales and angiosperms is briefly discussed.

Key words: Ecological wood anatomy, *Ephedra*, Ephedraceae, Gnetales, gymnosperms, wood anatomy, wood evolution.

INTRODUCTION

Because of the inherent phylogenetic and structural interest of Gnetales, one might expect that wood and bark anatomy of *Ephedra*, *Gnetum*, and *Welwitschia* had been extensively investigated. In fact, our present knowledge is based upon study of only a few species of *Ephedra* and *Gnetum*; the secondary xylem of the single species of *Welwitschia* is incompletely known. The account by Martens (1971) summarizes what has been reported about wood anatomy in *Ephedra*—a few features for a few species: *E. californica* (Jeffrey 1917), *E. distachya* L. and *E. monostachya* L. (Thompson 1912); and *E. trifurca* (Chamberlain 1935). The ambitious monograph on gymnosperm wood by Greguss (1955) has minimal coverage of Gnetales: a description of *E. distachya* only, plates for that species and for *E. major* Host. and *E. viridis*. Even at the generic level, much has remained to be learned. The analysis by Martens (1971) of ontogenetic changes in rays requires modification. The occurrence of numerous small calcium oxalate crystals

on outer surfaces of wood cells and secondary phloem cells is all but universal in *Ephedra*, but this feature has not been hitherto reported. A forerunner to the present study explored near-vessellessness in the genus (Carlquist 1988).

The concept that all species of *Ephedra* are alike anatomically, implicit in the work of such authors as Stapf (1889), proves not to be true with respect to wood anatomy. The occurrence of helical thickenings in vessels and tracheids of 10 North American species is a case in point. This feature, easily seen with a light microscope, has been previously unreported. Although less spectacular than helical thickenings, nature of growth rings, nature of ray histology, and several quantitative features of vessels and tracheids vary in significant ways at the species level in *Ephedra*. The limited amount of material hitherto studied is a result of the widespread nature of the genus: in dry areas on five continents, including some alpine areas difficult of access. Because *Ephedra* can be called a shrub (albeit with some treelike species), wood collections—which typically focus on arboreal species—have small holdings in the genus. Thus, field work has been required to obtain material of the North American species. Dr. Juan Hunziker of the Instituto Darwinion was very helpful in providing material of the South American species; some of these (*E. boelckei*) represented stem samples of large diameter.

The inherent phylogenetic interest of Gnetales is demonstrated in the recent works of Hill and Crane (1982), Crane (1985), Doyle and Donoghue (1987), and Crane and Upchurch (1987). In order to assess the origin of Gnetales, we need the detailed information given below on wood anatomy of *Ephedra*. Similarities between Gnetales and angiosperms have been stressed by such authors as Muhammad and Sattler (1982), although Thompson (1918) reached an opposite conclusion on much the same evidence. To what degree have the wood features of *Ephedra*, *Gnetum*, and *Welwitschia* evolved in parallel to those of angiosperms, to what extent are the features of these genera a syndrome related to the vessel-bearing habit and the consequences of vessel presence on how other wood features evolve?

Within *Ephedra*, some features by which species differ may be susceptible to phylogenetic interpretation (e.g., rays of *E. americana*), but most of the features by which species of *Ephedra* differ from each other are best interpreted in terms of rapid and sensitive adaptation to ecology and habit. *Ephedra* is often regarded as a shrub of extreme desert situations. However, *Ephedra* ranges in the New World from the equator to at least 50°S and nearly an equal distance into North America. *Ephedra* ranges from a little below sealevel (California) to over 4000 m (Andes of Argentina). Wood anatomy is compared with climate in the present study.

One North American species (*E. pedunculata*) and one South American species (*E. tweediana*) qualify as climbing shrubs. One South American shrub (*E. boelckei*) is a tree, although some *Ephedra* specimens from warmer North American deserts (e.g., *E. californica*, *E. trifurca*) can develop stems of diameter comparable to those of large trees. Some *Ephedra* species are small alpine subshrubs (*E. rupestris*). Features of wood anatomy can be correlated with these various habits. In addition, some species typically or frequently have horizontal stems that become buried in sand (*E. californica*, *E. trifurca*). Wood of these underground stems is compared in the present study with wood of upright stems. Wood of roots of *Ephedra* has not been studied previously; it proves to be distinctive and like that of underground stems.

By considering recent papers as well as Stapf's (1889) monograph, one can cite about 47 valid species of *Ephedra* for the world. Half of these (24) are New World species. All valid New World species are studied here, except for the poorly known *E. gracilis* Phil. ex Stapf. Stapf's (1889) scheme is given below, with addition of species described subsequently, as recognized in the papers by Cutler (1939), Hunziker (1949), and Roig (1984).

Section *Alatae*

Tribe *Habrolepides*: *E. boelckei*, *E. multiflora*, *E. torreyana*, *E. trifurca*.

Section *Asarca*

Tribe *Asarca*: *E. aspera*, *E. californica*, *E. clokeyi*, *E. fasciculata*, *E. funerea*.

Section *Ephedra* (Section *Pseudobaccatae* of Stapf 1889)

Tribe *Antisyphiliticae*: *E. americana*, *E. andina*, *E. antisyphilitica*, *E. breana*, *E. coryi*, *E. gracilis*, *E. frustillata*, *E. nevadensis*, *E. ochreatea*, *E. pedunculata*, *E. rupestris*, *E. triandra*, *E. tweediana*, *E. viridis*.

Because my data, as well as other lines of evidence, suggest that Stapf's classification may need modification, the New World species have been arranged alphabetically in Table 1.

Wood and bark samples of all of the North American species of *Ephedra* have been collected in liquid-preserved form. This material offers a greater degree of precision in description of anatomical features than dried materials. For example, presence of nuclei and starch in the cells termed fiber-tracheids here can only be demonstrated in liquid-preserved material. Thus, an account of wood and bark anatomy in the New World species of *Ephedra* provides a better introduction to this topic than would the Old World species, for which my materials are mostly in dried form.

The presence of small wood samples (most of these from herbarium specimens) as well as large samples, mostly collected in the wild (Table 1, column 1) permits analysis of how ray dimensions and histology change with ontogeny. The phenomenon of angular ray cells in *Ephedra*, a characteristic of many of the species, is explained in the present study in ontogenetic terms.

As the summary of Martens (1971) shows, there is very little accurate information available on bark formation in *Ephedra*. Because most of the samples studied in the present paper have bark attached, study of bark anatomy proves convenient. Bark anatomy in *Ephedra* proves to be a matter of degree of presence of tannins and of five kinds of sclerenchyma cells.

MATERIALS AND METHODS

Wood samples collected by me and by Dorado (see Table 1) were preserved in 50% aqueous ethyl alcohol. This proved entirely adequate for establishment of presence of starch and nuclei in living cells. Most of the specimens available in dried form represent portions of herbarium specimens, as their small diameter (Table 1, column 1) suggests. However, some of these (*E. compacta*, *E. frustillata*, *E. rupestris*) are close to diameter of basal stems in nature because of the diminutive size of shrubs in some species. The samples available of *E. boelckei* are from mature plants. The material of *E. frustillata* from the Copenhagen Botanical Garden (provided by the late Dr. Rolf Dahlgren) was the only sample from cultivated material; all other samples were from the wild. Portions of the dried wood samples were boiled in water, then stored in aqueous 50% ethyl alcohol.

Table 1. Wood characteristics of *Ephedra*.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>E. americana</i> H. & B.	Carlquist 7040	18	N, F	73	36	750	2.7	1.8	11.0	12.7	.10	796	0	187	695	3.2	4.8	USP
<i>E. americana</i>	Davidson 3864	17	N	174	27	593	3.0	1.7	9.1	12.0	.18	610	0	231	682	2.3	4.0	USP
<i>E. andina</i> Poepp. ex Mey.	Carlquist 7165	17	N	130	32	748	2.3	1.8	10.9	10.8	.13	844	0	—	2632	4.8	2.6	USP
<i>E. antisiphilitica</i> Berland. ex Mey.	Carlquist 15816	19	N, F	55	30	782	3.5	1.7	15.5	12.2	.10	828	+	—	2355	8.5	3.2	USP
<i>E. antisiphilitica</i>	Carlquist 125817	15	N, F	69	34	697	2.5	1.7	14.6	11.8	.11	787	+	—	1196	4.7	2.9	usP
<i>E. aspera</i> Engelmann ex Wats.	Carlquist 15828	27	0	90	28	813	2.6	1.8	16.4	12.0	.17	844	+	—	>5000	9.0	4.0	usP
<i>E. boelckeii</i> Roig	Hunziker 11257	37	N, F	122	41	785	2.6	1.9	13.9	16.2	.35	846	0	—	3336	3.5	2.2	Usp
<i>E. boelckeii</i>	Hunziker 11258	48	N	69	49	941	3.0	2.0	15.6	15.0	.19	1007	0	—	1699	4.5	3.0	Usp
<i>E. breana</i> Phil.	Bartlett 20555	12	F, 0	88	21	473	2.2	1.2	7.3	10.0	.05	550	0	—	614	4.1	3.0	usP
<i>E. californica</i> Watson	Carlquist 15823	38	N, 0	91	39	746	2.2	2.3	13.0	14.8	.20	852	+	—	1560	5.7	4.2	usP
<i>E. californica</i> UPRIGHT STEM	Carlquist 15945	17	0	83	33	719	3.0	1.9	9.3	13.9	.17	714	+	—	1319	5.8	2.8	usP
<i>E. californica</i> UNDERGROUND STEM	Carlquist 15945	13	N	78	43	936	4.0	2.2	13.8	17.0	.25	923	+	—	2580	8.4	3.0	Usp
<i>E. californica</i> ROOT	Carlquist 15945	4	n	90	56	877	5.0	2.2	15.2	14.9	.24	1050	+	—	2118	8.3	4.0	USP
<i>E. clokeyi</i> Cutler	Carlquist 15922	17	0	38	29	807	4.5	1.6	10.7	12.9	.05	863	+	—	3786	9.0	4.9	usP
<i>E. clokeyi</i> CUTLER STEM	Carlquist 15942	17	0	42	35	656	2.6	1.8	10.9	12.6	.06	757	+	—	2249	6.0	5.0	usP
<i>E. clokeyi</i> ROOT	Carlquist 15942	12	n	86	44	1065	3.0	2.2	13.3	16.1	.23	1143	+	—	>5000	13.3	3.8	Usp
<i>E. clokeyi</i> STEM	Carlquist 15944	30	0	90	34	882	2.8	1.9	15.7	12.9	.18	907	+	—	>5000	12.0	4.5	usP
<i>E. clokeyi</i> ROOT	Carlquist 15944	20	n	63	41	969	2.5	2.1	14.2	16.5	.19	1086	+	—	>5000	19.2	3.2	usP
<i>E. compacta</i> Rose	Dorado 1564	6	N, 0	110	23	493	2.4	1.5	8.3	11.6	.10	499	0	167	958	3.4	2.2	Usp
<i>E. compacta</i>	Rzedowski 25758	8	N, F	107	27	537	2.5	1.4	9.8	12.2	.13	605	0	182	522	3.2	2.2	Usp
<i>E. coryi</i> Reed var. <i>viscida</i> Cut. STEM	Carlquist 15831	18	0	71	30	502	3.0	1.8	8.8	12.0	.07	588	+	—	2004	5.1	2.8	usP
<i>E. coryi</i> var. <i>viscida</i> ROOT	Carlquist 15831	7	n	124	57	959	2.6	2.6	16.5	14.3	.33	1078	+	—	2357	7.0	3.2	Usp
<i>E. coryi</i> var. <i>viscida</i> STEM	Carlquist 15833	14	0	63	32	592	2.5	2.1	13.1	13.0	.11	645	+	—	3521	5.6	3.0	usP
<i>E. coryi</i> var. <i>viscida</i> ROOT	Carlquist 15833	11	n	128	51	861	3.2	2.7	15.2	15.5	.37	926	+	—	>5000	6.3	2.8	usP
<i>E. fasciculata</i> A. Nelson	Carlquist 15859	15	0	76	35	693	2.6	1.9	12.9	13.4	.14	846	+	—	>5000	11.7	3.0	usP
<i>E. fasciculata</i>	Carlquist 15862	16	0	78	29	666	2.3	1.7	12.1	12.1	.11	746	+	—	>5000	9.5	2.7	usP
<i>E. frustillata</i> Miers	cult. Copenhagen	4	N	121	40	544	2.0	2.1	12.1	12.6	.18	647	0	—	2478	4.0	2.5	Usp
<i>E. frustillata</i>	Hauman 294	2	0	37	26	434	2.0	1.0	7.2	10.1	.02	522	0	—	961	3.4	2.2	Us
<i>E. funerea</i> Coville & Morton	Carlquist 15821	20	0	57	32	722	2.0	1.6	11.5	12.9	.09	757	+	—	>5000	9.7	2.2	USP

