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Sherwin Carlquist
Santa Barbara Botanic Garden

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WOOD ANATOMY OF CARYOPHYLLACEAE: ECOLOGICAL, HABITAT, SYSTEMATIC, AND PHYLOGENETIC IMPLICATIONS

SHERWIN CARLQUIST¹

*Santa Barbara Botanic Garden
1212 Mission Canyon Road
Santa Barbara, CA 93105*

ABSTRACT

Wood of Caryophyllaceae is more diverse than has been appreciated. Imperforate tracheary elements may be tracheids, fiber-tracheids, or libriform fibers. Rays may be uniseriate only, multiseriate only, or absent. Roots of some species (and stems of a few of those same genera) have vascular tissue produced by successive cambia. The diversity in wood anatomy character states shows a range from primitive to specialized so great that origin close to one of the more specialized families of Chenopodiales, such as Chenopodiaceae or Amaranthaceae, is unlikely. Caryophyllaceae probably branched from the ordinal clade near the clade's base, as cladistic evidence suggests. Raylessness and abrupt onset of multiseriate rays may indicate woodiness in the family is secondary. Successive cambia might also be a subsidiary indicator of secondary woodiness in Caryophyllaceae (although not necessarily dicotyledons at large). Although a small shrub, *Gymnocarpus* may be primitively woody, and because that genus appears primitive in many wood features the family as a whole may derive from woody ancestors, despite apparent secondary woodiness in many phylads. Systematic distribution of wood character states in the family corresponds closely to the Pax and Hoffmann system of three tribes and their progressive degrees of specialization (Paronychiaceae, Alsineae, Sileneae). Wood data support the idea that Caryophyllaceae represent a branch from near the base of the order Caryophyllales. Wood of Caryophyllaceae is highly xeromorphic, comparable in quantitative vessel features to wood of desert shrubs; insular species have less xeromorphic wood. Instances of storied and druse presence in axial and ray parenchyma are newly reported for the family, as is the inverted orientation of xylem, phloem, and periderm produced by a cambium at the periphery of the pith in *Dianthus caryophyllus*.

Key words: Caryophyllales, Centrospermae, Chenopodiales, druses, ecological wood anatomy, storied wood structure, successive cambia, xeromorphic wood.

INTRODUCTION

Few families of dicotyledons are so poorly known with respect to wood anatomy as Caryophyllaceae. The summary of wood histology of the family offered by Metcalfe and Chalk (1950) occupies only four lines. Quantitative data have been offered for wood of only one species (Fahn et al. 1986). Wood anatomy of Caryophyllaceae is, however, of great potential importance in relation to systematics, ecological wood anatomy, and phyletic change in habit. The lack of studies in wood anatomy of the family may be related to the predominantly herbaceous nature of the family. The woodiest representatives (likely the Hawaiian genus *Schiedea*) are small shrubs the basal stem diameter of which probably rarely exceeds 3 cm.

Caryophyllaceae have been invariably regarded as a member of the order formerly known as Centrospermae and currently termed Caryophyllales (less frequently, Chenopodiales), although Caryophyllaceae lack the betalains (betacyanins), glycoflavones, and some other compounds characteristic of other families

in the order (Wohlgart and Mabry 1968; Richardson 1981). Sieve-tube plastid ultrastructure shows similarities between Caryophyllaceae and certain other families of the order—Achatocarpaceae, Molluginaceae, and Stegnospermaceae (Behnke et al. 1983). A cladistic study (Rodman et al. 1984) shows Caryophyllaceae as branching from near the base of the order Chenopodiales, well distanced from the betalain-containing families. A wood study claims affinity between Stegnospermaceae and Caryophyllaceae (Bedell 1980). The DNA evidence presently available, based on *rbcL* data, places Caryophyllaceae in an advanced position in the order, departing from the clade near Chenopodiaceae (Chase et al. 1993). The present study offers some evidence on the phyletic status of Caryophyllaceae.

Wood anatomy of Caryophyllaceae proves to be of especial significance with relation to habit. No Caryophyllaceae are truly shrubby or arboreal. Habits in the family range from subshrubs to perennials with thickened roots to minimally woody perennials to annuals. Relating the range of habits to the rayless wood predominant in the family as well as to the presence of successive cambia (largely in roots rather than

¹ Address all correspondence to author at 4539 Via Huerto, Santa Barbara, CA 93110.

Table 1. Wood characteristics of Caryophyllaceae.

Species	Collection	1 VG	2 VD	3 VM	4 VL	5 VW	6 TL	7 TW
<i>Alsinidendron trinerve</i> H. Mann	Perlman 5448	1.53	22	149	218	2.0	324	2.2
<i>Arenaria macradenia</i> S. Wats.	Thorne 40688	2.32	16	603	197	2.7	321	2.4
<i>Dianthus caryophyllus</i> L.	Carlquist s.n.	1.60	14	482	114	3.0	253	4.4
<i>D. rupicolus</i> Bivona	cult. UCBBG	1.86	20	387	104	3.0	193	2.0
<i>Gymnocarpus salsoloides</i> Webb & Christ.	Carlquist 2535	1.10	27	284	118	2.5	257	4.1
<i>Gypsophila patrinii</i> Ser.	Smirnov 59	3.25	18	636	146	2.4	—	—
<i>Polycarpaea divaricata</i> Ait.	Carlquist 2731	2.17	26	371	114	3.9	173	2.7
<i>Schiedea adamantis</i> St. John	Weller & Sakai 847	1.76	18	427	154	2.4	256	2.5
<i>S. ligustrina</i> Cham. & Schlecht.	Weller & Sakai 846	2.15	18	318	196	2.6	292	2.3
<i>S. lydgatei</i> Hillebrand	Weller & Sakai 870	1.65	26	196	172	1.0	297	2.0
<i>Scopulophila rixfordii</i> (Bge.) Munz & Jtn.	Roos 6097	>15	16	?	178	2.4	—	—
<i>Silene fruticosa</i> L.	cult. UCBBG	3.15	13	398	127	3.0	183	2.0
<i>S. hawaiiensis</i> Sherff ROOT	Carlquist 8161	2.63	17	55	142	2.6	208	2.3
<i>S. hawaiiensis</i> Sherff STEM	Carlquist 8161	2.00	19	193	154	2.2	303	2.6
<i>S. spergulifolia</i> (Desf.) M. B.	Akhverdov, June 1948	2.20	8	699	113	2.5	205	4.1
<i>S. struthioloides</i> A. Gray	Carlquist 1924	1.73	9	494	98	2.4	186	2.0
<i>S. verecunda</i> (S. Wats.) Hitchc. & Maguire	Carlquist 8158	2.30	25	295	135	3.2	—	—
Above Caryophyllaceae averaged		3.14	19	374	146	2.6	247	2.1

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean lumen diameter of vessels at widest point, μm ; 3 (VM), mean number of vessels per mm^2 ; 4 (VL), mean length of vessel elements, μm ; 5 (VW), mean wall thickness of vessels, μm ; 6 (TL), mean length of imperforate tracheary elements, μm ; 7 (TW), mean wall thickness of imperforate tracheary elements, μm . Provenances of specimens are given in Materials and Methods.

stems) is one of the purposes of the present study. Caryophyllaceae are a family of crucial importance in demonstrating if wood anatomy can reveal whether a phylad is primarily or secondarily woody.

Woody Caryophyllaceae mostly occupy relatively dry habitats. Interesting in this connection is whether wood of Caryophyllaceae is markedly xeromorphic (for criteria of wood xeromorphy, see Carlquist 1988), and if so, in what ways. Insular representatives of a group usually tend to be less xeromorphic in various features than their continental relatives. Woody Caryophyllaceae are well represented on the Hawaiian Islands and the Canary Islands, so there is sufficient material to provide a comparison between woods of insular and continental representatives.

MATERIALS AND METHODS

Wood samples of *Alsinidendron* and *Schiedea* were kindly provided through the generosity of Anne Sakai and Steven Weller. The samples of *A. trinerve* and *S. ligustrina* were liquid-preserved, as were my collections of *Dianthus caryophyllus*, *Silene hawaiiensis*, and *S. verecunda*. Specimens of all other Caryophyllaceae were available in dried form. Only root wood was studied for *Gypsophila patrinii*, *Scopulophila rixfordii*, and *Silene verecunda*. Both stem and root wood (Table 1) was studied for *Silene hawaiiensis*. All collections other than the Weller and Sakai material are documented with specimens in the Rancho Santa Ana

Botanic Garden Herbarium; the Weller and Sakai collections are deposited at the University of California, Irvine.

Sliding microtome sections were successfully obtained for specimens of *Polycarpaea divaricata*, *Silene struthioloides*, and all species of *Schiedea*. These woods are relatively uniform in texture and are moderately hard. Other caryophyllaceous woods contain hard and soft portions intermixed, or (as in the roots of *Silene hawaiiensis* and *S. verecunda*) soft tissue only. The problems posed by woods such as these were successfully solved by use of ethylene diamine for softening followed by sectioning in paraffin (Carlquist 1982). Sections were stained in a safranin-fast green combination. Both paraffin sections and sliding microtome sections were used for scanning electron microscope (SEM) study. The former were mounted on aluminum stubs just as paraffin sections are mounted on glass slides, whereas the sliding microtome sections for SEM study were dried between glass slides before being placed on aluminum mounts with the aid of double-sticky tape. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Terminology follows that of the IAWA Committee on Nomenclature (1964) except for the terms vascular tracheid and vasicentric tracheid, which follow my definitions (Carlquist 1985), which I believe correspond to the intent of the IAWA Committee on Nomenclature (1964) as well as to the usage of Metcalfe and Chalk

(1950). The term "pervasive" axial parenchyma is proposed here for axial parenchyma present as the ground tissue of fascicular xylem instead of fibrous tissue (imperforate tracheary elements). This term was introduced in an earlier paper (Carlquist 1993). Vessel diameter is measured as lumen diameter at widest point.

