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Wood Anatomy of Calyceraceae with Reference to Ecology, Habit, and Systematic Relationships

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ABSTRACT

Qualitative and quantitative data are presented for secondary xylem of 14 species of four genera of Calyceraceae; root wood is studied for acaulescent perennials and one annual. The wood anatomy of most species of *Calycera* has character states identical to those seen in wood of most Asteraceae (including phylads of Asteraceae thought to be basic in that family). Goodeniaceae have two features (tracheids, diffuse parenchyma) more primitive than corresponding conditions in Asteraceae and Calyceraceae according to traditional criteria. Diversity in wood anatomy within Calyceraceae is explainable in terms of adaptation to particular ecological conditions. Although woods of the family as a whole are xeromorphic, most *Calycera* species show few adaptations to extreme xeromorphy. The highest degree of wood xeromorphy occurs in species of relatively high elevation or high latitude. The presence of pseudoscalariform pitting, with transitions to helical-banded secondary xylem vessels, very much like those of primary xylem, in *Boopis graminea* and *Nastanthus* spp., coupled with absence of libriform fibers (replaced by axial parenchyma) are probably related to expansion and contraction of the wood in response to fluctuation in moisture availability.

Key words: Asteraceae, Asteridae, ecological wood anatomy, Goodeniaceae, pseudoscalariform vessel pitting, storage in roots.

INTRODUCTION

Although the family Calyceraceae contains about 50 species in six genera (Hansen 1992; DeVore and Stuessy 1995), little has been reported concerning wood anatomy of the family. Wood structure has been described for a single species, *Calycera sessiliflora* (Carlquist 1983). Very likely, the limited accumulation of secondary xylem in most species may have caused this neglect. Although Höck (1894) said that the family consists of herbs, perennials, and subshrubs, all of the species could be characterized as herbaceous. The woodiest of the family have perennial stems (and roots) of relatively limited duration, with a xylem cylinder a few mm in thickness at most. The woodiest species are not woody subshrubs in the sense of the subshrubby species of *Erica* or *Vaccinium,* which are miniature shrubs; rather, the larger Calyceraceae appear merely as herbs that develop secondary xylem for a limited number of years.

Calyceraceae show a diversity of habits. For example, *Acicarpha tribuloides* is an annual that in cultivation may persist into a second season, although little secondary xylem is added during the second year. *Nastanthus,* on the other hand, is an acaulescent rosette perennial that has secondary xylem in the relatively succulent root. *Calycera calcitrapa* is reported to be 0.7 m tall (specimen label, *A. C. Gibson and A. T. Hunziker 3050,* RSA); such a species has woodiness maximal for the family. Some species, such as the beach species *Acicarpha spathulata,* are perennials with stems that produce adventitious roots, and thus the older portions of the stems do not add much secondary xylem once newer stem portions are rooted.

The diversity of habit in the family, although limited, is of great interest with respect to wood anatomy. In predominantly herbaceous families such as Asteraceae, wood anatomy tends to correspond to the habits of the component species rather than to the taxonomic system.

Ecology and habit are intimately interconnected, and so relating wood anatomy clearly to one of these concepts or the other is difficult. The acaulescent rosette perennial habit of *Nastanthus andina* is an ad-

aptation to high latitude and high elevation. Presumably, frost damage is minimized by this habit, although the root must serve for storage of water and photosynthates. Field observations show that pith of *Nastanthus* serves to store water (DeVore, unpublished data). The secondary xylem of *N. andina* must be analyzed with respect to both ecology and habit simultaneously. The secondary xylem of the root of *N. andina* can be compared to that of the stems of species of *Calycera* only when these factors are taken into account. In cladistic terms, the various expressions of secondary xylem in Calyceraceae would likely appear as a rich assemblage of autapomorphies. with relatively few symplesiomorphies or synapomorphies. Concepts concerning classification and phylogeny within Calyceraceae, whether based on macromorphology (Hansen 1992) or DNA data, taking macromorphology also into account (DeVore unpublished), have shifted considerably in recent years.

The relatively small number of species sampled here prevents any effective analysis of wood anatomy in terms of systematic comparisons within the family. However, data on wood anatomy are very pertinent in comparing the relationships of Calyceraceae. The families considered close to Calyceraceae in traditional systems include Goodeniaceae and Asteraceae. The results of Michaels et al. (1993) and Cosner et al. (1994) pair Goodeniaceae and Calyceraceae on a branch basal to Asteraceae. Obviously, wood anatomy of Asteraceae and Goodeniaceae merits comparison with that of Calyceraceae.

MATERIALS AND METHODS

Material of all species studied came from herbarium specimens except for that of *Acicarpha tribuloides*, which was cultivated. Roots and stems of that species were preserved in 50% aqueous ethanol. The amount of stem or root wood present on herbarium specimens of particular species dictated the choice of taxa to be examined: if little more than primary xylem is present on a specimen, its xylem is not really comparable to secondary xylem one or more mm in thickness. Possibly field work devoted primarily to finding plants with a maximum amount of secondary xylem would have yielded samples with more secondary xylem than represented in some of our specimens, but likely not very much more. As noted in Table 1, stems were used except for *Nastanthus andina* and *N. polycephala*, in which plants are acaulescent and the upper portions of taproots were selected for study of secondary xylem. Basal stem portions transitional to hypocotyl were selected in *Boopis graminea* and *Calycera sympaganthera*.

In order to prepare sections, all materials were treated with ethylene diamine, infiltrated in a tertiary butyl alcohol series, embedded in paraffin, and sectioned on a rotary microtome according to the methods of Carlquist (1982). Sections were stained in a safranin-fast green combination. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

The means for vessels per group, vessels per mm², vessel diameter, vessel length, and libriform fiber length (Table 1) are based on 25 measurements with few exceptions. Figures for vessel pit diameter, vessel wall thickness, and libriform fiber wall thickness are based on conditions judged to be typical. Vessels per group is calculated based on a solitary vessel = 1, a pair of vessels in contact = 2, etc. Anatomical terms are based on the IAWA Committee on Nomenclature (1964), except for vasicentric tracheids, which are defined as in Carlquist (1985). The term "pervasive" parenchyma is used here, as it was by Carlquist and Boggs (1996), to denote secondary xylem in which imperforate tracheary elements are absent or infrequent, and in which, therefore, vessels are embedded in a background of axial parenchyma (e.g., Fig. 12, 18). In longitudinal section, such axial parenchyma where adjacent to rays simulates upright ray cells (which are common in Calyceraceae). Thus, ray height and width cannot be accurately determined in Calyceraceae with pervasive axial parenchyma, nor can the presence of uniseriate rays be detected. This accounts for absence of quantitative data on rays for some of the species in Table 1.

Collection and locality data for the species studied are as follows: *Acicarpha spathulata* R. Br., *Fosberg 48520* (POM), low beach ridge, Restinga de Jacarepaguá, south of Lagos Marapendi, Est. Guanabara, Brazil; *A. tribuloides* Juss., *Carlquist 8172* (SBG), cultivated in Santa Barbara from seeds provided by Copenhagen Botanic Garden; *Boopis anthemoides* Juss., *G. Tell 27-XI-1962* (RSA), Alrededores Sierra de la Ventana, Partido de Tornquist, Prov. Buenos Aires, Argentina; *B. graminea* Phil., *DeVore 1249* (OS, OSH, T), grazed, damp fields in Valle de las Nieblas, Region del Biobio, Prov. de Nuble, Chile; *Calycera calcitrapa* Griseb., *Gibson & Hunziker 3050* (RSA), km 147 about 55 km SE of Villa Union, Argentina; *C. crassifolia* (Miers) Hicken, *DeVore & Delucci 1833* (OS, OSH, T), back dune area, Cabo San Antonio to the south of Buenos Aires, Prov. de Buenos Aires, Argentina; *C. eryngioides* Remy, *DeVore 1303*, procumbent annual, ski slope in grazed area at Lagunillas, Prov. Santiago, Chile; *C. herbacea* Cav., *DeVore 1216* (OS, OSH, T), disturbed wet area, Laguna del Maule, 2100 m, Region de Maule, Prov. Talca, Chile; *C. sessiliflora* Phil. Argentina, *Burkart 18510* (RSA); *C. spinulosa* Gill ex Miers, *DeVore 1728* (OS. OSH, T), sandstone carenitel outcrop, 1300 m, 3 km SE of Potrerillos, Depto. Tupangato, Prov. Mendoza, Argentina; *C. sympaganthera* (R. & P.) Kuntze, *DeVore 1284* (OS, OSH,

Table 1. Wood features of Calyceraceae.

