INTRODUCTION

Although much work has been done on the family Polemoniaceae, most notably on experimental taxonomy, studies on the anatomy of the family have been remarkably few. Grant's (1959) summary of systematic work, as well as the compilation of Metcalfe and Chalk (1950) demonstrates the paucity of studies. No investigation of wood anatomy of Polemoniaceae has been generated since those summaries were prepared. To be sure, few studies on wood anatomy of predominantly herbaceous families have been done until the past two decades. Wood accumulation is limited in Polemoniaceae (Acanthogilia and Cantua are the only genera in which maximal stem diameter typically exceeds 2 cm). Therefore few specimens of polemoniaceous wood are present in wood collections, and data on wood anatomy are accordingly scanty. In addition, the woodier species of Polemoniaceae are mostly from the Cordilleran areas (often granitic zones) of North and South America, areas which have been little visited by those collecting wood samples or studying wood anatomy.

Because the majority of species in Polemoniaceae are herbaceous, one is faced with the question as to whether the family is primarily or secondarily woody, and whether if the family is primitively woody, any secondarily woody species occur in the family. Wood anatomy should be viewed carefully in attempting to answer these questions.

Although the affinities of Polemoniaceae do not seem highly controversial, composition of the order (sometimes called Polemoniales) varies appreciably from one phylogenetic system to another. Wood anatomy is a pertinent line of evidence for placement of the family. Distinctive groupings have been recognized within the family (Brand 1907; Grant 1959). Comparison of data on wood anatomy to these taxonomic concepts is undertaken here.

Woody Polemoniaceae occupy a series of ecological niches most of which could be described as dry. These habitats invite comparison to wood anatomy results. The following commentary (data original and from Brand 1907) is intended to facilitate these comparisons. Cobaea is a vine of shady cloud-forest areas of the Cordillera from northern Chile to southern Mexico. The specimen in the present study was taken from a specimen cultivated in Claremont. Cantua is a shrub of dry slopes of the montane or subalpine central Andes from Ecuador to northernmost montane Chile. Branched from the base, Cantua shrubs often reach 2 m and are the woodiest species in the
family. Of the species in the present study, *C. buxifolia* Juss. ex Lam. and *C. flexuosa* (R. & P.) Pers. were collected in the wild in Peru, whereas woods of *C. cuzcoensis* Infantes Vera and *C. pyrifolia* Juss. were collected from specimens cultivated in the Rancho Santa Ana Botanic Garden.

*Loeselia*, a primarily Mexican genus, consists mostly of somewhat woody annuals or perennials. *Loeselia involucrata* G. Don occurs in dry spots in Central America, whereas *L. mexicana* (Lam.) Brand is a small shrub from central and southern Mexico, where it grows in exposed montane places. Both collections of *Loeselia* were derived from wild-occurring plants, although the illustrations of *L. mexicana* (Fig. 15–17) represent sections made from a plant cultivated in the Rancho Santa Ana Botanic Garden.

*Huthia caerulea* Brand is a shrub to 1 m on dry montane slopes near Arequipa, Peru, whereas *H. longiflora* Brand is a small shrub which occupies lower slopes in the same province (Gibson 1967). Wood of both species was derived from wild-occurring plants, but represents medium-sized twigs rather than basal portions of plants.

*Ipomopsis* is characteristically branched from near the base of the plant, and is more often suffrutescence than shrubby. Formerly a section of *Gilia* (Brand 1907), *Ipomopsis* was recognized as a genus by Grant (1956). *Ipomopsis* ranges from northern Mexico into the United States, particularly the Southwest. *Ipomopsis rubra* (L.) Wherry occurs in the southwestern U.S. in sandy or rocky places in open woods. *Ipomopsis aggregata* (Pursh) V. Grant is distributed in dry sandy areas of the western U.S. *Ipomopsis longiflora* (Torr.) V. Grant is limited to sandy hills in New Mexico and adjacent areas.

Recently segregated from *Ipomopsis* is a distinctive shrub or subshrub of Baja California, *Acanthogilia gloriosa* (Bge.) Day & Moran. It occurs on granitic outcrops in or near washes in the thorn scrub zone of the peninsula.

*Leptodactylon*, once included in *Gilia* (Brand 1907) can be characterized as a shrub, although it may often be a small matlike subshrub when it grows at higher elevations; at most, it rarely exceeds a meter in height at lower elevations, where it tends to reach maximal size. *Leptodactylon californicum* H. & A. subsp. *californicum* ranges from sandy coastal hills near Lompoc, California (Michener 4068) to granitics in the Santa Ana Mountains (Michener 3979), San Gabriel Mts. (Carlquist 15645) and San Emigdio Mts. (Michener 3990). *Leptodactylon pungens* (Torr.) Rydberg subsp. *hallii* (Parish) Mason wood studied here (Michener 3941) was collected on a dry granitic ridge of San Benito Co., California. *Leptodactylon pungens* subsp. *pulchriflorum* (Brand) Mason material (Michener 4005) was collected at Tioga Pass, an alpine granitic area of the central Sierra Nevada of California.

*Eriastrum*, once included in *Gilia*, consists of 14 species native to dry areas of the western U.S. (Mason 1945). *Eriastrum densifolium* (Benth.) Mason is a short-lived perennial (2–5 years) branched from near the base. The collection Carlquist 15798 of *E. densifolium* subsp. austromontanum
(Craig) Mason was made in a dry sandy chaparral area of Cajon Pass, San Bernardino Mts., California, whereas the collection Michener 3992 came from a similar dry chaparral area of the San Emigdio Mts. The species *E. densifolium* as a whole occurs in montane and desert localities all of which can experience winter frost. *Eriastrum densifolium* subsp. *mohavense* (Craig) Mason occurs in Joshua Tree Woodland from San Bernardino Co. to Inyo Co., California.