Localities for the collections studied are as follows (for author citations see Table 1): *Alsinidendron trinerve* (Perlman 5448), Pu'u Kalena, Oahu, Hawaii; *Arenaria macradenia* (Thorne 40688), Aliso Canyon (Mojave Desert), Los Angeles County, California; *Dianthus caryophyllus* (Carlquist, s.n.), cultivated, Los Angeles, California; *D. rupicolus* (cultivated at University of California Botanical Garden, Berkeley); *D. sp.* (Tobey 2026), Tegrul, Gemusane, Turkey; *Gymnocarpos salsoloides* (Carlquist 2535), Teno, Tenerife, Canary Islands, Spain; *Gypsophila patrinii* (Smirnov 59), NW slope of Lake Baikal, Irkutsk Region, Russia; *Polycarpaea divaricata* (Carlquist 2731), Barranco del Puente, La Palma, Canary Islands, Spain; *Schiedea adamantis* (Weller & Sakai 847), Diamond Head, Oahu, Hawaii; *S. ligustrina* (Weller & Sakai 846), southern Waianae Mts., Oahu, Hawaii; *S. lydgatei* (Weller & Sakai 870), Kamalo Gulch, Molokai, Hawaii; *Scopulophila rixfordii* (Roos 6097), limestone crevices, Leadfield, Grapevine Mts., Inyo Co., California; *Silene hawaiiensis* (Carlquist 8161), Kilauea Overlook, Hawaii Volcanoes National Park, Hawaii, Hawaii; *S. fruticosa* (cultivated at the University of California Botanical Garden, Berkeley); *S. spergulifolia* (Akhverdov, June 1948), Vedensky District, Armenia; *S. struthioloides* (Carlquist 1924), Haleakala Caldera, Maui, Hawaii; *S. verecunda* (Carlquist 8158), Mt. San Antonio, Los Angeles Co., California.

ANATOMICAL RESULTS

Growth Rings

Because woody Caryophyllaceae mostly inhabit dry sites that experience only brief rainy seasons, growth rings are present in stems of most of the species studied. The only exceptions to this (habit and habitat correlations in parentheses) occur in *Alsinidendron trinerve* (understory shrub in wet forest); *Gypsophila patrinii* (root); *Schiedea ligustrina* (Fig. 13) (moderated island climate); *Scopulophila rixfordii* (root); *Silene hawaiiensis* stem and root (moderated island climate, moderately moist zone with minimal seasonality); and *S. verecunda* (Fig. 25) (root). The lack of seasonality in wood of roots is likely related to succulence of roots in Caryophyllaceae, although these roots occur in some species of highly seasonal habitats.

Growth rings in *Gymnocarpos salsoloides* occur only occasionally (not visible in the portion shown in Fig. 1). Growth rings in this species take the form of

one or two layers of marginal axial parenchyma. The leaves in this species are succulent, which may be related to lack of marked fluctuation in vessel diameter. Succulents at large typically have wood in which vessel diameter does not fluctuate greatly; narrow vessels (which provide conductive safety) and wide vessels (which accommodate larger volumes of flow during periods of active growth) are of selective value in species with broader, thinner leaves. *Polycarpaea divaricata*, also from a dry, frost-free lowland Canarian locality, has nonsucculent leaves and moderate fluctuation in vessel diameter (Fig. 6). A similar condition was observed in *Schiedea adamantis*. More pronounced fluctuation in vessel diameter (as well as difference in fiber-tracheid staining capability between earlywood and latewood) occurs in *S. lydgatei* (Fig. 17).

Minimal fluctuation in vessel diameter in *Dianthus caryophyllus* (Fig. 26) may be related to the cultivated provenance of the specimen. Earlywood in *D. rupicolus* and *Silene fruticosa* consists of wider vessels in a background of libriform fibers, while latewood contains narrow vessels and a few vasicentric tracheids in a background of axial parenchyma. Vessel diameter fluctuates more markedly in *D. sp.* (Tobey 2026), which is a specimen from a wild area; growth rings in this species are much like those in stems of *Arenaria macradenia* or *Silene spergulifolia*. *Arenaria macradenia* (Fig. 11) has very narrow vessels and vascular tracheids formed in parenchymatous background in latewood. The parenchymatous ground tissue continues in earlywood in which wide-lumened vessels are formed. Libriform fibers supplant axial parenchyma as vessel diameters lessen within a growth ring. The same features are shown even more dramatically in the stems of *Silene spergulifolia* (Fig. 18). In the first two years of secondary growth in this stem (Fig. 19), however, libriform fibers are not formed and vessels occur in a ground tissue of axial parenchyma. Vessel diameter in *Silene struthioloides* (Fig. 22, 23) fluctuates little within a single year. Rather, vessels are narrower or wider within a particular year's growth, presumably dependent on water availability.

Presence or absence of fibers in particular stems of Caryophyllaceae has been noted by Metcalfe and Chalk (1950). In the portion of an older horizontal stem of *Dianthus caryophyllus* studied here, libriform fibers are present throughout most of the wood, but are absent in the most recently formed portions. The reverse was observed in stems of *Schiedea globosa* H. Mann (collected at Hanauma Bay, Oahu), a more nearly herbaceous plant than other species of *Schiedea*. In the upright flowering stems of this plant, secondary xylem begins with vessels within a parenchyma background; later-formed secondary xylem consists wholly of libriform fibers and vessels.

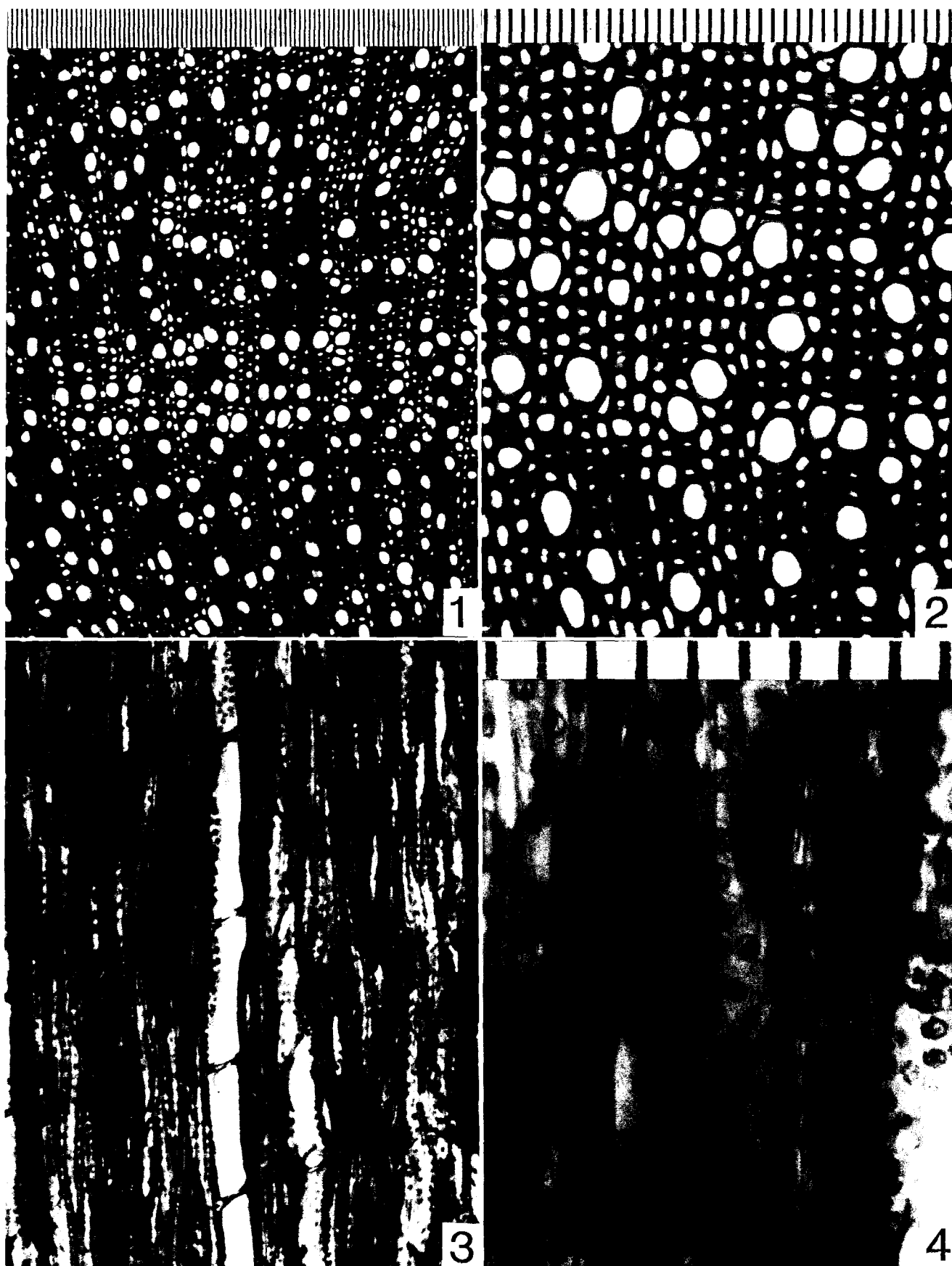


Fig. 1-4. Wood sections of *Gymnocarpus salsoloides* (Carlquist 2535).—1. Transection; vessels are essentially solitary.—2. Portion of transection; axial parenchyma is scanty vascentric, with a few diffuse cells.—3. Tangential section; uniseriate rays are inconspicuous.—4. Portion of tangential section, showing bordered pits on tracheids; ray cell to left of center, bottom. (Fig. 1, scale above Fig. 1 [divisions = 10 μ m]; Fig. 2, 3, scale above Fig. 2 [divisions = 10 μ m]; Fig. 4, scale above Fig. 4 [divisions = 10 μ m].)