Species	Collection	1 VG	2 VM	3 VD	4 VL	5 VW	6 PD	7 FL	8 FW	9 MH	10 MW	11 UR	12 ME
Acicarpha spathulata	Fosberg 48250	1.50	301	16	180	2.6	4	231	2.6	>500	4.6	—	9
A. tribuloides	Carlquist 8172 Stem	1.73	428	18	256	2.5	4	417	3.0	>500	7.5	—	11
	Carlquist 8172 Root	1.32	246	29	134	1.8	4	195	2.5	733	18.0	—	11
Boopis anthemoides	Cabrera 14777	1.52	374	25	222	2.1	2.5	235	3.2	?	?	?	15
B. graminea	DeVore 1249	3.08	892	11	210	2.2	5	338	5.5	?	?	?	2.6
Calycera calcitrapa	Gibson 3050	1.54	177	27	214	2.2	3	355	2.6	915	3.4	157	33
C. crassifolia	DeVore 1833	1.77	194	37	216	2.2	4	364	3.0	1317	3.8	177	41
C. eryngioides	DeVore 1303	1.84	364	24	227	2.4	5	352	3.0	458	2.8	71	15
C. herbacea	DeVore 1206	>20	458	28	201	2.5	5	?	3.0	>500	6.0	?	12
C. sessiliflora	Burkart 18510	1.84	182	48	304	2.5	5	608	2.5	902	3.4	217	80
C. spinulosa	DeVore 1728	2.06	287	28	227	2.6	5	302	4.4	?	5.5	?	22
C. sympaganthera	DeVore 1284	2.48	775	11	210	2.6	4	?	3.0	?	?	?	3.0
Gamocarpha alpina	DeVore 1250	5.55	2170	9	108	2.4	5	—	—	—	?	?	0.5
Nastanthus andina	DeVore 1728	5.50	784	16	164	2.6	6	—	—	—	?	?	3.4
N. polycephala	Werdermann 345	15.6	1326	9	228	2.6	6	—	—	?	?	?	0.2
Calyceraceae, averages		4.79	572	21	206	2.4	4.7	340	3.2	>500	4.0	155	18.3

Key to columns: 1 (VG), mean number of vessels per group; 2 (VM), mean number of vessels per mm^2; 3 (VD), mean lumen diameter of vessels, μm; 4 (VL), mean vessel element length, μm; 5 (VW), vessel wall thickness, μm; 6 (PD), axial diameter of pits on lateral vessel walls, μm; 7 (FL), mean libriform fiber length, μm; 8 (FW), libriform fiber wall thickness, μm; 9 (MH), mean multiseriate ray height, μm; 10 (MW), mean multiseriate ray width, cells; 11 (UR), mean uniseriate ray height, μm; 12 (ME), Mesomorphy Ratio (vessel lumen diameter times vessel element length divided by number of vessels per mm^2). Author citations and collection data in Materials and Methods. ? = measurements not feasible; — = structure not present.

T), burnt area of *Araucaria* and *Nothofagus* forest, 1 km down the road from Piedra del Aguila, Prov. de Malleco, Chile; *Gamocarpha alpina* (Poepp. ex. Less.) H. V. Hansen, *DeVore 1250* (OS, OSH, T), top of ridge behind hotel at Termas de Chillan, 2000 m, Region del Biobio, Provincia de Nuble, Chile; *Nastanthus andina* (Miers) H. V. Hansen, *DeVore 1723* (OS, OSH, T), alpine terminal moraine, Los Hormones, Prov. de Mendoza, Chile; *Nastanthus polycephala* (Phil.), *Werdermann 1345* (UC), Peru.

RESULTS

Growth Rings

There is little or no evidence of growth rings in *Acicarpha tribuloides* (stem, Fig. 1), *Calycera calcitrapa* (Fig. 14), and *C. crassifolia* (Fig. 16). Very likely in material of these species, the secondary xylem represents a single year's accumulation. In the root of *A. tribuloides* (Fig. 3), the small fiber-free zone of vessels at the outside of the secondary xylem represents secondary xylem formed during a second season. In *Boopis anthemoides* (Fig. 5, 6), the appearance of the transection suggests two growth rings and a portion of a third; the last is characterized by smaller, less abundant vessels. A shift from fiber-free to fibrous secondary xylem in *B. graminea* (Fig. 10) may represent secondary xylem from two successive years. In the root illustrated for *Nastanthus andina*, three successive growth rings are present; these growth rings are characterized by noticeably wider vessels in earlywood. In *Calycera herbacea*, there is a shift from wood composed of narrow vessels (Fig. 18, bottom fifth of photograph) to wood with wide vessels (top four-fifths of photograph). Without knowing the growing conditions, interpretation of this sequence is uncertain, but wood from two successive years is likely present.

Smaller vessels at the periphery of the wood samples were observed in *Acicarpha tribuloides* (root, Fig. 3, top), *Calycera calcitrapa*, *C. crassifolia*, *C. herbacea*, and *C. spinulosa*. Narrower vessels terminating secondary xylem accumulation characterize annnuals and short-lived perennials in Asteraceae (Carlquist 1966). This condition is likely common in annuals of various families, and represents adaptation to lowered moisture availability as the plant ceases growth.

Quantitative Vessel Features

None of the genera studied has characteristically solitary vessels (Table 1, column 1): minimal degree of vessel grouping is seen in the genera *Acicarpha* (Fig. 1, 3). The range in the family is from 1.32 to more than 20 vessels per group. Examples of extensive vessel grouping are shown by *Nastanthus andina* (Fig. 12) and *Calycera herbacea* (Fig. 18). Intermediate degrees of vessel grouping are illustrated for *Boopis anthemoides* (Fig. 5, 6), *B. graminea* (Fig. 10), *C. calcitrapa* (Fig. 14), and *C. crassifolia* (Fig. 16).

Vessel density (Table 1, column 2) ranges widely (177 to 2170 vessels per mm^2), but the lower limit recorded for the family is relatively high compared with, say, dicotyledonous rain forest trees, which often have fewer than 30 vessels per mm^2. The relatively
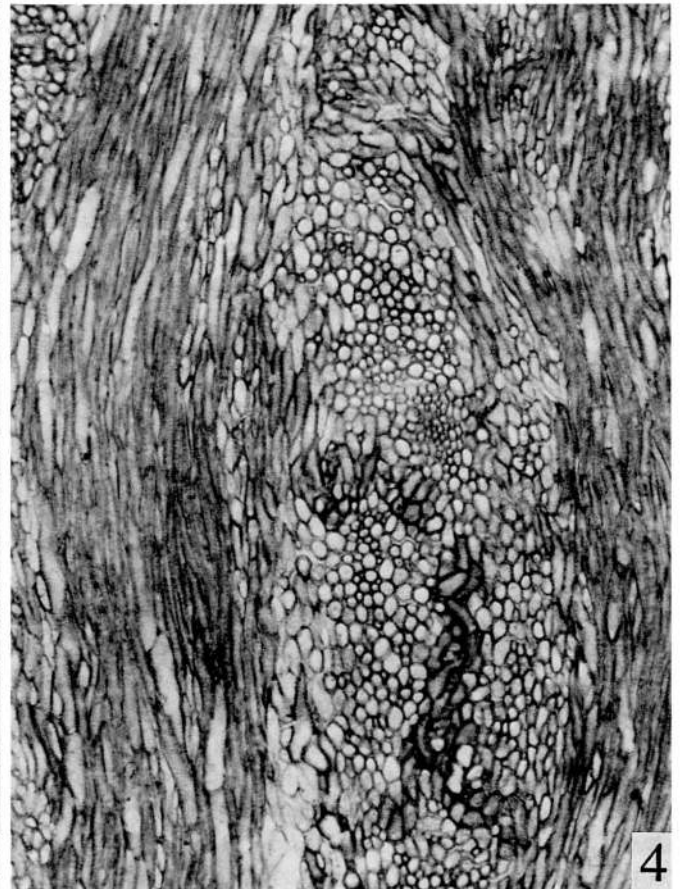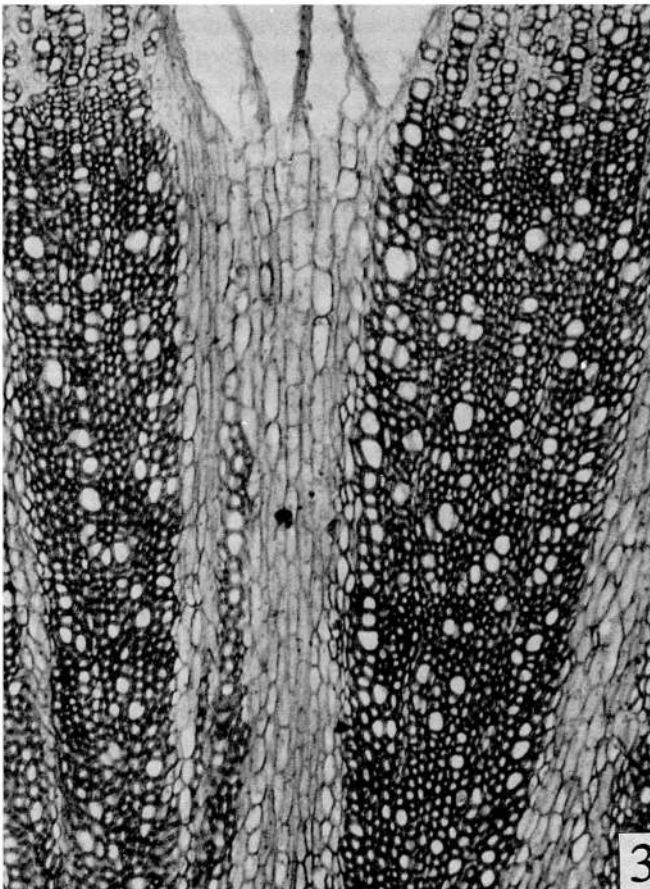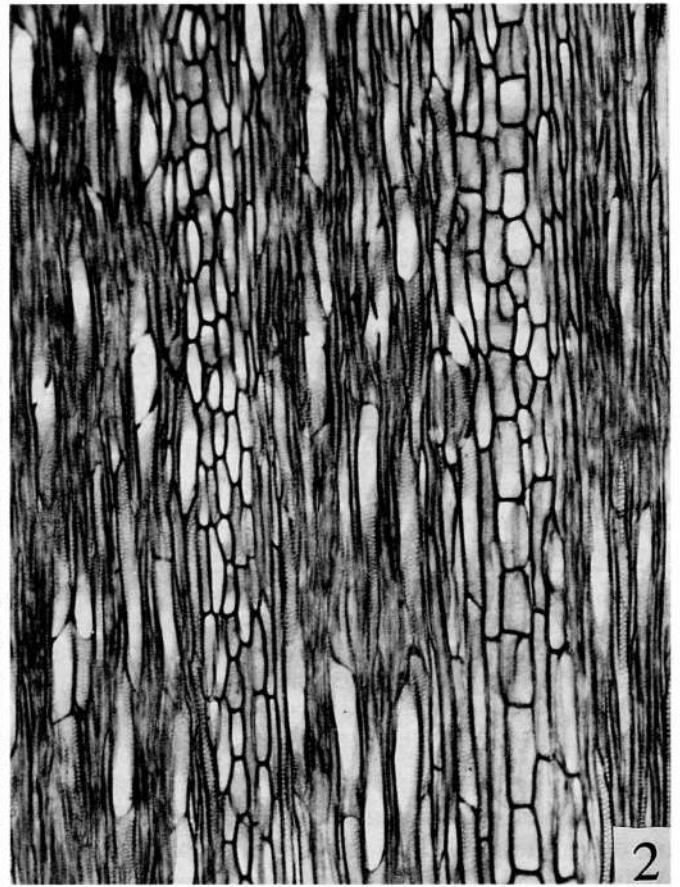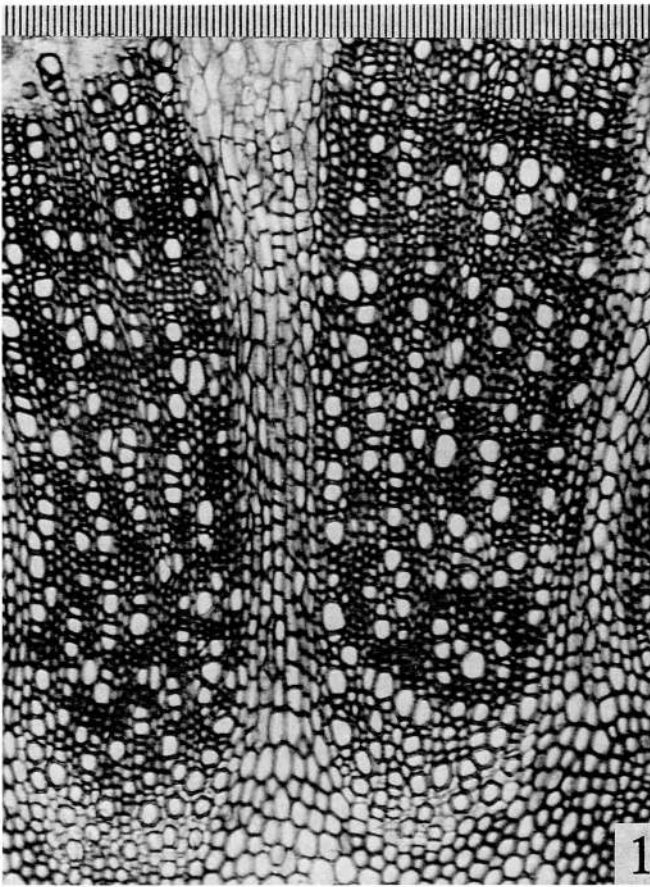
great vessel density in Calyceraceae is illustrated in Figs. 1, 3, 4, 5, 10, 12, 14, 16, and 18.