In sum, the ecological areas occupied by the Polemoniaceae of the present study are, except for habitats of *Cobaea*, characteristically dry much of the year. Some species occupy areas where frost can occur during half of the year or more (*Leptodactylon pungens*), although very likely none of the South American species experience frost unless the frost is mild and short-lived. Adaptations by wood to the physiological drought created by frost are very likely much the same as adaptations to aridity, although our understanding of these adaptations where wood is concerned are quite incomplete. Polemoniaceae are a group in which we ought to expect xeromorphic features in wood. Xeromorphic features may not be progressively more extreme beyond a certain point; mechanisms which effectively shut down the plant during a dry period of four months may not need to be heightened appreciably to insure persistence through an eight-month period of drought. Polemoniaceae has species in such a range of regimes; moreover, the strong fluctuation between seasons and between wet years and dry years ought to be evident in growth rings of Polemoniaceae. Of the genera of the family included in the present study, the North American genera represent much more radiation into a broad spectrum of dry habitats than do the South American species. The nature of wood anatomy in the various taxa may provide clues about physiological tolerances of particular construction patterns.

**MATERIALS AND METHODS**

Because stems of *Cantua* offer sufficient wood for sectioning on a sliding microtome, specimens of that genus were incorporated into the wood-slide collection at the Rancho Santa Ana Botanic Garden. The availability of wood of two species of *Cantua* and one of *Loeselia*, planted in the Botanic Garden by Dr. Verne Grant, was an additional inducement for study of woods. Likewise, a few specimens of *Leptodactylon californicum* growing in the Botanic Garden provided wood suitable for sectioning, leading to the observation that wood in that species is rayless (Carlquist 1970). However, study of additional species of the family, leading to a survey of the shrubs and woody herbs with respect to wood anatomy, had not been contemplated. The reason for this was at least partly technical. Woods of small twigs are difficult to section on a sliding microtome. Woods in which growth rings
Table 1. Wood characteristics of Polemoniaceae.

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<td>1.26</td>
<td>5.3</td>
<td>211</td>
<td>12</td>
<td>5.8</td>
<td>215</td>
<td>21</td>
<td>2.00</td>
<td>UVA</td>
<td>0.11</td>
<td>14</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Legend: 1 = portion of plant (R - root; S - stem; SS = small stem, less than 5 mm in diameter); 2 = mean vessel diameter, µm; 3 = mean number of vessels per mm²; 4 = mean vessel-element length, µm; 5 = mean number of vessels per group; 6 = mean vessel wall thickness, µm; 7 = mean length of imperforate tracheary elements, µm; 8 = mean diameter of imperforate tracheary elements at widest point, µm; 9 = mean wall thickness of imperforate tracheary elements, µm; 10 = mean height of multiseriate rays, µm; 11 = mean height of uniseriate rays, µm; 12 = mean width of multiseriate rays, µm; 13 = mean width of multiseriate rays, cells; 14 = ray histology as seen in radial section (u = upright cells; s = square cells; p = procumbent cells; upper case designates predominant type; only cell types present shown; upright cells indicated as present in some species which are nearly rayless); 15 = growth-ring type according to classification of Carlquist (1980); 16 = Vulnerability (vessel diameter divided by vessels per mm²); 17 = Mesomorphy (vulnerability multiplied by vessel-element length).
are characterized by latewood bands of parenchyma (e.g., *Ipomopsis aggregata*) tend to split into fragments when sectioned on a sliding microtome. Woods difficult to section for the above reasons proved entirely amenable to a recently-devised technique (Carlquist 1982a) which permits successful sectioning with a rotary microtome after softened woods have been embedded in paraffin. Sections were stained with safranin alone, or counterstained with fast green. Counterstaining permitted better observation of pitting details. Most wood samples were available in dried form. However, the Michener collections were preserved in formalin-acetic-alcohol.

Table 1 summarizes quantitative and qualitative data for the species studied. Means are based on 24 measurements per feature unless otherwise stated. In *Cobaea*, vessel diameter and number of vessels per mm² are based upon measurement of wide vessels only, since narrow vessels as seen in transection merge with imperforate tracheary elements in diameter and morphology. In *Eriastrum*, ray dimensions and morphology are given, but these are based on the limited number of rays present; *Eriastrum densifolium* can still be described as near-rayless. Ray width data are not given for *Ipomopsis aggregata* because the ray cells are thin walled and collapsed in the wood section preparations.

The kindness of the curators of the Herbarium of the University of California, Berkeley, and the Herbarium of the Rancho Santa Ana Botanic Garden, who permitted use of their materials, is gratefully acknowledged. Dr. David C. Michener contributed specimens he collected in Mexico and California, listed in Table 1. Mr. Vincent M. Eckhart sectioned most of the wood samples in this study and collected data on most of them. Other aspects of this investigation represent the work of the senior author. No attempt has been made to study wood of species with very little wood accumulation because information obtainable from such specimens is dubiously comparable to the data from woody species.

**ANATOMICAL DESCRIPTIONS**

**Growth rings.**—As can be seen from Table 1, the South American Polemoniaceae have little growth-ring activity, can mostly be designated as Type IB (vessels fluctuating little in diameter, imperforate tracheary elements little affected) according to an earlier growth-ring classification system (Carlquist 1980). Examples of this can be seen for *Cobaea scandens* Cav. (Fig. 1), *Huthia longiflora* (Fig. 12), and *Ipomopsis rubra*. *Cantua buxifolia* (Fig. 10), *C. flexuosa* (Fig. 5), and *Loeselia mexicana* (Fig. 15) can be said to belong to Type IE because of fluctuation in wall thickness of imperforate tracheary elements with respect to seasons. The bands of thinner-walled fiber-tracheids or libriform fibers in *Cantua* and *Loeselia* do not constitute parenchyma.

