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WOOD ANATOMY OF PORTULACACEAE AND HECTORELLACEAE: ECOLOGICAL, HABITAT, AND SYSTEMATIC IMPLICATIONS

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ABSTRACT

Qualitative and quantitative wood data are given for 13 species of 10 genera of Portulacaceae (secondary xylem from additional species of *Anacampseros* and *Lewisia* were studied but not quantitatively analyzed). Most Portulacaceae show modifications that can be related to the succulent habit, including wide, tall rays mostly composed of thin-walled cells; total or partial substitution of axial parenchyma for libriform fibers; and modified patterns of pitting on lateral walls of vessels. Pseudo-scalariform pitting is more common in Portulacaceae than in other dicotyledon families. In vessels of *Anacampseros* wood, wide helical bands of secondary wall material are present. Similar helices (but without the unusual width) occur in the wood of *Lewisia* and *Hectorella*. Woods of Portulacaceae as a whole are markedly xeromorphic with respect to vessel element dimensions, vessel density, and vessel grouping; wood of *Lewisia* and *Hectorella* is especially xeromorphic. Xeromorphism is not so pronounced in succulent dicotyledons at large. Woods of species of Portulacaceae with less marked adaptation to succulence show close resemblance to woods of Didiereaceae and woodier Cactaceae, suggesting the validity of the suborder Portulacineae, which includes these three families plus Hectorellaceae and Basellaceae. The wood of *Hectorella* is very similar to that of *Lewisia rediviva* and contains no features not also observed in Portulacaceae. Tracheidlike idioblasts in rays of *Anacampseros* are likely not homologous with wide-band vascular (or vasicentric) tracheids in fascicular secondary xylem of globular cacti. Dark-colored mucilage idioblasts in Portulacaceae are likely to be a homoplasy; they occur in a scattering of Caryophyllales.

Key words: Caryophyllales, Centrospermae, ecological wood anatomy, Portulacineae, succulence, tracheoidal idioblasts, xeromorphic wood.

INTRODUCTION

The present paper continues a series of studies on wood anatomy of Caryophyllales (Centrospermae of earlier authors) begun with a survey of woods of Caryophyllaceae (Carlquist 1995a). Some caryophyllalean families, such as Cactaceae, have been studied extensively by other authors and will not be covered in this series. The work of these authors, however, will be cited in the concluding paper of this series. The wood of a family now widely regarded as an outgroup of Caryophyllales, Plumbaginaceae, has been surveyed recently (Carlquist and Boggs 1996). Polygonaceae are widely regarded as an outgroup of Caryophyllales and a sister family of Plumbaginaceae (Rodman et al. 1984; Giannasi et al. 1992; Rettig et al. 1992; Downie and Palmer 1994; Williams et al. 1994; Downie et al. 1997). A survey of wood anatomy of Polygonaceae is planned.

Despite the fact that Caryophyllales are one of the best studied orders of angiosperms (Mabry 1977; Behnke and Mabry 1994), relatively little attention has been paid to wood anatomy of most families of Cary-

ophyllales. Metcalfe and Chalk (1950) summarized data on wood of several species of Portulacaceae, both data obtained by them and data from other authors. Gibson (1994) added some qualitative details for several species of Portulacaceae. The paucity of information relates partly to the nonwoody nature of most species of the family. Studies on wood anatomy have traditionally emphasized woody species while neglecting herbaceous species. Another reason for neglect of wood anatomy of Portulacaceae is the worldwide distribution of the family: a comprehensive collection of wood samples is thereby difficult to obtain, and wood samples must be preserved in liquid for shipment. Wood samples of dicotyledons are traditionally preserved by drying, but succulence is extensive in Portulacaceae and the family is thus little represented in xylaria. One of the reasons for studying the wood anatomy of Portulacaceae is that it demonstrates various kinds of stem succulence, and shows how wood of a group of dicotyledons has become modified to accommodate water storage and mechanical strength to divergent degrees.

The present study is not maximally comprehensive for the family, which is relatively large (19 genera, 500 species: Cronquist and Thorne 1994). However, a large

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proportion of the family is herbaceous. An attempt is made here to study a sampling of the woodier representatives and, by way of comparison, some herbaceous species. Wood of the cushion-plant family Hectorellaceae (*Hectorella caespitosa* on New Zealand and *Lyallia kerguelensis* Hook f. on Kerguelen: Philipson 1993) has not been studied hitherto. Hectorellaceae were included within Caryophyllaceae earlier (Pax and Hoffmann 1934), although some more recent authors have included the family in Portulacaceae (Cronquist 1981; Rodman 1994). Cronquist and Thorne (1994) recognize Hectorellaceae as a family, but concede they deliberately use narrow definitions of families for convenience in referring to segregate families. *Hectorella* contains betalains (Yoong et al. 1975; Mabry et al. 1978) and thus clearly belongs to Caryophyllales. The family has not been included in recent studies on molecular systematics, but its inclusion within the suborder Portulacineae seems very likely on the basis of macromorphology.

Although cladograms based on macromorphology and on DNA studies are not entirely in agreement, the closeness of Portulacaceae to Didiereaceae and to Basellaceae is often emphasized, and Cactaceae are usually placed near this trio of families (e.g., Rodman 1994). One of the purposes of the present study is to offer data concerning the five families of Portulacineae and to determine whether wood data are in accord with this grouping. Assuming this suborder as a natural group, what kinds of wood diversification have occurred?

Habit is of overriding significance in interpretation of wood patterns. Portulacaceae range from woody shrubs (*Portulacaria*, *Talinella*) or subshrubs (*Talinum*, *Talinopsis*) that have succulent to semisucculent leaves and stems to very succulent subshrubs (*Cistanthe*) or rosette herbs that are succulent in texture (*Lewisia*). The diverse types of wood in Portulacaceae must be examined first in terms of habit and ecology. Differences that do not appear correlated with these diverse habits may be considered within systematic contexts.

MATERIALS AND METHODS

Advances in intrafamilial systematics of Portulacaceae have been made in recent years (Carolin 1987; Hershkovitz 1991), and generic concepts in those studies have been followed. Wood of *Talinella boiviniana*, *Talinopsis frutescens*, and *Hectorella caespitosa* was available from dried specimens (Table 1). These specimens were boiled and stored in 50% aqueous ethanol. The texture of wood in Portulacaceae ranges from very soft to moderately soft, and only one species (*Talinella boiviniana*) was judged to have wood suitable for sectioning on a sliding microtome. For the remaining spe-

cies, woods were treated with ethylene diamine, embedded in paraffin, and sectioned on a rotary microtome (Carlquist 1982). Strength of ethylene diamine solutions and length of exposure to this chemical varied with softness of a given wood.

Sections were stained with a safranin-fast green combination corresponding to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen 1940). Some paraffin sections (e.g., Fig. 25) were mounted on aluminum stubs, cleansed of paraffin, sputter coated, and examined with scanning electron microscopy (SEM). Macerations were prepared by means of Jeffrey's Fluid and stained with safranin.

Sources of the specimens were as follows: *Anacampseros alstoni* Schönl., *Carlquist 8169* (SBG), cultivated, Santa Barbara; *A. alta* Poelln., *Carlquist 8167* (SBG), cultivated, Santa Barbara; *A. densifolia* Dint., cultivated, Huntington Botanical Gardens (H-44401); *A. marlothii* Poelln., cultivated, Huntington Botanical Gardens (H-46898); *A. retusa* Poelln., cultivated, Huntington Botanical Gardens (H-23384); *A. telephiastrum* DC., *Carlquist 8168* (SBG), cultivated, Santa Barbara; *Calypotrothea somaliana* Gilg, cultivated, Huntington Botanical Gardens (H-57630); *Ceraria fruticulosa* Pears. & E. L. Stephens, *Carlquist 8170* (SBG), cultivated, Santa Barbara; *Cistanthe guadalupense* (Dudley) Carolin ex Hershkovitz, *Carlquist 480* (RSA); *Hectorella caespitosa* Hook. f., Old Man Range near Alexandra, central Otago, South Island, New Zealand, *Beckstrom 1098* (RSA); *Lewisia cantelovii* Howell, cultivated, Rare Plant Research, Portland, Oregon; *L. cotyledon* (Wats.) Robinson var. *howellii* (Wats.) Jeps., summit of Siskiyou Mountains, 3 km SW of Dry Lake, Lookout, Siskiyou Co., California, *Ownbey 1751* (RSA); *L. rediviva* Pursh, *Carlquist 8157* (RSA), tree-line, Mt. San Antonio, Los Angeles County, California; *L. rupicola* C. S. English, cultivated, Rare Plant Research, Portland, Oregon; *Portulaca* sp., cultivated, Huntington Botanical Gardens (H-54247; native to Kenya); *Portulacaria afra* Jacq., cultivated, Claremont, California; *P. armiana* E. V. van Jaarsveld, cultivated, Huntington Botanical Gardens (s.n.); *Talinella boiviniana* Baill., SJRW-44451, Madagascar; *Talinopsis frutescens* A. Gray, limestone ridges, west slope of Pyramid Peak, Doña Ana Co., New Mexico, *Fosberg S3581* (POM); *Talinum paniculatum* (Jacq.) Gaertn. cultivated, Santa Barbara; *T. triangulare* (Jacq.) Willd., *Carlquist 8165* (SBG), cultivated, Waimea Falls Park, Oahu, Hawaii.

Terminology of wood anatomical features follows the usages of the IAWA Committee on Nomenclature (1964). The term "pseudoscalariform" refers to pits on lateral walls of vessels; these pits are much widened laterally, but still have an alternate pattern rather than one in which ends conform to cell wall angles. The term "pervasive" axial parenchyma is used for species

Table 1. Wood characteristics of Portulacaceae and Hectorellaceae.