Table 1. Continued.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Collection																	
<i>E. multiflora</i> Phil. ex Stapf	5	0	81	23	517	2.2	1.4	11.4	10.3	.11	610	0	—	786	3.1	2.5	Usp
<i>E. multiflora</i> Martin 503	3	0	100	24	685	2.2	1.0	5.3	8.8	.03	786	0	—	581	3.0	2.2	Usp
<i>E. nevadensis</i> Watson	12	0	87	33	556	2.3	1.9	12.8	13.5	.16	639	+	—	3126	7.9	2.6	usP
<i>E. nevadensis</i> Carlquist 15849	20	0	64	33	519	2.5	2.1	9.9	12.3	.08	593	+	—	1675	6.8	3.2	usP
<i>E. ochreate</i> Miers	9	N	173	26	434	2.0	1.5	7.7	12.1	.08	594	0	—	1169	3.8	2.0	Usp
<i>E. ochreate</i> Soriano 4149	5	N, 0	119	22	435	2.3	1.4	6.3	8.4	.04	459	0	—	1040	3.3	1.8	Usp
<i>E. pedunculata</i> Engelmann ex Watson	18	n	137	41	780	2.2	1.6	12.9	12.8	.23	832	0	150	819	3.1	2.3	usP
<i>E. pedunculata</i> Carlquist 15819	29	n	202	43	1006	2.2	2.3	14.0	14.9	.49	1018	0	209	901	3.3	2.4	usP
<i>E. rupestris</i> Benthams	7	0	<1	21	399	2.5	1.0	4.5	8.0	.00	449	0	—	618	4.6	2.4	Usp
<i>E. torreyana</i> Watson	22	0	66	35	649	2.6	2.5	16.9	12.8	.14	745	+	—	1030	5.5	2.8	usP
<i>E. torreyana</i> Carlquist 15832	22	0	76	27	626	2.3	2.1	12.9	13.1	.13	666	+	—	2016	5.4	2.6	usP
<i>E. triandra</i> Tul.	5	N, F	175	22	595	2.2	1.4	7.0	10.7	.11	658	0	152	1134	3.1	2.6	Usp
<i>E. triandra</i> Bartlett 20654	4	N	187	20	491	2.5	1.4	7.2	13.4	.19	575	0	—	1071	3.4	2.8	Us
<i>E. trifurca</i> Torr. UPRIGHT STEM	51	N	47	47	1083	2.8	2.3	11.8	18.1	.14	1133	0	—	968	6.3	3.0	usP
<i>E. trifurca</i> UNDERGROUND STEM	12	N	80	52	875	2.5	2.1	12.1	16.4	.20	1021	0	—	1450	5.0	3.2	usP
<i>E. trifurca</i> MADw-11270	22	0	27	40	503	2.6	2.2	11.2	13.7	.05	619	0	—	781	5.3	2.8	usP
<i>E. trifurca</i> Wolf 3123	14	N, 0	32	36	724	2.6	1.9	12.2	13.6	.06	735	0	—	679	5.3	3.6	usP
<i>E. tweediana</i> Fisch. & Mey.	9	n	291	26	574	2.5	2.0	10.2	12.3	.35	579	0	—	1033	3.1	2.0	Us
<i>E. viridis</i> Coville	17	0	66	43	677	2.6	2.6	13.6	13.2	.11	731	+	—	1781	8.4	3.0	usP
<i>E. viridis</i> Carlquist 15840	32	0	57	37	796	2.5	2.5	17.9	12.4	.12	779	+	—	1593	6.5	2.5	usP
<i>E. viridis</i> Carlquist 15846																	

Key to columns: 1, diameter of sample excluding bark, mm; 2, latewood vessels compared to earlywood vessels in growth rings (F = vessels fewer, N = vessels appreciably narrower, n = vessels only slightly narrower, 0 = vessels absent); 3, mean number of vessels per mm²; 4, mean vessel diameter (lumen) at widest point, μ m; 5, mean vessel element length, μ m; 6, mean vessel wall thickness, μ m; 7, mean number of series of perforations per perforation plate; 8, mean number of perforations per perforation plate; 9, mean diameter of perforations, μ m; 10, mean area of perforations per mm² of transection, mm²; 11, mean tracheid length, μ m; 12, helical thickenings in tracheids and vessels (+ = present, 0 = absent); 13, mean height of uniseriate rays, μ m; 14, mean height of multiseriate rays, μ m; 15, mean width of multiseriate rays at widest point, cells; 16, mean wall thickness of ray cells, μ m; 17, ray histology (upper case = predominant cell type, U = upright, S = square, P = procumbent). All information applies to upright stems unless otherwise stated. For further information, see Materials and Methods.

Table 2. Wood anatomy of *Ephedra* with relation to habit.

Habit category	Mean vessel diameter, μm	Perforation area/ mm^2
Equatorial shrubs (2)	32	0.14
N. Temperate shrubs, stems (13)	32	0.10
Large N. Temperate shrubs, stems (6)	36	0.13
Lianoid shrubs (3)	37	0.36
Treelike shrubs (2)	45	0.27
High-alpine shrub (1)	21	0.00

Specimens in 50% ethyl alcohol were sectioned on a sliding microtome; no softening techniques were required. Sections varied in thickness, but 16–18 μm thickness proved optimal because thickness of such sections was not excessive for photomicrography, yet one could observe reasonably broad areas of contacts between cells in them.

Some sections were stained with safranin, and counterstained to varying degrees with fast green. Fast green proved useful in demonstrating presence of nuclei and in differentiating pit membranes of tracheids and fiber-tracheids (for example, pit membranes in fiber-tracheid to fiber-tracheid pits are thickened like tori on tracheid-to-tracheid pits).

For most species, unstained sections were retained and dried between slides. These were used for SEM observation. SEM photographs were obtained with an ISI WB-6 scanning electron microscope at the Rancho Santa Ana Botanic Garden.

Macerations were prepared with Jeffrey's fluid and stained in safranin. Macerations were employed for determining length of vessel elements and tracheids, as well as for counting number of perforations per perforation plate.

Provenance of the specimens studied is as follows: *Ephedra americana*, Carlquist 7040, Tarma, Peru; *Davidson* 3864, W of Epizana, Cochabamba, Bolivia.—*Ephedra andina*, Carlquist 7165, Parque Nacional Campana de la Dormida, Chile.—*Ephedra antisiphilitica*, Carlquist 15816, Sonora, Texas; *Carlquist* 15817, Langley, Texas.—*Ephedra aspera*, Carlquist 15828, Oatman, Arizona.—*Ephedra boelckei*, Hunziker 11527, 11528, Mendoza Prov., Argentina.—*Ephedra breana*, Bartlett 20555, Sierra de los Colorados, Iglesia, San Juan Prov., Argentina.—*Ephedra californica*, Carlquist 15823, Kelbarker Road, Kelso, California; *Carlquist* 15945, Whitewater (between Palm Springs and Cabazon), California.—*Ephedra clokeyi*, Carlquist 15922, Joshua Tree National Monument, California; *Carlquist* 15942, Cottonwood Springs, California; *Carlquist* 15944, N of Cottonwood Springs, California.—*Ephedra compacta*, Dorado 1654, between Teotongo and Coixtahuaca, Oaxaca, Mexico; *Rzedowski* 25758, Tepelmema, Coixtahuaca, Oaxaca, Mexico.—*Ephedra coryi* var. *viscida*, Carlquist 15831, Tuba City, Arizona; *Carlquist* 15833, Kayenta, Arizona.—*Ephedra fasciculata*, Carlquist 15859, 15862, Kelso, California.—*Ephedra frustillata*, cultivated in Copenhagen Botanic Garden, Denmark (source of seeds not known); *Hauman* 294, Santa Cruz Prov. (Patagonia), Argentina.—*Ephedra funerea*, Carlquist 15821, Newberry, California.—*Ephedra multiflora*, Cabrera 31822, Salta Prov., Argentina; *Martin* 503, Antofagasta Prov., Chile.—*Ephedra nevadensis*, Carlquist 15844, Utah-Arizona Line, Arizona; *Carlquist* 15849, Bishop, California.—*Ephedra ochreatea*, Hicken 12, Mendoza Prov., Argentina; *Soriano* 4149, La Pampa Prov., Argentina.—

Table 3. Wood anatomy of *Ephedra* with relation to organography.