In *Acanthogilia gloriosa* (Fig. 26, 28), *Eriastrum densifolium*, and *Ipomopsis tenuifolia* (Gray) V. Grant, Type XI can be said to be present because
Fig. 1–4. Wood sections of *Cobaea scandens* (Carlquist 7394). —1. Transection. Exceptionally wide vessels present. —2. Tangential section. Rays absent. —3. Transection, vessel above. The majority of cells in the bottom quarter of the photograph are axial parenchyma; two smaller vessels, lower right. —4. Radial section. Simple perforation plate interconnecting fibriform vessel elements, center. (Fig. 1–2, magnification scale above Fig. 1 [finest divisions = 10 μm]; Fig. 3, scale above Fig. 3 [divisions = 10 μm]; Fig. 4, scale above Fig. 4 [divisions = 10 μm].)
vessels fluctuate in diameter and parenchyma bands are formed seasonally. The most extreme form of Type XI is represented by *I. aggregata* (Fig. 19, 22) because in the parenchyma, which is apparently terminal and formed at the end of a growing season, imperforate tracheary elements are wholly replaced by parenchyma.

Type V growth rings can be designated for *Leptodactylon* (Fig. 33, 35) and *Phlox diffusa* Benth. because not only do vessels vary in diameter with respect to growth rings, they markedly fluctuate in abundance seasonally. Type VA is the most extreme manifestation: vessels are not formed in all or much of the latewood; this condition is represented in *Leptodactylon pungens* subsp. *pulchriflorum* and subsp. *pungens* (Fig. 35) as well as in *Phlox diffusa*. In Type VB, vessels are fewer in latewood but imperforate tracheary elements are relatively uniform throughout the growth ring. Type VB occurs in *Leptodactylon pungens* subsp. *hallii*. In Type VD, vessels are fewer in latewood and tracheids are narrower in latewood. Type VD can be said to occur in *Leptodactylon californicum* (Fig. 33) and this species was cited earlier as an example of this growth ring type (Carlquist 1980).

**Vessel elements.**—Figures on mean vessel diameter, mean vessel-element length, and mean number of vessels per mm$^2$ are given in Table 1. Vessels are notably wide and few per mm$^2$ in *Cobaea* (Fig. 1, 3), although narrower vessels are not included in these figures. Notably narrow vessels, numerous per mm$^2$, can be observed in *Eriastrum* and in *Leptodactylon* (Fig. 33, 35). The extremes represented by *Cobaea* and *Leptodactylon* encompass an exceptionally wide range. The values in vessel-element length are equally remarkable; figures range from a little more than 100 μm in *Leptodactylon* to approximately 400 μm in *Acanthogilia gloriosa* (Day 76-129), *Cantua buxifolia* (Carlquist 7005), and *Eriastrum densifolium* subsp. *austromontanum* (Michener 3992). Interestingly, where more than one sample of a species was examined, and where age could be determined by growth rings, vessel-element length decreased with age. The sample *Cantua buxifolia*, Carlquist 7005, with longer vessel elements, was nearly twice the diameter of the sample Carlquist 7025, with appreciably shorter vessel elements. In *Eriastrum densifolium* subsp. *austromontanum*, the collection Michener 3992, with shorter vessel elements, was from a stem five years old, whereas Carlquist 15798, with longer vessel elements, was from a stem three years old. In *Leptodactylon californicum* subsp. *californicum*, the collection Michener 3990 (12 years old) had vessel elements approximately half the length of those in Carlquist 15645 (five years old) or Michener 3979 (seven years old); the collection Michener 4068, with vessel elements of intermediate length, was eight years old. The most marked differences between collections could be demonstrated in *Acanthogilia gloriosa*, where long vessel elements characterize the three-year-old upper stem (Day 76-129), whereas vessel elements are about half as long in the basal stems from the collections Michener 4241
Fig. 5-9. Wood sections of *Cantua flexuosa* (Carlquist 7149). — 5. Transection. Band of thin-walled fibers runs obliquely across center. — 6. Tangential section. Multiseriate rays outnumber uniseriate rays. — 7. Radial section. Axial parenchyma strands run vertically, center. — 8. Walls of fiber-tracheids from radial section. Pits are simple. — 9. Wall of vessel from tangential section. Grooves interconnecting pits are seen at right on vessel wall. (Fig. 5-6, magnification scale above Fig. 1; Fig. 7, scale above Fig. 3; Fig. 8-9, scale above Fig. 4.)
and 4265, both of which exceed 20 years in age. That shortening of vessel elements happens ontogenetically within a stem is more easily shown by study of vessel elements in radial sections, and study of a radial section of *Ipomopsis aggregata* wood did show this. Thus, vessel-element length in Polemoniaceae varies markedly with respect to age, although other factors are evident also.

Transections of wood of Polemoniaceae show that most taxa have few vessels per group (Fig. 1, 12, 15, 24, 26, 28, 31, 33, 35). Only the South American genera *Cantua* (Fig. 5, 10) and *Huthia* (Fig. 12) show figures higher than 2.0 for number of vessels per group (Table 1, column 5); the true figure for *Cobaea scandens* would undoubtedly be higher than 2.0, but that species has both wide and narrow vessels; the latter are very difficult to identify and were deliberately omitted from the computation of number of vessels per group. Vessel grouping, where present, takes the form of radial chains (Fig. 5, 10, 12, 15). In *Ipomopsis aggregata*, vessel grouping is much greater in latewood than in earlywood zones (Fig. 22). The number of vessels per group shown in Table 1 may be somewhat higher than could be obtained if one could identify the tips of overlapping ends of fibriform vessel elements. Many if not all of the Polemoniaceae studied have an appreciable number of fibriform vessel elements, in which transections of the overlapping ends may give the appearance that there are two vessels side by side rather than overlapping tips of a single vessel.