Species	Collection	1 VG	2 VD	3 VM	4 VL	5 VW	6 VP	7 TL	8 TW	9 MH	10 MW	11 RH	12 MR
<i>Anacampseros marlothii</i>	H-46898	2.3	8	153	138	—	—	—	—	>500	>10	U	7.2
<i>Calyptrotheca somaliana</i>	H-57630	1.9	37	129	145	2.5	6	424	1.3	1201	>5	U	42
<i>Ceraria fruticulosa</i>	Carlquist 8170	3.2	30	321	105	2.6	6	371	3.5	1153	6.7	Us	9.8
<i>Cistanthe guadalupense</i>	Carlquist 480	1.9	39	85	167	4.5	7	—	—	3039	>15	USp	77
<i>Lewisia cotyledon</i>	Ownbey 1751	7.4	11	1085	104	—	5	—	—	449	3.6	U	0.1
<i>L. rediviva</i>	Carlquist 8157	>15	14	759	101	—	—	—	—	>500	>10	U	1.9
<i>Portulaca</i> sp.	H-54257	1.7	33	49	232	2.2	5	350	3.5	—	—	—	104
<i>Portulacaria afra</i>	cult. Claremont	1.5	43	22	156	3.0	2	386	2.6	696	6.3	USP	305
<i>P. armiana</i>	cult. Huntington B. G.	2.2	33	85	137	2.5	2	373	2.5	1762	4.4	USp	53
<i>Talinella boiviniana</i>	SJRw-44451	1.8	63	41	232	2.2	12	744	2.4	1893	4.1	USp	36
<i>Talinopsis frutescens</i>	Fosberg S3581	1.7	30	270	100	2.7	6	232	2.1	830	5.3	U	11
<i>Talinum paniculatum</i>	cult. Santa Barbara	1.9	34	78	195	1.8	6	375	2.5	—	—	—	85
<i>T. triangulare</i>	Carlquist 8165	1.8	28	95	167	1.7	6	343	1.3	1293	7.2	US	49
Portulacaceae, averaged		3.7	30	219	153	2.5	6	400	2.3	1269	8.7		60
<i>Hectorella caespitosa</i>	Beckstrom 1098	3.7	7	639	155	2.0	—	—	—	—	—	U	1.7

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean diameter of vessel lumen, μm ; 3 (VM), mean number of vessels per mm^2 ; 4 (VL), mean length of vessel elements, μm ; 5 (VW), mean thickness of vessel walls, μm ; 6 (VP) mean axial diameter of pits on lateral walls of vessels, μm ; 7 (TL), mean length of imperforate tracheary elements (libriform fibers), μm ; 8 (TW), mean wall thickness of imperforate tracheary elements; 9 (MH), mean height of multiseriate rays, μm ; 10 (MW), mean width of multiseriate rays, μm ; 11 (RH), Ray histology (U = upright, s = square, P = procumbent, lower case indicates the cell type is infrequent); 12 (MR), Mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per mm^2 . Author citations of binomials and additional collection data in Materials and Methods.

in which (as in *Hectorella* and *Lewisia*) vessels are embedded in a parenchymatous background (e.g., Fig. 33) in which libriform fibers are absent or scarce.

Vessel lumen diameter is measured as an average between widest and narrowest lumen diameter in vessels oval in transection. Lumen diameter has physiological significance with respect to conductive capabilities, and therefore is to be preferred to the diameter of a vessel including the wall, a convention used in earlier literature. Although the bands of the helically banded vessels (e.g., *Lewisia*) likely do not provide the same conductive characteristics as a solid wall of such width, the "apparent" lumen as one views these elements in transection is measured, rather than the distance across the cell from primary wall to primary wall. Mean number of vessels per group is calculated as a solitary vessel = 1, a pair of vessels in contact = 2, etc. Means presented in Table 1 are based on 20 measurements where possible except for wall thickness and pit diameter figures, which are based on conditions judged to be typical. Pit diameter on lateral walls of vessels is measured in an axial rather than in a lateral direction. Figures have been omitted from some items in Table 1 where neither accurate measurements nor reasonable estimates could be obtained. Because the wood of *Anacampseros* appears rather uniform, a single species has been selected for presentation with respect to quantitative data. For similar reasons, data for only two species of *Lewisia*, which represent the diversity observed within the genus, are in Table 1, although slides of other species were studied and viewed.

ANATOMICAL RESULTS

Growth Rings

Little seasonal fluctuation in diameter of secondary xylem cells is visible in transections of wood of Portulacaceae (Fig. 1, 15, 19, 23, 27). A small amount of cell diameter fluctuation is shown for a *Talinum paniculatum* stem in which two years of secondary xylem accumulation are present (Fig. 10); a little narrowing in the libriform fibers gives evidence that the bottom quarter of the photograph represents the first year of xylem accumulation.

Vessel Elements

The mean number of vessels per group (Table 1, column 1) indicates a moderate to high degree of vessel grouping in Portulacaceae. About equal numbers of solitary and paired vessels are evident in *Calyptrotheca somaliana* (Fig. 22), *Cistanthe guadalupense* (Fig. 17), *Portulacaria afra* (Fig. 19), *Talinella boiviniana* (Fig. 1), *Talinum paniculatum* (Fig. 6) and *T. triangulare* (Fig. 10). A greater degree of grouping (>2 vessels per group) was observed in *Anacampseros marlothii* (Fig. 25), *Ceraria fruticulosa*, *Lewisia rediviva* (Fig. 27, 28), other species of *Lewisia*, and *Hectorella caespitosa* (Fig. 31, 33).

Vessel lumen diameter (Table 1, column 2) averages 30 μm for the family, which is rather narrow compared with vessel diameter in dicotyledons at large (Metcalfe and Chalk, 1950, report the vessel diameter of dicotyledons at large as 94 μm , but their sampling is biased

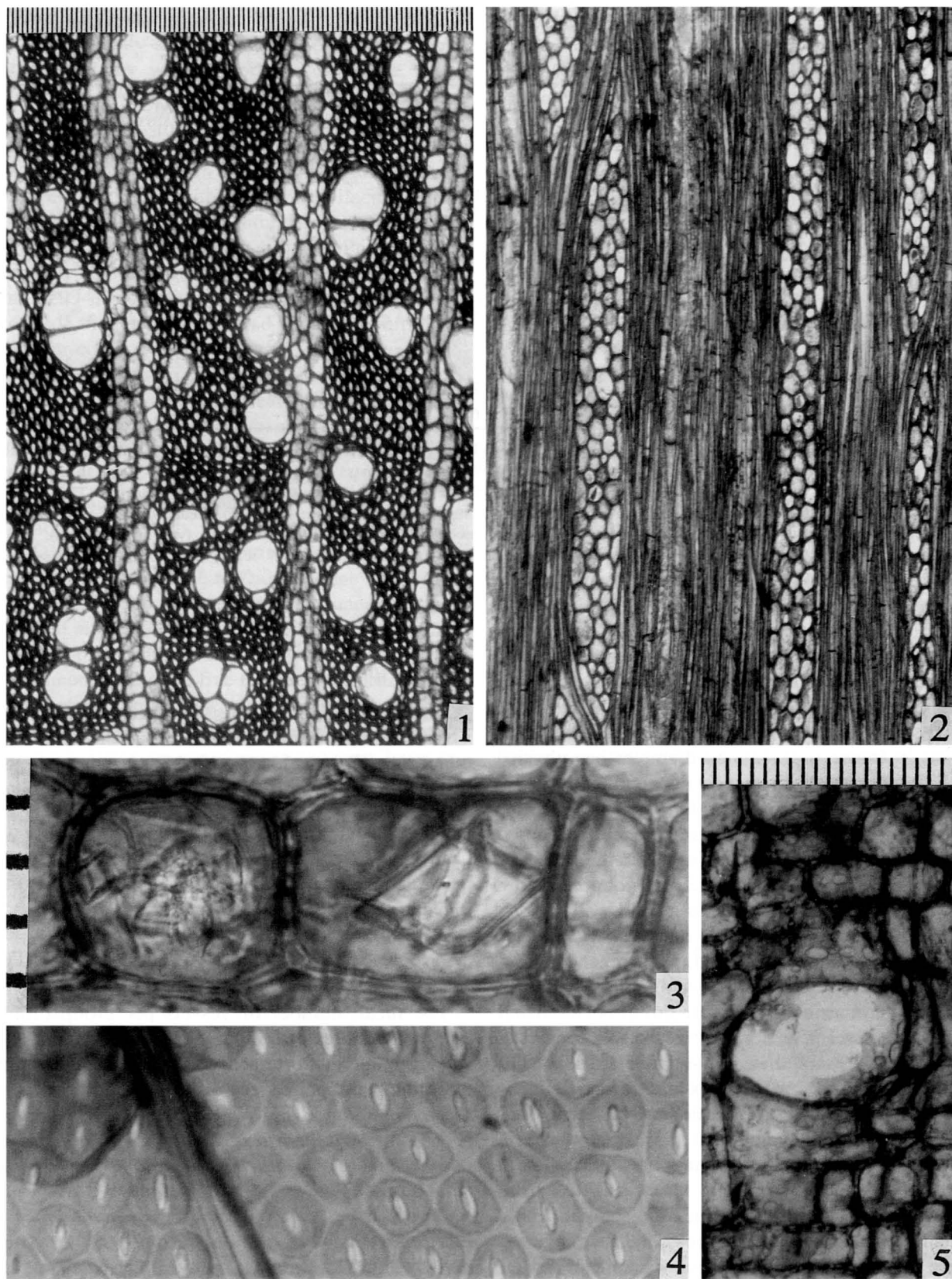


Fig. 1–5. Wood sections of *Talinella boiviniana*.—1. Transection; some vessels are notably wide, many are solitary. 2. Tangential section; rays are wide, tall.—3. Ray cells containing hexagonal crystals, mostly aggregated into druses.—4. Pitting on lateral wall of vessel from radial section; tyloses at upper left.—5. Perforated ray cell from radial section. (Fig. 1, 2, scale above Fig. 1; Fig. 3, 4, scale to left of Fig. 3; Fig. 5, scale above Fig. 5 [divisions in all scales = 10 μ m].)