Plant portion	Mean vessel diameter, μm	Perforation area/ mm^2
Upright stems (2)	35	0.12
Underground stems (2)	48	0.23
Roots (5)	50	0.27

Ephedra pedunculata, Carlquist 15815, 15819, Sonora, Texas.—*Ephedra rupes-*
tris, Hunziker 10504, Jujuy Prov., Argentina.—*Ephedra torreyana*, Carlquist 15832,
 Tuba City, Arizona; Carlquist 15835, Monument Valley, Arizona.—*Ephedra*
triandra, Bartlett 20654, San Rafael, Mendoza Prov., Argentina.—*Ephedra tri-*
furca, Carlquist 8036, E of Holtville, California; MADw-11270, New Mexico;
 Wolf 3123, Blythe, California.—*Ephedra tweediana*, Pastore s.n., Buenos Aires
 Prov., Argentina.—*Ephedra viridis*, Carlquist 15846, Grand Junction, Colorado;
 Carlquist 15846, Sherwin Summit (between Bishop and Lee Vining), California.
 Specimens documenting North American collections are located at RSA (Rancho
 Santa Ana Botanic Garden Herbarium). Specimens documenting South American
 collections (other than Carlquist specimens, which are at RSA), are located at SI
 (Instituto Darwinion, San Isidro, Argentina). Taxonomy of the New World *Ephe-*
dra species follows that of Cutler (1939), Hunziker (1949), and Roig (1984). These
 accounts supplant that of Stapf (1889) at the species level.

Nomenclature for wood terms is in accord with the IAWA Committee on
 Nomenclature (1964). Vessel diameter and perforation area per mm^2 are presented
 in Tables 1–3. Vessel diameter is based on widest lumen diameter. Perforation
 area per mm^2 is calculated: $(\text{mean perforation radius})^2 \times 3.14 \times \text{mean number}$
 of perforations per perforation plate $\times$ mean number of vessels per mm^2 . This
 computation proves to be more accurate as an indicator of conductive charac-
 teristic of *Ephedra* woods than vessel diameter. Perforation area per mm^2 is greater
 than vessel area per mm^2 in *Ephedra*, which one would expect because a multi-
 plicity of perforations on a perforation plate has a greater potential friction than
 a single large perforation (as in a specialized dicotyledon) or a vessel lumen. Means
 for features given in Tables 1–4 are based on 25 measurements (fewer if a structure
 is infrequent on a section) except for vessel wall thickness and tracheid wall
 thickness; for these two features, representative conditions were measured. Vessels
 per mm^2 is based on vessels, not vessel groups. Tracheids are much like fiber-
 tracheids in length, but an attempt was made to select tracheids only when mea-
 suring tracheid length by means of pitting (large, bordered in tracheids) and by
 means of helical thickenings (present in tracheids of ten species). Narrow vessels
 in *Ephedra* are similar to wider tracheids as seen in transection; discrimination

Table 4. Wood anatomy of *Ephedra* with relation to sample diameter.

Sample diameter	Vessel element length, μm	Tracheid length, μm	Height multiseriate rays, μm	Width multiseriate rays, cells
> 20 mm (9)	763	821	2268	5.4
< 6 mm (6)	526	602	901	3.7
All collections (42)	697	765		6.1

was attempted on the basis of dimensions of vessel elements as seen in macerations, where perforation plates could be seen.

RESULTS

Growth Rings

Growth rings are illustrated in Figures 1–16 as well as in enlarged format to show the role of tracheid and vessel diameter in Figures 17–20. The vessel features by which latewood differs from earlywood are given in Table 1, column 2. There are five main growth-ring types in *Ephedra*. Note should be taken, however, that degrees of intermediacy exist, even within a single stem. The designations of Table 1, column 2, are those believed to characterize most growth rings of a specimen, but variation can occur depending on severity of season. For example, *E. aspera* is characterized as having no vessels in latewood, but a few vessels may be found in latewood of a few growth rings.

1. Vessels only slightly narrower in latewood, but not noticeably fewer (“n” in Table 1, column 2). This condition is shown for *E. pedunculata* in Figure 1 (also enlarged, Fig. 17) and *E. tweediana* (Fig. 7). In this type, vessel diameter is constant until a short distance before the terminus of the growth ring. *Ephedra pedunculata* and *E. tweediana* are the two species in the New World that can be considered scandent. In addition, this growth-ring type characterizes roots of *E. californica*, *E. clokeyi*, and *E. coryi* var. *viscida* (Fig. 23, compare to stem, Fig. 21).

2. Growth rings with vessels appreciably narrower in latewood (“N” in table 1, column 2) characterize many species; they are illustrated here in Figures 2–5. Narrower vessels occur throughout the latter half of a growth ring in this type. Species in which growth rings have such narrower vessels include *E. americana* (Fig. 3), *E. boelckeii* (Fig. 2), *E. breana*, *E. compacta* (Fig. 4), *E. frustillata* (cult. Bot. Gard. Copenhagen), *E. ochreatea*, *E. triandra*, and *E. trifurca* (in part). Growth rings in *E. boelckeii* (Fig. 2) do not appear strongly dissimilar to those of *E. pedunculata* (Fig. 2), but this resemblance is due to similarity in vessel diameter. The vessels in *E. americana* (Fig. 3) and *E. aspera* (Fig. 4) are narrow and sparse even in earlywood, but they are narrower yet in latewood. These two species, therefore, are not referred to the same type found in *E. pedunculata* (Fig. 1).

3. In the latewood of growth rings, vessels may be fewer than in earlywood. This condition tends to occur in combination with the presence of narrower vessels in some growth rings. It may be seen in some growth rings in sections of *E. compacta* (Fig. 4), *E. multiflora* (Fig. 9), *E. triandra* (Fig. 5), and *E. viridis* (Fig. 8). Other species in which this condition is reported include *E. boelckeii* and *E. breana* (Table 1, column 2).

4. Latewood—at least the latter half of a growth ring—contains no vessels at all in some species of *Ephedra*. This condition is illustrated for *E. californica* (Fig. 18, 25), *E. fasciculata* (Fig. 11), *E. frustillata* (Fig. 19), *E. funerea* (Fig. 12), and *E. torreyana* (Fig. 6). Vessels may be restricted to the first quarter or less of the growth ring (Fig. 11, 12) or may become fewer in the center portions of a growth ring (Fig. 6). In some species, vessels are absent in latewood of some growth rings although in others in the same specimens, narrower vessels may be found (*E. breana*, *E. compacta*, *E. ochreatea*). In other species, vessels are absent in some growth rings of a specimen, but are fewer in number in others (stem of *E. coryi* var. *viscida*, Fig. 21; *E. viridis*, Fig. 8).

Fig. 1-4. Transections of *Ephedra* wood to show types of growth rings.—1. *E. pedunculata* (Carlquist 15819); vessels very little diminished in diameter and abundance in latewood.—2. *E. boelckei* (Hunziker 11257); vessels little diminished in diameter and abundance in latewood; narrow growth rings above.—3. *E. americana* (Carlquist 7040); vessels narrower in latewood.—4. *E. compacta* (Dorado 1654); vessels much narrower and fewer in latewood. (Fig. 1-4, magnification scale above Fig. 1 [divisions = 10 μm].)

Fig. 5-8. Transections of wood of *Ephedra*, to show growth rings.—5. *E. triandra* (Bartlett 10654); growth rings are wide, vessels narrower in latewood.—6. *E. torreyana* (Carlquist 15835); vessels absent in latewood.—7. *E. tweediana* (Pastore s.n.); several growth rings in which vessels are only a little narrower or fewer in latewood than in earlywood.—8. *E. viridis* (Carlquist 15840); growth rings fluctuate in histology; vessels are narrower and fewer than in earlywood. (Fig. 5-8, scale above Fig. 1.)

Fig. 9–12. Transections of wood of *Ephedra* to show growth rings and vessel characteristics.—9. *E. multiflora* (Cabrera 31822); vessels few or none in latewood.—10. *E. breana* (Bartlett 20555); considerable fluctuation in width and histology of growth rings; first growth ring outside of pith contains few vessels.—11. *E. fasciculata* (Carlquist 15862); vessels prominent in earlywood but fewer or none in latewood.—12. *E. funerea* (Carlquist 15821); vessels mostly absent in latewood. (Fig. 9, 10, 12, scale above Fig. 1; Fig. 11, scale above Fig. 11 [divisions = 10 μ m].)

Fig. 13–16. Transections of wood of *Ephedra* to show growth rings and vessel characteristics.—13–14. *E. ochreatea* (Soriano 4149).—13. Vessels sparse, very few in first growth ring (pith below).—14. Transection portion to show scarcity of vessels (below), few vessels in upper three growth rings.—15. *E. frustillata* (Hauman 294); growth rings narrow with few vessels.—16. *E. rupestris* (Hunziker 10504); growth rings evident (below); vessels probably entirely absent in this section. (Fig. 13, 15, 16, scale above Fig. 1; Fig. 14, scale above Fig. 11.)

Fig. 17–20. Transections of wood of *Ephedra* to show characteristics of vessels and tracheids.—17. *E. pedunculata* (Carlquist 15819); vessels diminish in size only in last portion of growth ring.—18. *E. californica* (Carlquist 15823); vessels wider in earlywood than in species with less marked growth rings; tracheids thicker walled than in other species.—19. *E. frustillata* (Hauman 294); vessels narrower in earlywood than in species with less marked growth rings.—20. *E. fasciculata* (Carlquist 15859); numerous narrow growth rings, demarcated mostly by wider tracheids rather than wide vessels. (Fig. 17–20, scale above Fig. 11.)

5. In a few species of *Ephedra*, vessels are absent in growth rings or nearly so. In these instances, growth rings are demarcated by juncture of wide earlywood tracheids with narrower latewood tracheids. The best example of this condition is shown for *E. rupestris* (Fig. 16). In this section, probably only a single vessel is present (see also Carlquist 1988). *Ephedra frustillata* (Fig. 15; portion enlarged, Fig. 20) and *E. ochreatea* (Fig. 13, 14) show that some growth rings begin with a few vessels, whereas others contain only wider tracheids in earlywood. Although the *E. rupestris* illustrated represents a nearly vesselless condition, the *E. ochreatea* example illustrates a transection in which some growth rings have no vessels in earlywood (at least in some places on the section), whereas in others, vessels are present in earlywood and are either fewer, or less numerous, or absent in latewood (Fig. 13, 14).

The above account suggests that there is considerable variability in growth-ring expression as well as type, and therefore phenotypic modifiability is evident (note the difference in the two successive growth rings of Fig. 27). The ecological significance of this is discussed in a later section of this paper.