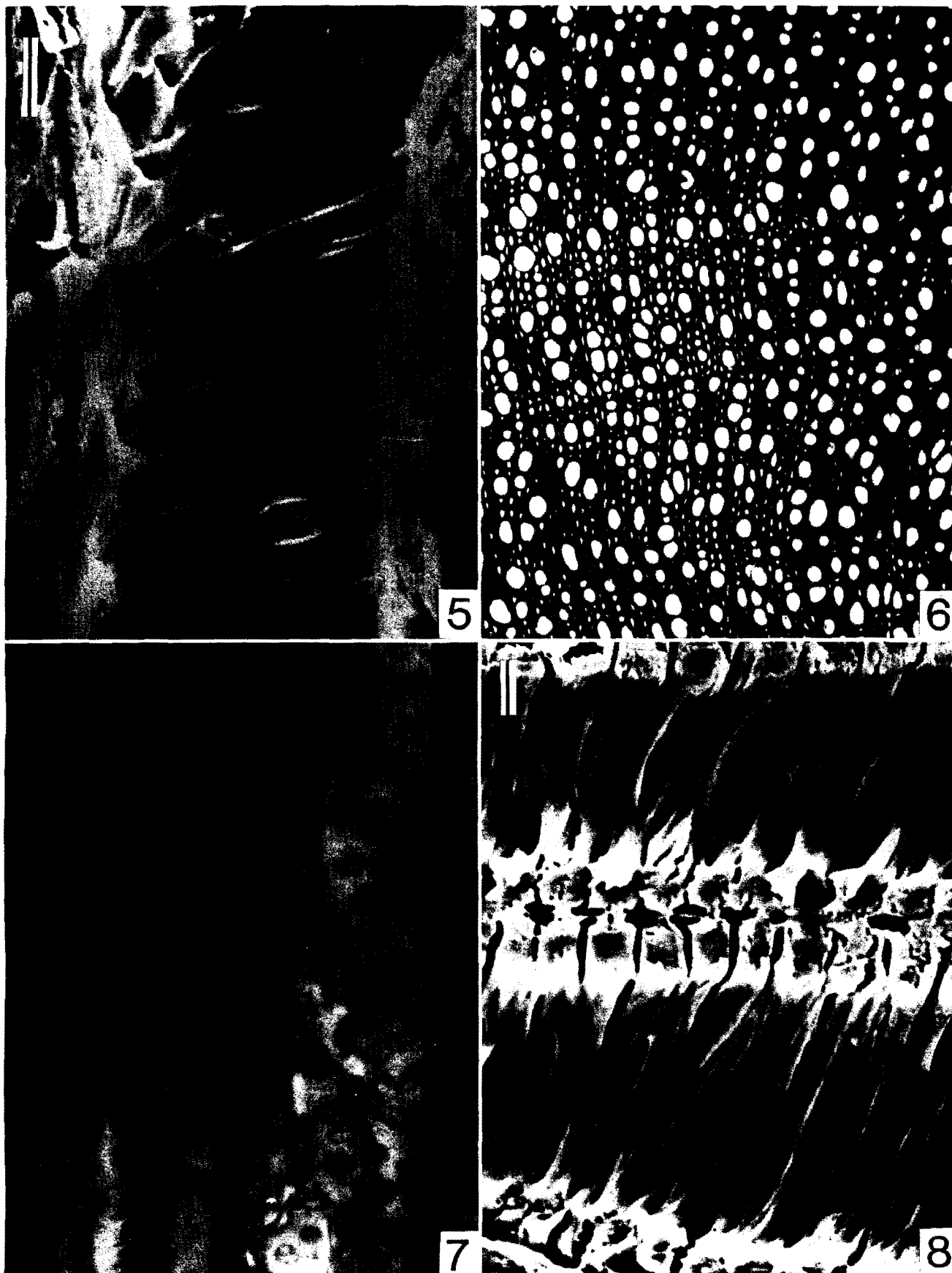


Fig. 5–8. Wood sections of *Gymnocarpus* and *Polycarpaea*.—5. *Gymnocarpus salsoloides* (Carlquist 2535), SEM photograph of vessel wall from tangential section, showing helical sculpture on wall.—6–8. *Polycarpaea divaricata* (Carlquist 2731).—6. Transection showing indistinct growth rings.—7. Portion of transection, showing bordered pits in vessels.—8. SEM photograph of two vessels from tangential section; grooves interconnect pit apertures. (Fig. 5, 8, bar at upper left = 5 μ m; Fig. 6, scale above Fig. 1; Fig. 7, scale above Fig. 4.)

Vessel Elements

Vessel grouping (Table 1, column 1) is minimal (fewer than 1.20 vessels per group) in *Gymnocarpus salsoloides* (Fig. 1, 2), the only species in this study in which tracheids rather than libriform fibers form the ground tissue of the wood. In all other Caryophyllaceae, fiber-tracheids or libriform fibers are present and vessel grouping is greater. *Alsinidendron trinerve* (Fig. 12) has 1.53 vessels per group, but the figure is higher in the remaining Caryophyllaceae other than *Gymnocarpus*. Groups of vessels are almost indefinitely large in *Scopulophila rixfordii* (Fig. 9; no libriform fibers are present in xylem, only narrower and wider vessels). Vessel grouping in woods of Caryophyllaceae often takes the form of radial chains (Fig. 12, 13, 17, 23), although pore multiples are also present, especially in latewood (Fig. 11, 18).

Mean vessel diameter (Table 1, column 2) ranges from a low of 8 μm in *Silene spergulfifolia* (Fig. 18, 19) and 9 μm in *S. struthioloides* (Fig. 22, 23) to 26 μm in *Polycarpha divaricata* (Fig. 6) and *Schiedea lydgatei* (Fig. 17) and 27 μm in *Gymnocarpus salsoloides* (Fig. 1, 2). One should note that the wider vessels of Caryophyllaceae are still relatively narrow compared to the vessels of dicotyledons at large (trees of wet forests typically have a mean vessel diameter in excess of 100 μm). The average vessel diameter figure for Caryophyllaceae studied here, 19 μm , is comparable to that for Californian desert shrubs, 25.9 μm (Carlquist and Hoekman 1985: vessel diameter in that study computed from outside dimension rather than lumen width). The Caryophyllaceae sampled include wood of mesic species and wood of succulent roots, and while neither category qualifies as mesomorphic, wood of Caryophyllaceae as a whole is strongly xeromorphic.

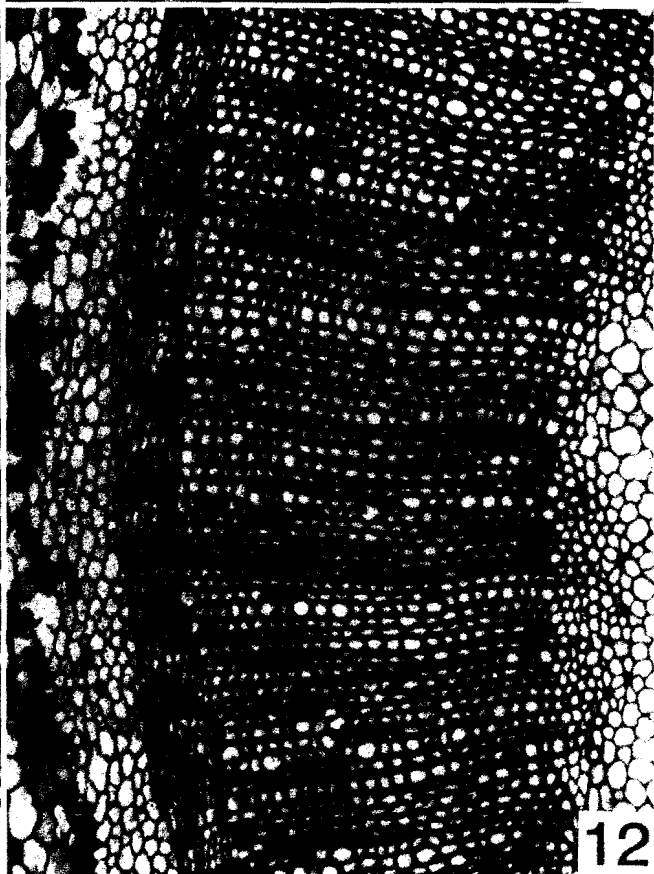
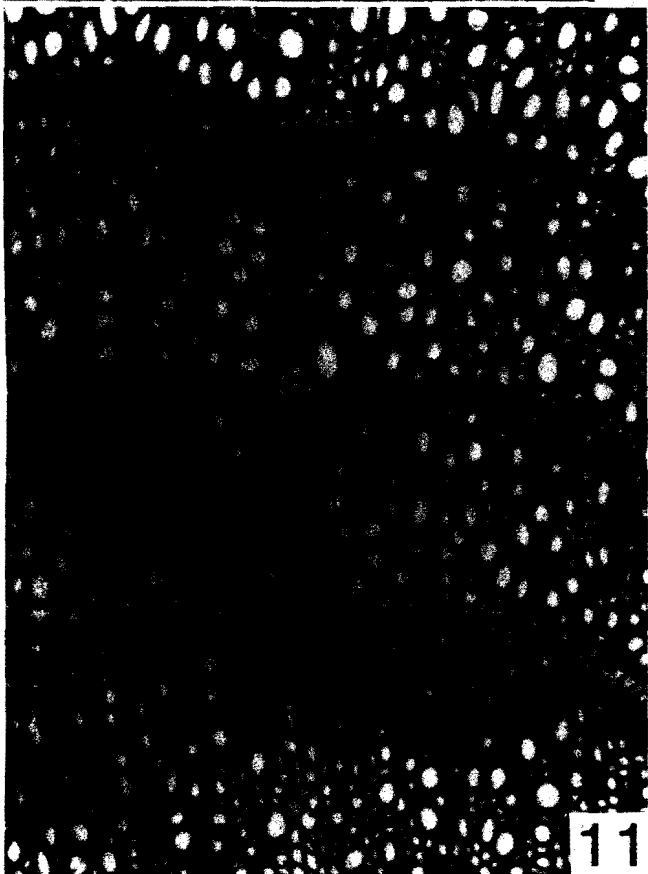
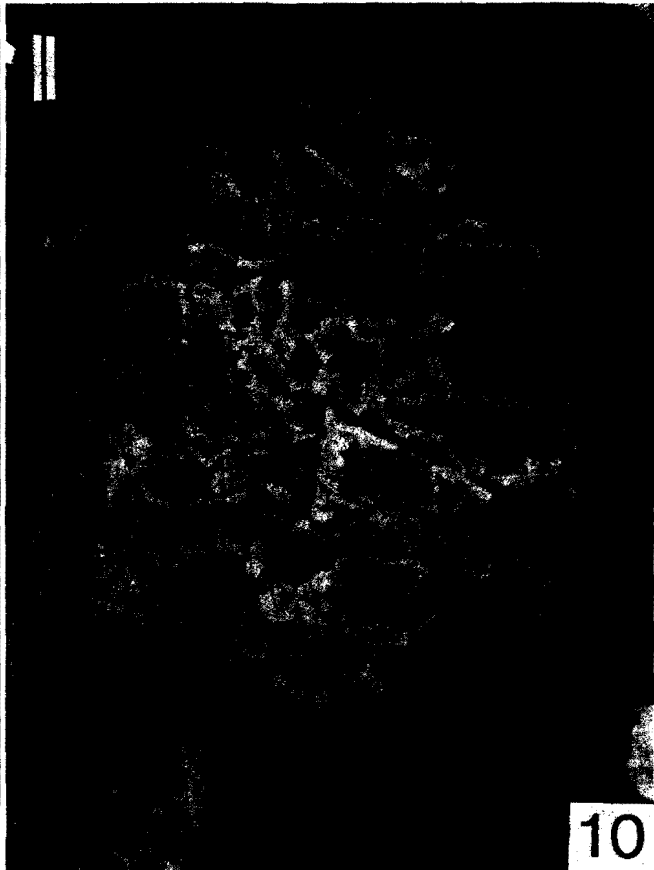
Vessel density (Table 1, column 3) has often been thought to show an inverse relationship (admittedly with exceptions of various degrees) to vessel diameter. Vessel density is notably high (above 300 per mm^2) in most Caryophyllaceae (Fig. 1, 2, 5, 9, 11, 13, 22, 25, 26). For those species with wide rays (e.g., *Silene struthioloides*) or successive cambia (*Scopulophila rixfordii*), rays and conjunctive tissue were not included in the areas scanned for vessel density data collection. Relatively low vessel density (55 per mm^2) was observed in the succulent roots of *Silene hawaiiensis*. In all other species, vessel density was within a range that is typical of more xeromorphic woods.