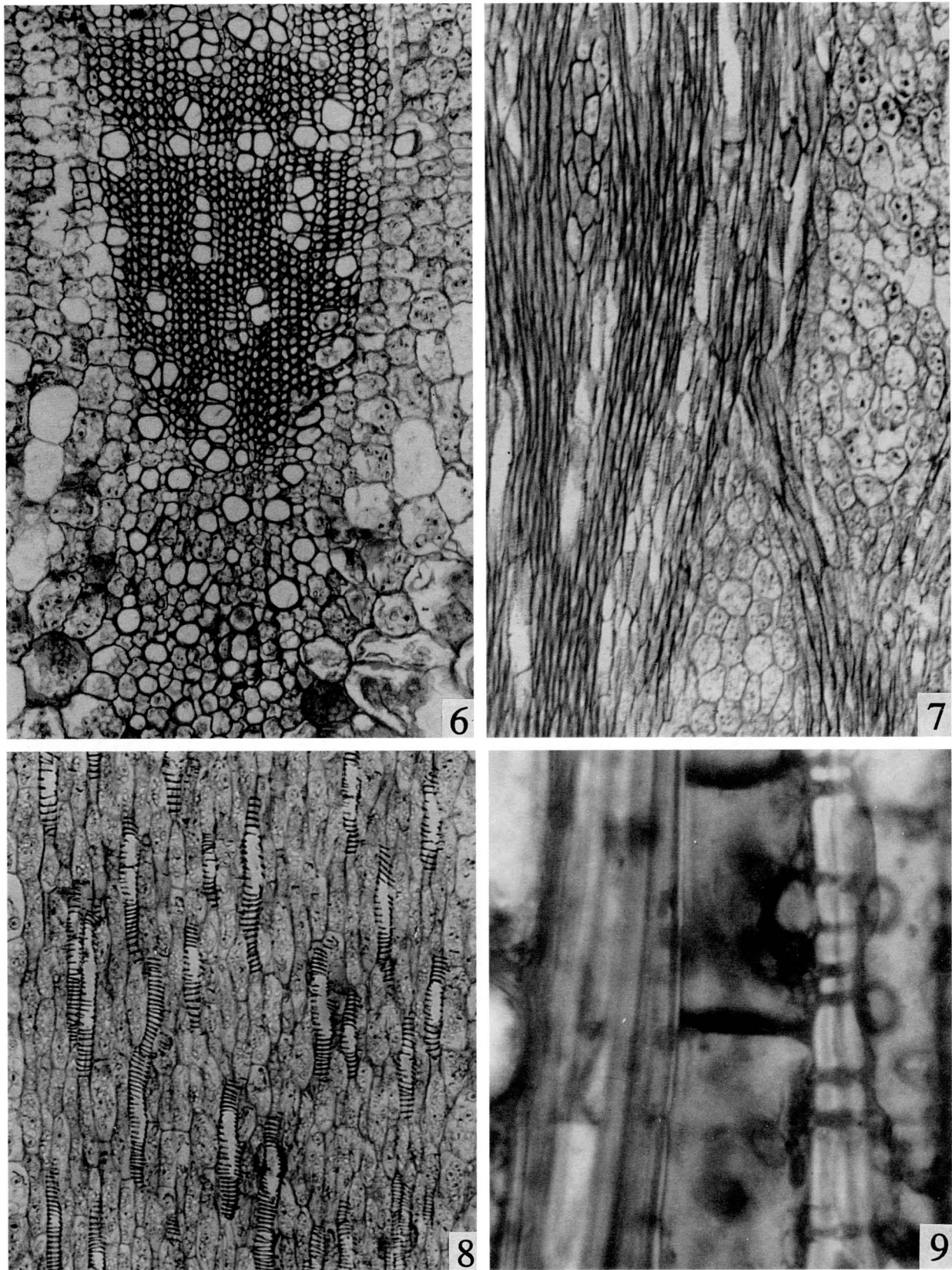


Fig. 6-9. Wood anatomy of *Talinum* and *Talinella*.—6-8. *Talinum triangulare*.—6. Transection; secondary xylem in upper half of photograph has fibers; secondary xylem (and late metaxylem) in lower half of photograph is fiber-free.—7. Tangential section of fibrous wood; rays wide, tall.—8. Tangential section of fiber-free secondary xylem; vessels have mostly scalariform pitting.—9. *Talinella boiviniana*; septate fiber from radial section; two dark transverse septa are present; wall of septate fiber in sectional view, right, has vestigially bordered pits. (Fig. 6-8, scale above Fig. 1; Fig. 9, scale to left of Fig. 3.)

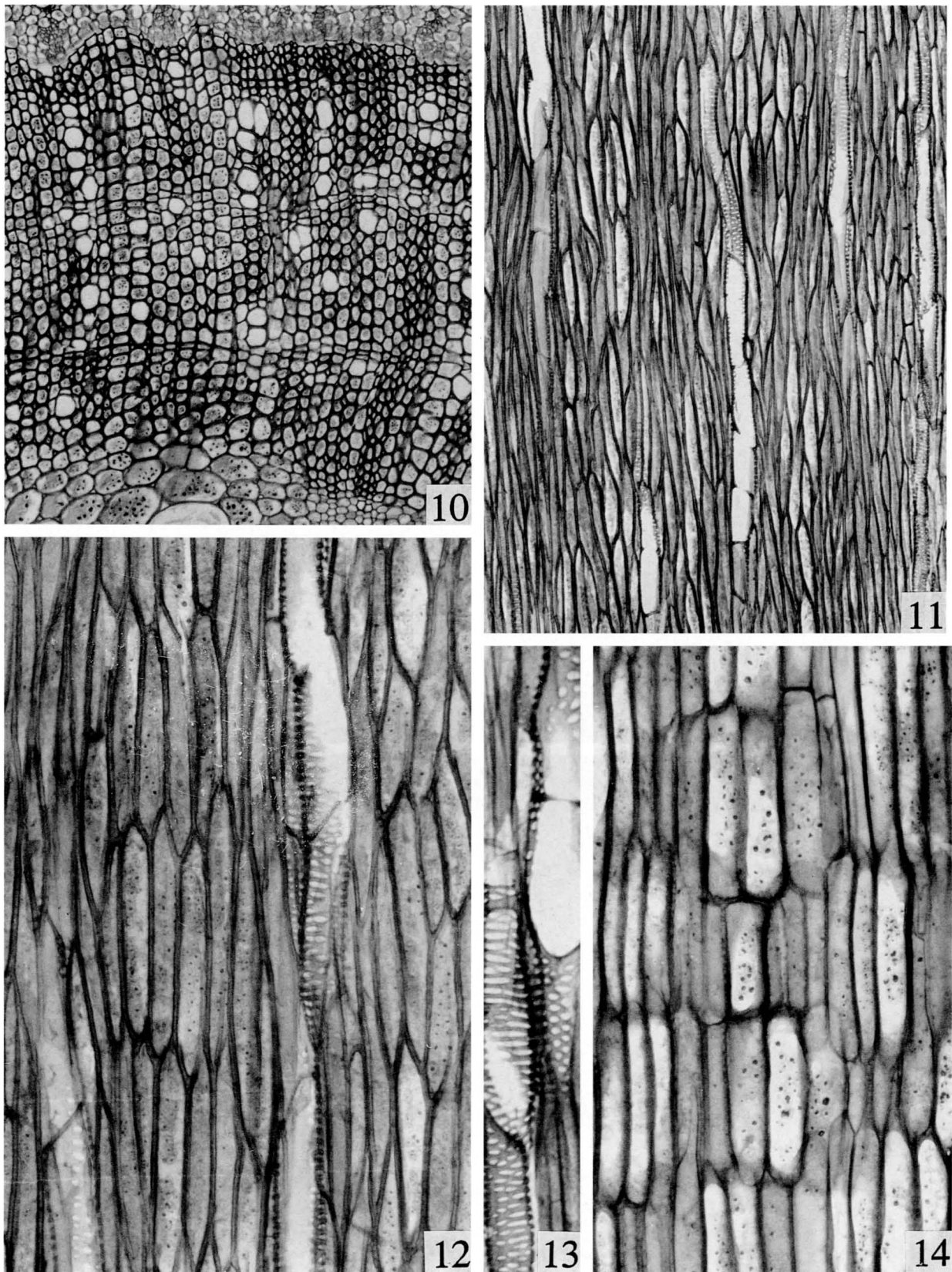


Fig. 10–14. Wood sections of *Talinum triangulare*.—10. Transection, showing a two-year accumulation of secondary xylem.—11. Tangential section, showing rayless condition.—12. Tangential section; the “potential ray area” at left consists of storied fibers; gray spots in fibers are starch grains.—13. Vessels from tangential section; alternate pitting in vessel at right, pseudoscalariform pitting in vessel at left.—14. Radial section, showing starch-filled cells that are intermediate between upright cells and libriform fibers in a “potential ray area.” (Fig. 10, 11, scale above Fig. 1; Fig. 12–14, scale above Fig. 5.)