Vessel lumen diameter (Table 1, column 3) is often considered to be inversely proportional to vessel density. Calyceraceae offer no notable exceptions to this. Vessel lumen diameter is Calyceraceae as a whole is very narrow: the figure for Asteraceae as a whole is 46 μm; the figure for dicotyledons as a whole (admittedly, a sampling biased toward trees) is 88 μm (Metcalfe and Chalk 1950). These comparisons are estimates based on subtracting twice the likely mean vessel wall thickness from the outside vessel diameter, which is what is given in those publications. Despite the approximations of these comparison figures, the dramatically narrow mean lumen diameter of vessels of Calyceraceae is evident.

The mean length of vessels of Calyceraceae (Table 1, column 4) is 206 μm, which is not notably shorter than the mean for Asteraceae, 235 μm (Carlquist 1966). However, the mean vessel element length for dicotyledons as a whole is 600 μm (Metcalfe and Chalk 1950). Despite the shortness of mean vessel element length in Calyceraceae, there is a marked range in means within the family, from 108 to 304 μm.

Vessel wall thickness (Table 1, column 5) is relatively uniform in the family. This is of interest because pitting types of vessels vary so widely in the family.

The axial diameter of pits in vessel walls ranges widely, from 2.5 to 6 μm. The widest pits with respect to axial dimension occur in *Nastanthus,* in which pseudoscalariform pits are so elongate in a lateral dimension that helical bands like those characteristic of primary xylem vessels are achieved in some vessels.

Qualitative Vessel Features

All vessel elements in Calyceraceae have simple perforation plates. Species that have vessels surrounded by libriform fibers have alternate pits circular to oval in outline (*Acicarpha* spp., *Boopis* spp., *Calycera crassifolia, C. eryngioides,* and *C. sympaganthera.* Alternate pitting is shown for *C. crassifolia* (Fig. 21, above), but in this species, laterally elongate pits also occur (elsewhere on Fig. 21). Such laterally elongate pits are also illustrated for *C. herbacea* (Fig. 20). These laterally elongate pits are termed pseudoscalariform here, because the ends of the pits do not correspond to cell faces, as they do in true scalariform pits. Pseudoscalariform pits in dicotyledons at large often co-occur with alternate pits, as in Fig. 21, and likely

represent a form of alternate pitting in which lateral elongation of alternate pits has occurred. Pseudoscalariform pits are common in predominantly herbaceous phylads. In the Calyceraceae studied, pseudoscalariform pitting is common in *Boopis graminea, Calycera calcitrapa, C. eryngioides, C. herbacea, C. sessiliflora, c. spinulosa, Gamocarpha alpina, Nastanthus andina,* and *N. polycephala.* In Calyceraceae in which vessels are embedded in pervasive parenchyma, pseudoscalariform pits are so elongate that the wall patterns approach helical bands like those in primary xylem; a few true helical elements may also be present, as in *N. andina* (Fig. 13) and *N. polycephala.*

Faint helical thickenings on a secondary wall (not to be confused with the helical bands mentioned above), sometimes known as "tertiary helical thickenings" were observed on the vessel walls of *Boopis anthemoides* (Fig. 9).

Imperforate Tracheary Elements

Calyceraceae have two types of imperforate tracheary elements: vasicentric tracheids and libriform fibers. Vasicentric tracheids were observed in *Acicarpha tribuloides* (root and stem) and *Boopis anthemoides.* Vasicentric tracheids are notably abundant in the latter species.

Libriform fibers in Calyceraceae have small simple pits. Length of libriform fibers (Table 1, column 7) in the family is about 1.5 times the length of vessel elements.

Libriform fiber wall thickness (Table 1, column 8) is relatively thin. In many families of dicotyledons (e.g., arboreal Fabaceae), libriform fiber wall thickness is twice the thickness of the walls the fibers accompany. Typical conditions for libriform fibers in Calyceraceae are illustrated in Figs. 1, 3, 5, 6, 10 (above), 14, and 16. Libriform fibers were not observed in *Calycera sympaganthera, Gamocarpha alpina, Nastanthus andina,* and *N. polycephala.* Few libriform fibers were observed in *Calycera herbacea* (Fig. 18), *C. spinulosa,* and *C. sympaganthera.* In the last-named species, libriform fibers were present in a few bands near the periphery of the wood sample; the material of this species was derived from a stem-root transition region. The transection of wood of *Boopis graminea* shows a fiber-bearing cylinder (Fig. 10, above) surrounding a fiber-free core (Fig. 10, below).

