Wood, stem, and root anatomy of Basellaceae with relation to habit, systematics, and cambial variants

SHERWIN CARLQUIST
Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, California 93105 U.S.A.

Accepted: June 24, 1997

Summary

Wood data from wider stem, root, and root-stem transition of a mature plant of Anredera baselloides are analyzed for quantitative and qualitative features. Distinctive characters of A. baselloides include presence of successive cambia in wider stem, root, and root-stem transition; other types of cambial variants are newly reported for the family. Systematic distribution of successive cambia in Caryophyllales does not parallel cladistic schemes for the order, and possible reasons are advanced. Wood features other than successive cambia are compatible with relationship to the other families of Portulacinae (Cactaceae, Didiereaceae, Hectorellaceae, Portulacaceae) except for features related to habit, particularly the scandent habit. These features (mostly newly reported for Basellaceae) include restriction of vessels to central portions of fascicular areas (vessels thereby likely protected from torsion); some vessels wide but many narrow; all ray cells and ray-adjacent axial parenchyma with thin walls; (interxylary) phloem strands in ray-adjacent axial parenchyma (with cambia that augment the phloem strands); and intraxylary phloem. Tubers contain pith phloem strands adjacent to which cambia produce secondary xylem and phloem. Druses and mucilage cells in cortex and rays and storying in axial xylem cells are newly reported for Basellaceae.

Key words: "Anomalous" secondary growth, cambial variants, Caryophyllales, Centrospermae, lianas, successive cambia.

1. Introduction

The family Basellaceae (4 genera, 40 species: CRONQUIST & THORNE 1994) is of special interest within Caryophyllales in a number of respects. All species are vining or lianoid, a habit relatively unusual in the order, although found in agdestoid and petiverioid Phytolaccaceae, Bosea (Amaranthaceae), Bougainvillea (Nyctaginaceae), and a few species of pereskioid cacti. The family is also distinctive in its tubers, which are not like stems elsewhere in Caryophyllales. The stems, roots, and tubers are capable of indefinite longevity in some species, such as the one studied here, Anredera baselloides, for which an unusually mature specimen was available. Numerous anatomical characteristics of wood, stems, and roots are reported for the first time because of the excellence of this material. Only stems of limited diameter were available to METCALFE & CHALK (1950) and GIBSON (1994).

The likelihood that wood anatomy is strongly influenced by the scandent habit of Basellaceae provides problems in systematic interpretation in wood anatomy. Basellaceae have been placed in the suborder Portulacinae (THORNE 1992, BEHNKE 1994, CRONQUIST & THORNE 1994, NOWICKE 1994, 1996), which is usually construed as containing Cactaceae, Didiereaceae, Hectorellaceae, and Portulacaceae. RODMAN et al. (1984) and RODMAN (1994) made a case for inclusion of Aizoaceae in the same clade as the families of Portulacinae (but see MANHART & RETTIG 1994).

Cactaceae, Didiereaceae, Hectorellaceae, and Portulacaceae lack successive cambia (METCALFE & CHALK 1950, RAUH & DITTMAR 1970, GIBSON 1994, CRONQUIST 1998). Anredera baselloides (H. B. K.) BAillon, Basella rubra L., and Ullucus tuberosus CALDAS of the Basellaceae were reported to have successive cambia (MOROT 1884, PFEIFFER 1926), and successive cambia are mentioned for the family by PANIKKAR & BHAMBIE (1974); more recent authors have not mentioned these reports. In addition, cambial variants other than successive cambia are present in A. baselloides and are described below. The distribution of successive cambia in Caryophyllales is of considerable potential phyletic significance: about half of the families and genera of the order have successive cambia, but the systematic distribution of these taxa does not correspond in a parsimonious fashion with the position of these taxa in cladograms. Therefore, successive cambia
present a curious situation in the interpretation of phyl
lesis of Caryophyllales. Genetic, developmental, and
functional nature of successive cambia in the order are
in need of elucidation, and Basellaceae are central to
analysis of these questions. In Caryophyllales, success-
usive cambia can be found in succulent roots (Caryo-
phyllales, Chenopodiaceae, Nyctaginaceae: PFEIFFER
1926, METCALFE & CHALK 1950) as well as lianaid
stems (Nyctaginaceae: ESAU & CHEADLE 1969) or in
stems subshrubs (Heliophytum: GIBSON 1978) or trees
(Phytolaccaceae: WHEAT 1977, MIKESSELL 1979), so
factors other than habit must be involved. Caryophylla-
les in general, and Basellaceae in particular, are keys to
understanding of structure, functional significance, and
phylogenetic nature of successive cambia in vascular plants.