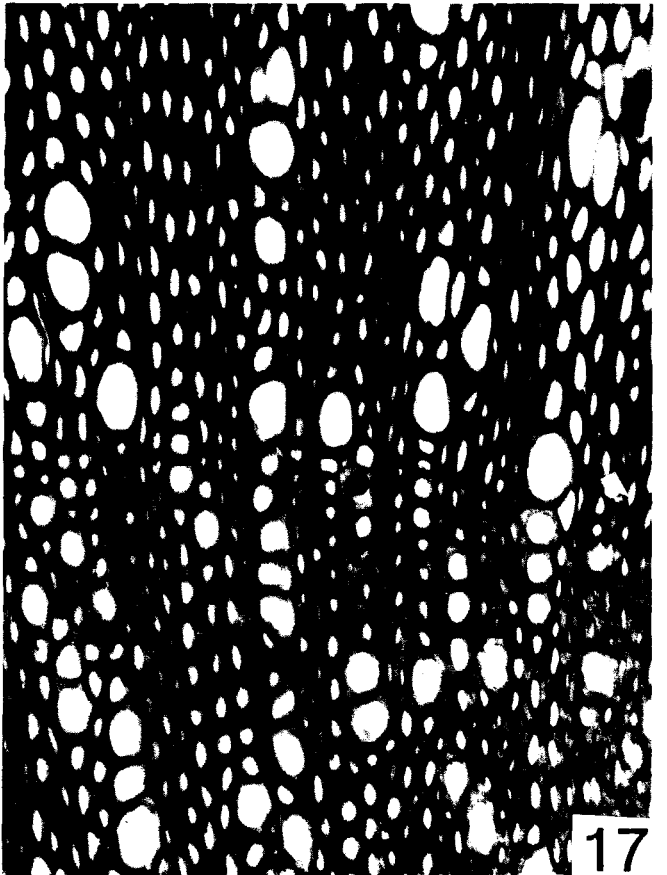
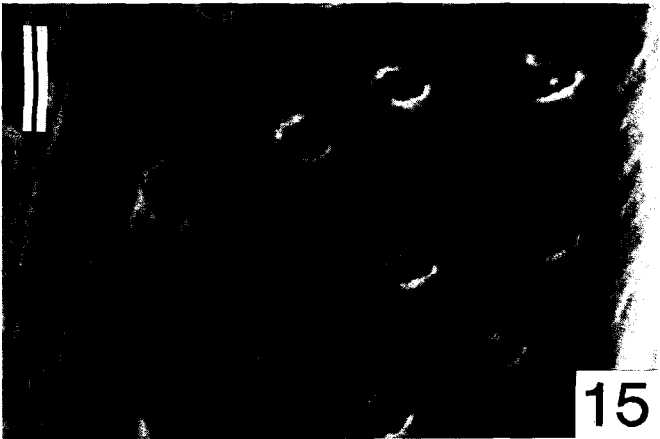
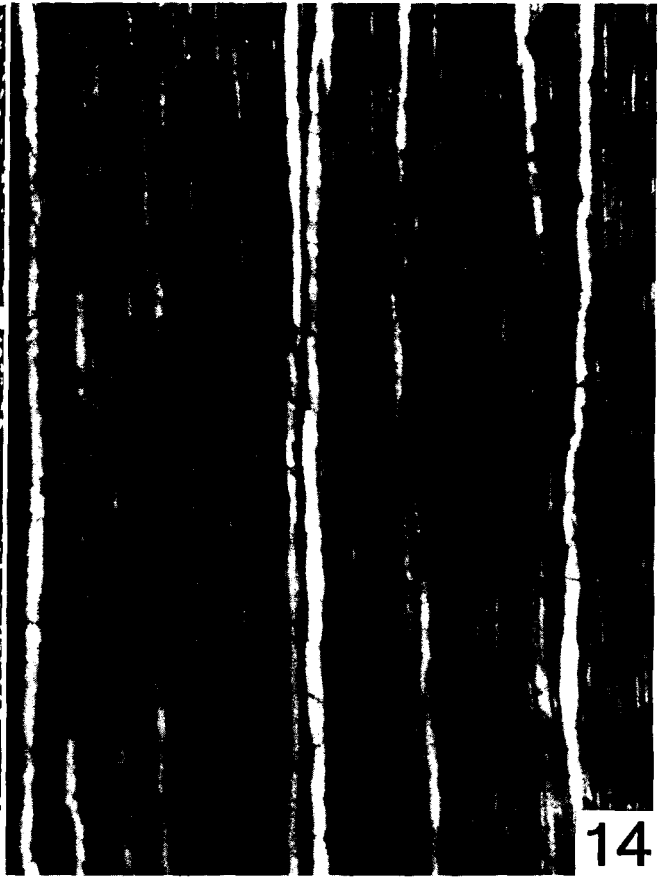
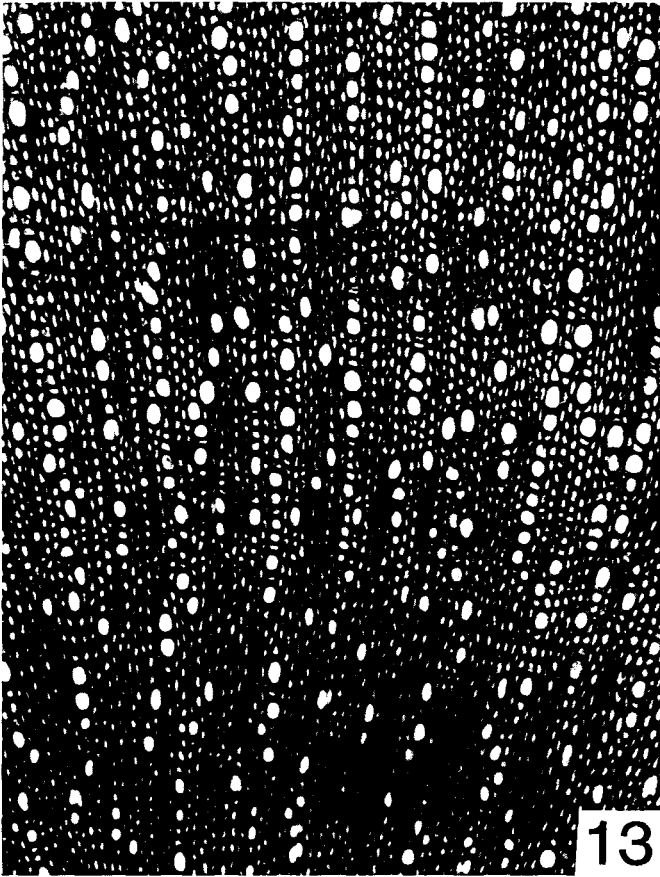
Vessel element length (Table 1, column 4) is notably short in Caryophyllaceae, as shown for *Gymnocarpus salsoloides* in Fig. 3. The longest mean vessel element length (218 μm) was observed in the species from the most mesic locality, *Alsinidendron trinerve*. Mean vessel element length in this species is not markedly greater than that for Caryophyllaceae as a whole (150 μm), however. In turn, the figure for the family as a whole is not much greater than that in the species with shortest vessel elements: *Silene spergulfifolia* (113 μm) and *Dianthus caryophyllus* (114 μm).

Vessel wall thickness (Table 1, column 5) ranges from 2.0 μm in *Alsinidendron trinerve* (Fig. 12), *Dianthus rupicolus*, *Schiedea lydgatei* (Fig. 17) and *Silene fruticosa* to 3.9 μm in *Polycarpha divaricata* (Fig. 6, 8). Thicker vessel walls (3.2 μm) occur in one wood that has pervasive parenchyma, *Silene verecunda* (Fig. 25), although that is not characteristic in woods with a fibrous background, such as *Gypsophila patrinii*.