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Fig. 1–4. Wood sections of *Acicarpha tribuloides.*—1–2. Stem.—1. Transection, showing limited thickness of secondary xylem accumulation.—2. Tangential section; rays are all multiseriate with upright cells, extensions of primary rays.—3-4. Root—3. Transection; nonfibrous secondary xylem at extreme top was formed during a second season.—4. Tangential section; very wide rays, procumbent cells common. (Fig. 1–4, scale above Fig. 1 [divisions = 10 μm].)
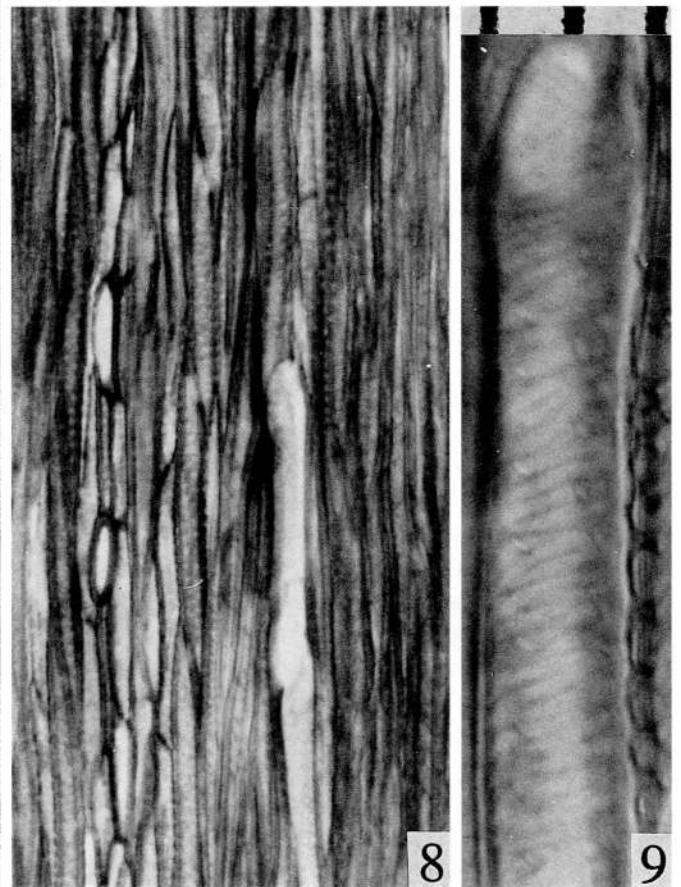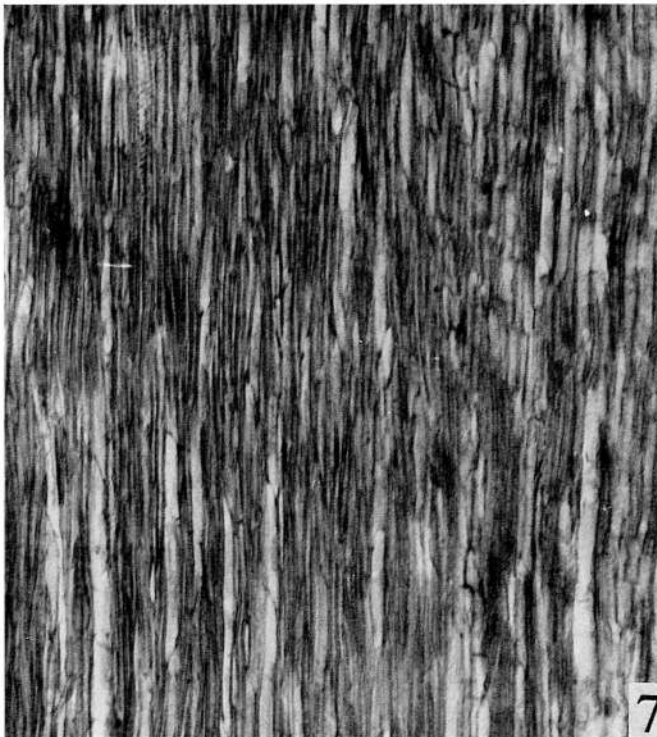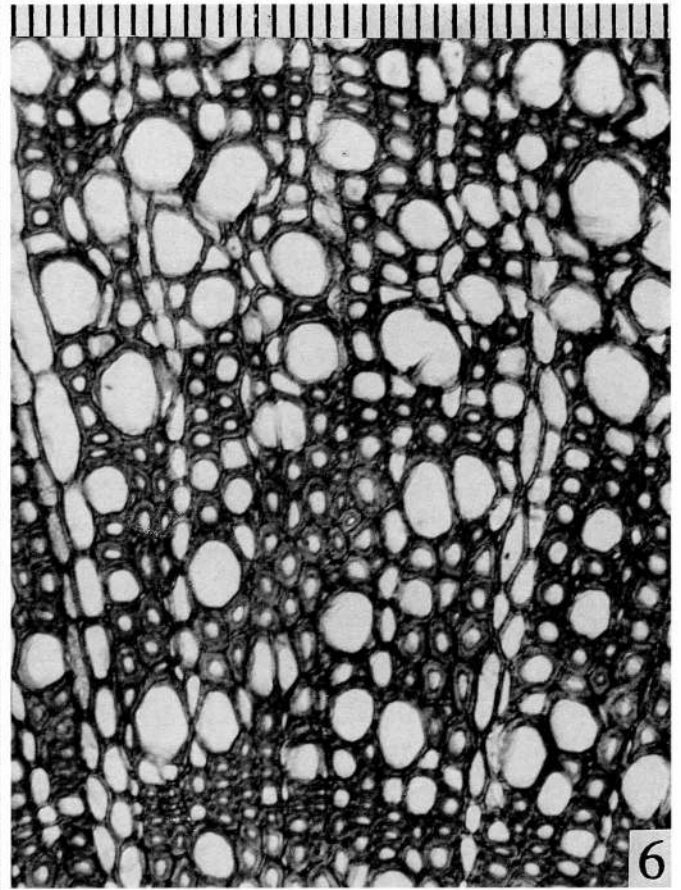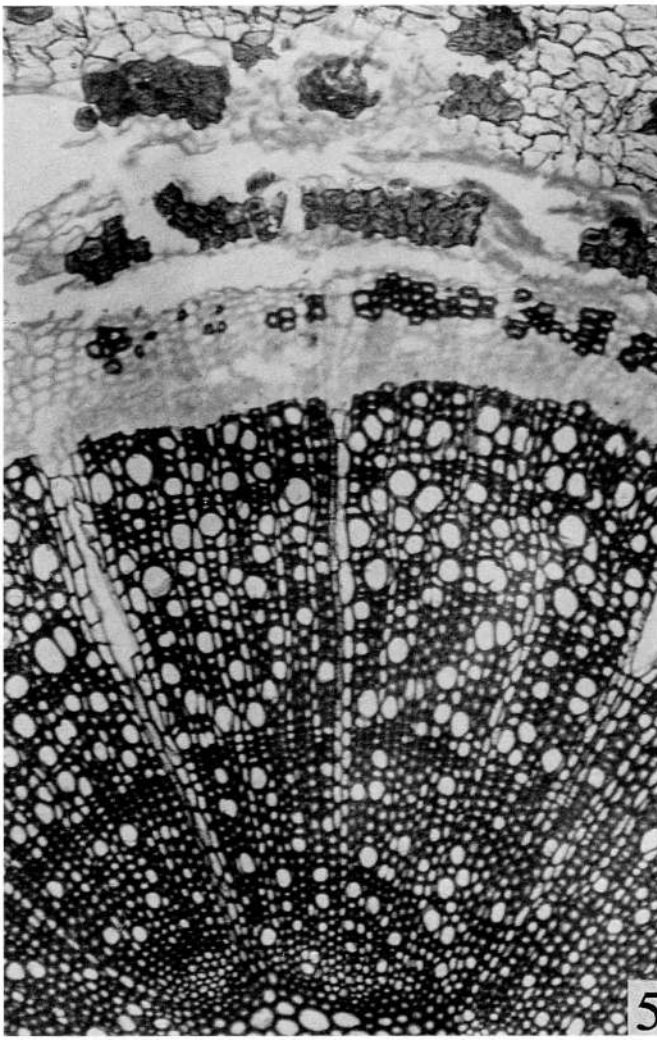
Axial Parenchyma

The type of axial parenchyma common in woodier Calyceraceae is scanty vasicentric, an incomplete sheath of cells one cell thick around vessels or vessel groups. This was observed in *Acicarpha spathulata, A. tribuloides* (stems only), *Boopis anthemoides, Calycera calcitrapa, C. crassifolia* (parenchyma very scarce), *C. eryngioides, C. sessiliflora,* and *C. spinulosa.* A few diffuse axial parenchyma cells were noted in *C. calcitrapa* and *C. spinulosa.*

Pervasive axial parenchyma (axial parenchyma forming a background to vessels, with few or no imperforate tracheary elements present) may be considered a replacement for fibrous tissue in particular species. Pervasive axial parenchyma characterizes *Calycera sympaganthera, Gamocarpha alpina, Nastanthus andina* (Fig. 12), and *N. polycephala.* Pervasive axial parenchyma with some areas of libriform fibers is present in *Boopis graminea* Fig. 10) and *Calycera herbacea* (Fig. 18). No axial parenchyma was observed in the roots of *Acicarpha tribuloides.*

Axial parenchyma subdivided into strands of two cells was observed in *Acicarpha spathulata, A. tribuloides* (stems), *Boopis anthemoides, Calycera calcitrapa, C. crassifolia, C. eryngioides, C. sessiliflora, S. spinulosa,* and *C. sympaganthera.* Only undivided axial parenchyma was observed in *Boopis graminea, Calycera herbacea, Gamocarpha alpina, Nastanthus andina,* and *N. polycephala;* however, axial parenchyma in these species has only thin primary walls. Subdivision of such cells may be difficult to see, particular since primary walls are often collapsed in these species. In the species listed with parenchyma in strands of two cells, walls were lignified, so that the strands of two cells could be identified with certainty.

Rays

The woodier species of Calyceraceae have narrow multiseriate rays plus uniseriate rays. This condition is most clearly shown by *Calycera calcitrapa* (Fig. 15) and *C. crassifolia* (Fig. 17). In the former species, uniseriate rays outnumber multiseriate rays, whereas the reverse is true in *C. crassifolia.*

Height of multiseriate rays (Table 1, column 9), width of multiseriate rays (column 10), and height of uniseriate rays (column 11) are given for species in which ray dimensions can be determined easily on account of presence of lignified walls on ray cells. Species with nonlignified ray cell walls (e.g., *Boopis graminea,* Fig. 11), also mostly have pervasive axial parenchyma with thin nonlignified walls. In these species, a tangential section cannot reveal clearly the limits between a ray with upright ray cells and adjacent axial parenchyma cells. In species with such rays and axial parenchyma, ray dimensions can not be ascertained accurately, nor can the presence or absence of uniseriate rays be established. Cellular preservation is less for cells with nonlignified cell walls, providing an additional reason for difficulty in determining limits of rays.

If one compares data on multiseriate ray height and width for the species of Calyceraceae (Table 1, columns 9 and 10), one finds notably wide, tall rays in *Acicarpha spathulata, A. tribuloides* (Fig. 2, 4) and *Calycera herbacea* (Fig. 18). In these species, primary rays are extended with very little change during secondary growth. There may be no rays in fascicular areas (Fig. 19). In the species of Calyceraceae with narrower, shorter rays, there is more modification of rays during secondary growth.