The materials studied here may all belong to a single
species, A. baselloides (H. B. K.) BAILLON (see below).
This is not regarded as a limitation to the present study,
the purpose of which is to establish the presence of par-
ticular histological features rather than to explore diver-
sity within the family. Anredera baselloides, however,
may attain a large size than other species in the family,
and thus may represent the nature of wood and cambial
activity and other histological features in stems and
roots better than immature material of other species.
New data on Basellaceae are important because a series
of studies on Caryophyllales is in progress, and more
data on character states of these families are needed to
develop concepts of evolution of anatomical conditions
in the order. Data on Didiereaceae (RAUH & DITTMAR
1970) and Cactaceae (several papers by GIBSON, see
GIBSON 1994) have been contributed by others. The pre-
sent series includes a study of Caryophyllaceae (CARL-
QUIST 1995) and Portulacaceae (CARLQUIST & BOGGS
1998), as well as a study of a family considered an outgroup
of Caryophyllales, Plumbaginaceae (CARLQUIST & BOGGS
1996).

2. Materials and methods

All specimens were fixed in 50% aqueous ethanol; stems
and roots of Basellaceae are too succulent for drying to be
a feasible means of preservation. Liquid preservation is ad-
avantageous in fixing thin-walled cells such as mucilage cells,
phloem, and parenchyma, whereas woody dicotyledons have
wood that often consists wholly of cells with rigid lignified
walls. Sections were prepared using the schedule of CARL-
QUIST (1982), in which ethylene diamine is employed as a sof-
tening agent prior to paraffin sectioning. Wide vessels and
fibrous tissue embedded in a background of thin-walled tissue
cannot be satisfactorily sectioned on a sliding microtome. Sec-
tions were stained with a safranin-fast green combination.
Macerations of secondary xylem were prepared with Jeffrey’s
solution and stained with safranin.

The mature specimen that forms the basis for the descrip-
tions below is clearly referable to Anredera baselloides
[= Boussingaultia baselloides H. B. K. and Anredera scandens
(L.) MOOJ]. This plant was supplied to me by STEVE MORGAN
(Botanic Garden, University of California at Riverside), it was
probably at least 40 years old, and had been cultivated at a
residence in La Verne, California. The portions designated as
"upper stems" were not twigs but upper portions of the main
stem, about 2 cm in diameter. The root-stem transition features
a swollen form, wider than the stem above this region and
about 10 cm in diameter. The root selected for sectioning was
a portion of the main root about 5 cm in diameter. The tubers
are potato-like branches from the main stem at ground level,
and were about 3 cm in diameter in the plant studied. Stem and
root materials of relatively large specimens identified as Bouss-
ingaultia cordifolia TENORE and B. gracilis MIERS were
available through the courtesy of the Los Angeles State and
County Arboretum, Arcadia, California. ULRICH (1934) con-
cluded that these two taxa are conspecific with A. baselloides.
However, SPERLING (1987) found that both B. cordifolia and
B. gracilis belong to a species separate from A. baselloides,
and that this species should be called Anredera cordifolia
(TENORE) STEENIS. No anatomical differences (except those
related to the occurrence of vessels in the central portionsof fascicular areas, with libriform fibers adjacent to rays. In determin-
ing number of vessels per mm² of transsection, ray areas were excluded from
the portions surveyed here. Had rays been included, the figu-
res for vessels per mm² would have been much lower, especially
in tubers. Number of vessels per group is calculated as a
solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc.;
however, the narrow vessels adjacent to wide vessels are so
numerous that number of vessels cannot be accurately calcu-
lated. Vessel lumen diameter is measured as an average be-
tween wide and narrow axes of a vessel lumen as seen in trans-
section in order to present a more accurate image of the rhe-
ological capabilities of vessels. Both wide and narrow vessels
were included in the means, although the two categories were
also studied separately with respect to vessel element length.