Vessel Density

Mean vessel density is given for the collections studied in Table 1, column 3. There is an extraordinarily wide range, from 291 vessels per mm² in *E. tweediana* to less than one in *E. rupestris* (Fig. 16), for which a representative figure cannot really be computed because the *E. rupestris* collection studied is so close to vessellessness (Carlquist 1988). The two species with the highest density are the scandent species *E. pedunculata* (Fig. 1) and *E. tweediana* (Fig. 7). Both of these species achieve great vessel density by virtue of maintaining throughout latewood the same vessel density characteristic of earlywood. Vessel densities were computed by scanning transections in a random fashion without avoiding rays; consequently, species with wide rays tend to show lower vessel densities. The mean vessel density for the collections studied is 95 vessels per mm². Vessel densities above 95 vessels per mm² were observed in *E. americana*, *E. andina*, *E. boelckei* (Fig. 2), *E. compacta* (Fig. 12), *E. coryi* var. *viscida* (roots only: Fig. 23), *E. ochreatea* (Fig. 13), *E. pedunculata* (Fig. 1), *E. triandra* (Fig. 5), and *E. tweediana* (Fig. 7).

Vessel Diameter

Mean vessel diameter (lumen diameter) is given for the collections studied in Table 1, column 4, and sections enlarged to show characteristic vessel diameter conditions are presented here as Figures 17–20. Figures 1–16, 21, and 23 are also illustrative of a range of vessel diameter conditions.

In dicotyledons, vessel diameter is approximately inversely proportional to vessel density (Carlquist 1975), but in *Ephedra* this correlation is more weakly represented. In *E. boelckei* (Fig. 2) and *E. pedunculata* (Fig. 1) vessels are both relatively wide and dense. This is also true in roots of *Ephedra*, as in *E. californica*, *E. clokeyi*, and *E. coryi* var. *viscida* (Fig. 23).

Vessel Element Length

Mean vessel element length is presented in Table 1, column 5. The mean length for vessel elements of all collections studied is 697 μ m. Thus, notably long vessel

Fig. 21-24. Comparison of stem wood (Fig. 21, 22) and root wood (Fig. 23, 24) of *E. coryi* var. *viscida* (Carlquist 15831).—21. Transection; vessels relatively narrow in earlywood but even fewer and narrower in latewood.—22. Tangential section; rays relatively narrow and numerous.—23. Transection; vessels relatively wide, varied little in diameter with respect to growth rings.—24. Tangential section; rays very tall, few; tracheids storied (termini of cells in middle of photograph). (Fig. 21-24, scale above Fig. 1.)

Fig. 25-28. Comparison of wood of upright stems (Fig. 25, 26) and horizontal underground stems (Fig. 27, 28) of *E. trifurca* (Carlquist 8036).—25. Transection; vessels are narrow.—26. Tangential section; rays are relatively numerous and narrow.—27. Transection; vessels are relatively wide.—28. Tangential section; rays are wide and tall. (Fig. 25-28, scale above Fig. 1.)

elements (over 800 μm) were observed in *E. aspera*, *E. boelckeii*, *E. californica*, *E. clokeyi*, *E. coryi* var. *viscida*, *E. pedunculata*, and *E. trifurca*. All of these represent wood samples collected in the field (rather than removed from herbarium specimens) and are shrubs of medium to large size (or in the case of *E. pedunculata*, *Carlquist 15819*, a climbing shrub of mature size).

Vessel Wall Thickness

The figures of Table 1, column 6 reveal that most species have values for vessel wall thickness in a narrow range between 2.0 μm and 3.0 μm . Wall thickness more than 4.0 μm , a rare condition, was observed in *E. californica* (underground stem, root) and *E. clokeyi* (*Carlquist 15911* stem).

Perforation Plates and Lateral Wall Pitting of Vessels

Ephedra has long been noted for its foraminate perforation plates. These consist of a group of circular perforations comparable to the circular outlines of pit cavities on lateral walls of *Ephedra* vessels or, for that matter, bordered pits on conifer tracheids. These are illustrated here in Figures 29–38 and in Figure 61 (upper right). Thompson (1912, 1918) reports occasional perforations (as defined on the basis of wide apertures and correspondingly reduced borders) that retain pit membranes (bearing tori) in *Ephedra*. Such perforationlike pits (usually no more than one or two per perforation plate) were observed frequently in the present study. They usually are located not in the central portion, but at the top or bottom of the perforation plate and thus represent a kind of transition to the lateral wall pitting. In Figure 35, the central five “perforations” have retained pit membranes, an unusual condition.

There are various possible ways to quantify the perforation plate features of *Ephedra*. Several are offered here. In Table 1, column 7, the number of series of perforations per perforation plate is given. If anywhere in a perforation plate two perforations lie in a lateral pair rather than in a single vertical line, the plate is said to have two series (Fig. 30, 33, 36, 37). If perforations form only a single line, the figure “1” was assigned (e.g., Fig. 29, 35, 38). Three series of perforations are illustrated here in Figures 31 and 32. In general, the number of series of perforations relates to the width of the vessel; a single series of perforations often characterizes narrow latewood vessels.

Mean number of perforations per perforation plate (Table 1, column 8) has been calculated for the collections studied. This figure correlates (but weakly) with vessel diameter. The low mean number of perforations per perforation plate is reached in *E. rupestris* (Fig. 29); the highest figure was that for *E. viridis*, 17.9. The mean figure for all collections studied is 13.0.

Mean diameter of perforations (Table 1, column 9) shows variation within the genus. Care is required in developing random measurements, and I selected no more than 4 perforations per perforation plate in assembling the data. The data of Table 1, column 9 range from a diameter of 8.0 μm in *E. rupestris* to 18.0 μm in stems of *E. trifurca*.

The total mean area of perforations per perforation plate can easily be calculated. However, a more meaningful figure proves to be perforation plate area multiplied

Fig. 29–34. Details of vessels and perforation plates in *Ephedra* wood.—29. *E. rupestris* (Hunziker 10505); vessel from maceration.—30–34. SEM photographs of perforation plates from radial sections.—30. *E. boelckei* (Hunziker 1125); borders on perforations are minimal.—31. *E. pedunculata* (Carlquist 15819); perforations are large.—32. *E. californica* (Carlquist 15832); perforation plate is biseriate to triseriate.—33–34. *E. viridis* (Carlquist 15841).—33. Helical thickenings can be seen near perforations and on adjacent tracheids.—34. Fiber-tracheid containing starch grains to right of perforation plate. (Fig. 29, scale above Fig. 11; Fig. 30–34, bracket at upper right in Fig. 30 [bracket = 10 μ m].)

Fig. 35–38. Perforation plates of *Ephedra* wood from radial sections.—35–37. *E. andina* (Carlquist 7165).—35. Perforations retain pit membranes.—36. Perforations clearly bordered.—37. Perforations without pit membranes, right; perforations occluded by deposits, left.—38. *E. compacta* (Dorado 1654); narrow borders are evident on perforations (perforations of only one vessel are seen; wall of facing vessel has been removed by sectioning). (Fig. 35–37, bracket scale at top right, Fig. 30; Fig. 38, scale at top right [bracket = 10 μ m].)

by number of vessels per mm^2 (Table 1, column 10). This figure, in effect, is the proportion of each mm^2 of transection devoted to conduction by perforations. The wide range of values in the genus for this figure is susceptible to ecological interpretation and is discussed in that connection below.

Borders may be found on perforations to various extents. The most common pattern is near-absence of borders on perforations—especially in earlywood vessels. Some—but not all—latewood vessels may have wider borders on perforations. *Ephedra americana* and *E. andina* (Fig. 35–37) are distinctive in having borders relatively well developed on perforations, although the difference from what one sees in other species is only one of degree.

Lateral wall pits of vessels have wide borders, so that the pit apertures are relatively narrow (Fig. 33, top center; Fig. 35, top center). Greguss (1955) figures laterally elongate pit apertures for lateral wall vessel pits of *E. distachya* and *E. viridis*. This appearance may, in fact, be related to occurrence of wall sculptures, such as helical thickenings (not figured by Greguss) rather than conformation of the apertures *per se*.

Tracheids

Tracheid length is given for the collections in Table 1, column 11. The mean tracheid length for all collections is $765\ \mu\text{m}$. Most collections have tracheids about 10% longer than vessel elements; in fact, the ratio between mean tracheid length and mean vessel element for all collections is 1.109. There are three samples for which measurements yielded vessel element length a little longer than tracheid length: *E. californica*, Carlquist 15945, upright stem; *E. californica*, Carlquist 15945, underground stem; *E. viridis*, Carlquist 15846 (Table 1). Perhaps by using a larger number of measurements for these collections, I could have obtained figures in which mean tracheid length was greater than vessel element length. However, the results are presented without remeasuring by way of showing that this situation can occur, even though it is infrequent.

Correlations mentioned above between vessel element length and stem size also holds true for tracheid length—as would be expected in view of the parallel between vessel element length and tracheid length.

Figures were obtained on tracheid diameter, but these seemed too unreliable to include in the final presentation. Species with wider vessel elements tend to have wider tracheids as well. Tangential diameter of tracheids is relatively conservative in *Ephedra* (compared to radial diameter, which fluctuates in accordance with growth rings).

Tracheid wall thickness parallels vessel wall thickness. Although detailed data have not been included in Table 1, measurements for this feature showed that tracheid walls tend to be about $0.2\text{--}0.6\ \mu\text{m}$ thicker than vessel walls in any given specimen of *Ephedra* wood. Tracheids with walls thicker than $4.0\ \mu\text{m}$ were recorded in *E. antisiphilitica*, *E. aspera*, and *E. californica* (Carlquist 15945, underground stems and roots).

Tracheids of *Ephedra* have large circular fully bordered pits. This pitting has been figured by various authors (Chamberlain 1935; Jeffrey 1917; Mertens 1971; Thompson 1912, 1918) and is illustrated here in Figure 49 (left half of photograph) and Figure 50 (extreme left; also tracheid pits are visible in face view, just to right of center).