Ray histology can be most reliably determined from the woodier species of the family. Although radial sections are required for determining presence of upright, square, and procumbent cells, illustrations of tangential sections are cited here as showing cell shapes, but they do so only inferentially. The stems of *Acicarpha tribuloides* have rays composed almost exclusively of upright ray cells (Fig. 2), whereas procumbent cells predominate in rays of *A. tribuloides* roots (Fig. 4). Procumbent cells were commonly observed only in roots of *A. tribuloides.* The rays of Calyceraceae show a pronounced tendency toward upright cells. This is shown clearly in *Boopis anthemoides* (Fig. 7, 8) and *B. graminea* (Fig. 11). Procumbent cells are short in their vertical dimensions in *Calycera calcitrapa* (Fig. 15) and *C. crassifolia* (Fig. 17), so limits of rays are determined rather easily in these species.

Ray cell walls are relatively thin: about 1–1.5 μm in *Boopis anthemoides* (Fig. 6, 8) and *Calycera calcitrapa* (Fig. 15). Only simple pits were observed in ray cell walls of the family.

Storying

No evidence of storying, either in vessel elements, axial parenchyma, libriform fibers, or rays, was seen

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Fig. 5–9. Sections of stem of *Boopis anthemoides.*—5. Transection; bark above shows three-year secondary phloem accumulation, the increments demarcated by fibers; secondary xylem below also represents a three-year accumulation, with very weakly demarcated growth rings.—6. Transection of secondary xylem to show fibers and, adjacent to vessels and thinner walled than fibers, a few axial parenchyma cells.—7–9. Tangential sections.—7. Rays inconspicuous because their upright cells blend into fibrous background.—8. A multiseriate ray, left, with markedly upright cells.—9. A vessel showing helical thickenings on the secondary wall ("tertiary helical thickenings"). (Fig. 5, 7, scale above Fig. 1; Fig. 6, scale above Fig. 6 [divisions = 10 μm]; Fig. 9, scale above Fig. 9 [divisions = 10 μm].)
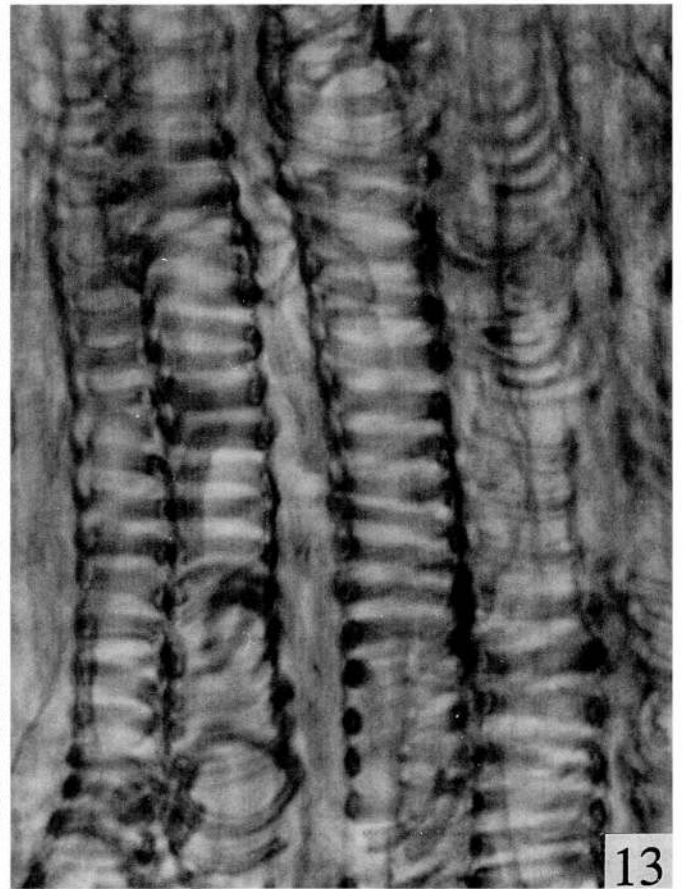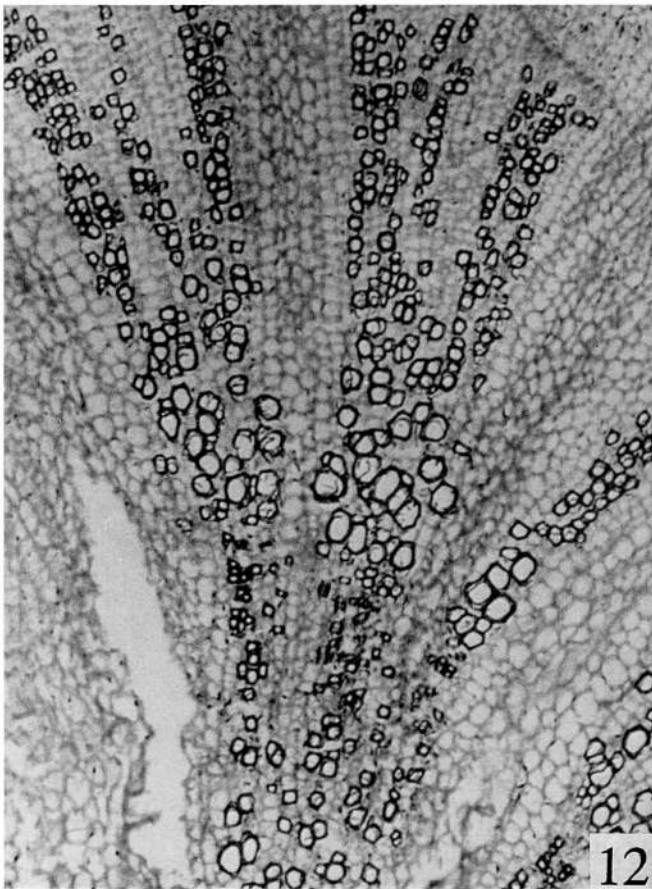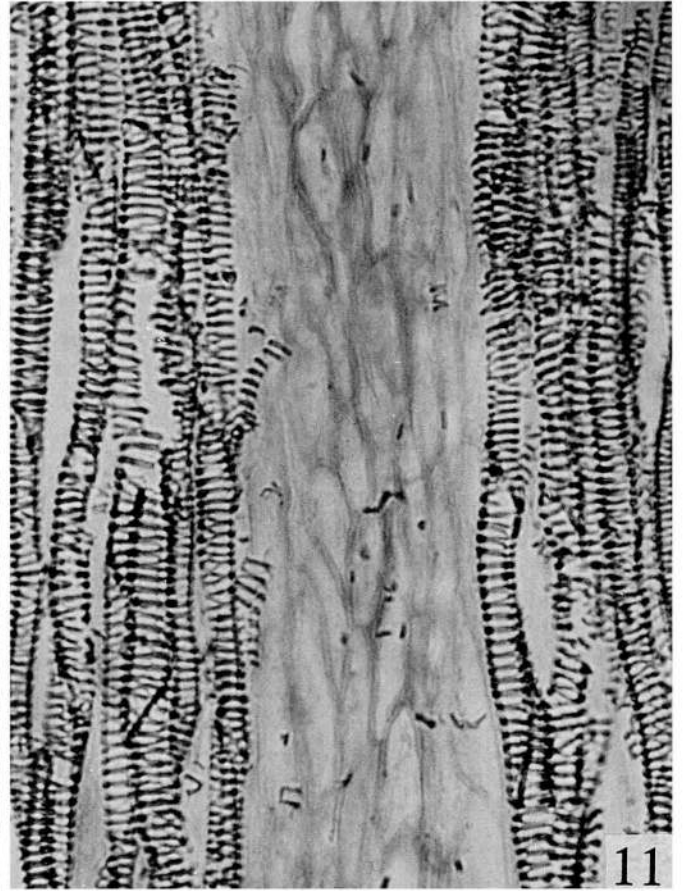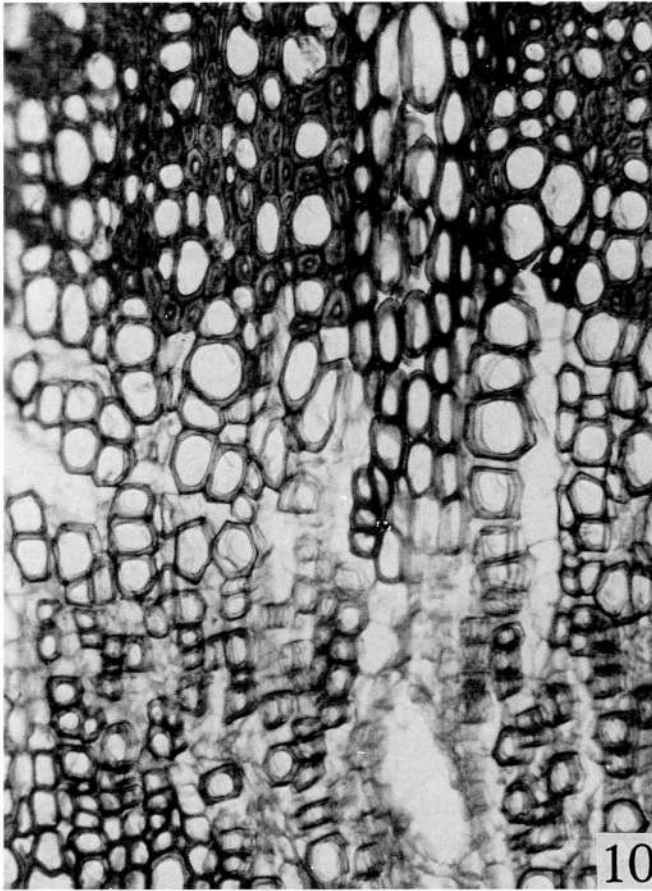
in any of the Calyceraceae studied. The accumulations of secondary xylem are minimal in the family, however, and storying is more likely to appear with increase in diameter of a stem or root.