Figs. 1-4. Photographs of sections of stem of Anredera basel-
loides. 1-2. Transsections. 1. Section to show formation of a
second increment of vascular tissue (above) by a cambium
formed in the cortex; vascular tissue formed by the first cam-
bium below (sp = secondary phloem, sx = secondary xylem).
2. Vascular tissue formed by cambium that originated in the
stem cortex; thin-walled axial parenchyma partially subdivi-
des the fibrous portions of the secondary xylem. 3. Tangential
section to show histology of fascicular area and ray portion
dr = druse, If = libriform fiber, mc = mucilage cell, wv = wider
vessel). 4. Vessel wall from tangential section; grooves inter-
connect pit apertures (above). Fig. 1, scale above Fig. 1 (finest
divisions = 10 μm); Fig. 2, scale above Fig. 2 (divisions
= 10 μm); Fig. 3, scale above Fig. 3 (divisions = 10 μm); Fig.
4, scale above Fig. 4 (divisions = 10 μm).
The term “pseudoscalariform” refers to lateral wall pits of vessels in which the pit is laterally elongate, like a scalariform pit but derived from an alternate pattern (whereas ends of scalariform pits are aligned to wall angles). All quantitative data are derived from products of the first cambium.

3. Anatomical descriptions

The anatomy of the upper stem (2 cm diameter) is described completely; the root and the root-stem transition descriptions omit items in which structural conditions are identical to those of the upper stem. Illustrations prepared from the root and for the root-stem transition are however, cited under those categories.

Upper stem (Figs. 1–4). Successive cambia present, products of a second cambium observable in the material available (Figs. 1, 2). Accumulation of secondary xylem and phloem much less than that produced by the first cambium, but orientation similar. Intraxylary phloem present adjacent to pith. Growth rings absent. Mean number of vessels per group, > 15. Vessels dimorphic in diameter, the narrow vessels located mainly in radial strips interconnecting the groupings of wider vessels. The portions of fascicular areas adjacent to rays are composed of libriform fibers and strips of thin-walled axial parenchyma; the libriform fibers and thin-walled axial parenchyma may be described as ray-adjacent, therefore. Mean vessel diameter, 31 μm. Mean number of vessels per mm², 251. Mean vessel element length, 221 μm; mean length of wide vessels, 182 μm; mean length of narrow vessels, 264 μm. Mean thickness of vessel wall, 2.2 to 7.2 μm (wider vessels are thicker walled). All vessels with simple perforation plates. Lateral wall pitting composed mostly of oval pits (Fig. 4), the axial diameter of which is about 12 μm. Grooves intersect some pit apertures (Fig. 4, above), and some pits are quite elongate laterally (pseudoscalariform), especially on the wider vessels. All imperforate tracheary elements are libriform fibers with minute slitlike simple pits. Mean length of libriform fibers, 405 μm. Mean wall thickness of libriform fibers, 2.8 μm. Axial parenchyma present as scanty vasicentric cells with lignified walls formed in strands of two cells. Axial parenchyma also present as thin-walled cells adjacent to rays; in transsection, these parenchyma zones appear as indentations in the outlines of the fibrous fascicular xylem (Fig. 2, bottom; see also Fig. 7, lower right). Ray-adjacent axial parenchyma in strands of two cells or not subdivided; a few strands subdivided into strands of four or more cells each of which contains a druse also present in the ray-adjacent axial parenchyma. Phloem strands present within some of the ray-adjacent axial parenchyma. Rays multiseriate only, mean width = 7.8 cells. Mean ray height > 500 μm. Rays composed of thin-walled nonlignified cells. Ray cells most commonly square as seen in radial section, less commonly upright or procumbent. Mucilage cells and cells bearing a single druse each present in rays (Fig. 3). Vague storying present in vessels, axial parenchyma, and libriform fibers; storying clear in sieve-tube elements. Stem cortex with scattered druse-bearing idioblasts and scattered idioblastic sclereids or sclereid nests. Sclerenchyma very rare in secondary phloem; and only present in older secondary phloem. Sclerenchyma absent in periderm.