Fiber-tracheids ("Axial Parenchyma")

Fibriform cells with secondary walls, one or more nuclei per cell at maturity, and no septation (very rarely subdivided into two or more cells) have been reported in *Ephedra* by Strasburger (1891), Boodle and Worsdell (1894), Thompson (1912), Greguss (1955), and Martens (1971). These cells, as correctly noted by Martens (1971), are interconnected with tracheids by bordered pit pairs; the pits and their borders are not as large as those interconnecting one tracheid with another tracheid, but one must describe the fiber-tracheid to tracheid pits as fully bordered. Pits interconnecting two fiber-tracheids have vestigial borders (Fig. 48, lower right) as seen with SEM; with the light microscope, such pit pairs tend to appear either simple or vestigially bordered; the pit membranes of these pit pairs are lenticular in sectional view, recalling the tori of gymnospermous tracheid pits. The cells I am terming fiber-tracheids are called parenchyma cells by Mertens (1971). Because of the nucleate nature of these cells, designation of them as parenchyma has justification. However, nucleated fibers in dicotyledons are not termed parenchyma. In the present study, these nucleated cells are termed fiber-tracheids for the following reasons:

1. In conifers, axial parenchyma cells occur in strands, and have nonbordered pits on the parenchyma side—half-bordered pit pairs where facing tracheids (Greguss 1955).

2. The markedly bordered pits of the *Ephedra* fiber-tracheids where they are in contact with tracheids are strongly suggestive of origin of the fiber-tracheids from tracheids; indeed, that interpretation is given by Thompson (1912).

3. In *Gnetum gnemon* L., parenchyma that subdivides into strands like axial parenchyma strands of dicotyledons is present; pits are *simple* on these parenchyma cells. *In addition*, however, *Gnetum gnemon* also has septate fiber-tracheids. These latter cells are judged here to be comparable to the fiber-tracheids of *Ephedra*. Lianoid species of *Gnetum* apparently lack the axial parenchyma strands.

4. Pit membranes of the tracheid to fiber-tracheid pit pairs bear tori. The lenticular pit membranes (as seen in sectional view of the fiber-tracheid to fiber-tracheid pit pairs also suggests a toruslike conformation.

5. The fiber-tracheid to fiber-tracheid pit pairs are vestigially bordered in at least some *Ephedra* species (Fig. 48–50), and fiber-tracheid to ray cell pit pairs are always clearly bordered on the fiber-tracheid side in *Ephedra*.

6. The lengths of fiber-tracheids are apparently much like those of the tracheids in any given sample of *Ephedra* wood.

7. Wall thickness and diameter of the fiber-tracheids are identical with those of tracheids in *Ephedra*. In transection, the fiber-tracheids can be distinguished from tracheids only by presence of contents (contents can be demonstrated with certainty only in liquid-preserved material).

Contents of fiber-tracheids, as seen in stained liquid-preserved material, are, in addition to cytoplasm and nuclei (Fig. 45, left; Fig. 47), starch (Fig. 34, right; Fig. 48), and dark-staining droplets (Fig. 49, 50) much like those of ray cells. There seems little doubt that the function of what are termed fiber-tracheids here is much like that of parenchyma cells—a statement that could also be made of septate or nucleate fiber-tracheids or libriform fibers in dicotyledons.

As seen in wood transections of *Ephedra*, the grouping of the fiber-tracheids can be minimal, or diffuse (using the appropriate terms as applied to dicotyledon woods). The tangential grouping, "diffuse-in-aggregates," is common in *Ephedra* woods where fiber-tracheids are more abundant. Clusters of several fiber-tracheids, about as wide tangentially as radially, are also evident in some species. The fiber-tracheids of *Ephedra* are generally less abundant in latewood than in earlywood. Although different specimens show slightly different degrees of fiber-tracheid abundance and also some modally different groupings (e.g., fiber-tracheids are more abundant in *E. aspera*, with narrow bands frequent and diffuse and diffuse-in-aggregates cells not so common compared to those latter types in most species). Differences among species are difficult to quantify. Moreover, species for which liquid-preserved material was not available (the South American species) are more difficult to characterize with respect to the fiber-tracheid distributions. Distributions are best seen in transections. In dried material, however, pitting that permits one to identify fiber-tracheids is best seen in longitudinal sections.

Wall Sculpture in Vessels and Tracheids

Some New World species of *Ephedra* have smooth walls on vessels and tracheids (Fig. 39), but almost half have helical thickenings (Fig. 40–46, 48–50). The occurrence of helical thickenings in vessels and tracheids has been tabulated in Table 1, column 12. As this listing shows, all of the North American species except *E. compacta*, *E. pedunculata* (Fig. 39), and *E. trifurca* have helical thickenings, whereas none of the South American species do. If a species has helical thickenings in vessels, it has them in tracheids also, although the thickenings in tracheids are usually not so crass as those in vessel elements. The present account is the first report of these thickenings. Although Greguss (1955) figured wood of *E. viridis*, a species that has these thickenings, he has apparently missed the thickenings, or figured them only as elliptical pit apertures on vessels.

Somewhat less conspicuous helical thickenings were observed in *E. antisiphilitica* (Fig. 42), *E. aspera*, *E. californica*, *Carlquist 15823* (Fig. 40, 41), *E. clokeyi* (roots only), and *E. funerea*. This is apparently not constant within a species, because prominent helical thickenings occur in *E. californica*, *Carlquist 15945*. Where less conspicuous, helical thickenings appear to fade out at points (Fig. 40–42). They may be narrow and more numerous (Fig. 40) or wider and fewer (Fig. 41, 42). The thickenings may appear as a pair of ridges flanking pit apertures (Fig. 40, 41). If thickenings are crasser, such a relationship is not evident (Fig. 42–46).

More conspicuous thickenings appear more nearly continuous around a vessel wall (Fig. 43–46). The angle varies from nearly horizontal (Fig. 43, 45, 46) to almost 45° (Fig. 44). A layering of the wall may be evident (streaks in Fig. 44), or fine, tapering tips of thickenings can be seen in some vessels (Fig. 45). An instance in which a rough texture appeared superimposed on thickenings (Fig. 46) is very likely not a warty wall, but rather a deposition of droplets of a secondary plant product; vessel elements further away from the ones photographed lacked the roughening. The helical thickenings in tracheids form an angle of 45° or more with the horizontal (Fig. 48; fainter in Fig. 49, 50).

Rays

Ray characteristics are illustrated in Figures 51–58, as well as in comparisons of stem wood with that of roots (Fig. 21–24) and upright stem wood with that of

Fig. 39-42. Vessel walls from radial sections of *Ephedra* wood, to show degrees and kinds of wall sculpturing.—39. *E. pedunculata* (Carlquist 15819); vessel wall is smooth.—40-41. *E. californica* (Carlquist 15823).—40. Fine striationlike thickenings, often in pairs with relation to pit apertures.—41. Thickenings are wider than in Fig. 40, tend to fade out in places.—42. *E. antisiphilitica* (Carlquist 15816); thickenings moderately pronounced, but tend to fade out in places. (Fig. 39-42, bracket indicating scale at upper right in Fig. 39.)

Fig. 43-46. Vessel walls with prominent helical thickenings from radial sections of *Ephedra* wood.—43. *E. torreyana* (Carlquist 15835); helical thickenings nearly transverse.—44-46. *E. viridis* (Carlquist 15841).—44. Thickenings oblique; wall layering apparent.—45. Thickenings in narrow vessel (center) and in adjacent tracheid (right); fiber-tracheid at left.—46. Granular appearance on helical thickenings, very likely due to deposits of a secondary plant product. (Fig. 43-46, bracket scale in Fig. 39.)

horizontal underground stems (Fig. 25–28). Table 1, columns 13 and 14 list mean heights of uniseriate and multiseriate rays, respectively, for the collections studied. Column 13 shows by absence of figures for many collections that uniseriate rays are common only in *E. americana* (Fig. 51), *E. compacta*, and *E. pedunculata*. Uniseriate rays are moderately common in one collection of *E. triandra*, but they are only occasional in the other species, in which they are so infrequent (often only one or two per tangential section) that no figure is reported in Table 1.

Height of multiseriate rays varies greatly (Table 1, column 14). In collections in which more than one third of the rays in a given tangential section were incomplete, owing to not being entirely contained within the segment sectioned, multiseriate rays were reported as “>5000 μm ” in height. The significance of variation in ray height is considered below with respect to ontogeny.

In some species, such as *E. americana* (Fig. 51) and *E. tweediana* (Fig. 54), mean ray width at widest point falls below 4.0 cells (Table 1, column 15). Species in which mean ray width at widest point exceeds 4.0 cells are illustrated here: *E. boelckeii* (Fig. 53), *E. coryi* var. *viscida* roots (Fig. 24), *E. trifurca* upright stem (Fig. 26), and *E. trifurca* underground stems (Fig. 28).

Ray-cell wall thickness (Table 1, column 16) shows an appreciable range: from 1.8 μm in *E. ochreatea* to 5.0 μm in *E. clokeyi*. This feature appears to be relatively constant within particular species. Ray-cell walls in *Ephedra* appear to have several layers that shrink apart upon drying, as shown in Figure 70. This feature was noted in SEM photographs of ray cells in several species.

The symbols of Table 1, column 17, denote predominance of upright, square, or procumbent cells. Rays specified as “Us” lack procumbent cells. If all three cell shapes are about equally abundant in a wood, all three are shown in upper case; otherwise, only the predominant cell type is in upper case.

Upright cells may appear as sheathing cells along rays composed predominantly of procumbent cells (Fig. 55), but upright cells tend to be much commoner at tips of rays (Fig. 56, above; Fig. 52, center below). Predominance of upright cells is illustrated here for *E. boelckeii* (Fig. 53), *E. frustillata* (Fig. 57), *E. triandra* (Fig. 58), and *E. tweediana*. Rays in which upright, square, and procumbent cells are about equally abundant are illustrated here for *E. americana* (Fig. 51).

Contents of ray cells commonly include starch grains (Fig. 59–61). Starch grains are spherical to slightly oval (Fig. 60) and may be irregular in outline by virtue of a small amount of mutual compression (Fig. 60). In slides prepared according to the usual methods (Fig. 61), dehydration of sections results in formation of dark-appearing air spaces in the centers of starch grains. Droplets of dark-staining compounds are also common in ray cells of *Ephedra*. These are illustrated in Figure 62.

Ray cells bear pits circular to oval in outline as seen in face view (Fig. 66). Pits in ray-cell walls, as seen in sectional view, are simple to bordered. The most common condition, characteristic of the genus, is shown in Figure 62: horizontally oriented walls bear moderately sparse pits that are simple or slightly bordered, whereas the tangentially oriented walls (vertical in Fig. 62) have numerous bordered pits per unit length of wall.

A striking feature characteristic of rays in some *Ephedra* wood samples is the occurrence of ray cells that run in a diagonal rather than a tangential direction.