Deposits and Crystals

Wood cells of Calyceraceae are notably free of deposits of secondary compounds. Starch grains were not observed. Druses were observed in cortex and pith of *Acicarpha spathulata,* but not in wood; no crystals other than these were observed in any Calyceraceae. Resinlike droplets, such as those often seen in woods of Asteraceae, were not recorded for any species in the present study.

ECOLOGICAL AND HABITAL CONCLUSIONS

Species of *Calycera* can be characterized as short-lived perennial herbs or facultative annuals. The cylinder of wood is only about 1–2 mm thick at most in the species studied at stem bases and adjacent root portions; distal to this region, there is less secondary xylem. Wood of *C. calcitrapa* (Fig. 14, 15) and *C. crassifolia* (Fig. 16, 17) is characterized by presence of libriform fibers as in many woody dicotyledon species. Presence of the fibers relates to the self-supporting nature of stems in these species. Woods of these species deviates from the pattern of typical woody dicotyledons in having pseudoscalariform pitting (some alternate pitting also present) and in having predominantly upright ray cells. These features are characteristic of woods that exemplify paedomorphosis (Carlquist 1962). Woods of *Calycera* show fewer features of paedomorphosis than the remaining species, as mentioned below. If the wood plan of *Calycera* is basic to the family as a whole, herbaceousness is likely basal to the family.

Species of Calyceraceae other than the above show even more numerous indications of paedomophosis and therefore a likely herbaceous ancestry. *Boopis anthemoides* has few rays, and ray cells are so predominantly upright that they are easily confused with libriform fibers and axial parenchyma cells. Shorter ray cells and more numerous rays would be expected if secondary growth continued for an extended period of time (several more years), so these features may relate to the relatively short life span in *B. anthemoides.*

Acicarpha tribuloides is an annual or nearly so. The limited amount of secondary xylem is related to the annual habit of this species, as are the rays. The rays are little-modified extensions of primary rays, and very few rays originate from cambium in the fascicular areas. The great width and height of rays of some Calyceraceae correlated with brevity of secondary xylem activity. *Acicarpha spathulata* and *Calycera herbacea* exemplify this ray condition.

The species of *Gamocarpha* and *Nastanthus,* as well as *Calycera spinulosa* and *C. sympaganthera* have multiseriate rays difficult to measure because their abundant thin-walled axial parenchyma adjacent to rays resembles their thin-walled ray cells. The presence of both abundant thin-walled axial parenchyma and wide, tall thin-walled rays could relate either to storage or water or storage of photosynthates, or both. Starch remnants were not observed in the materials examined, but preparation methods may not have been suitable for preservation of starch. Another possibility is that Calyceraceae store photosynthates mostly as inulin, a polysaccharide known to occur as a storage compound in Calyceraceae (Hansen 1992), and that therefore starch remnants would not be expected in anatomical preparations. The high elevation and high latitude localities of *Nastanthus* in particular, and some species in other genera are subject to cold and drought, and storage of water as well as photosynthates are likely functions for root parenchyma as a result of seasonal extremes.

Pseudoscalariform pitting in vessels with transitions to helical bands like those of primary xylem (Fig. 13) is very common in the secondary xylem of roots of *Nastanthus* and in some other species. Secondary xylem vessels with pseudoscalariform pitting transitional to helical band patterns are potentially capable of greater bending or even expansion and contraction (in the case of helical bands) than vessels with walls composed of continuous secondary wall material interrupted only by circular or oval pits. The occurrence of vessels with more flexible wall patterns suggests expansion and contraction of stem vessels and roots related to water storage.

Helical thickenings on the secondary walls of vessels of *Boopis anthemoides* ("tertiary helical thickenings," not to be confused with the helical bands mentioned above) are an indication of xeromorphy (e.g., Carlquist 1966). Marked growth rings occur in secondary xylem of several species of Calyceraceae; the

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Fig. 10–13. Wood sections of Calyceraceae.—10-11. *Boopis graminea.*—10. Transection; vessels in a parenchyma background below; vessels embedded in libriform fibers in subsequently formed secondary xylem, above.—11. Tangential section; multiseriate ray in center; vessels show laterally elongate (pseudoscalariform) pits.—12-13. *Nastanthus andina,* secondary xylem of root.—12. Transection; two-year accumulation of wood, showing wide rays, pervasive axial parenchyma, and marked difference between diameter of earlywood vessels (bottom; center) and latewood vessels.—13. Vessels from tangential section; pseudoscalariform pitting transitional to helical bands—a pattern consisting only of helical bands is nearly achieved. (Fig. 10, 11, scale above Fig. 6; Fig. 12, scale above Fig. 1; Fig. 13, scale above Fig. 9.)
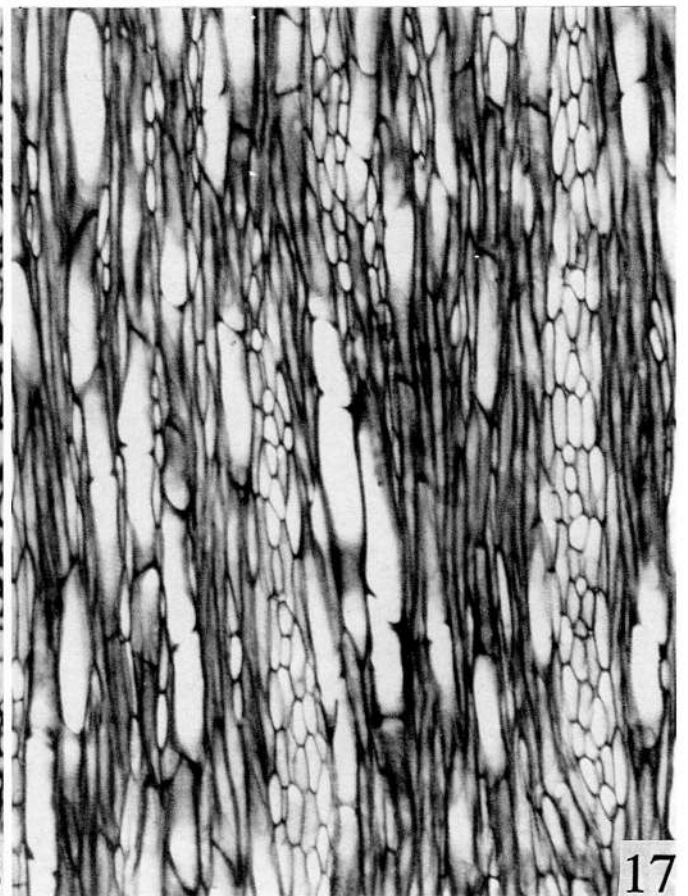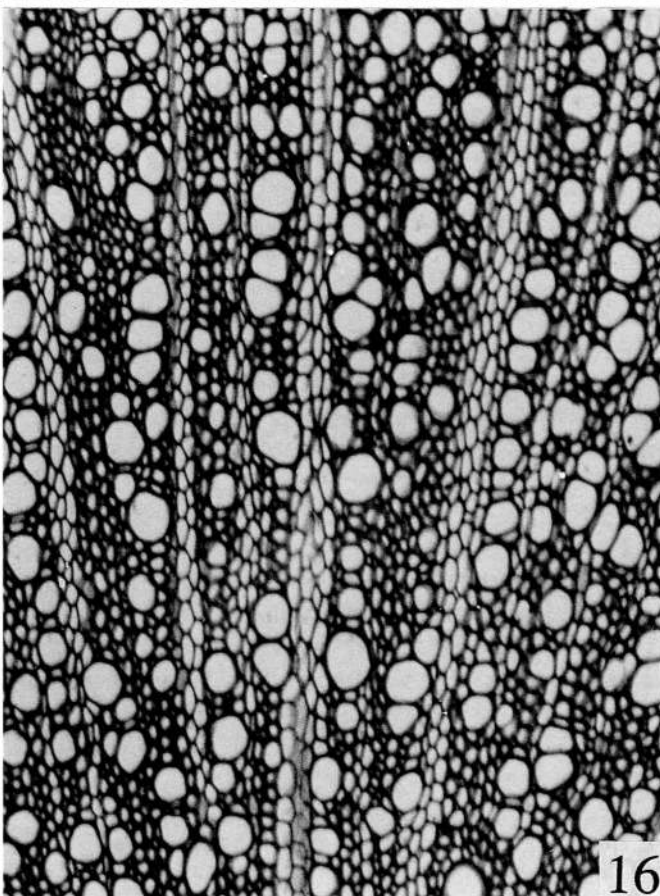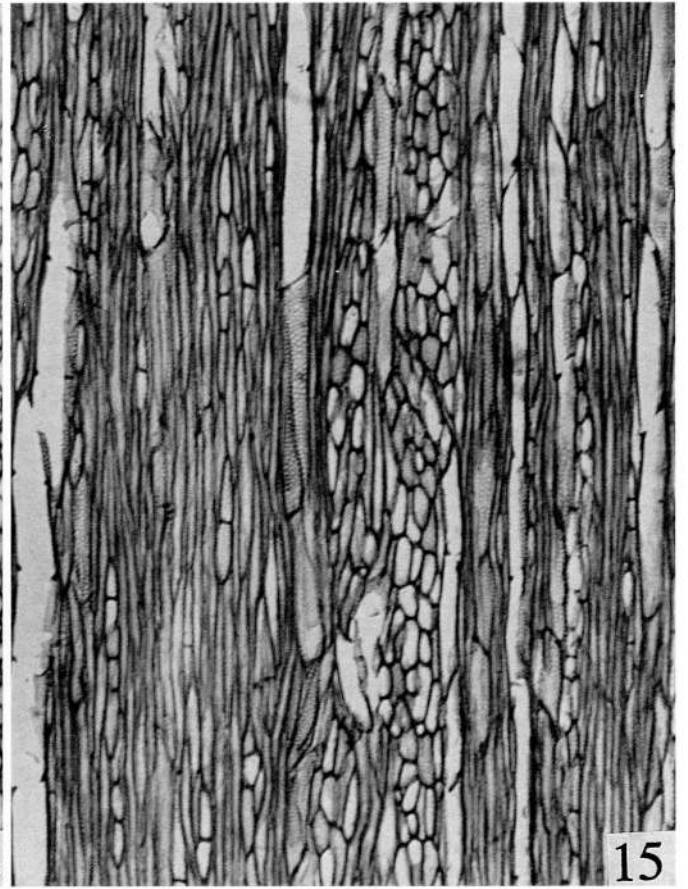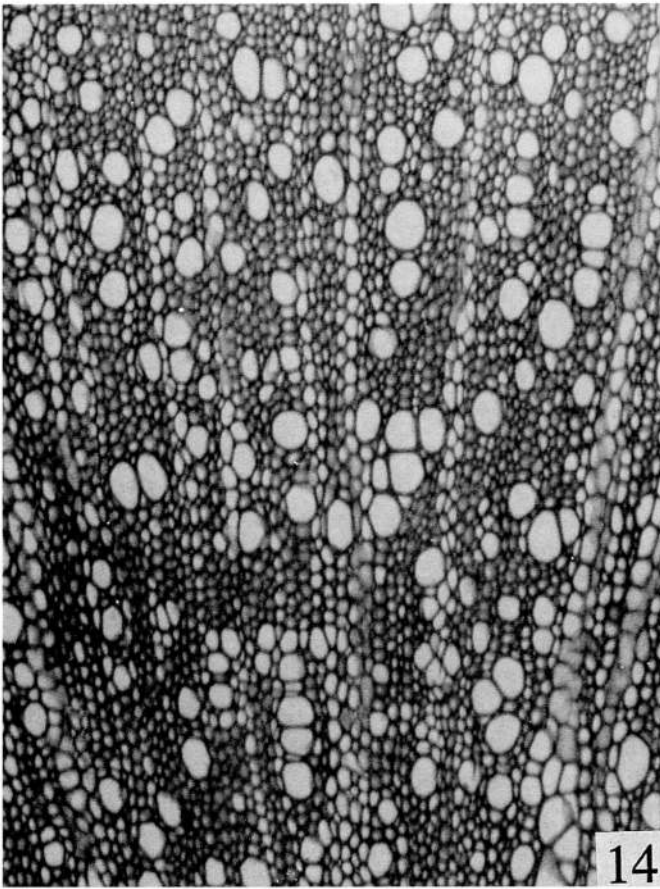
distinctness of these growth rings is indicative of strong seasonality, and the latewood in such growth rings is indicative of xeromorphy. In some species in which the wood sample terminates in narrower vessels, the addition of secondary xylem ends in a more xeromorphic pattern indicative that the last-formed secondary xylem was formed under conditions of lessening water availability.