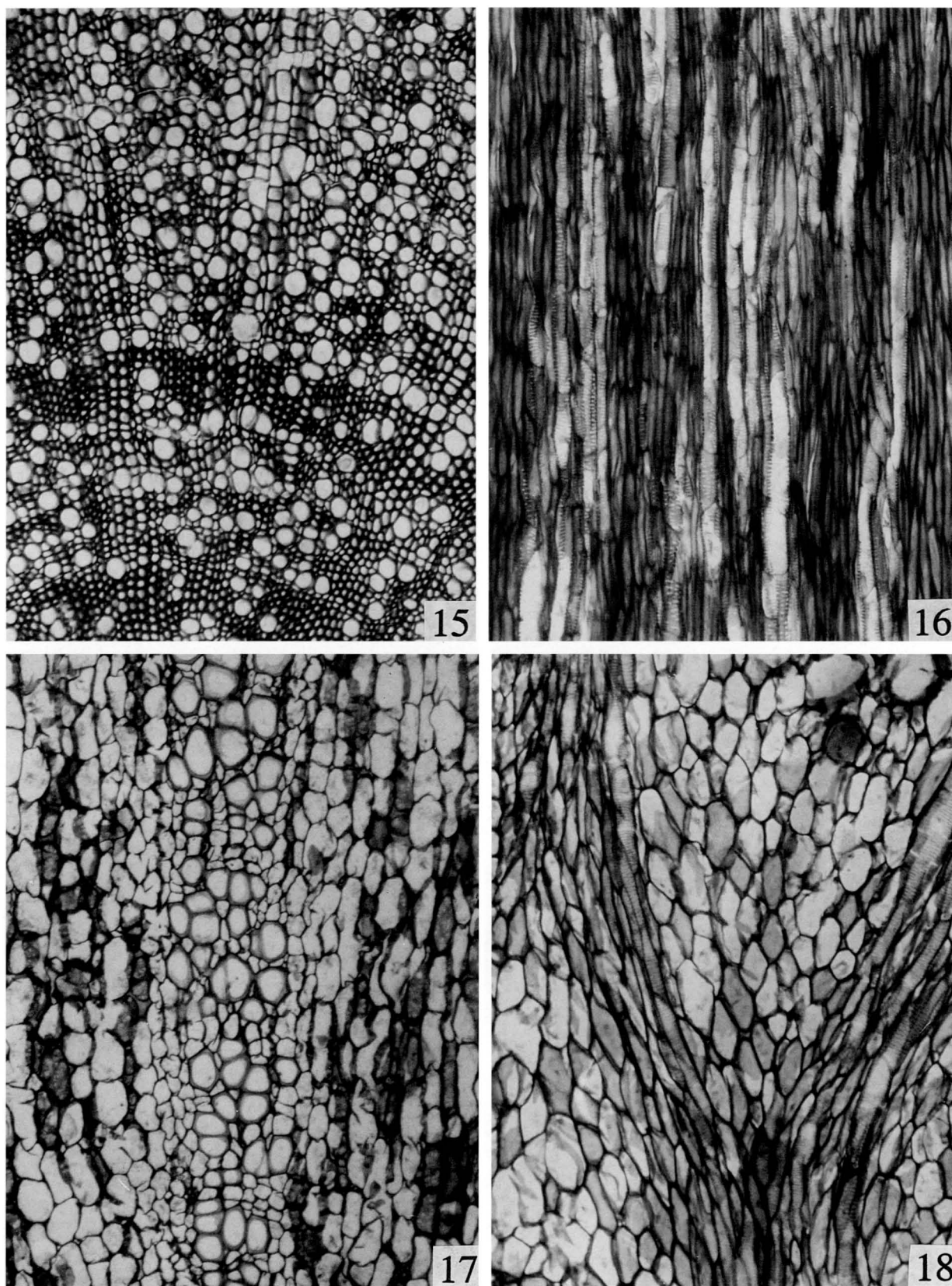


Fig. 15–18. Wood sections of *Talinopsis* and *Cistanthe*.—15–16. *T. frutescens* stem.—15. Transection; vessels narrow; wood begins rayless (bottom), develops rays during secondary growth.—16. Tangential section; libriform fibers vaguely storied.—17–18. *C. guadalupense* stem.—17. Transection; fascicular xylem lacks libriform fibers.—18. Tangential section; rays wide, tall. (Fig. 15–18, scale above Fig. 1).

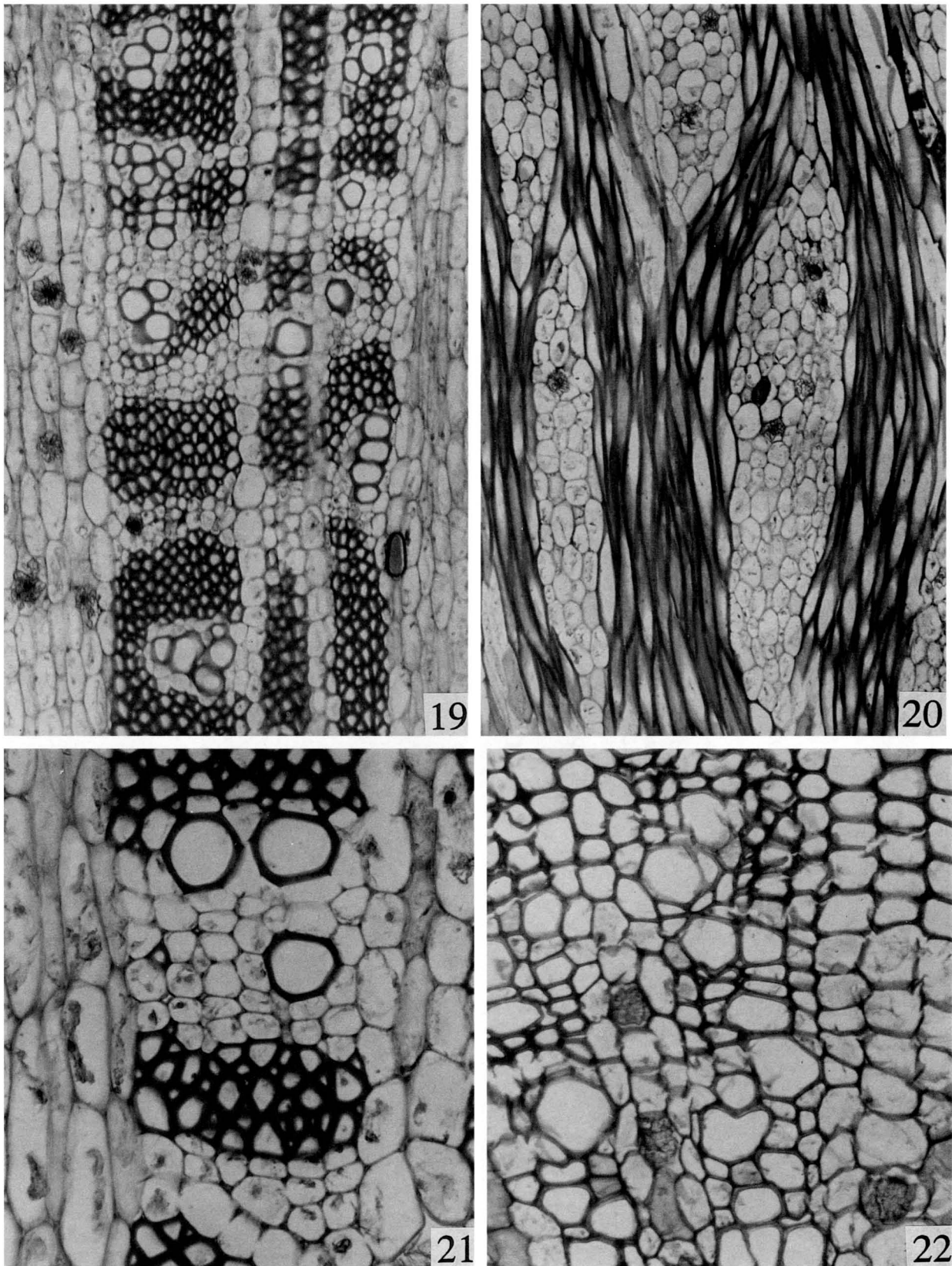


Fig. 19–22. Sections of *Portulacaria* and *Calyptrorhiza*.—19–21. *Portulacaria afra*.—19. Transection; banded axial parenchyma present.—20. Transection portion to show thick walled vessels and libriform fibers and two bands of axial parenchyma.—21. Portion of transection; fibers in tangential bands separated by axial parenchyma.—22. *C. somaliana* transection; libriform fibers thin walled; druses (dark gray) in a few ray cells. (Fig. 19, 20, scale above Fig. 1; Fig. 21, 22, scale above Fig. 5.)