Fig. 47–50. Details of fiber-tracheids and tracheids of *Ephedra* wood.—47. *E. fasciculata* (Carlquist 15862), light photomicrograph of transection; fiber-tracheids may be identified by presence of protoplast (gray) in cell lumen; cells without protoplasts are vessels or tracheids.—48. *E. nevadensis* (Carlquist 15844), SEM photograph of radial section; two tracheids (helical thickenings are present in them) and two fiber-tracheids (small granular deposits are present in them).—49–50. *E. viridis* (Carlquist 15841), light photomicrograph of tangential sections.—49. Tracheids (left) containing helical

Ray cells bearing these walls may be only slightly distorted from rectangular into rhomboidal shapes, as in the section of *E. pedunculata* (Fig. 63), or they may be narrowly rhomboidal, with walls much distorted, as *E. viridis* (Fig. 64). Sometimes a herringbonelike pattern is achieved, with two adjacent (or fused) rays containing cells radiating in different directions in the rays or ray segments, as shown in *E. fasciculata* (Fig. 65: clear in ray at left; a few diagonal cells in the ray near right edge of photograph also).

The explanation for diagonally oriented ray-cell walls becomes evident upon examination of sections such as the one illustrated in Figure 63. Note that in this photograph, the angle of the ray-cell walls follows the distance by which the terminus of the growth ring is offset to the left as compared to the right of the ray. Thus, the angle of ray-cell walls represents a mechanism whereby rays can accommodate differential growth of adjacent xylem segments. The herringbonelike effect sometimes encountered results from presence of a narrow wedge of axial secondary xylem between two rays with diagonal walls in them. If the narrow intervening axial segment disappears ontogenetically, the two rays with different diagonal orientations in cell walls (Fig. 65) are united.

Ray cells as seen in radial sections may also show displacement of cell walls in a diagonal direction as a result of accommodation to offset xylem segments. This is seen to a small degree in Figure 56.

Ray cells with diagonal wall orientation were seen in all *Ephedra* species studied here except for *E. breana*, *E. compacta*, *E. frustillata*, *E. multiflora*, *E. ochreatea*, *E. rupestris*, *E. triandra*, and *E. tweediana*. All of these were represented in this study by samples of small diameter, which thereby minimally show changes related to ontogenetic tendencies.

Storied Structure

Although no species of *Ephedra* clearly has storied wood, a near-storied appearance was visible in a few samples. The most striking of these is in the root of *E. coryi* var. *viscida* (Fig. 24: tips of tracheids are adjacent or at a similar level in center of photograph).

Crystals

Early in the progress of this study, I noticed a granular-appearing material between ray cells of *Ephedra trifurca*. Because of the occurrence of small (but visibly crystalline with light microscopy) calcium oxalate crystals in *Welwitschia*, I suspected that even more minute crystals might be present among ray cells of *Ephedra*. Because the granular material was too fine to resolve with a light microscope, SEM examination was the method of choice. As shown in Figures 67–70 and Figure 60 (below), minute rhomboidal crystals, typical in their shape of

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thickenings; at right, fiber-tracheids with granular deposits; the pits between adjacent fiber-tracheids have small borders.—50. Tracheids and fiber-tracheids (the latter with dark contents; pits between two adjacent fiber-tracheids (far right) are bordered. (Fig. 47, 49, 50, magnification scale above Fig. 47 [divisions = 10 μ m]; Fig. 48, scale in Fig. 39.)

Fig. 51-54. Tangential sections of *Ephedra* wood to show ray characteristics.—51. *E. americana* (Carlquist 7040); rays are narrow multiseriate plus uniseriate.—52. *E. viridis* (Carlquist 15840), rays are mostly wide multiseriate with occasional sheathing cells along the edges of rays with predominantly procumbent cells.—53. *E. boelckei* (Hunziker 11257); rays are wide multiseriate, composed predominantly of upright cells.—54. *E. tweediana* (Pastore s.n.); many ray cells are markedly upright. (Fig. 51-54, scale above Fig. 1.)

Fig. 55-58. Sections of *Ephedra* woods to show ray characteristics.—55. *E. torreyana* (Carlquist 15835), tangential section; upright sheathing cells along margins of the ray, which contains procumbent cells mostly, may be seen.—56. *E. pedunculata* (Carlquist 15819), radial section; rays are predominantly procumbent; oblique walls evident in many cells.—57. *E. frustillata* (Hauman 294), tangential section; dark-staining compounds occur in the ray cells, which are markedly upright.—58. *E. triandra* (Bartlett 20654), radial section; ray cells (right of center) are all upright. (Fig. 55-58, scale above Fig. 11.)

Fig. 59–62. Details of ray cells and ray cell contents in *Ephedra* wood.—59. *E. compacta* (Dorado 1654), SEM photograph of tangential section; starch grains visible in two cells; nature of pits evident in a third.—60. *E. viridis* (Carlquist 15840), SEM photograph of ray cell (above) and associated intercellular space (below) from radial section; angular starch grains are present in the ray cell, minute calcium oxalate crystals occur in the intercellular spaces.—61. *E. trifurca* (Carlquist 8036), light photomicrograph from radial section; starch grains (dark spots in centers) in ray cells.—62. *E. coryi* var. *viscida* (Carlquist 15831), light photomicrograph of radial section; pits on tangential walls (vertical) are bordered; pits on horizontal walls are simple or less prominently bordered. (Fig. 59, scale in Fig. 39; Fig. 60, scale at upper right [bracket = 10 μ m]; Fig. 61, 62, scale above Fig. 47.)

Fig. 63–66. Sections of *Ephedra* wood to show details of ray cells.—63. *E. pedunculata* (Carlquist 15819), transection; angular walls in ray cells are oriented so as to form an adjustment to the offset between the wood portion at left and that to the right.—64. *E. viridis* (Carlquist 15846), transection; ray cells between two adjacent wood portions are markedly oblique because offset between the two portions is considerable.—65. *E. fasciculata* (Carlquist 15859), transection; ray cells at left are markedly oblique; to the right of them, a narrow upright wood portion, then a ray in which some ray cells are oblique.—66. *E. pedunculata* (Carlquist 15819), SEM photograph of ray cells from radial section; crystals are not present in the intercellular spaces between the cells. (Fig. 63–65, scale above Fig. 11; Fig. 66, scale in Fig. 39.)

calcium oxalate crystals, are indeed present not only among ray cells (Fig. 60, 69–70), but also among vessels, tracheids, and fiber-tracheids as well (Fig. 67, 68). The crystals are more abundant among ray cells than among axial xylem cells, perhaps because spaces among ray cells are larger. The crystals tend to be present more abundantly in spaces among cells, and to be more sparsely present on faces where cells are in contact. Where present, the minute crystals are often abundant. When dislodged by sectioning, the crystals leave impressions in the wall surfaces (Fig. 68). The crystals are rhomboidal in outline or rectangular in appearance, depending on their orientation.

Crystals were not observed in the wood of *E. compacta* or *E. pedunculata* (Fig. 66). Crystals were observed to be relatively sparse in wood of *E. frustillata*, *E. multiflora*, *E. rupestris*, and *E. tweediana*. However, in species in which the crystals were absent or sparse in wood, minute crystals could readily be observed in axial phloem or in phloem rays, which universally contain crystals in the collections studied. Greatest abundance of crystals was noted in *E. aspera*, *E. californica*, and *E. trifurca*. The above data represent the first report of crystals in wood (or phloem) of *Ephedra*. Minute calcium oxalate crystals have been reported on outer surfaces of epidermal cells and cortical parenchyma (Martens 1971, p. 24, 35). Although crystals are often present inside ray cells of *Gnetum*, no crystals were observed inside the ray cells of *Ephedra*.

Bark, Secondary Phloem, and Periderm

As reported by Thompson (1912) and other workers, *Ephedra* has sieve cells and no companion cells. It also has axial phloem parenchyma (the source for periderm formation in older stems). An unreported feature of considerable interest is the occurrence of minute calcium oxalate crystals, much like those shown for secondary xylem in Figures 67–70. Axial (vertical) cells of secondary phloem of *Ephedra* bear the minute crystals on their outer surfaces abundantly at places adjacent to intercellular spaces. Because intercellular spaces are larger and more abundant in phloem rays than in axial phloem, minute crystals appear in larger quantities in phloem rays than in axial phloem. The minute crystals are more abundant in phloem rays than in xylem rays in *Ephedra*. As mentioned above, crystals were seen in phloem even in those species in which crystals could not be observed among xylem cells (*E. compacta*, *E. pedunculata*). The minute calcium oxalate crystals are thus universal in the New World species with respect to phloem.

In Figure 71, one may see phloem parenchyma (axial) throughout most of the photograph. Only in the lower portion of the photograph, adjacent to secondary xylem, are sieve cells—already being crushed—evident. A single file of ray parenchyma cells (center) is shown. These three cell types are present in all secondary phloem of *Ephedra*. The quantity of phloem parenchyma produced by *E. pedunculata* is more than that characteristic of other species.

In addition to sieve cells, axial phloem parenchyma, and phloem ray parenchyma, the following cell types occur in bark of *Ephedra*: (1) dark-staining fibers, perhaps of a slightly gelatinous nature (less bright with polarized light than ordinary fibers), formed within secondary phloem; (2) sclereids matured from axial parenchyma cells; (3) suberized phellem; (4) phelloderm, small in quantity except where the phelloderm consists of sclereids and there more abundant; (5) sclereids

Fig. 67–70. SEM photographs of wood sections of *Ephedra* woods to show minute calcium oxalate crystals in intercellular spaces or adherent to outer surfaces of wood cells.—67. *E. californica* (Carlquist 15823), radial section; crystals on surfaces of tracheids.—68. *E. torreyana* (Carlquist 15835), radial section; crystals on surfaces of tracheids.—69. *E. ochreatea* (Hicken 12), tangential section; crystals on outer surfaces of ray cells.—70. *E. trifurca* (MADw-11270), tangential section; crystals between ray cells. (Fig. 67, magnification scale at upper right [bracket = 10 μ m]; Fig. 68, 69, scale in Fig. 60; Fig. 70, scale at upper right in Fig. 70 [bracket = 10 μ m].)

formed in the phloem rays. These cell types and their abundance as observed in species of the present study are described below.