The vessel-to-vessel and vessel-to-imperforate tracheary element pits are basically alternate in Caryophyllaceae and typically range from 4 to 5 μm in vertical dimension of the pit cavity (Fig. 4, 7); larger pits (6 μm) were observed only in *Alsinidendron trinerve*. Laterally elongate pits characterize vessels of *Arenaria macradenia*, *Dianthus caryophyllus* (Fig. 27–29), *Gypsophila patrinii* (Fig. 30), *Scopulophila rixfordii*, *Silene spergulfifolia* (Fig. 21), *S. struthioloides*, and *S. verecunda*. These laterally elongate pits are termed pseudoscalariform here: in shape they are like those of scalariform pitting in being laterally elongate, but rather than lining up in vertical series on wall faces, they are staggered, illustrating that they may have been derived from lateral elongation of alternate pits. Pseudoscalariform pits are not subdivided by narrow strands of secondary wall material in *Gypsophila patrinii* (Fig. 30); there are slender strands that run vertically across a few pits in vessels of *Dianthus caryophyllus* (Fig. 29), and wider strands across a few pits in vessels of *Silene spergulfifolia* (Fig. 21). The list of species with pseudoscalariform pitting is the same as the list of species with pervasive vessel-to-parenchyma pitting. In *Dianthus rupicolus* and *Silene fruticosa*, pits on the latewood vessels are somewhat larger, and with bigger apertures, than pits on the earlywood vessels (which face mostly libriform fibers rather than parenchyma, but pitting is alternative, not really pseudoscalariform. Pseudoscalariform pitting occurs in vessel-

Fig. 9–12. Wood photomicrographs of Caryophyllaceae.—9–10. *Scopulophila rixfordii* (Roos 6097), transection of root.—9. Vascular stands, formed by successive cambia.—10. Druse as seen by SEM.—11. *Arenaria macradenia* (Thorne 40688), transection showing four growth rings; marginal axial parenchyma alternates with bands of libriform fibers.—12. *Alsinidendron trinerve* (Weller 5448), transection of stem showing rayless secondary xylem; pith at right, cortex at left. (Fig. 9, 11, 12, scale above Fig. 1; Fig. 10, bar at upper left = 5 μm .)





to-parenchyma pitting; in some of the species with these pits, libriform fibers occur in some zones, yet pseudoscalariform pitting on vessels occurs throughout the wood. In *Silene struthioloides*, which has pseudoscalariform pitting, vessels are embedded in a background tissue of libriform fibers (Fig. 24). The woodiness of this species is exceptional in the genus, and the pitting pattern may have been retained from an ancestry in which parenchyma was abundant in fascicular secondary xylem.

Vessels of *Polycarpaea divaricata* have circular pit cavities (Fig. 7). However, grooves interconnect pit apertures (Fig. 8). Pit apertures in vessels of Caryophyllaceae are typically narrowly elliptical.

Helical sculpture is not evident in vessels of Caryophyllaceae, with a few notable exceptions. Pairs of faint thickening bands accompany pit apertures in vessels of stems of *Silene hawaiiensis*. These are most clearly seen in narrow vessels. With light microscopy, helical sculpturing in vessels of *Gymnocarpus salsoioides* is so faint it would most likely be regarded as dubiously present by most observers. With SEM, thickenings are clearly present, although they are not pronounced (Fig. 5). Helical sculpture was also observed with SEM in vessels of *Schiedea ligustrina* (Fig. 15, 16). Curiously, in the example of more pronounced thickenings shown in Fig. 16, the thickenings run counter to the direction of the pit apertures.

Imperforate Tracheary Elements

In Caryophyllaceae as a whole, length of imperforate tracheary elements (Table 1, column 6) averages 257 μm , which is 1.71 times the average vessel element length (150 μm) for the species studied. Woods of some species lack imperforate tracheary elements: roots of *Gypsophila patrinii*, *Scopulophila rixfordii*, and *Silene verecunda*.

Caryophyllaceae are striking in terms of diversity of

imperforate tracheary elements. *Gymnocarpus salsoioides* has fully bordered pits on imperforate tracheary elements (Fig. 3, 4). These cells are therefore tracheids according to the IAWA Committee on Nomenclature (1964). The mean pit cavity diameter of these tracheids is 4.2 μm . Tracheids like these have been reported in *Gymnocarpus decandrum* Forssk. by Fahn et al. (1986).

Fiber-tracheids that have pits with vestigial borders 0.5–1.5 μm in diameter were observed in *Alsiniden-dron trinerve*, *Polycarpaea divaricata*, and all of the species of *Schiedea*. The species studied in *Arenaria*, *Dianthus*, and *Silene* lack borders on pits of imperforate tracheary elements, which are therefore termed libriform fibers.

Wall thickness of imperforate tracheary elements (Table 1, column 7) ranges from 2.0 μm (*Silene struthioloides*, Fig. 23) to 4.8 μm (*S. spergulifolia*, Fig. 20).

A few layers of vascular tracheids were observed in the latewood of *Schiedea lydgatei*. These are inconspicuous and easily overlooked. In *Silene spergulifolia*, the cells that appear to be extremely narrow vessels in latewood (e.g., Fig. 18, top) when examined in longitudinal sections and in macerations usually lack perforation plates and thus are mostly vascular tracheids. On the other hand, the wood of *Scopulophila rixfordii* (Fig. 9) has what appear to be very narrow vessels randomly intermixed with wider ones. Some of these apparently narrower vessel elements do have perforation plates, but others do not. These latter cells should be termed vasicentric tracheids because of their distribution.

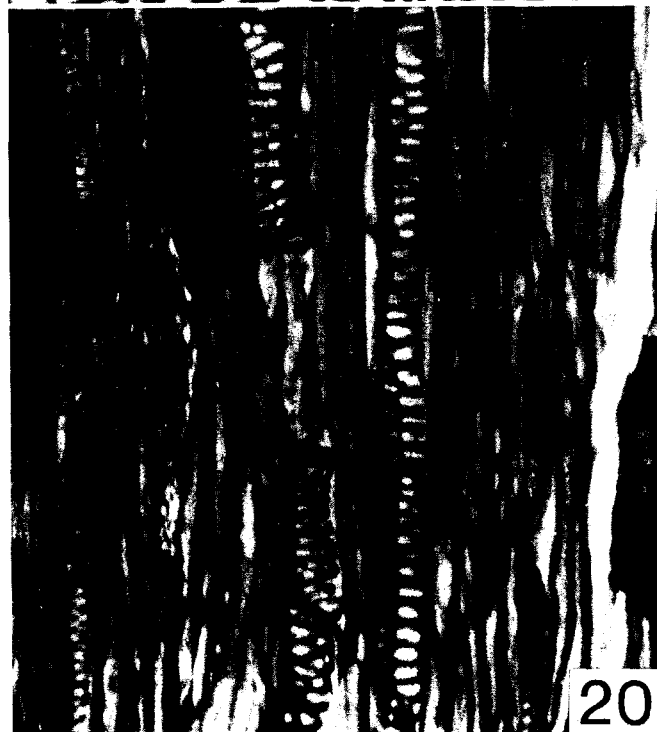
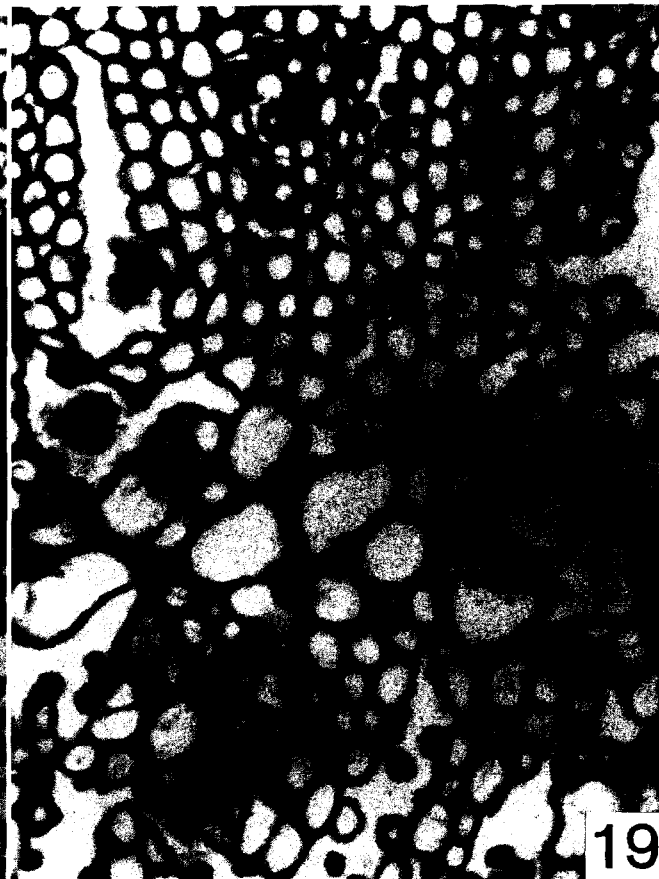
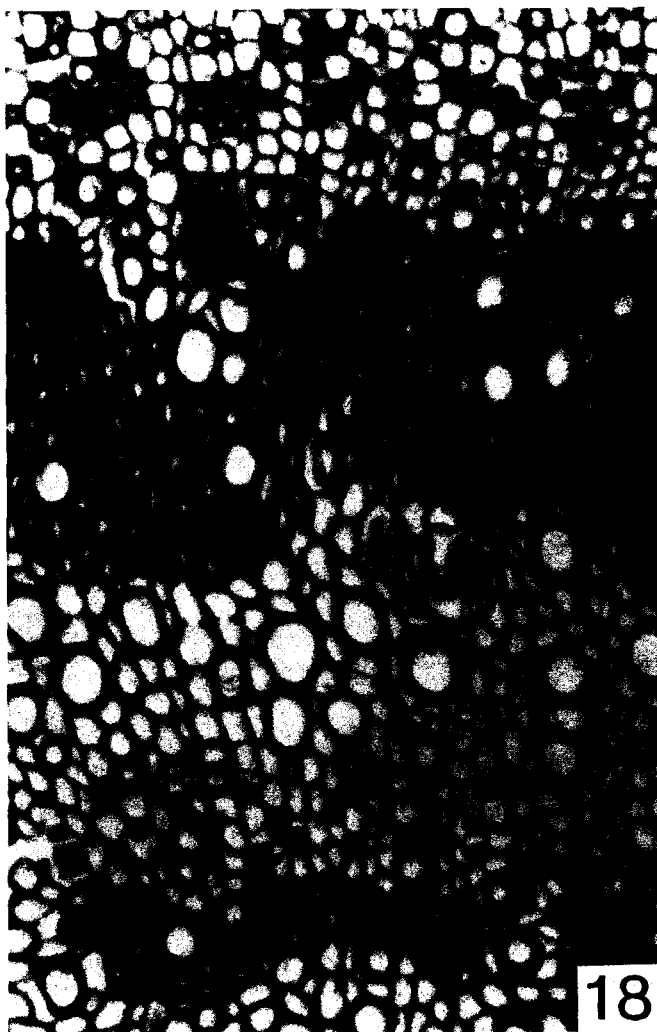
Axial Parenchyma