Root (Figs. 5, 6). Vascular tissue produced by a second (successive) cambium portions present in cortex, but the vascular tissue produced by them mostly oriented tangentially rather than radially. Vessel restriction present (Fig. 5, 6). Mean number of vessels per group, > 15. Mean vessel diameter, 36 μm. Mean number of vessels per mm², 301. Mean vessel element length, 206 μm; mean length of wider vessel elements, 173 μm; mean length of narrower vessel elements, 243 μm. Mean wall thickness of vessels ranging from 2.6 μm (narrower vessels) to 7.5 μm (wider vessels). Lateral wall pitting commonly composed of pits circular, polygonal, or oval in outline, about 12 μm in diameter; pseudoscalariform pitting common in wider vessels. Mean length of libriform fibers, 500 μm. Mean wall thickness of libriform fibers, 5.0 μm. Thin-walled axial parenchyma adjacent to the rays appearing as indentations in the fibrous margins of the fascicular areas (Fig. 5, upper right; Fig. 6, upper right). If fascicular areas are narrow, thin-walled axial parenchyma may interrupt radial continuity of the radial bands of fibrous tissue (Fig. 5, left of center). Ray-adjacent axial parenchyma frequently with phloem strands (Fig. 6, “rp”). Rays (other than those that are extensions of primary rays) originate in an abrupt fashion, rather than as uniseriate or biseriate rays that widen. Mean width of rays, 6.0 cells. Ray cells most commonly upright or square, less commonly procumbent. Occasional mucilage cells and occasional sclereids or sclereid nests in cortex, periderm free from sclerenchyma.

Root-Stem Transition (Figs. 7–13). Vascular strands produced from the second cambium oriented either radially or tangentially. Growth rings absent (Fig. 7). Divisions of secondary xylem of root (5–6) and root-stem transition (7–8) of Anredera baselloides. 5. Varied widths of fascicular areas; one near left appears discontinuous because fibrous strands alternate with axial parenchyma. 6. Two strands of ray-adjacent intraxylary phloem (rp). 7. Fascicular area in which abrupt origin of a multiseriate ray (above) has occurred. Section to show that libriform fibers (lf) are adjacent to a ray, whereas narrow vessels (nv) lie in the central portion of a fascicular area, between wider vessels; a strand of ray-adjacent phloem (light gray) is located above the strand of libriform fibers. Fig. 5, 7, scale above Fig. 2; Fig. 6, 8, scale above Fig. 3.
sions in parenchyma result in breakage and displacement of fascicular areas (Fig. 10). Vessels dimorphic in Diameter (Figs. 7, 8), the narrower vessels forming radial chains interconnecting the larger vessels. Number of vessels per group, > 15. Mean diameter of vessels, 38 \( \mu \text{m} \). Mean length of vessel elements, 184 \( \mu \text{m} \); length of wider vessel elements, 147 \( \mu \text{m} \); length of narrower vessel elements, 208 \( \mu \text{m} \). Lateral wall pits of vessels circular, about 12 \( \mu \text{m} \) in axial diameter with grooves interconnecting pit apertures; pits laterally elongate (pseudoscalariform) in some wider vessels (Fig. 12). Mean length of libriform fibers, 451 \( \mu \text{m} \). Mean wall thickness of libriform fibers, 2.8 \( \mu \text{m} \). Thin-walled axial parenchyma adjacent to rays in strands separated from each other by libriform fibers (Fig. 7–9). Thin-walled axial parenchyma cells in strands of one or two cells (Fig. 11). Phloem present in some of the ray-adjacent parenchyma strands (Fig. 8, 9, 12). Cambial activity that produces secondary phloem developing between libriform fibers and the phloem strands (Fig. 9, “c”). Rays composed of procumbent, square, and upright cells in about equal numbers.