Simple perforation plates characterize all of the Polemoniaceae studied, both in primary and in secondary xylem (e.g., Fig. 23). However, double perforation plates were observed in a scattering of species throughout the family, including *Eriastrum densifolium* subsp. *austromontanum* (Fig. 18), *E. densifolium* subsp. *sanctorum* (Mlnk.) Mason, *Huthia longiflora* (Fig. 13), *I. rubra*, and *Loeselia mexicana*. Double perforation plates appear to be related to more elongate overlap areas of vessel elements, which in turn tend to be present on fibriform vessel elements, as was noted in Hydrophyllaceae (Carlquist and Eckhart 1984).

Lateral wall pitting of vessels, regardless of what type of cell is in contact with an area of vessel wall, consists of alternate circular bordered pits in Polemoniaceae (Fig. 4, 18). However, variations on that pattern occur in some species which bear elliptical pits on vessels, intermixed with circular pits: *Eriastrum densifolium* subsp. *austromontanum*, *Huthia caerulea*, *Leptodactylon californicum*, and *L. pungens*. In *Ipomopsis aggregata*, some elliptical pits occur on earlywood vessels, but in the latewood bands in which vessels occur embedded in parenchyma, much-widened pits characterize vessels (Fig. 23). These are not to be confused with the helical bands on primary xylem vessels, although there is a moderate degree of resemblance superficially; this situation has been clarified elsewhere (Carlquist and Eckhart 1984).
Fig. 10–14. Wood sections of *Cantua* and *Huthia*.—10–11. *Cantua buxifolia* (Carlquist 7005).—10. Transection. Vessels in radial rows.—11. Tangential sections. Multiseriate and uniseriate rays about equally abundant.—12–14. *Huthia longiflora* (Weberbauer 3782).—12. Transection. Vessels mostly in radial rows.—13. Portion of radial section. A double perforation plate is seen, center.—14. Tangential section. Rayless condition evident. (Fig. 10–11, 12, 14, magnification scale above Fig. 1; Fig. 13, scale above Fig. 4.)
Fig. 15–18. Wood sections of *Loeselia* and *Eriastrum*.—15–17. *Loeselia mexicana* (Carlquist XII-1970, cultivated in the Rancho Santa Ana Botanic Garden).—15. Transection. An inconspicuous growth-ring margin lies above the center of the photograph.—16. Tangential section. Erect ray cells predominate.—17. Septate fiber-tracheids from radial section.—18. *Eriastrum densifolium* subsp. *austromontanum* (Carlquist 15798). Radial section. Double perforation plate at left. (Fig. 15–16, magnification scale above Fig. 1; Fig. 17–18, scale above Fig. 4.)
Helical sculpture may be found on vessels of some Polemoniaceae. In its least pronounced form, it is present as a pair of very small ridges beside each pit, as in *Acanthogilia* (Fig. 29). Such ridges were also observed in *Leptodactylon pungens* subsp. *pulchriflorum*. Grooves interconnecting pit apertures were observed in *Cantua flexuosa* (Fig. 9), *C. cuzcoensis*, and *C. pyrifolia*. The ridges beside pit apertures in *Leptodactylon* may be present in a more pronounced form: pairs of adjacent ridges coalesced into helical bands (the “spirals” or “tertiary helical thickenings” of some authors). These were seen in *L. californicum* and *L. pungens* subsp. *hallii*.

Imperforate tracheary elements.—In dicotyledons at large, imperforate tracheary elements can be defined as tracheids (pits fully bordered, approximately as dense as those on vessels), fiber-tracheids (pits with vestigial borders and/or pits less dense than those on vessels), and libriform fibers (pits simple). Using these definitions, one can characterize *Eriastrum densifolium*, *Ipomopsis tenuifolia*, and *Leptodactylon* (all taxa studied) as having tracheids. Fiber-tracheids may be said to be present in *Acanthogilia gloriosa*, *Cantua pyrifolia* (borders on pits very reduced), *Huthia caerulea*, *H. longiflora*, and *Ipomopsis* (all species studied except *I. tenuifolia*), and *Loeselia mexicana* (borders very reduced: Fig. 17). Libriform fibers can be said to occur in *Cantua buxifolia*, *C. cuzcoensis*, *C. flexuosa* (Fig. 8), and *Loeselia involucrata*, since borders were not observed on pits in these species. Septate fibers were observed in *Cantua cuzcoensis*. The imperforate tracheary elements of *Loeselia mexicana* (Fig. 17) must be termed septate fiber-tracheids. The fiber-tracheids of *Cobaea scandens* have gelatinous inner walls which shrink away from outer walls in prepared slides. The libriform fibers of *Cantua buxifolia* could be described as slightly gelatinous, because prepared slides of wood sections feature splitting which extends the length of the pit aperture; this is presumably an artifact induced by withdrawal of water from the section.

If one computes a ratio between the imperforate-element length and vessel-element length, one obtains figures which range from 2.30 (*Cantua flexuosa*) to 1.12 (*Leptodactylon californicum*). Most species in Polemoniaceae fall between 1.30 and 1.80.

Axial parenchyma.—Axial parenchyma of all Polemoniaceae could be described as basically vasicentric scanty, with an incomplete sheath—sometimes only or or two cells instead of a sheath—around vessels or vessel groups as seen in transection. Axial parenchyma is more abundant in *Cantua flexuosa* than in other Polemoniaceae, and sheaths are typically complete, often more than one cell thick in places; in radial sections, several adjacent parenchyma strands may therefore be seen in places (Fig. 7).