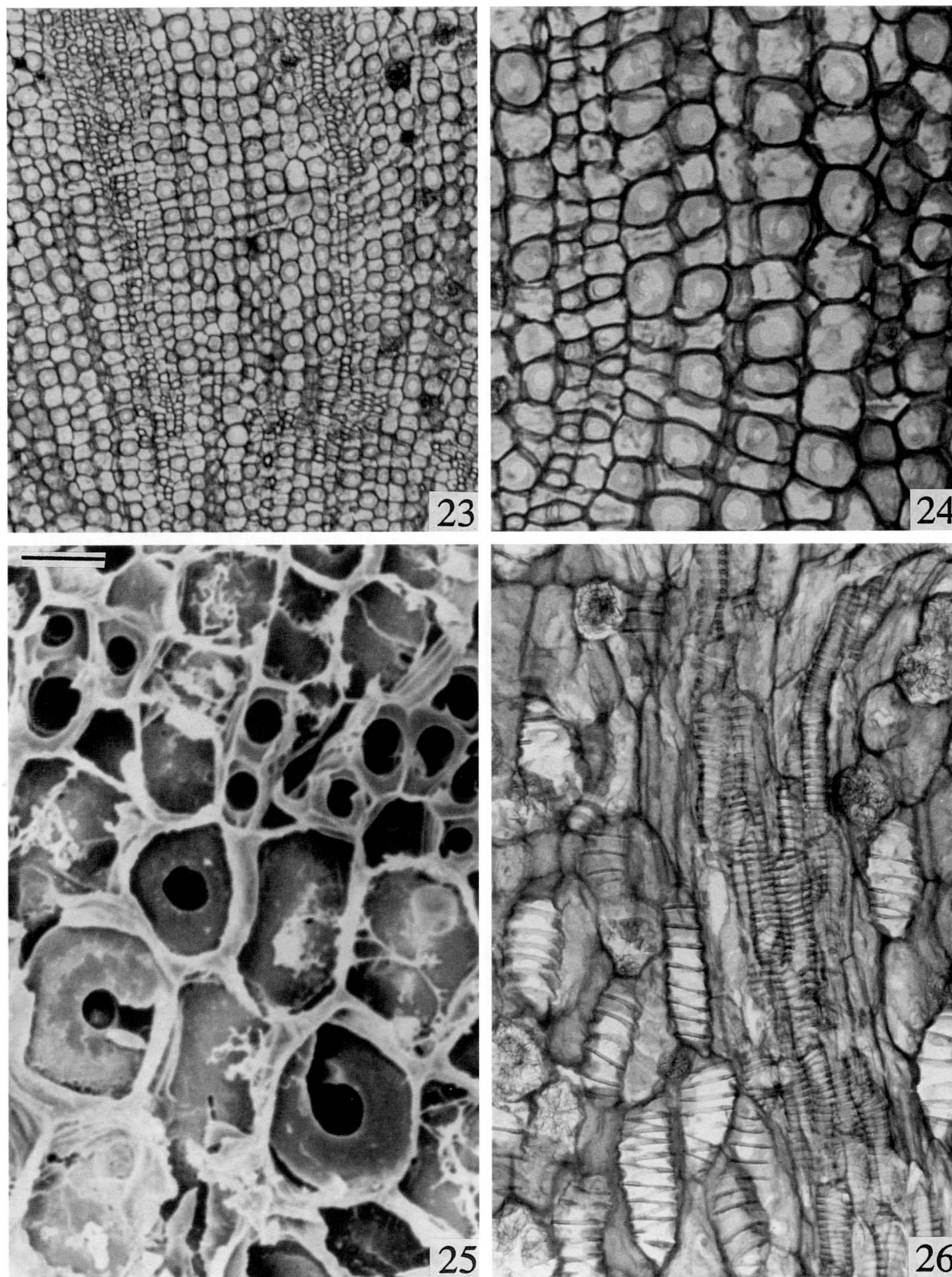


Fig. 23–26. Wood sections of *Anacampseros marlothii*.—23. Transection; two fascicular zones and portions of wide rays are present.—24. Transection portion to show narrow vessels in fascicular portion strip two cells wide from top to bottom of photo near left edge) and rays with wide-helix idioblasts.—25. Transection (SEM photograph) to show wide-helix idioblasts (bottom two-thirds of photo) in a ray and wide-helix vessels in a fascicular area (top third of photo).—26. Tangential section, showing fascicular area containing vessels (top to bottom, to right of center) and, left and right, rays containing wide-helix idioblasts. (Fig. 23, scale above Fig. 1; Fig. 24, 26, scale above Fig. 5; Fig. 25, scale at upper left = 20 μm .)

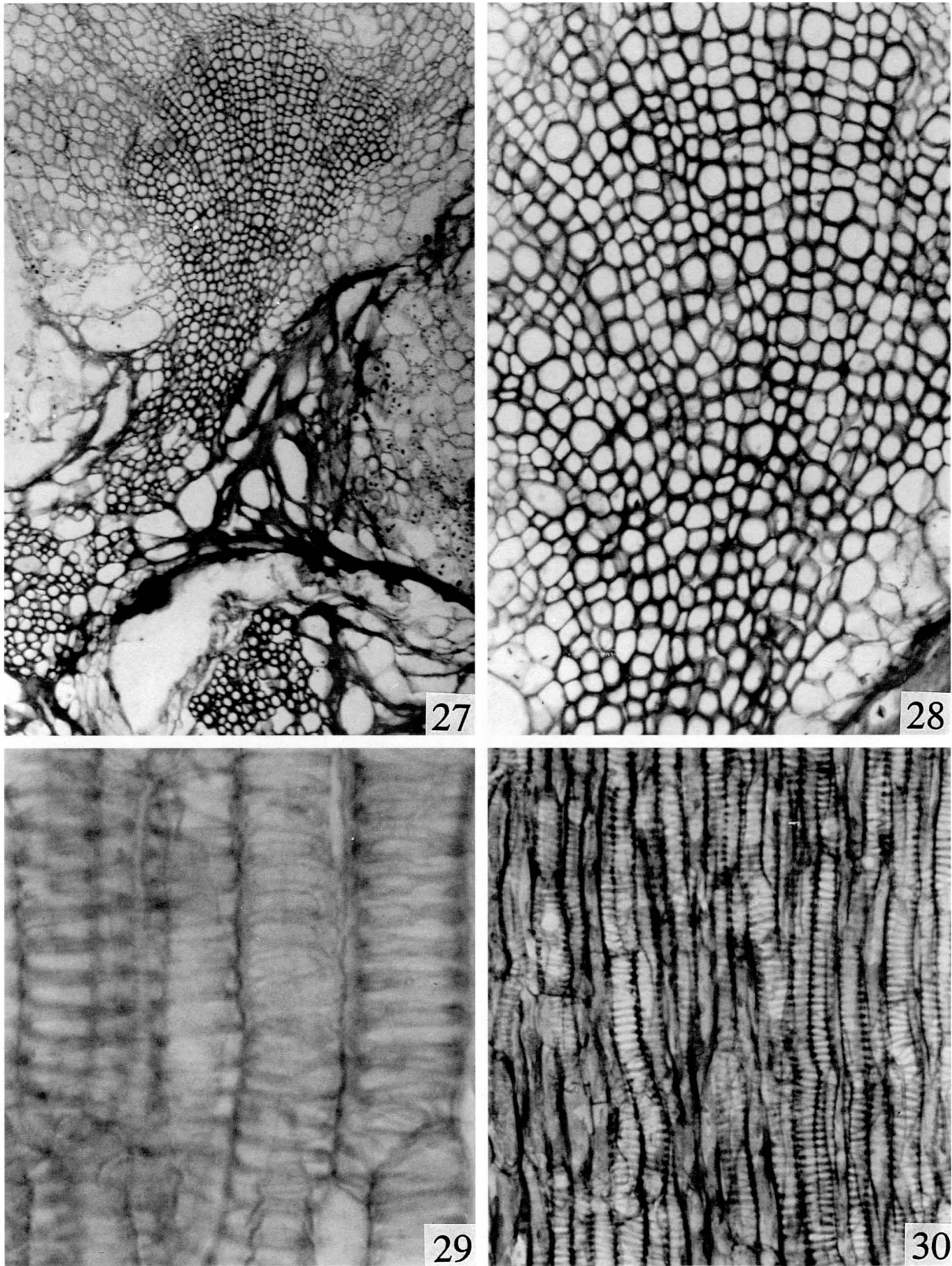
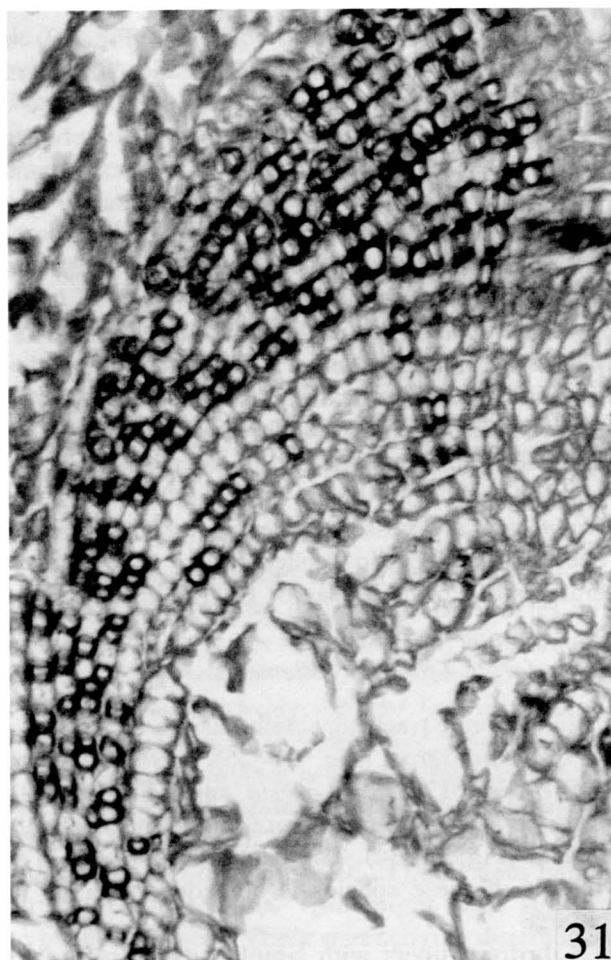
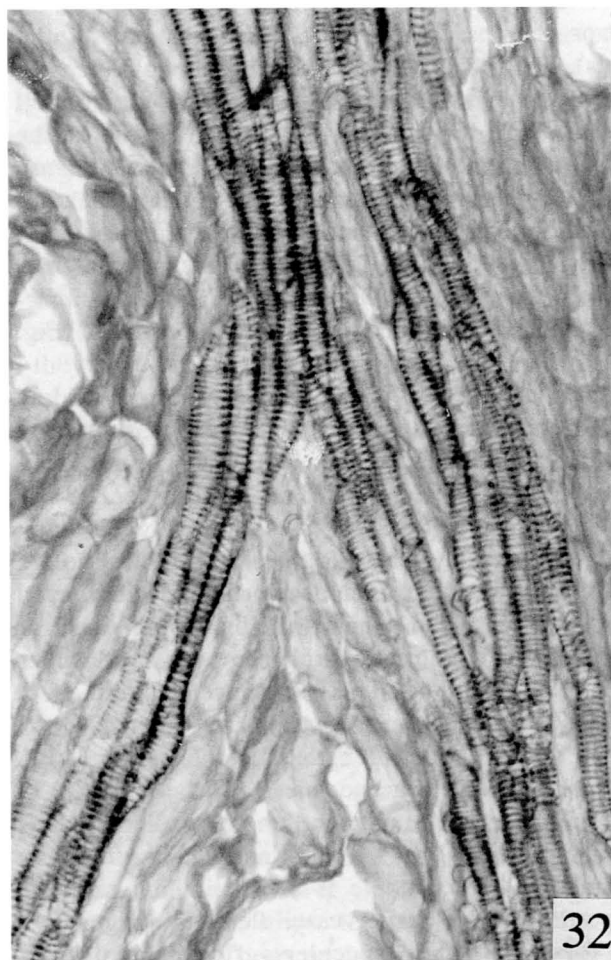