Dark-staining phloem fibers are apparently present in all of the *Ephedra* species studied. Although not evident in the section shown of *E. pedunculata* (Fig. 71), *E. multiflora* (Fig. 72), *E. breana* (Fig. 73), *E. viridis* (Fig. 74), or *E. frustillata* (Fig. 75), phloem fibers can be found in whole mounts of strands of bark of these species. Species in which the dark-staining phloem fibers were observed in small quantity include *E. boelckei*, *E. funerea*, and *E. rupestris*. Moderate quantities of phloem fibers were recorded in bark of *E. americana*, *E. antisiphilitica*, *E. compacta*, *E. coryi* var. *viscida* (stem and root), *E. ochreata*, *E. torreyana* (Fig. 76), *E. trifurca*, and *E. viridis*. Large quantities of the dark-staining phloem fibers were observed in bark of *E. californica*, *E. clokeyi* (stem and root), *E. fasciculata*, *E. nevadensis*, *E. triandra*, and *E. tweediana*. These phloem fibers are yellowish in unstained material, which accounts for the intensity of their coloration (dark red with safranin) when stain is applied. The phloem fibers are identical in staining characteristics to the fibers that occur at the periphery of the pith in stems of *Ephedra* (Fig. 5, 7, 10, 14, 15). The distinctive coloration, staining, and wall appearance (less refractive than walls of sclereids in *Ephedra*) of the phloem fibers suggest that their wall chemistry differs from that of ordinary fibers, a matter that needs further investigation.

Phloem sclereids that mature from axial parenchyma cells and which stain pale pink with safranin, occur in some species of *Ephedra*. Not truly abundant in any species, they are maximally present in bark of *E. triandra* (Fig. 77). Phloem sclereids can be distinguished from phloem fibers by virtue of staining characteristics, wider lumina (phloem fibers have very narrow lumina) with associated moderate wall thickness, and the fact that the sclereids, derived from strands of axial phloem parenchyma, occur as strands (as seen in longisection). In addition to *E. triandra*, phloem sclereids were observed in bark of the following species: *E. breana*, *E. fasciculata*, *E. nevadensis*, *E. ochreata*, *E. torreyana*, and *E. tweediana*.

Suberized phellem in *Ephedra* bark consists of thin-walled cells, most commonly found as accumulations four to eight cell layers thick. These cells are most clearly shown in Figures 72 and 75. They are also present in Figure 73 (top) and Figure 74 (top). The phellem cells stain pale red with safranin. Phellem cells of this type were observed in most of the specimens studied, and suitable preparations (phellem becomes dissociated easily from stem sections cut on the sliding microtome) might reveal it to be universally present in the genus.

Tannin-filled phellem cells may occur in isolated fashion (Fig. 76, right) or as prominent bands of cells (Fig. 75; Fig. 76, left). Species other than those of the figures just cited in which tanniferous phellem was noted include *E. antisiphilitica*, *E. californica*, *E. clokeyi*, *E. coryi* var. *viscida*, *E. fasciculata*, *E. frustillata*, *E. funerea*, *E. ochreata*, *E. pedunculata*, *E. torreyana*, *E. triandra*, *E. trifurca*, *E. tweediana*, and *E. viridis*.

Ephedra is unusual among woody vascular plants in having phelloderm that matures into sclereids. A periderm may contain as many as five or six layers of phelloderm sclereids (Fig. 77). The phelloderm sclereids stain pale pink, like the phloem sclereids, with safranin. As seen in longisection, the phelloderm sclereids are elongate and rectangular in shape. In addition to the species represented by these figures, phelloderm sclereids were noted in *E. aspera*, *E. breana*, *E. cali-*

Fig. 71-75. Transections of bark from *Ephedra* stems.—71. *E. pedunculata* (Carlquist 15819); secondary phloem is devoid of sclerenchyma.—72. *E. multiflora* (Cabrera 31822); two zones of thin-walled phellem cells are present; wood and collapsed secondary phloem at bottom of photograph.—73. *E. breana* (Barlett 20555); sclerenchyma-free secondary phloem above wood, and at outside of stem, larger thin-walled phellem cells.—74. *E. viridis* (Carlquist 15846); dark deposits are evident in two zones of secondary phloem.—75. *E. frustillata* (Hauman 294); extensive dark-staining deposits present. (Fig. 71-75, scale above Fig. 11.)

Fig. 76–77. Sections of *Ephedra* wood to show bark anatomy.—76. *E. torreyana* (Carlquist 15838), transection; occasional dark-staining fibers are present in phloem (below center).—77. *E. triandra* (Bartlett 20654), transection; from top to bottom, collapsed phellem, phelloderm sclereids, old secondary phloem containing sclerified axial parenchyma plus dark-staining fibers, secondary phloem with dark-staining fibers, younger secondary phloem, wood; sclereids are present in ray area near left edge of photograph. (Fig. 76–77, scale above Fig. 11.)

fornica, *E. clokeyi*, *E. compacta*, *E. coryi* var. *viscida*, *E. ochreata*, *E. trifurca*, and *E. tweediana*.

Phloem ray cells converted from parenchyma into sclereids may be variously shaped. Shown here are rhomboidal cells (Fig. 74, left) and narrow cells corresponding to what would be termed upright ray cells as seen in a radial section (Fig. 77, left). Species of *Ephedra*, in addition to those in the figures just cited, in which phloem ray sclereids were observed include *E. antisiphilitica*, *E. californica*, *E. clokeyi*, *E. compacta*, *E. coryi* var. *viscida*, *E. funerea*, *E. nevadensis*, *E. ochreata*, *E. torreyana*, *E. trifurca*, and *E. tweediana*.

All of the above special cell types cited as present in bark are undoubtedly of wider systematic occurrence in the New World species than the above listings indicate. The near-absence of sclerenchyma in some (*E. multiflora*, *E. pedunculata*) may represent a species characteristic. The abundance of sclerenchyma in the bark of *E. triandra* is likewise noteworthy. *Ephedra triandra* is also the only species in the present study in which pith sclereids were noted: scattered among the thin-walled pith cells in this species are cells with lignified walls several times as thick as those of the parenchyma cells surrounding them.

CONCLUSIONS

Wood Anatomy and Habit

Table 2 presents data on comparative vessel diameter and perforation area per mm² for categories based primarily on habit. Size of plant and ecology are taken

into account secondarily. Vessel area per mm^2 could have been used instead of diameter, but perforation area per mm^2 appears to be the more reliable indicator of conductive characteristics of vessels. Most South American samples have been omitted from Table 2 because they did not represent stem diameter of optimal size (most were derived from herbarium specimens).

Large shrubs and equatorial shrubs appear to have slightly greater conductive capacity than the average of North American shrubs. Because transpirational rates are probably not markedly seasonal in equatorial shrubs, this may be expected: vessels are more abundant in latewood of the equatorial shrubs than they are in temperate shrubs. The lianoid species (*E. pedunculata*, *E. tweediana*) have a perforation area per mm^2 of transection threefold greater than that of the North American shrubs. This correlates with the data obtained in dicotyledonous vines and lianas (Carlquist 1975, p. 206). The stems available of *E. tweediana* were not very large, so perhaps the figure given for lianas is, in fact, lower than what would have been obtained had mature wood samples been available.

The treelike *E. boelckei* has a perforation area higher than that of the North American shrubs but lower than that of the lianas. This parallels the situation in dicotyledons (Carlquist 1975, p. 206).

The nearly vesselless shrub *E. rupestris* ("high alpine shrub" in Table 2) has by virtue of vessel paucity a virtually nil perforation area per mm^2 of transection. An accurate figure cannot be obtained under such circumstances, and may vary from one plant to another (perhaps depending on microhabitats).

The best interpretation of *Ephedra* wood suggested by the data of Table 2 is that conductive area (judged by any of several possible definitions) increases with increase in the size of the transpirational crown (green stem surface) of the plant. The transpirational crown of a lianoid *Ephedra* is large compared to stem diameter. Also, lianoid species of *Ephedra* have more numerous and wider vessels in latewood than do other species (this applies to stems, not roots).

Thus, the central principle that appears operative in construction of *Ephedra* wood is that with increased transpiration (lianas, large shrubs), vessels (both wider and more numerous per mm^2) represent an adaptation to conduction of larger volumes of water per unit time. Vessels thus tend to promote conductive efficiency, but theoretically they do not offer the potential conductive safety of a comparable area of tracheids. Air bubbles that could spread from one vessel element so as to disable an entire vessel cannot spread from one tracheid into a neighboring tracheid because the bubbles cannot traverse pit membranes of tracheids. Presence of vessels in *Ephedra* wood may lower potential conductive safety. However, the reduction in safety occurs in precisely those *Ephedra* species that have greater water availability and thereby in those species a (small) diminution in conductive safety has little or no negative effect.

Wood Anatomy and Organography

Data comparing vertical upright stems, underground (horizontal) stems, and roots are presented in Table 3. The collections selected for data on upright stems are the same collections for which data on underground stems and/or roots are also available. The term underground stem refers to prostrate stems that become buried as sand drifts over a shrub. Underground stems by this definition are permanently buried, and do not reemerge; upright branches are innovated on them, as are roots.

The values for perforation area per mm^2 for roots (Table 3) are more than twice those for upright stems, and the range in the roots measured (0.19–0.37) even reaches into the range observed in lianoid stems. In fact, roots have growth rings like those of lianoid stems, with latewood vessels numerous and with little diminution in diameter. This contrast can be seen clearly by comparing Figures 21 and 22 (stem) with Figures 23 and 24 (root). In addition to vessel features, rays are wider and taller in roots as compared to stems (see also Table 1, ray data for *E. clokeyi* and *E. coryi* var. *viscida*); this difference is visible if one compares Figures 22 and 24.

If one compares underground stems, upright stems, and roots (Table 3), one finds that perforation area per mm^2 and vessel diameter for underground stems are much closer to values typical of roots than those typical for upright stems. However, one does not see markedly narrower latewood vessels in underground stems (compare Fig. 25 with Fig. 27); in this respect, underground stems differ from roots. Earlywood vessels are quite large in underground stems (Fig. 27). Thus, the perforation area per mm^2 and vessel diameter of underground stems are due not to similarity between earlywood and latewood (as in roots), but to a marked fluctuation in size between earlywood and latewood vessels. Rays of underground stems do not appear statistically different from rays of upright stems (see Table 1, ray data for *E. californica* [Carlquist 15945] and *E. trifurca* [Carlquist 8036]). However, the ray cells of underground stems may be larger than those of upright stems (compare Figures 26 and 28). In dicotyledons, wider vessels are characteristic of roots (Patel 1965). Roots and underground stems of *Ephedra* have conductive characteristics much like stems of lianoid *Ephedra* species. Larger rays in roots and larger ray cell size in underground stems may relate to a storage function (storage of starch or water or both) for wood of underground structures as compared to wood of aerial stems.

Ontogeny

The data of Table 4 show a clear increase in vessel element length and tracheid length with increase in stem diameter. These changes are not surprising in view of the curves presented for conifers and vessel-bearing dicotyledons by Bailey and Tupper (1918). There has been relatively little comment in wood literature on change in vessel diameter with age. In a scattering of studies, one can find evidence that vessel diameter tends to increase with age (e.g., Carlquist 1984). Clearly, the data of Table 1 show that vessel diameter increases with age. This can be shown within a given sample as well as by comparing wood samples of different diameters.