Axial parenchyma may also be present as narrow bands, as in *Acanthogilia gloriosa* (Fig. 26, 28) or wider bands, as in *Ipomopsis aggregata* (Fig. 19, 22). Parenchyma is more abundant in earlywood than in latewood of *Er-
Fig. 19-23. Wood sections of *Ipomopsis aggregata* (*Hall 5138*).—19. Transection. Rays are nonlignified.—20. Tangential section of fascicular area. No rays evident.—21. Tangential section showing rays, latewood vessels in a parenchyma matrix.—22. Portion of transection showing latewood (center). Latewood vessels are surrounded by parenchyma.—23. Radial section of latewood vessels in parenchyma band. Radially much widened, alternate bordered pits present on vessels (Fig. 19-21, magnification scale above Fig. 1; Fig. 22, scale above Fig. 3; Fig. 23, scale above Fig. 4.)
iastrum densifolium, but is not present as a band. The banded parenchyma of A. gloriosa and I. aggregata can be grouped with the thin-walled libriform fibers of Cantua (Fig. 5), and all are probably manifestations of fiber dimorphism (Carlquist 1958). Axial parenchyma is more abundant in Cobaea scandens than in other Polemoniaceae, but cells may be distributed variously and do not appear referable to fiber dimorphism; perhaps the parenchyma distribution in this species represents increase in abundance of vasicentric parenchyma.

Axial parenchyma cells are subdivided into strands of two to three cells in the taxa with shorter fusiform cambial initials, as in Eriastrum densifolium; strands are longer (three to five cells) in species with longer cambial initials, as in Cantua flexuosa (Fig. 7).

Vascular rays.—Rays may be present or absent in Polemoniaceae. Leptodactylon may be deemed basically rayless, as noted earlier (Carlquist 1970). Most samples in this genus are entirely rayless (e.g., Fig. 34), but larger wood samples may have a few inconspicuous rays one or two cells high (Fig. 36). Eriastrum densifolium can be termed near-rayless; woods lack rays near pith, but stems which are more than three years old show presence of rays, and a nearly normal-appearing complement of rays occurs in stems five years old or older. Huthia is rayless at first; the specimen of H. longiflora (Fig. 14) showed no rays at all. Cobaea scandens (Fig. 1, 3) lacks rays.

As can be seen from the data in Table 1, most Polemoniaceae have both multiseriate and uniseriate rays. This is illustrated here for Cantua flexuosa (Fig. 6), C. buxifolia (Fig. 11), Loeselia mexicana (Fig. 16), Ipomopsis longiflora (Fig. 25), Acanthogilia gloriosa (Fig. 27, 30), and Ipomopsis rubra (Fig. 32). In the genera which are not rayless or near-rayless, multiseriate rays are more frequent than uniseriate rays. In Ipomopsis aggregata (Fig. 20, 21), uniseriate rays are so scarce they may be regarded as effectively absent. In Acanthogilia gloriosa (Fig. 30) and Ipomopsis tenuifolia, all rays are uniseriate close to the pith, but some of these become multiseriate later on (Fig. 27), although in these species uniseriate rays remain more abundant than multiseriate rays.

Procumbent ray cells predominate in rays of only a few species: Cantua buxifolia (in Carlquist 7025, the larger of the two samples studied), C. flexuosa (Fig. 6), in which the wood sample was the largest studied in the family, and Ipomopsis aggregata (Fig. 21). In Acanthogilia gloriosa, the smaller stems have rays composed of erect cells only (Fig. 20), whereas in the large stems, rays are composed predominantly of procumbent cells in the central portions of multiseriate rays, with uniseriate wings of multiseriate rays and uniseriate rays composed of erect cells. In Cantua cuzcoensis, erect and procumbent cells were observed to be about equally frequent, with approximately square cells predominating. With the exception of the species named above in this paragraph, erect ray cells exclusively compose the rays of
Fig. 24–27. Wood sections of *Ipomopsis* and *Acanthogilia*. — 24–25. *Ipomopsis longiflora* (*Waterfall 10355*). — 24. Transection. Vessels are mostly not grouped. — 25. Tangential section. Uniseriate rays outnumber multiseriate rays, all cells erect. — 26–27. *Acanthogilia gloriosa* (*Michener 4241*). — 26. Transection. Two parenchyma bands in lower half of photograph. — 27. Tangential section. Multiseriate rays present, with procumbent cells in center of rays; uniseriate rays more abundant than multiseriate rays. (Fig. 24–27, magnification scale above Fig. 1.)
Polemoniaceae studied. One may note that these species can all be described as near-rayless.

Ray cells are moderately thin and lignified throughout the species studied, and pits interconnecting ray cells lack borders. The rays in *Ipomopsis aggregata* (Fig. 19, 21) are thin-walled, however, with no lignification. The rays in this species are also exceptionally tall and wide. In other species, width of rays, whether expressed in microns (Table 1, column 12) or cells (column 13) is greater in larger and older specimens of a species as compared to ray width in smaller specimens of those species, respectively.

**Other features.**—Polemoniaceae can be characterized as having nonstoried wood structure. However, vague storying could be seen in a few places in wood of *Loeselia mexicana* (Fig. 16). Starch was observed in rays, axial parenchyma, and tracheary elements of *Acanthogilia gloriosa* and *Cantua flexuosa*. Presence of starch in imperforate tracheary elements means that they must be regarded as nucleate. Absence of starch in collections other than those of the two species may be attributed at least in part to method of preservation (drying) and treatment (boiling, soaking in ethylene diamine) before sectioning.