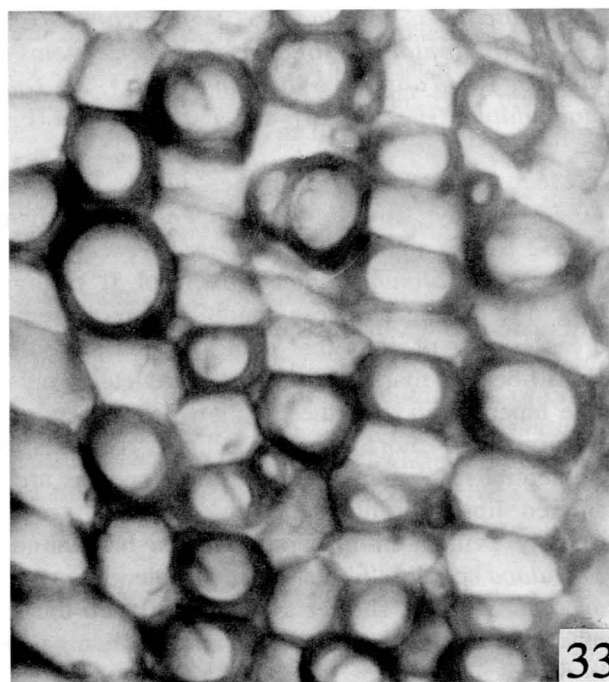
Fig. 27–30. Wood sections of *Lewisia*, from hypocotylar portions of older plants.—27–29. *L. rediviva*.—27. Transection; xylem has broken into several segments as a result of expansion of the vascular core.—28. Transection portion; vessels are narrow, numerous and libriform fibers are absent.—29. Vessels from radial section; secondary wall portions are intermediate between helical thickenings and pseudoscalariform pitting, but closer to helical thickenings.—30. *L. cotyledon* tangential section; uniseriate rays are inconspicuous; libriform fibers are absent. (Fig. 27, scale above Fig. 1; Fig. 28, 30, scale above Fig. 5; Fig. 29, scale to left of Fig. 3.)



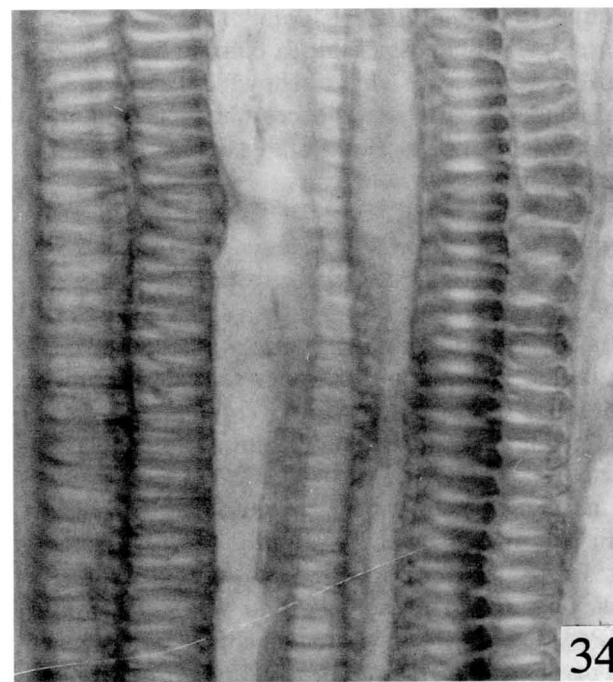
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Fig. 31–34. Wood sections of *Hectorella caespitosa* stems.—31. Transection; a curved wedge of fascicular secondary xylem is present.—32. Tangential section; wide rays and vessels shown.—33. Portion of transection; axial parenchyma is scattered among the narrow vessels; libriform fibers are absent.—34. Vessels from radial section; pattern of secondary wall is intermediate between pseudoscalariform pitting and helical thickenings. (Fig. 31, 32, Scale above Fig. 5; Fig. 33, 34, scale to left of Fig. 3.).

in favor of trees, which characteristically have wider vessels). The species of Portulacaceae that has the widest vessels is *Talinella boiviniana* (Fig. 1); also well above average for the family are the vessels of the markedly succulent species *Cistanthe guadalupense* (Fig. 17) and *Portulacaria afra* (Fig. 19, 21). The transverse sections of other species show relatively narrow vessels (Fig. 6, 10, 15). Extremely narrow vessels characterize *Anacampseros marlothii* (Fig. 23), *Lewisia rediviva* (Fig. 27, 28), and *Hectorella caespitosa* (Fig. 31).

Vessel density (Table 1, column 3) ranges widely within Portulacaceae. Very low density is shown by *Portulacaria afra* (Fig. 19), whereas very high densities occur in the species of *Lewisia* (Fig. 27, 28) as well as in *Hectorella caespitosa* (Fig. 31, 33). Many Portulacaceae have very wide multiseriate rays (e.g., Fig. 7, 18). Rays were included in the areas surveyed for vessel density, but even so, the figures obtained for vessel density were rather high compared with other groups of dicotyledons. This result is related to the fact that in most Portulacaceae vessels are very narrow.

Mean vessel element length (Table 1, column 4) is very short in Portulacaceae (mean for the family, 153 μm). The mean vessel element length for dicotyledons as a whole is 649 μm (Metcalf and Chalk 1950). As noted above, their sample is biased in favor of tree species that tend to have vessel elements longer than those found in shrubs, succulents, or perennial herbs (Carlquist 1975).

Vessel wall thickness (Table 1, column 5) is notably thin in Portulacaceae. This is shown in Figures 1, 6, 10, 15, and 22. A notable exception is provided by *Portulacaria afra* (Fig. 19, 21). Those genera with secondary xylem vessels with thin primary walls to which are attached helices of secondary wall material—*Anacampseros* (Fig. 24, 25, 26), *Lewisia* (Fig. 29, 30), and *Hectorella* (Fig. 33, 34) form a special case that will be discussed later.

Axial diameter of pits on lateral walls of vessels is given in Table 1, column 6. Pits are circular in outline and alternate in *Portulaca* sp. and *Talinella boiviniana* (Fig. 4). Pits are circular and alternate to pseudoscalariform in *Portulacaria afra*, *P. armiana*, *Talinum paniculatum* (Fig. 13), and *T. triangulare*. The size of pits in the two species of *Portulacaria* is notably small. Pits are scalariform and pseudoscalariform on vessels of *Ceraria fruticulosa* and *Talinum triangulare*. Pseudoscalariform pitting exclusively characterizes *Calypotrothea somaliana* and *Cistanthe guadalupense*. Laterally wide annular or helical secondary wall thickening bands characterize vessels of all species of *Anacampseros* (Fig. 25, 26). Helical secondary wall thickening bands that are not so abnormally wide laterally but rather like helical thickening bands seen on primary xylem tracheary elements in most vascular

plants, are seen in *Lewisia cotyledon* (Fig. 30) and *L. rediviva* (Fig. 29). Occasional pseudoscalariform pitting occurs in vessels of *L. rediviva*. There are occasional secondary wall interconnections between the helices in vessels of *Lewisia*; these suggest a transition to pseudoscalariform pitting. The secondary xylem vessels of *Hectorella* have helical thickenings with occasional interconnections of secondary wall material between the helices (Fig. 34).

All vessels of Portulacaceae have simple perforation plates. Although globular cacti have tracheids with wide annular or helical bands of secondary wall material (Boke 1957; Gibson 1973; Mauseth et al. 1995) as well as some vessels, all of the tracheary elements with laterally wide bands in fascicular xylem of *Anacampseros* are vessel elements, and no vascular tracheids or vasicentric tracheids were observed in macerations of Portulacaceae or Hectorellaceae.

Imperforate Tracheary Elements

Imperforate tracheary elements are lacking in stems of *Anacampseros* (Fig. 23–26), *Cistanthe guadalupense* (Fig. 17, 18), *Lewisia* spp. (Fig. 27–30), the roots of *Talinopsis frutescens*, and in the stems of *Hectorella* (Fig. 31–34). The background tissue in which vessels of these species is embedded is axial parenchyma.

Libriform fibers with simple pits characterize *Ceraria fruticulosa*, *Portulaca* sp., *Portulacaria afra* (Fig. 19–21), *P. armiana*, *Talinopsis frutescens* (stems only; Fig. 15, 16), *Talinella boiviniana* (Fig. 1, 2), *Talinum paniculatum* (Fig. 10–14), and *T. triangulare* (Fig. 6–8).

Mean length of libriform fibers (Table 1, column 7) ranges widely: from 744 μm in *Talinella boiviniana* to 232 μm in stems of *Talinopsis frutescens*. In *Portulaca* sp., *Talinum paniculatum*, and *T. triangulare* (Fig. 11, 12), near rayless conditions are present. Ray areas consist of cells that could be considered either short fibers or markedly elongate (vertically) ray cells. The tapering ends of these cells (Fig. 12) suggest libriform fibers more than ray cells. If the cells in the “potential ray” areas of these three species are considered libriform fibers, a dimorphism in ray cells (clearly evident in macerations) can be claimed. In *Portulaca* sp., the “fibers” of the “potential ray areas” average 212 μm , shorter than, but close to the length of vessel elements in that species (232 μm) whereas libriform fibers of the fascicular areas average 352 μm in length.

In the earlier portions of secondary xylem of *Talinum triangulare* (Fig. 6, bottom, Fig. 8) there are no libriform fibers. In later-formed secondary xylem, (Fig. 6, top, Fig. 7), libriform fibers are present.

Mean wall thickness of libriform fibers is shown in

Table 1, column 8. The mean thickness for the family is notably low for the family, and this condition is shown for *Calypotrothea somaliana* (Fig. 22) and *Talinum triangulare* (Fig. 6). Thicker walled libriform fibers are present in *Portulaca* sp., *Portulacaria afra* (Fig. 9–21), and *P. armiana*.

Septate fibers were observed in wood of *Talinella boiviniana* (Fig. 9) and *Talinum triangulare*. Libriform fibers in Portulacaceae typically have very small simple pits. However, very small vestigial borders were observed in at least some sectional views of fibers of *Talinella boiviniana* (Fig. 9), for which fiber-tracheids could therefore be cited. A few tyloses (Fig. 4) were observed in *Talinella boiviniana*.