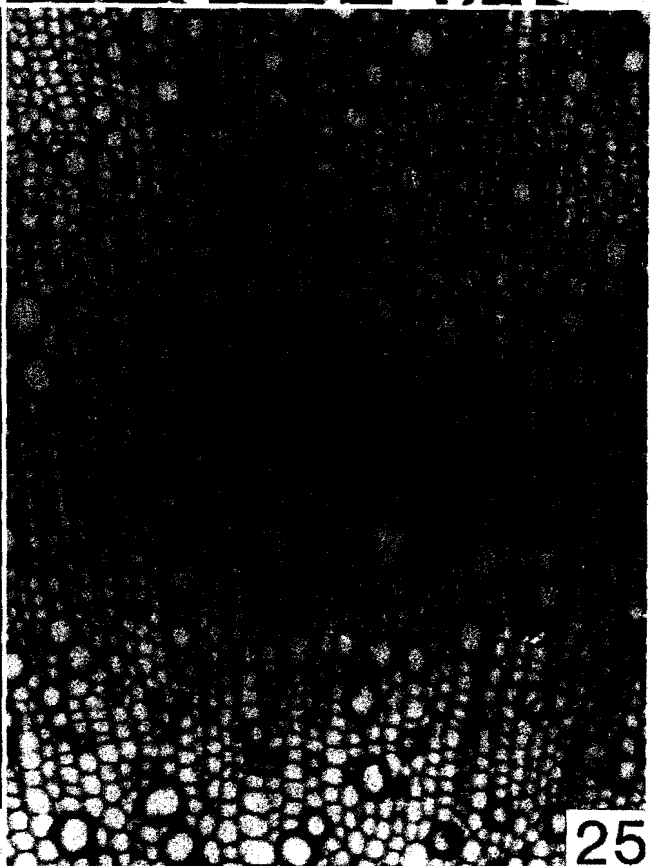
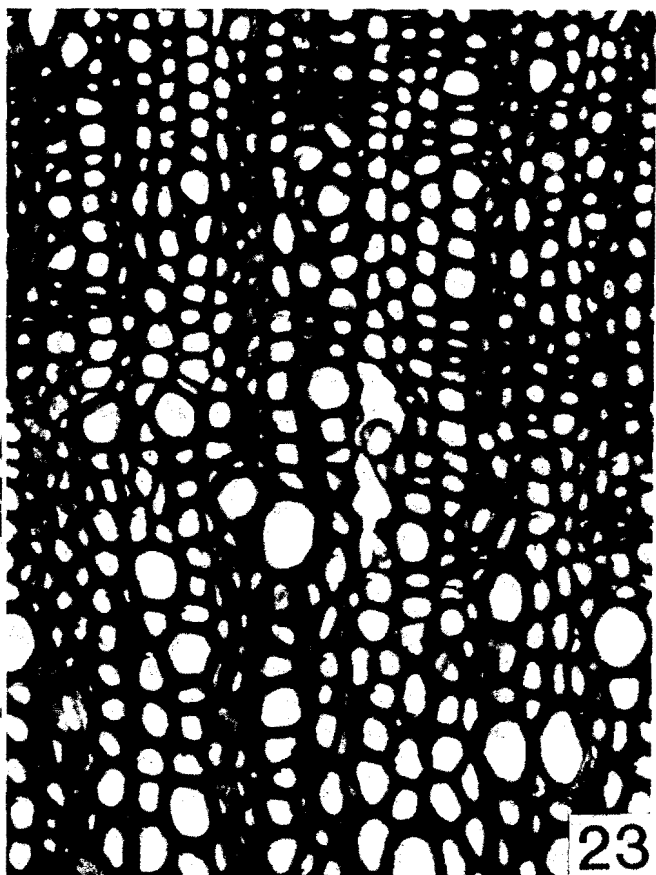
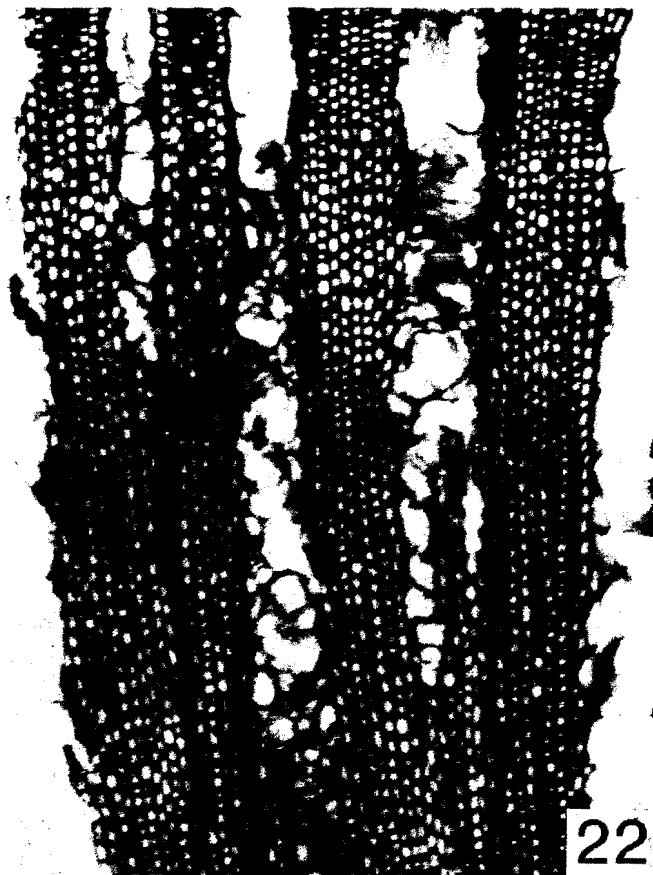
Pervasive axial parenchyma occurs in the roots of *Gypsophila patrinii*, *Scopulophila rixfordii* (Fig. 9), and *Silene verecunda* (Fig. 25). As noted by Metcalfe

← Fig. 13–17. Wood sections of *Schiedea*.—13–16. *S. ligustrina* (Weller 846).—13. Transection; vessels in radial chains.—14. Tangential section showing rayless condition.—15–16. SEM photographs of vessel walls from tangential section.—15. Faint striations on vessel wall.—16. Helical sculpture that runs counter to direction of pit apertures.—17. *S. lydgatei* (Weller s.n.), portion of transection showing lighter-staining latewood (below), darker staining earlywood (above). (Fig. 13, 14, scale above Fig. 1; Fig. 15, 16, bars at upper left in each photograph = 5 μm ; Fig. 16, scale above Fig. 2.)

→ Fig. 18–21. Wood sections of *Silene spergulifolia* (Akhverdov, June 1948).—Transection showing latewood and earlywood vessels embedded in bands of marginal parenchyma, fibers formed midseason.—19. Transection near pith, showing absence of fibers in first-formed secondary xylem.—20. Tangential section showing vessels in a parenchyma band.—21. SEM photograph of vessels from tangential section; pits are laterally elongate. (Fig. 18–21, scale above Fig. 2; Fig. 21, bar at upper left = 5 μm .)

Fig. 22–25. Wood sections of *Silene*.—22–24. *S. struthioloides* (Carlquist 1924).—22. Transection showing wide rays (one originating, to right of center) composed of thin-walled cells that have collapsed.—23. Transection showing a growth ring containing larger vessels (below) succeeded by a growth ring with smaller vessels (above).—24. Tangential section showing absence of uniseriate rays.—25. *Silene verecunda* (Carlquist 8158) root, transection showing vessels of various width and pervasive parenchyma. (Fig. 22, scale above Fig. 1; Fig. 23–25, scale above Fig. 2.)





and Chalk (1950), certain other Caryophyllaceae have axial parenchyma in bands that alternate with the parenchyma bands. These parenchyma bands can be called marginal parenchyma in some species because they are positioned at the end and beginning of growth rings, as in *Arenaria macradenia* (Fig. 11), *D. rupicolus*, *Dianthus* sp. (Tobey 2026), *Silene fruticosa*, and *S. spargulifolia* (Fig. 18). The parenchyma bands in *Arenaria macradenia*, *D. sp.*, and *S. spargulifolia* include the narrow latewood vessels as well as large earlywood vessels; midseason vessels of intermediate diameter are embedded in a ground tissue of libriform fibers. Axial parenchyma formed in a less predictable fashion, with no evident relationship to growth rings, was observed in *Dianthus caryophyllus* (Fig. 26). Marginal parenchyma consisting of bands only a single cell wide (rarely two) was observed in *Gymnocarpus salsoloides*, and was reported in *G. decandrum* by Fahn et al. (1986). In addition to banded axial parenchyma, scanty vasicentric parenchyma characterizes many Caryophyllaceae; it is seen clearly in *Gymnocarpus salsoloides* (Fig. 2). Occasional diffuse cells can also be seen in that species (Fig. 2). Scanty vasicentric parenchyma was recorded for *Alsinidendron trinerve* (in which the cells have thin primary walls only), *Polycarpaea divaricata*, and all species of *Schiedea* (very rare in *S. ligustrina* and *S. lydgatei*), and *Silene struthioloides*. In the earlywood of *Dianthus rupicolus*, in which libriform fibers occur, no axial parenchyma was observed adjacent to vessels. In *Silene fruticosa*, some of the earlywood vessels embedded in the libriform fibers are associated with a few vasicentric axial parenchyma cells.

Axial parenchyma of Caryophyllaceae as seen in longisection usually consists of cells that are not subdivided into strands. Strands of 2–3 cells occur in *Gymnocarpus salsoloides* and were reported for *G. decandrum* by Fahn et al. (1986). Starch was observed in axial parenchyma of *Schiedea lydgatei*.

Rays

The generalization by Metcalfe and Chalk (1950) that woods of Caryophyllaceae are rayless does not hold for all species. It does hold, in the present study, for *Alsinidendron trinerve* (Fig. 12), *Schiedea* (all species: Fig. 13, 14, 17); and stems of *Silene hawaiiensis*. In the wood of *Dianthus rupicolus*, wood begins rayless, but in the outer wood, rays do finally originate.

A few uniseriate rays one or two cells high were observed in the wood of *Silene fruticosa*, which is otherwise rayless.

In *Arenaria macradenia* and *Gypsophila patrinii*, multiseriate rays are relatively common (mean height in *A. macradenia*, 529 μm). Multiseriate rays are also relatively common in *Silene struthioloides* (Fig. 22). *Silene struthioloides* has sufficient accumulation of secondary xylem so that one can see origins of rays. The multiseriate rays in this species and in *Dianthus rupicolus* originate abruptly, rather than by gradually widening of uniseriate or biseriate rays. Abrupt origin of multiseriate rays has been observed in Cucurbitaceae (Carlquist 1992) and Aristolochiaceae (Carlquist 1993). Wide multiseriate rays were also observed in roots of Caryophyllaceae in *Silene hawaiiensis* and *S. verecunda*. In all of the multiseriate rays as studied in radial section, ray cells are upright and thin walled, but a few procumbent cells were also seen in rays of *Arenaria macradenia* and *Silene struthioloides*.