**SYSTEMATIC CONCLUSIONS**

There is considerable diversity in wood anatomy of Polemoniaceae, apparently as a result of shift into various habits and habitats. Because the habits of the family include shrubs, vines, annuals, and perennials of various growth forms, and because these various habits relate to a wide range of habitats (mostly dry, except for *Cobaea*), few “marker” features with a distinctive systematic rather than habital or ecological distribution can be cited. In discussing systematic application of data, the scheme of the family offered by Grant (1959) may be used as a framework:

- Tribe A. Cobaeae: *Cobaea*
- Tribe B. Cantuae: *Cantua, Huthia*
- Tribe C. Bonplandieae: *Bonplandia, Loeselia*
- Tribe D. Polemonieae: *Polemonium, Allophyllum, Collomia, Gymnosteris, Phlox, and Microsteris*
- Tribe E. Gilieae: *Gilia, Ipomopsis, Eriastrum, Langloisia, Navarretia, Leptodactylon, Linanthus, Acanthogilia*

A basic pattern can be said to be common to the wood of all of these tribes. Features common to all species studied include: vessels with simple perforation plates; vessel walls with circular (or elliptical) nonvestured bordered pits on lateral walls, with or without accompanying helical sculpture; imperforate tracheary elements are tracheids (fiber-tracheids and libriform fibers in some phylads as specializations); axial parenchyma vasicentric scanty
Fig. 28–32. Wood sections of Acanthogilia and Ipomopsis. —28. Acanthogilia gloriosa (Day 76-129). —28. Transection. Three parenchyma bands of different degrees of distinctness seen. —29. Wall of vessel from radial section. Very faint ridges present in pairs beside pits. —30. Tangential section. Most rays uniseriate; all ray cells erect. —31–32. Ipomopsis rubra (Moore 6814). —31. Transection. Vessels in variously long radial rows. —32. Tangential section. Uniseriate rays more common than multiseriate rays, all ray cells erect. (Fig. 28, 30, magnification scale above Fig. 3; Fig. 29, scale above Fig. 4; Fig. 31–32, scale above Fig. 1.)
(banded parenchyma probably an innovation, not a modification of vasicentric scanty parenchyma in the taxa where bands occur); rays both multiseriate and uniseriate (one or the other absent in some taxa, evidently a specialization); ray cells erect except for central portions of multiseriate rays (rays all uniseriate near pith a specialization, raylessness probably not ancestral to the family but a specialization of certain genera within it).

The problem in defining a basic pattern and deriving others from it is that no genus in Polemoniaceae is primitive with respect to all features. *Cantua*, which has what one would term a primitive ray condition, has fiber-tracheids (with much reduced borders) or libriform fibers rather than tracheids. The genera with tracheids (*Eriastrum, Leptodactylon, Phlox*) seem specialized in having rayless or near-rayless structure, on the other hand. If one were to imagine a wood of a polemoniaceous plant primitive in all respects, one would choose, according to currently accepted concepts of primitiveness in dicotyledonous woods, the rays of *Cantua* combined with the tracheids of *Eriastrum, Leptodactylon, Phlox*, or *Ipomopsis tenuifolia*. This hypothetical primitive pattern assumes that the evolution from tracheids to fiber-tracheids to libriform fibers is unidirectional. Although patterns in wood evolution do tend to support this generalization, one cannot say categorically at this point in our knowledge of wood anatomy that no degree of reversion can occur. Interestingly, the genera with tracheids are all north-temperate in distribution; *Cantua, Cobaea, Huthia*, and *Loeselia* all have fiber-tracheids with vestigially-bordered pits or libriform fibers. Absence of tracheids in the South American genera might have forestalled radiation of these phylads into dry habitats, whereas the physiological advantages of tracheid presence (localization of air embolisms to imperforate cells) may have permitted radiation of the north-temperate genera into numerous habitats of a dry nature.

The wood of Polemoniaceae is remarkably diverse, but the patterns are compatible with a hypothesis that the family is monophyletic. The only genus seriously questioned as belonging to Polemoniaceae is *Cobaea*, which is sometimes recognized as a segregate family (e.g., Dahlgren 1980). To be sure, the vining habit of *Cobaea* and the anatomical consequences of that habit would make it a distinctive element in any family in which it was the only vining species. The presence of vessel dimorphism in *Cobaea* is not a characteristic merely of that genus, but is widespread in all vines (Carlquist 1981). The abundance of axial parenchyma in *Cobaea* is also not unusual in vines. The absence of rays in *Cobaea* is indeed unusual; to the best of my knowledge, raylessness has not been reported in a dicotyledonous vine hitherto. However, raylessness and near-raylessness in Polemoniaceae are characteristics which may indicate that the rayless condition in *Cobaea* might be an indicator of its systematic affinity. Although pollen of *Cobaea* is distinctive (Erdtman 1953), it resembles that of Convolvulaceae or Polemoniaceae in its polyporate nature more closely than it resembles pollen of any
other family. The chromosome number of *Cobaea* is $2n = 52$ (Grant 1959). The hypothetical number $x = 9$ occurs in all of the other subfamilies of Polemoniaceae (along with putatively derived numbers in some tribes), and one might regard the chromosome number of *Cobaea* as a slight deviation from the hexaploid number $2n = 54$, which is, in fact, found in *Cantua* (Grant 1959). The pinnate leaves of *Cobaea* show resemblance to those of certain other Polemoniaceae (e.g., *Polemonium*). In sum, although *Cobaea* is easily the most distinctive genus in Polemoniaceae, it probably fits more closely into the concept of Polemoniaceae than into the bounds of any other family; whether or not to recognize it as a monogeneric family then becomes a matter of how one wishes to stress distinctiveness of genera by means of familial rank.