Quantitative vessel features have been combined into a ratio termed the Mesomorphy Ratio (vessel diameter times vessel element length divided by number of vessels per mm^2). Although this Ratio does not correspond to any single physiological function, it proves to be a sensitive indicator of ecology (e.g., Carlquist and Hoekman 1985), more useful than a single measure. Mesomorphy Ratio figures are given for Calyceraceae in Table 1, column 12. Vessel lumen diameter is used here rather than outside vessel diameter, as in earlier studies such as Carlquist and Hoekman (1985), because the lumen diameter corresponds to hydrological functions of the xylem. Adjustments can easily be made in figures in earlier studies that use outside vessel diameter, and the difference between the two measurements is usually not great in any case. Within Calyceraceae, higher Mesomorphy Ratio values characterize the species of *Calycera*, which are short-lived perennials or herbaceous subshrubs. Annuals (*Acicarpha*) have Mesomorphy values lower than the family average. Low Mesomorphy values are to be expected in annuals, because they tend to grow in areas where drought or cold are more extreme than in areas where short-lived perennials tend to occur. The lowest Mesomorphy Ratio values are found in *Boopis graminea* (2.6), *Gamocarpha alpina* (0.5), and the species of *Nastanthus* (3.4, 0.2). These species are all from relatively high elevations and latitudes (see locality data in Materials and Methods). Drought and freezing are more likely to occur in these habitats than in those of the remaining species of Calyceraceae studied here. Mesomorphy Values in the range of 0.2–3.4 are extremely low compared to those for other plants. The Mesomorphy Value for Californian desert shrubs was reported to be 20.9 (Carlquist and Hoekman 1985); even if the reported vessel diameter for those shrubs was reduced by 20% in order to convert vessel diameter to lumen diameter (and two thicknesses of the vessel wall is likely less than that), the California desert shrub Mesomorphy value would be 16.7. If the Mesomorphy value of the four species of Calyceraceae cited above is average, the figure is 1.7, whereas the mean for the remaining species is 22.9. There is only one other family in which such low Mesomorphy values have been recorded, Plumbaginaceae (Carlquist and Boggs 1996); the value reported (vessel lumen diameter used) was 4.1; the range of species in that family was from 0.5 to 30, a range quite similar to that for Calyceraceae.

PHYLOGENETIC AND SYSTEMATIC CONCLUSIONS

The sampling of the family is too small to offer any reliable criteria for use in systematics within the family. Even if a more nearly complete sampling could be made, most of the variations observed would likely be related to autapomorphies that represent adaptations by wood to ecology and habit for particular species.

Asteraceae, Calyceraceae, and Goodeniaceae have been considered close to each other in most phylogenetic systems that have used macromorpholology (e.g., Hansen 1992). Relationships among the three families based on molecular data have never been in close agreement. Michaels et al. (1993) and Cosner et al. (1994) found that Calyceraceae and Goodeniaceae were equally likely sister groups to Asteraceae. An expanded sampling of *rbcL* sequences from Goodeniaceae was used in the analysis of Asterales by Gustafsson et al. (1996) that indicated Goodeniaceae may be the sister group to Asteraceae. This result may have been due to unequal sampling of Goodeniaceae and Calyceraceae. Recently, Bremer and Gustafsson (1997) produced a second *rbcL* tree that equalized sequences from Goodeniaceae and Calyceraceae. This recent analysis shows Calyceraceae to be the sister group to Asteraceae. Analyses of *ndhF* sequence data (Jansen and Kim 1995) and combined *ndhF* and *rbcL* data (Kim and Jansen 1995) suggest Calyceraceae are the sister group to Asteraceae.

Morphological evidence has also suggested that Calyceraceae are the sister group to Asteraceae (DeVore and Stuessy 1995). However, the number of autapomorphic features among members of Asteraceae (e.g., the indusium in Goodeniaceae, the pendulous ovule in Calyceraceae) and the lack of shared characters among these families make cladistic analyses difficult.

What does wood anatomy show concerning the interrelationships of these families? Wood of Asteraceae characteristically has, in all of the tribes (and thus likely symplesiomorphically) vessels with simple perforation plates; lateral wall pitting composed of alternate circular bordered nonvestured pits; libriform fibers