In *Dianthus arboreus* L., Tellini (1939) described and figured radially oriented multiseriate strips of parenchyma in the secondary xylem, but claims these species are not rays, and that rays are not present in this species. Rather, Tellini regarded these as proliferations from axial parenchyma. However, Tellini's figures appear to contradict this interpretation, because what seem to be rays cross the cambium, and extend part way into both xylem and phloem, much like what I have seen in the abrupt origin of rays in *Silene struthioloides*. Moreover, several such multiseriate rays that originate later in the ontogeny of secondary xylem could be seen in my material of *Dianthus caryophyllus*. Wood of the unidentified *Dianthus* from Turkey (Tobey 2026) shows, in tangential sections, numerous typical multiseriate rays (cells of which contain large numbers of druses). These features also occur in the rays that occur in outer wood of *D. rupicolus*. Thus, normal multiseriate rays do occur in *Dianthus*. In the earliest-formed secondary xylem of my material of *D. caryophyllus*, there are some strips of parenchyma 1–2 cells wide in which radial subdivision of these parenchyma cells may have contributed to the width of these strips. Such proliferation may be what caused Tellini to claim that rays were absent in *Dianthus arboreus*.

In *Gymnocarpus salsoloides*, there are inconspicuous uniseriate (rarely biseriate) rays (Fig. 3). These

Fig. 26–29. *Dianthus caryophyllus* (Carlquist s.n.), sections of older horizontal stem.—26. Transection showing secondary xylem below from normal cambium above; below in photograph cambium has formed in the pith, yielding xylem (two dark patches) to the outside, phloem to the outside, and a periderm (bottom of photograph).—27. Tangential section through a zone of axial parenchyma, showing rayless condition.—28. Portion of tangential section showing vessels with laterally elongate pits.—29. SEM photograph of vessel from tangential section showing laterally elongate (pseudoscalariform) pits traversed by a few narrow strands of wall material. (Fig. 26, scale above Fig. 1; Fig. 27, scale above Fig. 2; Fig. 28, scale above Fig. 4; Fig. 29, bar at upper right = 5 μm .)



average 189 μm in height and are rarely more than three cells in height. Cells of these rays are upright, and their tips often overlap as seen in tangential section. Uniseriate rays of this description were reported in *Gymnocarpus decandrum* by Fahn et al. (1986). A few uniseriate rays like those of *Gymnocarpus salsoioides* were observed in the wood of *Polycarpaea divaricata*.

Crystals

Druses are present in woods of the family (Fig. 10, 31). The druses of Caryophyllaceae, as studied by SEM, are distinctive in that they are composed not of rhombohedral (prismatic) crystals but of chiplike or wedgelike fragments (Fig. 10, 31).

Druses were observed in axial parenchyma of *Arenaria macradenia*, *Dianthus caryophyllus*, *Gypsophila patrinii*, and *Silene spergulifolia*. They occur in rays of *Arenaria macradenia*, *Dianthus* sp. (Tobey 2026), *Gypsophila patrinii*, and *Silene verecunda*. Druses are common in the conjunctive tissue (parenchyma between vascular strands produced by successive cambia) of *Scopulophila rixfordii* (Fig. 9, dark spots). Based upon the slides studied here of *Arenaria macradenia*, I reported druses in rays of *Arenaria macradenia* earlier (Carlquist 1988); the remaining reports above are new.

Storying

Patches of storied axial parenchyma and vessel elements, sometimes with storied libriform fibers as well, were observed in tangential sections of wood of *Dianthus caryophyllus*, *Polycarpaea divaricata*, and *Silene spergulifolia*. Storying has not hitherto been reported in Caryophyllaceae, but it has been reported in three other families of Caryophyllales: Amaranthaceae, Chenopodiaceae, and Nyctaginaceae (Metcalf and Chalk 1950). The species of Caryophyllaceae that exhibit storied wood structure are precisely the ones that have the shortest vessel elements. Vessel element length is extremely short in species with storied structure in dicotyledons at large (Bailey and Tupper 1918; Bailey 1923).

Cambial Variants

Pfeiffer (1926) reports cambial variants for the family; I presume these to be successive cambia forming strands of vascular tissue like those of *Scopulophila rixfordii* (Fig. 9). The tribe Paronychieae is richest in this cambial type, whereas it has been reported in only one species of subfamily Silenoideae (Pfeiffer 1926). All instances of successive cambia reported thus far are in roots, except for three genera which have successive cambia in both stems and roots: *Cometes*, *Corrigiola*, and *Pollichia* (Pfeiffer 1926).

A unique form of successive cambial activity is newly reported here for horizontal older stems of *Dianthus caryophyllus* (Fig. 26). At the periphery of the pith in this material, a cambium produces vascular tissue in inverse orientation—phloem to the inside and xylem to the outside. In addition to producing phloem on its internal face, this cambium yields a periderm internal to the phloem (Fig. 26, bottom).

ECOLOGICAL CORRELATIONS

Vessel features demarcate Caryophyllaceae as markedly xeromorphic: vessel elements are short, narrow, and numerous per mm^2 of transection (for further comments on wood xeromorphy, see Carlquist 1988). The features for all Caryophyllaceae studied here averaged are as follows (in parentheses, figures for Californian desert shrubs from Carlquist and Hoekman 1985): vessels per group, 3.14 (2.62); vessel diameter, 19 μm (26 μm); vessels per mm^2 , 372 (361); vessel element length, 146 μm (190 μm). In all four features, the Caryophyllaceae sample studied here yields means indicative of more xeromorphy than the means for the Californian desert shrubs, despite the fact that only a few of the species studied come from localities as dry as desert sites, namely *Arenaria macradenia*, *Gymnocarpus salsoioides*, and *Scopulophila rixfordii*. One species studied here, *Alsinidendron trinerve*, comes from a frequently cloudy wet forest area where it is an understory shrub. Although the wood of *Alsinidendron* is less xeromorphic than that of the closely related *Schiedea* in quantitative features of vessels, the difference is not great despite the fact that the *Schiedea* species were collected in dry lowland localities.

Another comparison of potential interest is between insular and mainland Caryophyllaceae. This comparison is feasible because so many insular species of Caryophyllaceae have been utilized in the present study. *Dianthus rupicolus* and *Silene fruticosa* have been omitted from this comparison because their ecology is maritime continental—intermediate between insular and inland continental—and because the samples were from cultivated specimens, which one would expect to have more xeromorphic wood expressions than wild-growing plants. Quantitative vessel features of insular species averaged are as follows (means for combined continental species in parentheses): number of vessels per group, 1.76 (2.34); vessel diameter, 20.6 μm (14.0 μm); number of vessels per mm^2 , 304 (605); vessel element length, 153 μm (143 μm). The insular species are more mesomorphic than the continental species in all of these features. Another way to express this is to combine three vessel features into the Mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per mm^2). The figure for the insular species for this ratio is 10.37, whereas the

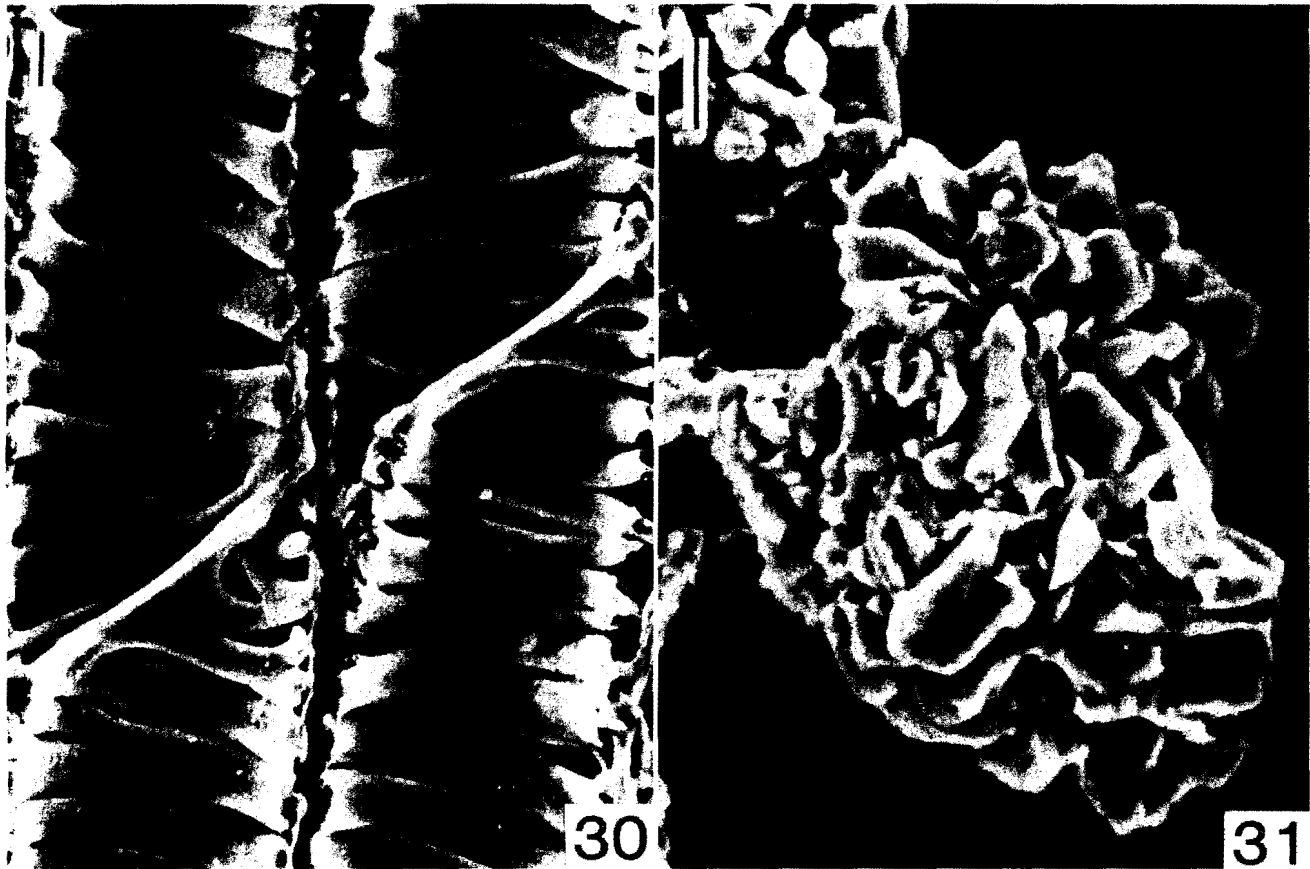


Fig. 30–31. *Gypsophila patrinii* (Smirnov 59), SEM photographs from tangential section of root wood.—30. Pits on vessels are markedly elongate laterally, resulting in a pattern that mimics a scalariform condition or even simulates helical thickenings in a primary xylem vessel.—31. Druse from rays. (Bars at upper left in each figure = 5 μm .)

continental species yield the value 3.31. While one can say that the woods of insular species show less xeromorphy, as might be expected if insular climates are less extreme, the difference is not huge. One should note that some insular species grow in localities that are in effect deserts: *Gymnocarpus salsoloides* (Teno, Tenerife) and *Silene struthioloides* (Haleakala Caldera, Maui).