If one compares the hypothetical basic pattern of woods in Polemoniaceae to the wood anatomy reported for other families of tubiflorous dicotyledons, one can find other families in which tracheids are present: Convolvulaceae (Metcalfe and Chalk 1950; Mennega 1969), Hydrophyllaceae (Carlquist et al. 1983; Carlquist and Eckhart 1984), Goodeniaceae (Carlquist 1969) and Dipsacaceae (Carlquist 1982b). Although most Solanaceae and Boraginaceae have libriform fibers, tracheids have been reported in a very small number of species in those families (Metcalfe and Chalk 1950). Degrees of difference between the wood patterns of Polemoniaceae and those of other families are probably greater (e.g., Verbenaceae, Bignoniaceae) and therefore need not be considered at present. Convolvulaceae and Solanaceae are the families most frequently cited as close to Polemoniaceae (Cronquist 1981; Dahlgren 1980; Takhtajan 1980; Thorne 1976). Since wood anatomy does not conflict with this placement, a detailed comparison of wood anatomy of Polemoniaceae with families other than Convolvulaceae and Solanaceae does not seem warranted at present. One may select, however, one other feature—chromosome number—to show that the situation is not a simple one, and that evolutionary patterns in the tubiflora families of dicotyledons need further elucidation. If $x = 9$ is the basic number for Polemoniaceae, the only other families with $x = 9$ mentioned in this paragraph are Hydrophyllaceae, Dipsacaceae, and Goodeniaceae (the latter also has $x = 8$ and 7), using the compilation of Raven (1975) as a guide. Convolvulaceae appear to be based on $x = 7$, Solanaceae on $x = 12$ according to Raven. Obviously integration of numerous kinds of evidence is needed.

### EVOLUTION OF HABIT

Is the Polemoniaceae primitively woody, secondarily woody, or possibly both? A wood such as that of *Cantua* or of *Loeselia* shows no evidence of secondary woodiness. One might have wished wood in these genera to have tracheids, and thus be primitive in all respects so as to serve as a basic plan.
for the family. Similar considerations apply to *Acanthogilia* and *Ipomopsis* (specialized in some species, however, in having only uniseriate rays near the pith). The presence of both multiseriate and uniseriate rays in the four genera just named is the condition hypothesized to be primitive in dicotyledons (Kribs 1935). Increase in width of the multiseriate rays and in procumbency of cells in the multiseriate rays during growth of the stem both occur in these genera, and are features cited as typical of dicotyledonous woods by Barghoorn (1941a). The occurrence of raylessness introduces other possibilities, however. We must note that raylessness and near-raylessness are essentially identical, since woods which begin as rayless often eventually do develop rays as growth continues, although some never acquire rays (Barghoorn 1941b). Raylessness seems to characterize phylads which are in the process of evolving from an herbaceous ancestry to a somewhat woodier condition; raylessness thus represents a sudden conversion of potential ray areas, which would be mechanically weak, into imperforate tracheary elements, which are mechanically stronger (Carlquist 1970). It is too early in the progress of comparative studies of wood to assert unequivocally that raylessness always must indicate phylesis from herbaceous to woody. Rayless annuals are few (Carlquist and Eckhart 1984); although minimally woody, annuals are not necessarily exceptions to the idea of phylesis from herbaceous to woody in rayless phylads; adaptation to erect habit may favor production of fibers rather than rays, for example.

The pervasive presence of erect ray cells in Polemoniaceae suggests an herbaceous tendency in many of the genera, since tubiflorous families of dicotyledons generally have procumbent cells fairly abundantly in multiseriate rays of woody species, less abundantly in herbaceous species (e.g., Asteraceae, Carlquist 1966). In a species in which erect ray cells are present exclusively, and in which short fusiform cambial initials occur (and thereby short imperforate tracheary elements) only minor modification is necessary to convert potential ray areas to zones of fibers. Although criteria for herbaceousness in wood anatomy are few, the wood of *Cantua* and *Loeselia* seems to offer no contradiction to a hypothesis that Polemoniaceae may have had a woody ancestry. However, Polemoniaceae if primitively woody may have shifted rapidly to herbaceous modes of structure, and probably ancestors were not very woody in any case. The tribes Polemoniæae and Gilieæae may be ancestrally herbaceous. The ancestors of the rayless and near-rayless genera *Cobaea*, *Eriastrum*, *Leptodactylon*, and *Phlox* can be hypothesized to have been herbaceous. *Cantua* seems to form shrubs of indefinite size, whereas the relatively finite size of *Leptodactylon* shrubs may be related to its rayless or near-rayless nature.

The ratio between imperforate tracheary-element length and vessel-element length is smallest in the genus *Leptodactylon*, greatest in *Cantua*. Although this ratio is in general not at all an indicator of habit, but over
broad areas of dicotyledons an indicator (high values) of specialization, the low value in *Leptodactylon* may be related to the rayless nature, since imperforate tracheary elements must simulate ray cells in length for raylessness to occur. There is no apparent relationship between values for this ratio and whether tracheids or libriform fibers are the imperforate tracheary element in genera of Polemoniaceae.

Wide vessels and vessel dimorphism are characteristic of *Cobaea*, just as in other vines (Carlquist 1981). As noted above, the rayless nature of *Cobaea* is an unusual one for vines, however. *Cobaea* never becomes a strikingly woody vine, however; its diameter and longevity are finite. Therefore, wide zones of thin-walled parenchyma (rays) which would provide flexibility among fascicular areas as they evidently do in woody vines are not of selective value in *Cobaea*. Alternatively, raylessness may be regarded as a limitation which has prevented *Cobaea* from evolving into a woody vine.