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Fig. 14–17. Wood sections of *Calycera*.—14–15. *C. calcitrapa*.—14. Transection; one year of secondary xylem accumulation is included in the photograph.—15. Tangential section; uniseriate rays are more common than multiseriate rays.—16–17. *C. crassifolia*.—16. Transection; solitary vessels are about as common as grouped vessels, although groups are mostly of two or three vessels each.—17. Tangential section; multiseriate rays are more common than uniseriate rays. (Fig. 14–17, scale above Fig. 1.)
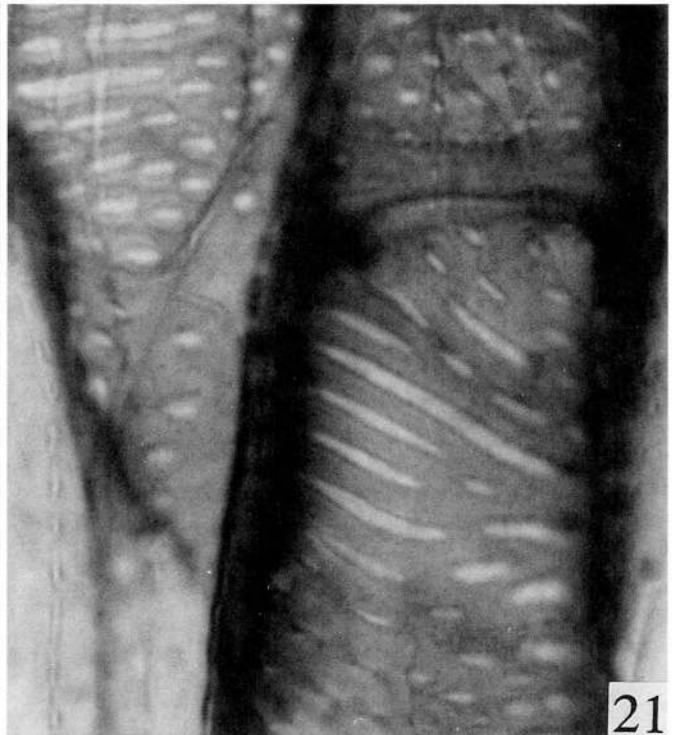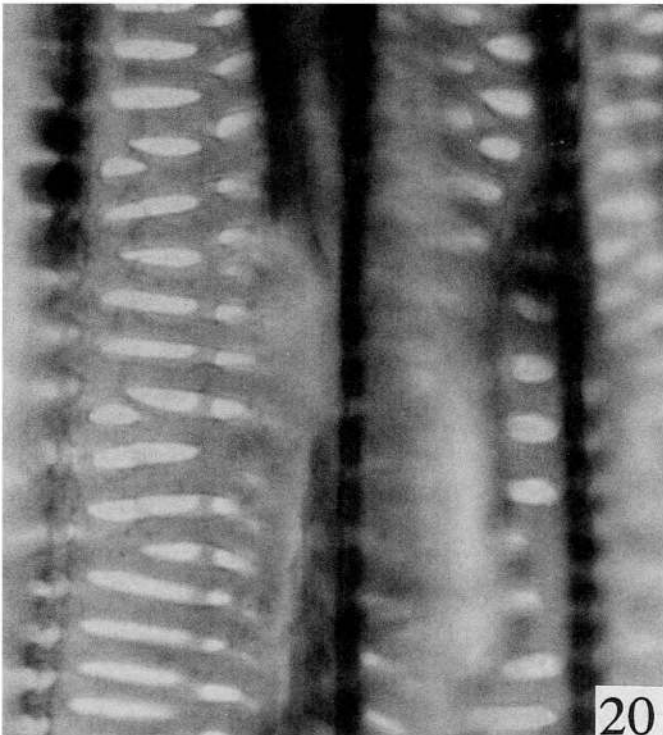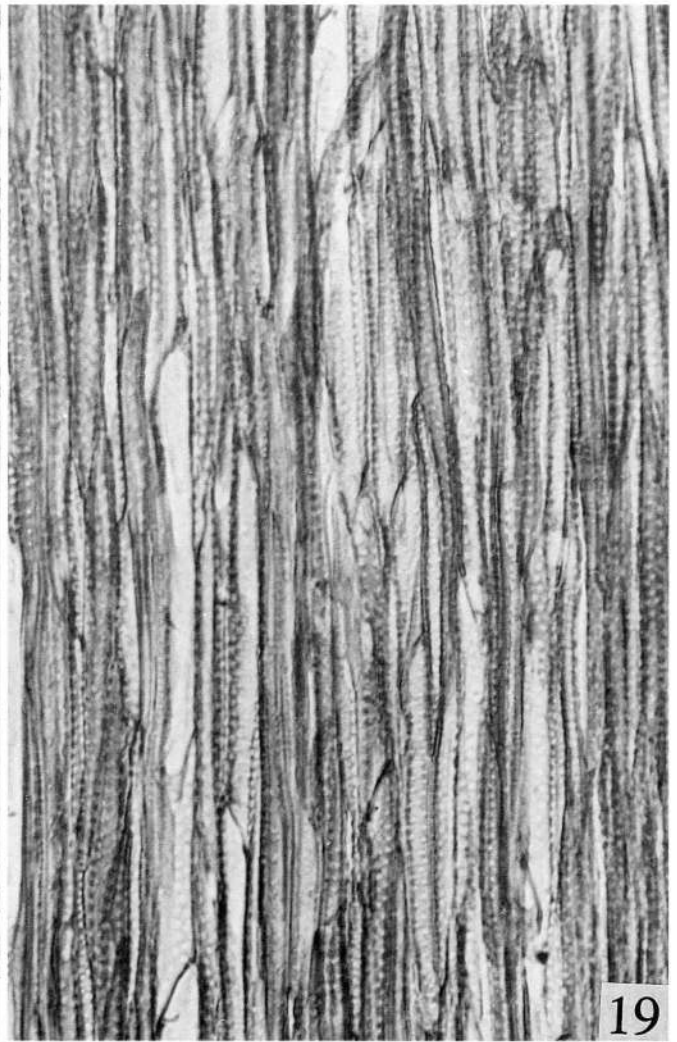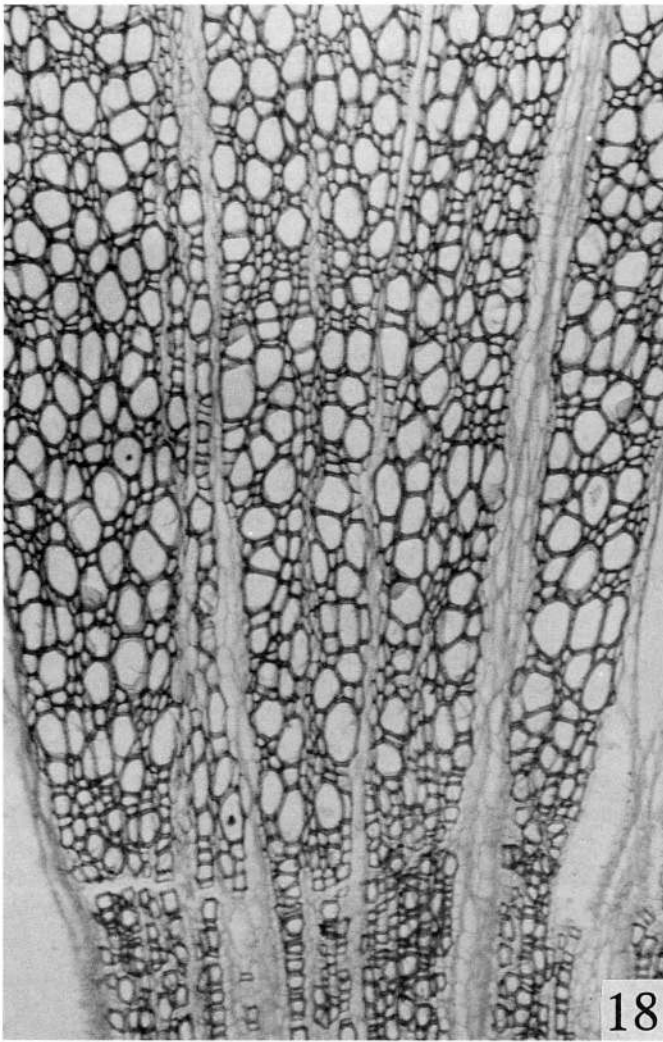
with simple pits (in addition, vasicentric tracheids in a few species); vasicentric scanty axial parenchyma, in strands of two or several cells; both multiseriate and uniseriate rays, referable to Heterogeneous Type II of Kribs (1935); wood is storied wood in a few genera, but nonstoried wood basic for the family (Carlquist 1966). All of these features may be found in species of *Calycera,* so that a position for Calyceraceae basal to Asteraceae is reflected in wood anatomy. The genera of Calyceraceae other than *Calycera* exhibit some character states other than those listed above for Asteraceae, and these represent adaptations to particular habits or ecological conditions.

The present study does not necessarily indicate that *Calycera* is basal within Calyceraceae on the basis of wood anatomy. Note should be taken that *Moschopsis,* a genus not included in this study because of lack of suitable material, is shown as basal within the family (along with "*Boopis I*") by DeVore and Stuessy (1995). Assuming that *Calycera* does reflect the basic plan of wood in Calyceraceae, wood data are compatible with the traditional view of close relationship between Calyceraceae and Asteraceae.

As noted above, such workers as Michaels et al. (1993) pair Goodeniaceae with Calyceraceae, and therefore wood of Goodeniaceae should be considered in connection with Calyceraceae. Goodeniaceae have tracheids (or fiber-tracheids) as imperforate tracheary elements rather than libriform fibers. Goodeniaceae also have apotracheal (diffuse) rather than vasicentric axial parenchyma (Carlquist 1969). In these two features, Goodeniaceae have more primitive character states according to traditional interpretations (see Carlquist 1988) than do Calyceraceae. Taking that into account, wood anatomy does not rule out Goodeniaceae as basal to Asteraceae, although wood anatomy would favor a hypothesis in which Calyceraceae and Asteraceae are sister families at the end of a clade in which Goodeniaceae are basal to those two families.

Wood anatomy is of dubious usefulness in construction of cladograms within the family Calyceraceae because most character state progressions relate to particular ecological or habital shifts, and where this is true, one is likely dealing with a series of autapomorphies. Moreover, only root wood can be studied feasibly for some Calyceraceae, whereas stem wood has been studied for others, and these two kinds of wood may not be comparable.

Woodiness, at least of a moderate degree, seems basal in Asteraceae (Carlquist 1966), but if so, evolution into herbaceous habits has likely occurred numerous times in that family, as has secondary woodiness (Carlquist 1962, 1966, 1974). Groups basal within the Asteridae clade may be primitively woody (e.g., Cornaceae), but ray structure and vessel pitting suggest that Calyceraceae are basically an herbaceous or minimally woody phylad.

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Fig. 18–21. Wood sections of *Calycera.*—18–20. *C. herbacea.*—18. Transection; there is a marked change in vessel diameter from bottom fifth to upper four-fifths.—19. Tangential section of a fascicular zone in which no rays are evident.—20. Vessel walls from tangential section. Pits are basically alternate, but some so widened laterally that they appear scalariform (and are better termed pseudoscalariform).—21. *C. crassifolia.* Vessels from tangential section; pits range from oval to much widened laterally. (Fig. 18, scale above Fig. 1; Fig. 19, scale above Fig. 6; Fig. 20, 21, scale above Fig. 9.)

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