Axial Parenchyma

The type of axial parenchyma distribution likely basal in Portulacaceae is to be expected in species with less parenchymatization of secondary xylem related to succulence. Such species have scanty vasicentric axial parenchyma. These species include *Talinella boiviniana* (Fig. 1, 2), *Talinopsis frutescens* (stems only: Fig. 15), and *Talinum triangulare* (Fig. 6, top). Vasicentric parenchyma is very scarce in *Talinum paniculatum* and absent in *Portulaca* sp.

In *Portulacaria afra* (Fig. 19, 21), one sees banded paratracheal parenchyma. One might term some of these bands confluent. These parenchyma distributions were also observed in *Ceraria fruticulosa* and *Portulacaria armiana*. In species of Portulacaceae not mentioned above in connection with axial parenchyma, libriform fibers are absent and parenchyma is present instead. This parenchyma type has been termed pervasive (Carlquist 1995b; Carlquist and Boggs 1996). Axial parenchyma cells are also present between vessel groups but are also scattered within vessel groupings (Fig. 6, bottom; Fig. 8, 17, 23, 25, 27, 28, and 33).

Axial parenchyma occurs in strands of two cells in some species (*Ceraria fruticulosa*, *Portulacaria afra*, *P. armiana*, *Talinella boiviniana*, *Talinum paniculatum*, and *T. triangulare*). Strands composed of one or two cells were observed in *Calypotrothea somaliana*, *Lewisia rediviva*, and *Talinopsis frutescens*. Strands of only a single cell characterize *Anacampseros* spp., *Cistanthe guadalupense*, and *Lewisia cotyledon*.

Rays and Raylessness

Vascular rays in secondary xylem of Portulacaceae are all multiseriate (Fig. 2, 7, 18, 20, and 32). Uniseriate rays are so infrequent as to be negligible except in *L. cotyledon howellii*. Multiseriate rays are relatively tall and wide (Table 1, columns 9 and 10). Rays are composed predominantly of upright cells (Table 1, column 11; Fig. 12). Only in *Portulacaria afra* are procumbent cells common in rays (Fig. 20). The stem of

P. afra studied here was from near the base of a relatively large shrub. Because the proportion of procumbent cells increases during secondary growth in most dicotyledons, the abundance of procumbent cells in *P. afra* likely relates to sample diameter. However, even in *P. afra*, upright, square, and procumbent cells are about equally abundant.

As noted above, one can say that *Portulaca* sp. and *Talinum paniculatum* (Fig. 11, 12) have either multiseriate rays composed of fibriform upright cells, or else they have rayless woods in which short libriform fibers occupy potential multiseriate ray areas.

Ray cells have lignified walls in *Talinella boiviniana* (Fig. 2) and *Talinopsis frutescens* stems (Fig. 15, 16). Secondary xylem in the stems of *Calypotrothea somaliana* (Fig. 22) begin with lignified ray cells, but later nonlignified cells are formed in rays. The cells in “potential” ray areas of *Portulaca* sp. and *Talinum paniculatum* have lignified secondary walls. However, the remaining species of Portulacaceae have nonlignified ray cell walls (Fig. 6, 17, 19, 20, 23–26, 28, 31, and 32). In the Portulacaceae that have lignified ray cell walls, cell walls are usually only 1.2 to 1.6 μm in thickness.

Anacampseros is unique among the Portulacaceae studied in possessing tracheoidal idioblasts in rays of the secondary xylem (Fig. 25, lower two-thirds of photograph; Fig. 26, lower left plus two idioblasts near right margin). These cannot be termed tracheids because they occur idioblastically and thus do not form continuous vertical series that would represent a conductive tissue. Longisections of the wide bands of these idioblasts show that the wide bands of secondary wall material are annular rather than helical, and that the bands are only slightly bordered. In contrast, the wide helical bands in vessels of fascicular secondary xylem of *Anacampseros* are clearly bordered. The bands on the walls of the ray idioblasts are much wider laterally than those of the fascicular xylem (Fig. 25, 26). SEM study shows that primary walls of the tracheoidal idioblasts in rays of *Anacampseros* are not perforated.

Perforated ray cells were observed in *Talinella boiviniana* (Fig. 5). This is a first report of this cell type for Portulacaceae.

Cambial Variants

Some authors have considered that secondary xylem in which very narrow fascicular areas are separated from each other by wide rays constitutes an unusual cambial condition, although one can argue this is merely one expression of a continuum. In any case, the roots of *Talinopsis frutescens* show very narrow fascicular areas and very wide rays. In older plants of *Lewisia*, the secondary xylem cylinder often becomes

separated into segments of irregular shape (Fig. 27). This could be regarded as a cambial variant. Similar conformations of secondary xylem may be seen in *Hectorella* (Fig. 31). However, the cambial variant so characteristic of Chenopodiaceae and some other families of Caryophyllales, successive cambia producing concentric bands of vascular tissue separated by conjunctive tissue, is absent in the Portulacaceae studied.

Storied Structure

Storied structure is not characteristically present in any of the Portulacaceae studied. However, some storying in the fibriform ray cells of *Talinum paniculatum* is evident (Fig. 12), and vague storying may be seen occasionally in fibers of a few other species, such as *Talinopsis frutescens* (Fig. 16).

Crystals and Cell Contents

Druses in rays were observed in *Anacampseros marlothii* (Fig. 23, right; Fig. 24, left) and all other species of *Anacampseros* and in *Calyptrorhiza somaliana* (Fig. 22), *Ceraria fruticulosa*, *Cistanthe guadalupense*, *Portulacaria afra* (Fig. 19, 20), *P. armiana*, *Talinella boiviniana* (Fig. 3), and *Talinum triangulare*. Druses in axial parenchyma were observed in *Calyptrorhiza somaliana*. Crystals hexagonal in outlines were observed in addition to druses in ray cells of *Talinella boiviniana*.

Dark colored idioblasts are present in rays of *Ceraria frutescens*, *Cistanthe guadalupense*, *Portulacaria afra* (Fig. 19, 20), and *P. armiana*.

Starch was observed in rays of *Lewisia cotyledon*, *Talinella boiviniana*, *Talinum paniculatum* (Fig. 14), and in libriform fibers of *Portulaca* sp., *Talinum paniculatum* (Fig. 14) and in axial parenchyma of *Lewisia cotyledon*.

ECOLOGICAL AND HABITAT CONCLUSIONS

Portulacaceae as a whole are succulent. Genera and species of the family differ in degree of stem succulence, but all can be considered to have at least a moderate degree of leaf succulence. Stem succulence in dicotyledons is often correlated (with exceptions) with increased parenchymatization within the secondary xylem. In the present study, *Talinella* is the only genus that does not illustrate parenchyma presence greater than would be expected in wood of a typical woody dicotyledon. If one imagines the wood of ancestors of Portulacaceae to be relatively nonsucculent and to have wood features in accordance with nonsucculent habits, *Talinella* would represent wood that should be like that of ancestral types in its scanty vasicentric parenchyma, its absence of other types of axial parenchyma and its relatively narrow rays.

Stems of *Talinopsis frutescens* have wood similar to the wood of *Talinella*. However, roots of *Talinopsis frutescens* are notably succulent and feature maximal modification for water storage: wide rays, narrow fascicular areas, and complete substitution of parenchyma for fibers in the fascicular areas. The differences between the stems and roots of *Talinopsis* represent extremes in lack of parenchymatization and maximal parenchymatization, respectively. *Portulaca* sp. and *Talinum paniculatum* have wood similar to that of *Talinopsis* stems, but with a close approach to raylessness; these species show a minimal parenchymatization. The absence or near-absence of axial parenchyma in *Portulaca* sp., and *Talinum paniculatum* likely correlates with their near-raylessness, since this correlation is all but universal in rayless dicotyledon woods.

In *Portulacaria*, increased parenchymatization is evident in the bands of apotracheal axial parenchyma and in the somewhat increased volume of rays, which, like the axial parenchyma have thin, nonlignified cell walls.

In *Cistanthe guadalupense* and *Anacampseros* spp., rays are wide and have thin walled cells, and fascicular areas are fiber-free, just as in the roots of *Talinopsis*. *Cistanthe* and *Anacampseros*, therefore, represent maximal degrees of parenchymatization related to succulence, and this can be said of *Lewisia* also.

The wide-banded tracheoidal idioblasts of rays of *Anacampseros* resemble the vascular tracheids of globular cacti (figured by Boke 1957; Gibson 1973; Mauseth 1993; Mauseth and Plemons 1995; Mauseth et al. 1995). These idioblasts in *Anacampseros* doubtless function as water storage cells that contract as water is withdrawn from them, but do not collapse because of the bands of secondary wall material. Such idioblasts have not been reported in rays of cacti, but the wide-helix vascular tracheids of globular cacti are doubtless similar in function. Mauseth et al. (1995) suggest that cacti with wide-band tracheids are related to resistance to cavitation, but there is very little evidence as yet about negative pressures in cacti that have the wide-band tracheids or about negative pressures in other cacti. If narrow vessels are more resistant to cavitation (and thereby likely indicative of high negative pressures), as shown by Hargrave et al. (1994), one might think succulents to have narrow vessels if cavitation resistance is of significance for succulents. However, succulents as a whole have rather wide vessels: a mean of 72 μm in a sampling of succulents, as opposed to a mean of 29 μm in a sampling of desert shrubs (Carlquist 1975, p. 206). Wide-helix tracheary elements or tracheoidal idioblasts have been reported by Arnott (1960) in leaves of the fern *Botrychium*, by Carlquist (1960) in the leaves of *Achlyphila* (Xyridaceae or Abolbodaceae), and in the leaves of *Setchellanthus* (S. Carlquist and R. Miller, unpublished), a

monotypic genus currently referred to Capparaceae for which data in support of separate familial status are soon to be published. One can hypothesize some degree of expansion and contraction with respect to changes in water availability in all of these, but not so markedly in *Achlyphila* and *Botrychium* leaves. Idioblasts, tracheids, or vessel elements with the laterally wide rings or helices of secondary wall material, therefore, have probably evolved several times independently, and although they may be an ideal response for water storage, obviously their apparent scarcity in vascular plants argues for the effectiveness of other mechanisms (chiefly parenchyma cells without such thickening bands) as water storage devices. When one views transections of wide-band idioblasts, vessels, or tracheids with a light microscope, they may at first glance appear to be thick-walled fibers, so that instances of their occurrence may well have been overlooked. Gibson (1977) regarded the wide-band vascular tracheids of cacti as homologs of libriform fibers. They might more logically be regarded as homologs of vessel elements with wide helical bands, such as those that occur in fascicular secondary xylem of *Anacampseros*.