**ECOLOGICAL CONCLUSIONS**

Three quantitative features were used to develop the indices Vulnerability (Table 1, column 16) and Mesomorphy (column 17): vessel diameter, number of vessels per mm$^2$, and vessel-element length. These indices show that only *Cobaea* and *Cantua* can be termed mesomorphic based on wood anatomy. The other species have mesomorphy values that extend from 111 downward to 4.6. Notably low values characterize *Leptodactylon* and *Phlox diffusa*. In the genera other than *Cantua, Cobaea, Leptodactylon,* and *Phlox*, wood anatomy may not be closely keyed to the environment because stems can die back to a woody caudex, thereby rendering adaptations of those stems to dry conditions irrelevant: in *Leptodactylon* and *Phlox diffusa*, which have evergreen leaves, such dieback does not occur, so wood and leaf anatomy must represent effective adaptations to the water relations problems presented by extended dry (and/or cold) seasons. Even *Cantua* has a habit which minimizes the necessity for adaptation by wood anatomy to a dry climate. *Cantua* is branched from the base, and size of shoots produced and thereby added to the water economy of the plant, or extent of shoots which die and thereby are withdrawn from the water economy of the plant, relate to the abundance of rainfall during a season. In addition, size and number of leaves, and production of long shoots and short shoots differentially are other mechanisms *Cantua* has for taking advantage of wet seasons or surviving dry ones. A plant with leaves and wood closely adapted to dry conditions is probably less well able to take advantage of wet seasons than one which is more flexible.

There is a steady fall in vessel-element length during growth of a stem in Polemoniaceae. This is what would be predicted in a predominantly herbaceous group of dicotyledons according to the theory of paedomorphosis
(Carlquist 1962). Obviously shorter vessel elements characterize some species and genera (*Leptodactylon*), longer ones other species and genera (*Cantua*) in the family. However, within any given species, length of vessel elements seems primarily related to age of plant. Of course, the older the plant, the shorter the vessel elements would mean that if short vessel elements confer greater xeromorphy to a wood, older plants are more xeromorphic.

The nature of imperforate tracheary elements in the family is unusually diversified for a family of dicotyledons. The most notable aspect of this is the presence of tracheids in *Eriastrum densifolium, Ipomopsis tenuifolia, Leptodactylon* (all taxa), and *Phlox diffusa*, with fiber-tracheids and libriform fibers in the other taxa studied. The ecological value of woods in which tracheids occur has been stressed and related to desert and dry chaparral habitats (Carlquist 1980). Radiation of woody *Eriastrum* and *Leptodactylon* species into a large series of dry habitats (some of them very dry and some physiologically dry because of freezing in winter) may be based on this anatomical characteristic. The absence of tracheids in the South American genera and in *Loeselia* may account for the relatively restricted patterns of radiation of those genera into dry habitats.

In the taxa in which tracheids occur, vessel grouping would be expected to be very low—perhaps below 1.3 or 1.4—according to a theory offered elsewhere (Carlquist 1984). That value is exceeded in some of the collections of the tracheid-bearing taxa, although only by a little (Table 1, column 5). Values in excess of 1.3 might be the result of counting overlapping ends of two fibriform vessel elements in a vertical file as two vessels rather than one. Also, where number of vessels per mm$^2$ is very elevated, as it is in Polemoniaceae of xeric habitats, chance dictates that more numerous contacts occur between vessels than would be the case if vessels per mm$^2$ were few. If vessels are confined to earlywood very largely, and if they are relatively large in diameter, the chance of contacts resulting in groupings is greater than if vessels were narrower than they are in earlywood and if vessels were randomly distributed throughout a growth ring. Thus the theory of vessel grouping (Carlquist 1984) is still applicable. In the taxa of Polemoniaceae with fiber-tracheids or libriform fibers, vessel grouping does offer an avenue of safety through redundancy.

Various forms and degrees of helical sculpture occur in Polemoniaceae. Helical sculpture does appear to be correlated with xeromorphy, and *Leptodactylon*, which tends to be the most xeromorphic genus in most respects, has the most pronounced helical sculpture in vessels.

Growth rings vary within Polemoniaceae. Relatively mild growth-ring activity (Type I) is evidenced by *Cantua, Huthia*, and *Loeselia*; all of these are subtropical. Type I growth rings also occur in species of *Ipomopsis* with short-lived stems (some lasting only a single year). The species designated as having Type V growth rings show not only wider but more numerous
vessels in earlywood and have tracheids as imperforate tracheary elements. Vessels tend to be fewer in latewood than earlywood (VB, VD) and the tracheids may be wider in earlywood than in latewood (VD). Vessels may be absent in latewood or nearly so (VA). These distinctive types of growth-ring activity seem related to the highly seasonal climates, featuring long periods of drought or cold, in which Leptodactylon and Phlox diffusa grow. The latewood in Type V growth rings has maximal safety (greatest in VA) because tracheids are the cell type most abundant in latewood.

Seasonal production of parenchyma in addition to vessel diameter fluctuation characterize Type XI growth rings (Acanthogilia, Eriastrum, Ipomopsis aggregata). Seasonality of parenchyma and its possible significance in a dry climate have been explored in an accompanying paper (Carlquist and Eckhart 1984). Starch reserves in parenchyma may serve not only for production of new foliage and flowers, but for innovation and maintenance of conduction by virtue of the increased osmotic pressure that hydrolysis of starch into sugar might create. Where vessels or vessel groups are surrounded by parenchyma in latewood bands, as in Ipomopsis aggregata, laterally widened pits tend to occur, simulating the situation seen in some Hydrophyllaceae (Carlquist and Eckhart 1984).

Banded parenchyma in Polemoniaceae may be seen in its most incipient form in Cantua, where bands of thinner-walled libriform fibers or fiber-tracheids are produced annually or seasonally. This seems an instance of fiber dimorphism (Carlquist 1958). The well-marked narrow parenchyma bands in Acanthogilia gloriosa and the conspicuous wider bands of Ipomopsis aggregata would be the end products of such fiber dimorphism. These two species occur in some notably dry localities, and the seasonal parenchyma bands are very likely related to xeric ecology.

LITERATURE CITED


Footnote

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