Other putatively xeromorphic features that occur in the wood of Caryophyllaceae include helical sculpturing in vessels and type of imperforate tracheary element. Helical sculpture occurs in vessels of *Gymnocarpus salsoloides*, *Polycarpaea divaricata*, and *Schiedea ligustrina*. These species do not have highly pronounced helical sculpturing in vessels. Nevertheless, these occurrences are of great interest, because helical sculpturing is sometimes thought to be associated only with cold, and can be found in some genera (e.g., *Cornus*) that never occur in dry areas. In fact, helical sculpturing may occur in species that grow in cold areas in some instances, but in other groups the habitat is a dry one. The three species of Caryophyllaceae with helical sculpturing in vessels occur in areas that experience no frost.

Gymnocarpus has tracheids rather than fiber-tracheids or libriform fibers. It also has a low number of vessels per group (1.10). This is one more instance that affirms that vessel grouping is minimal (essentially restricted to random contacts between vessels governed by vessel density and vessel diameter) if tracheids are the type of imperforate tracheary element present. Tracheids can serve as a conductive system subsidiary to vessels, theoretically serving for conduction should the vessels embolize (Carlquist 1984); the conductive capabilities of tracheids are sufficient to render the selective value of vessel grouping minimal. According to this hypothesis, fiber-tracheids and libriform fibers are nonconductive or essentially so, so that vessel grouping offers a redundancy (while maintaining conductive pathways) valuable should some vessels embolize. Vessel groupings should be greater the more xeromorphic the locality where such woods are involved. All Caryophyllaceae other than *Gymnocarpus* have fiber-tracheids or libriform fibers, and of these species, the least degree of vessel grouping does occur in the species from the most mesic locality, *Alsinidendron trinerve*. A low degree of vessel grouping in *Di-*

anthus caryophyllus may indicate the greater degree of water availability in cultivation.

Growth rings in Caryophyllaceae do not show dramatic differences in vessel diameter in the range of what one sees in temperate species of *Quercus*. However, most localities inhabited by woody Caryophyllaceae have a wet season with short availability of a modest quantity of moisture. The most pronounced growth rings are in two species of desert areas, *Arenaria macradenia* and *Silene spergulifolia*. Roots tend to store water in those Caryophyllaceae with perennial woody roots, and this should lessen the likelihood of growth ring formation. Indeed, growth rings are absent in the roots of *Gypsophila patrinii*, *Scopulophila rixfordii*, *Silene hawaiiensis*, and *S. verecunda*.

HABITAT CORRELATIONS

Caryophyllaceae are best described, when maximally woody, as subshrubs; none qualifies as a shrub in the sense of shrubby Fabaceae or Rosaceae. Woody Caryophyllaceae could, in fact, be regarded merely as woody herbs. The occurrence of raylessness is pertinent in this regard. Raylessness has often been associated with phylesis from herbaceousness toward increased woodiness (Barghoorn 1941; Carlquist 1970, 1988). In Caryophyllaceae, raylessness is most pronounced in *Alsinidendron* and *Schiedea* (the latter perhaps the woodiest genus of the family). Uniseriate rays without multiseriate rays characterize *Gymnocarpus* and may be found sparsely in *Polycarpaea*. Multiseriate rays appear characteristic of the majority of remaining Caryophyllaceae studied here, except for the stems of *Dianthus caryophyllus* (a few multiseriate rays) and *Silene spergulifolia* (no rays). One can conclude that Caryophyllaceae are by no means a rayless family, and that if raylessness is an indicator of secondary woodiness, the family might be primitively woody, but with evolution of herbaceousness in most of the family and secondary woodiness in some phylads. Successive cambia, reported here in *Scopulophila* and *Dianthus*, and reported in 19 genera of the family by Pfeiffer (1926), have been regarded by some workers as an indication of secondary woodiness in phylads that mostly lack normal cambial activity (see discussion in Carlquist 1988). This is probably not true in typically woody phylads (e.g., particular species of *Bauhinia* of the Fabaceae are characterized by either a normal cambium or successive cambia). The raylessness, lack of either multiseriate rays or uniseriate rays, abrupt origin of multiseriate rays, and occurrence of successive cambia in Caryophyllaceae may be indicative of loss of particular features of normal cambial activity. Normal cambial activity is not a single phenomenon, but a series of phenomena. Loss of capability for production of rays, or production of par-

ticular kinds of rays, can occur without loss of capability for production of axial tissue, for example.

The occurrence of libriform fibers in *Arenaria*, *Dianthus*, and *Silene spergulifolia* is noteworthy in that it seems related to habit. Libriform fibers in the horizontal basal stem of *Dianthus caryophyllus* may cease to be formed once maximal stem diameter has been attained, if the stem studied is typical: optimal mechanical strength has been attained by that time, but production of more conductive tissue is required. In *Schiedea globosa*, the reverse sequence is characteristic (vessels in a parenchyma ground tissue, followed by fiber-tracheids without parenchyma or vessels) of that species, and may correlate with the fact that the stem, as it produces an inflorescence and fruits, has a progressively increased requirement for mechanical strength.

Successive cambia in the roots of Caryophyllaceae may relate to the probable water and photosynthate storage functions of these roots. Successive cambia are a way of producing vascular tissue scattered throughout a parenchymatous ground tissue (the conjunctive tissue). If so, this would account for the fact that successive cambia are much less common in stems than in roots of Caryophyllaceae. Storage function could be achieved in alternative ways, such as bands of libriform fibers alternating with bands of (marginal) parenchyma (*Arenaria*, *Silene spergulifolia*) or pervasive parenchyma (roots of *Gypsophila patrinii* and *Silene verecunda*).

SYSTEMATIC AND PHYLOGENETIC CORRELATIONS

The interrelationships of families of Caryophyllales have interested numerous workers in recent years. The cladistic work of Rodman et al. (1984) places Caryophyllaceae near the base of the caryophyllalean clade. Bedell (1980) claimed a relationship between *Stegnosperma* (Stegnospemaceae) and Caryophyllaceae. The recent assemblage of *rbcL* data (Chase et al. 1993) shows Caryophyllaceae as a branch from well along the Caryophyllales clade, near Chenopodiaceae and Amaranthaceae.

Further knowledge of caryophyllalean woods is desirable before defensible conclusions can be reached. However, the present study does demonstrate the diversity of woods within the family, a key point in establishing its relationship. The wood of *Gymnocarpus* is of significance in this regard, because its tracheids and uniseriate rays are unlike the fiber-tracheids (*Alsinidendron*, *Polycarpaea*, *Schiedea*) or libriform fibers (other genera) and multiseriate rays (or raylessness) elsewhere in the family. The features of *Gymnocarpus* wood support the idea that Caryophyllaceae branched early from the caryophyllalean clade, other-

wise one would not expect tracheids or even fiber-tracheids in the family, and one might not expect rays. Wood of *Amaranthaceae* and *Chenopodiaceae* (libriform fibers, raylessness, storying, and with successive cambia rather than a single cambium), and the range of character-state expressions in caryophyllaceous wood could not be derived from that pair of families unless one hypothesized a large number of reversions to more primitive expressions. Wood features tend to be less reversible than other characters because of functional correlations between the wood characters (Carlquist 1988). *Stegnosperma* does have tracheids, but it also has successive cambia and both multiseriate and uniseriate rays. For *Stegnospermaceae* and *Caryophyllaceae* to be related, one would have to imagine an ancestor with tracheids, but with multiseriate and uniseriate rays (instead of only uniseriate rays, as in *Gymnocarpus*) and yet with no successive cambia. Genera with such ancestral wood features do exist in other families of *Caryophyllales*. At present the cladistic scheme of Rodman et al. (1984) is supported by the wood data.

The ancestors of *Caryophyllaceae* are likely to have been woody and to have had rays. If the entirety of *Caryophyllaceae* were rayless or had successive cambia, one could hypothesize ancestors to *Caryophyllaceae* that had lost normal cambial activity. The woods of *Gymnocarpus* and *Polycarpaea* suggest a normal woody ancestry for the family, even if they are not big shrubs. Interestingly, the Pax and Hoffmann (1934) system placed *Gymnocarpus* and *Polycarpaea* near the beginning of *Paronychieae*, the tribe they recognize as most primitive, although they had no wood data. The presence of tracheids rather than fiber-tracheids in *Gymnocarpus* also is in line with a basal placement in the family. All of the instances of successive cambia known thus far are in *Paronychia*, with the exception of a single species of *Silene* (Pax and Hoffmann 1934). The distribution of this feature in *Caryophyllaceae* needs more study, particularly with respect to roots.

Fiber-tracheids with much reduced pit borders are found in *Alsinidendron* and *Schiedea*, which fall into the central tribe of *Caryophyllaceae*, *Alsineae*, in the Pax and Hoffmann (1934) system. The raylessness of these two genera distances them from *Gymnocarpus* and *Polycarpaea*. However, *Arenaria*, which has multiseriate rays and nucleate libriform fibers, is also placed in *Alsineae*.

The third, and presumably most specialized, tribe in the Pax and Hoffmann system is *Sileneae*, and all of the genera of that subfamily studied here have libriform fibers rather than tracheids or fiber-tracheids. Wide multiseriate rays that originate abruptly occur in *Sileneae* but also in one genus of *Alsineae* (*Arenaria*).

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