Ray height clearly increases with age, as the data of Table 4 show. This parallels data in various studies of dicotyledons. Ray width also increases with age in *Ephedra*, a trend documented in dicotyledons by Barghoorn (1941). Another change in rays with age described by Barghoorn (1941) also occurs in *Ephedra* but is more difficult to document or is subject to exceptions: increasing procumbency of ray cells as stem diameter increases. For example, the upright ray cells in the relatively old stem of *E. boelckeii* (Fig. 53) seem about as abundant as the upright ray cells in the small stem of *E. tweediana* (Fig. 54). Nevertheless, in general most older rays in *Ephedra* seem to have more abundant procumbent cells, as in the section of *E. viridis* (Fig. 52), whereas in many smaller stems of *Ephedra* upright ray cells are more common (Fig. 57, 58). There is no pattern of

uniseriate wings on multiseriate rays in *Ephedra* as there is in many dicotyledons, nor is there any clear pattern in *Ephedra* of upright sheath cells on multiseriate rays that consist mostly of procumbent cells—a pattern common in some dicotyledons.

Ecology

The account above of vessel characteristics with relationship to habit shows that with respect to growth forms, the larger shrubs, lianas, and small trees have wider vessels. This may be a way of coping with the greater demands for conductive volume in plants with transpirational demands greater than those of the smaller shrubs. Although vessels are more vulnerable if they are wider (Ellmore and Ewers 1985; Ewers 1985), the vessels of *Ephedra* are at their widest not very wide compared with dicotyledons (mean vessel diameter in dicotyledons: 94 μm according to Metcalfe and Chalk 1950). Thus, *Ephedra* vessels do not seem to represent a marked diminution of safety. I am assuming that a wood composed wholly of tracheids would be the safest in a vesselless gymnosperm. That ultimate degree of vessel extinction has very nearly been reached in *Ephedra* in the case of *E. rupestris*, a high-elevation species of Argentina, as well as in a high-elevation population of *E. gerardiana* from Tibet (Carlquist 1988). One may assume that these localities are as extreme as any inhabited by *Ephedra* with respect to cold—and therefore physiological drought. Progressively greater degrees of vessel diameter (roughly an inverse of vessel density) is related to progressively greater plant size (Table 2, 4).

Plant size can be used as an approximate indicator of xeromorphy in *Ephedra*. In either high-alpine or high-latitude (notably in southern South America) *Ephedra* habitats, freezing is likely many days per year. If narrower vessels are less likely to embolize than wider vessels (Ellmore and Ewers 1985; Ewers 1985), decrease in vessel diameter (and correlative increase in vessel density) in *Ephedra* does correlate with lowered water availability, at least in terms of probable freezing. One must emphasize that with respect to precipitation, no *Ephedra* habitat qualifies as mesic. *Ephedra* habitats range from dry to very dry. Therefore, wider vessels (characteristic of moister localities) ought to occur in cultivated specimens. This expectation is realized in the cultivated specimen of *E. frustillata*, in which not only are vessels wider, they are more numerous per mm^2 (not expected if vessel diameter is inversely proportional to vessel density) as shown by Table 1.

Vessel characteristics related to conductive safety are also involved in growth ring phenomena. *Ephedra* species in the more extreme habitats have latewood that is vesselless or nearly so: *E. aspera*, *E. clokeyi*, *E. coryi* var. *viscida*, *E. fasciculata*, *E. frustillata*, *E. funerea*, *E. multiflora*, *E. nevadensis*, *E. torreyana*, *E. trifurca*, and *E. viridis*. Some of these species are in areas with notably severe winters (*E. coryi* var. *viscida*, *E. nevadensis*, *E. torreyana*, *E. viridis*). Vessels are slightly to markedly narrower or fewer than earlywood vessels—but not absent—in latewood of the remaining species. Those species with latewood vesselless or nearly so are producing latewood that is maximally resistant to embolism formation, whereas earlywood represents various degrees of concession (by greater vessel diameter and abundance) to conduction of greater volumes of water during the portion of the year when soil water availability rises above a minimal level.

Although vessel diameter is mentioned as a criterion of conductive efficiency

in the above discussion, comparisons listed earlier in this Conclusions section show that perforation area per mm^2 is a more important criterion than vessel diameter. Perforation area per mm^2 cannot readily be computed for latewood or earlywood separately in a given species. Hence vessel diameter is used as a rough approximation of conductive efficiency in the discussion on growth rings in the preceding paragraph.

Helical thickenings in vessels and tracheids, a feature newly reported for *Ephedra*, is conspicuously present in all North American species except for *E. compacta*, *E. pedunculata*, and *E. trifurca*. None of the South American species have helical thickenings. Helical thickenings have been hypothesized to represent a device for increasing wall surface in conductive cells, deterring (or possibly aiding in repair of) air embolisms (Carlquist 1983). The occurrence of helical thickenings in vessels and tracheids is markedly greater in dicotyledon species of colder areas in genera distributed in a range of climates. This seems to suggest a relationship between helical thickenings and safety of the conductive system. If this relationship is valid, one might have expected presence of helical thickenings to be more pronounced in woods of *Ephedra* plants from farther north latitudes and from higher elevations; this relationship appears to exist. The lack of sharply marked growth rings in some southerly populations of *E. californica* and *E. trifurca* is also an indication that adaptation to climatic extremes decreases from north to south.

One might think that absence of helical thickenings in wood of alpine and high-latitude South American species invalidates the above hypothesis. However, genetic information for production of helical thickenings may not originate readily, and if so, thickenings should not be expected in all of the sites where they would be adaptive. Such features as absence of vessels in latewood seem more readily evolved than helical thickenings in vessels and tracheids in *Ephedra*.

Starch storage is frequent in the fiber-tracheids and in ray cells of *Ephedra*. Starch storage undoubtedly relates to seasonality of the climates in which they occur. All of the species of *Ephedra* occur in climates that are seasonal, at least (equatorial populations of *E. americana*) with respect to rainfall.

Minute calcium oxalate crystals are virtually omnipresent on outer surfaces of wood ray cells and phloem ray cells and axial phloem cells in *Ephedra*; they are somewhat sparser (but clearly present) on outer surfaces of tracheary elements in *Ephedra*. Such crystals have been reported in epidermis of leaves and in some internal leaf cells of *Ephedra* (Martens 1971). Calcium oxalate crystals are generally considered as an herbivore deterrent, but that interpretation has generally been applied to calcium oxalate crystals borne internally in cells. The "spicular cells" of *Welwitschia* stems (presumably in secondary xylem) bear somewhat coarser calcium oxalate crystals on their outer surfaces (Martens 1971). A few examples can be cited from angiosperms, such as the often-mentioned crystal-coated astrosclereids in leaves of Nymphaeaceae. Evidently deterrence of wood-boring insects is a genuine problem in *Ephedra*, for many specimens I have cut in the field show tunneling of woods from such predation.

Other aspects of bark anatomy very likely play a role in deterrence of predators. The occurrence of dark brown-staining deposits (perhaps tannins), the presence of fiber strands, the development of phelloderm sclereids and the occurrence of other sclereids in bark may be mechanisms that retard insect damage.

Systematics and Evolution

One can see that the collections of *Ephedra* have differences in wood anatomy that can be interpreted most readily in terms of ecology. Many of these features are probably subject to environmental modification, as the collections of *E. frustillata* indicate so clearly. The degree of modifiability cannot be estimated at present, but would merit further investigation. One would like to know what quantitative vessel features would be modified, and to what extent, if *Ephedra* species were cultivated together in a single garden. A forthcoming study on wood anatomy of Old World species of *Ephedra*, in which cultivated specimens will play a considerable role, may offer useful data on this question.

A few qualitative wood features show highly distinctive systematic distribution within the genus. Rays are mostly wide and multiseriate in *Ephedra*. Three species of *Ephedra* (*E. americana*, *E. compacta*, and *E. pedunculata*) have uniseriate rays as abundant as multiseriate rays, and in these three species, multiseriate rays are never as wide as they typically are in other species. These three species have ray structure much like that of dicotyledons. Interestingly, these three species are tropical to subtropical, and occupy a central portion of the range of *Ephedra* in the New World. If one could apply the criteria of Kribs (1935) to *Ephedra*, one could cite these three species as having rays more primitive than those of other *Ephedra* species. Application of the Kribs criteria to *Ephedra* would be premature. One of the three species, *E. americana*, tends to have a greater degree of border retention on perforations of vessels than is characteristic in the genus. A greater degree of border presence would be expected to be a more primitive condition in the genus, based on the evolution of vessel elements from tracheids.

Ephedra has cells termed fiber-tracheids here because their pits are clearly bordered (fiber-tracheid to tracheid) or vestigially bordered (fiber-tracheid to fiber-tracheid), although pits are, when widest, still smaller than those of tracheids. In addition, the fiber-tracheids are not septate or subdivided into strands, although they are nucleate. Thompson (1912) believed that fiber-tracheids in *Ephedra* (termed parenchyma by various authors) are evolutionarily the product of what I would call tracheid dimorphism. I agree with Thompson's interpretation. In *Gnetum*, both fiber-tracheids (septate) and axial parenchyma strands (as in dicotyledons) can be present; this can be cited as an additional reason for calling the nucleated cells in *Ephedra* fiber-tracheids rather than parenchyma.

The occurrence of storying in *Ephedra* (in localized areas of wood in a few collections) may represent a specialized condition if concepts based on dicotyledons are applicable. However, the storying is minimal. Occurrence of storying in *Ephedra* may be related to the fact that fusiform cambial initials (and therefore tracheids and fiber-tracheids) are shorter in *Ephedra* than they are in other gymnosperms.

In recent years, a number of authors have revived interest in wood of Gnetales as an indicator of phylogenetic relationship to angiosperms. Such comparisons will be considered in detail in later papers of this series. The tracheids of *Ephedra* are unlike those of angiosperms in their large, torus-bearing, circular bordered pits. Primary xylem of *Ephedra*, like that of conifers, has tracheids that bear bordered pits *intercalated* into helical bordered bands; scalariform pitting, so common in metaxylem of angiosperms, is absent in *Ephedra*. The perforation

plates of *Ephedra* suggest derivation from tracheids like those of conifers rather than those of angiosperms. These facts, familiar to authors that have dealt with Gnetales, were used as arguments by Thompson (1912) for independent origins of angiosperms and Gnetales. Data of the present paper offer nothing contrary to Thompson's interpretation.

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