Vessels in *Lewisia* and *Hectorella* mostly have helical thickening bands transitional to pseudoscalariform pitting. This often takes the form of bands interconnecting helices. However, the secondary wall pattern is clearly longitudinally extensible and shrinkable, much as with the wide-banded vessels of *Anacampseros*. Worth noting with respect to habit is that *Lewisia* is acaulescent, so that libriform fibers would be of little selective value for support of stems. The cushion-plant habit of *Hectorella* likewise renders mechanical strength as conferred by fibers of minimal value. *Anacampseros* stems, if upright, are short, and in many species the stems are prostrate or else caudexlike; thus, the absence of libriform fibers in *Anacampseros* is understandable. *Cistanthe guadalupensis* can become a kind of succulent subshrub, but the heavy branches tend to trail somewhat on the ground rather than stand upright, so one can correlate absence of libriform fibers with the growth form in that species. *Ceraria*, *Portulacaria*, and *Talinopsis* have stiff, upright stems, so presence of libriform fibers in those genera correlates with habit. Interestingly, *Ceraria*, *Cistanthe*, *Portulacaria*, and *Talinopsis* stems have vessel walls thicker than the family average. Because the habits of these genera (with the exception of *Cistanthe*) feature libriform fibers and an upright habit (only moderately so in *Cistanthe*), the thickness of vessel walls may contribute to mechanical strength of stems. The main value of thick, lignified walls on vessels may be in contributing a secondary source of mechanical strength to plants. There has been little commentary

in the literature on reasons why vessels should have relatively thick, lignified secondary walls.

The presence of pseudoscalariform pitting in vessels of so many Portulacaceae may be related to lack of selection for a maximally strong vessel wall pattern. More rigid wall patterns, such as a wall bearing alternate circular bordered pits, are to be expected in woodier dicotyledons. The woodiest species in the present study, *Talinella boiviniana*, illustrates that pattern most clearly.

The rayless or near-rayless wood of *Portulaca* sp. and *Talinum paniculatum* suggests increased woodiness in this species compared with their ancestors. This interpretation is based on the trend established earlier (Carlquist 1970) for herbaceous phylads with a few woody representatives that are secondarily woody. This also applies to groups in which ray cells are predominantly upright, as in Portulacaceae (Carlquist 1962). Although basal representatives of Portulacaceae may have been woody, most of the species in the present study have woods characteristic of secondarily woody or less woody ("woody herb") dicotyledons.

Rays, axial parenchyma, and even libriform fibers are rich in starch in some of the Portulacaceae studied. Starch storage may be correlated with rapid production of flowers and fruits during the short wet season experienced by most succulent plants. Starch is likely present in wood cells of more species of Portulacaceae than reported here.

Abundant druses and (in *Talinella boiviniana*) hexagonal crystals are likely defenses for water-rich tissues against herbivores. The dark colored idioblasts may also have this significance.

Wood xeromorphy of Portulacaceae does not conform to the expectation one might have, based on earlier data for stem succulents. A sample of stem succulents (Carlquist 1975, p. 206) has means as follows: vessel diameter (wall included), 72 μm ; vessels per mm^2 , 64.2; vessel area per mm^2 , .087 mm^2 ; vessel element length, 259 μm ; Mesomorphy index (Table 1, column 12, defined in Table 1), 290. Figures for Portulacaceae are quite different. Mean vessel diameter for Portulacaceae as a whole (30 μm) is about half that in the 1975 succulent sample, as is vessel element length in the family (153 μm), and vessel density in the family (219 per mm^2) more than three times the value in the 1975 sample. The Mesomorphy value of Portulacaceae (60) is one-fifth that of the 1975 sample. If one examines the data of Table 1, one sees that very xeromorphic quantitative wood features characterize *Anacampseros* and *Lewisia* and account for some of the difference between Portulacaceae and the sampling of succulents used in Carlquist (1975). This is evident primarily in the Mesomorphy Ratio (Table 1, column 12), which is based on vessel diameter, vessel element length, and number of vessels per mm^2 of transection,

but also in the number of vessels per group (column 1). Thus, Portulacaceae show that a family which consists almost wholly of succulents has wood considerably more xeromorphic than wood of the average succulent. Xeromorphy and succulence are not mutually exclusive strategies in wood of dicotyledons. The wide rays and the presence of pervasive axial parenchyma in Portulacaceae are characteristics of wood of succulents.

SYSTEMATIC CONCLUSIONS

In recent systems, Portulacaceae have been closely grouped with Didiereaceae, Basellaceae, and Cactaceae into the suborder Portulacineae of Caryophyllales (Thorne 1983; Cronquist and Thorne 1994). Hectorellaceae belong to this alliance, whether treated within Portulacaceae or as a separate family. Portulacineae are a natural group according to the pollen data of Nowicke (1996), gene sequence data of Rettig et al. (1992), and the phenetic and cladistic results of Rodman (1994). The data of Downie and Palmer (1994) are not distant from this treatment. Studies using DNA have not considered Hectorellaceae because of lack of material, but the placement of that family in Portulacineae seems secure on the basis of other data sets.

The wood of Portulacineae is now relatively well known, with the exception of Basellaceae, which I am currently studying. Data on wood of Didiereaceae are available (Rauh and Dittmann 1970). Gibson (see papers by him listed in Gibson 1994) and Mauseth et al. (1995) have offered extensive data on Cactaceae. Conclusions about Portulacineae with respect to wood data must await study of other Caryophyllales.

If one compares wood of Portulacaceae and Hectorellaceae to that of Cactaceae and Didiereaceae, one finds very close agreement provided that one selects less-succulent species of Portulacaceae and woodier species of Cactaceae. Woods of *Talinella* and *Talinum triangulare* are very similar to woods of Didiereaceae and columnar Cactaceae. More-succulent Portulacaceae, with highly parenchymatized secondary xylem and secondary xylem with pseudoscalariform lateral wall pitting on vessels, show modification with respect to particular types of habits.

Within Portulacaceae, a few distinctive wood features seem of systematic significance. Notably small lateral wall pits occur on vessels of *Portulacaria* and contrast with vessel pits in the remaining Portulacaceae. *Ceraria*, grouped closely with *Portulacaria* by Carolin (1987) and Hershkovitz (1991), has much larger pits. However, the wood of *Ceraria* does resemble closely that of *Portulacaria* in having thick-walled libriform fibers in fascicular xylem and in having druses and dark-colored idioblasts in rays.

The distinctive wide-band idioblasts in rays of *An-*

acampseros differentiated that genus from others in the present study. These idioblasts are morphologically similar in appearance to the vascular tracheids in fascicular xylem of globular cereoid cacti. However, as noted above, the mode of occurrence of these cells is different in the two families. Moreover, *Anacampseros* does not appear to be basal within the schemes of Carolin (1987) or Hershkovitz (1991), further lessening the possibility that the two cell types are a sympleiomorphy. Unless new evidence comes to light, the wide-band idioblasts of *Anacampseros* rays and the wide-band tracheids of fascicular xylem of globular Cactaceae are nonhomologous and independently derived. Other wood anatomical features that differentiate genera include the small pit size of *Portulacaria* (both species) and the large pit size of *Talinella*. *Talinella* is the only genus which has hexagonal crystals in rays; it also has druses, found in most genera of Portulacaceae.

Gibson (1994) suggests dark-staining mucilage cells of Portulacaceae and Didiereaceae are a synapomorphy. These idioblasts have been recorded in *Ceraria*, *Cistanthe*, and *Portulacaria*. However, *Cistanthe* is distant from *Ceraria* and *Portulacaria* in the schemes of Carolin (1987) and Hershkovitz (1991). Moreover, dark-colored idioblasts have been reported from roots of *Saponaria officinalis* L. of the Caryophyllaceae (Pax and Hoffmann 1934), a species not close to Portulacaceae or Didiereaceae in phylogenies proposed thus far. Further study of dark-colored idioblasts and mucilaginous idioblasts within Caryophyllales is definitely needed. Cells corresponding to these terms have likely been overlooked in a number of species, if only because mucilaginous contents may be removed by some fixation and microtechnical methods commonly in use.

The diverse wood patterns of Portulacaceae clearly show that relatively few distinctive wood features are of use in infrafamilial systematics: most distinctive wood features relate closely to habit and ecology. The wood of *Lewisia* contains fiber-free fascicular xylem and numerous narrow vessels with secondary wall thickenings that are helical or transitional between helical and pseudoscalariform. These features doubtless relate to the distinctive succulent roots (and perhaps hypocotyls) of *Lewisia*, and thereby the wood of the genus may not indicate as isolated a position as its distinctive appearance might suggest. In the schemes of both Carolin (1987) and Hershkovitz (1991), *Lewisia* occupies a basal position, relatively far from the remainder of the family. The wood of *Hectorella* is surprisingly like that of *Lewisia*, but that similarity may relate to habit and xeromorphy (in the case of *Hectorella*, xeromorphy likely relates to frost rather than drought) rather than to phylogenetic closeness to Portulacaceae (note: the wood of *Hectorella* is from

stems, whereas the *Lewisia* wood is from hypocotyl—upper root regions). In any case, wood of *Hectorella* does not offer any reasons for placing that genus in a position far from Portulacaceae.

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