Multiseriate ray height, >500 \( \mu \text{m} \). Mean width of multiseriate rays, 7.8 cells. Storying present in ray-adjacent axial parenchyma (Fig. 11), some libriform fibers, phloem within ray-adjacent axial parenchyma (Fig. 12, left), narrow and wide vessels and vasicentric axial parenchyma (Fig. 12, right). Sclereids in older parts of secondary phloem only, appearing to be sclereids derived from phloem parenchyma, not phloem fibers. Intraxylary phloem present adjacent to the crushed pith, but no cambial activity adjacent to phloem strands observed (Fig. 13).

Tubers (Figs. 14–16). No cambium present in cortex, and therefore no vascular tissue outside of the main cylinder. Only a single cylinder of bundles present, no successive cambia observed. Secondary growth much greater in fascicular areas of the cylinder of bundles; interfascicular cambium relatively inactive (Fig. 14, “ic”). Mean number of vessels per group, > 15. Mean vessel diameter, 32 \( \mu \text{m} \). Mean number of vessels per

---

Figs. 9–12. Sections from root-stem transition region of Anredera baselloides. 9–10. Transsections. 9. Fascicular area to show wide vessels (upper right and lower left) interconnected by narrow vessels; libriform fibers also present; ray-adjacent interxylary phloem strands at upper left and lower right with origin of a cambium (c) adjacent to one of these. 10. Fascicular area broken and displaced by differential growth in ray parenchyma. 11–12. Tangential sections. 11. Section through thin-walled ray-adjacent axial parenchyma, showing storied condition; some parenchyma cells in strands of two. 12. Section through strand ray-adjacent interxylary phloem (sieve plates indicate storied nature of sieve-tube elements), narrow vessels (nv) and portions of a wide vessel (upper right). Fig. 9, 11, 12, scale above Fig. 3; Fig. 10, scale above Fig. 1.

---

4. Conclusions

4.1. Habit

Characteristics of wood anatomy of lianas and vines (as contrasted with that of trees) include presence of notably wide vessels; dimorphism in diameter of vessels; fibrous axial xylem relatively small in volume compared to vessel elements; abundant axial parenchyma; and wide, tall rays (Carlquist 1975, 1985). Although successive cambia certainly occur widely in non-lianoid plants, they are relatively more common than "normal" (single) cambia in lianoid plants (Carlquist 1985). This is illustrated clearly in Gnetales, in which all of the lianoid species have successive cambia (although one non-lianoid species, Welwitschia mirabilis Hook. f., also has successive cambia). Anredera baselloides agrees with all of these characteristics, although in distinctive ways. For example, a sample of vines and lianas (Carlquist 1975, p. 206) showed a mean vessel diameter of 157 \( \mu \text{m} \); non-lianoid dicotyledons with successive cambia had a mean vessel diameter of 68 \( \mu \text{m} \). Anredera baselloides has a mean vessel diameter less than either of these: from 31 \( \mu \text{m} \) in stems to 36 \( \mu \text{m} \) in roots. The photographs suggest that vessels are wider than 36 \( \mu \text{m} \) on average (Figs. 1, 5, 7, 13), but the fact that there are numerous vessels is not so evident.

---

FLORA (1999) 194 7
at low as at high power (Fig. 8). Because both wide and narrow vessels are present, one can say that vessels are dimorphic (the wide vessels are shorter, another criterion for dimorphism). If frequency were plotted against either vessel diameter or vessel element length, a bi-modal curve would not be obtained: narrow vessels are numerous and would form a spike on a curve, but wide vessels are relative few, and would create an attenuation of the curve. The wide range of diameters is unusual except for instances of marked ring porosity (e.g., deciduous species of Quercus). Narrow vessels (in addition to wide ones) are not uncommon in lianas, and may confer conductive safety (Carlquist 1985).

Vessel elements do not elongate appreciably after derivation from fusiform cambial initials. The narrow vessels of A. baselloides may elongate during maturation, but probably not to a marked extent because greater elongation of tracheary elements would likely create a nonstoried appearance, but the tracheary elements of the species are storied (Fig. 12). The storied pattern of sieve tube elements (Fig. 12) is a little less evident than that of vessel elements or axial parenchyma (Fig. 11).

Vessel restriction patterns, with libriform fibers adjacent to rays but vessels in the central portions of fascicular areas as seen in transection, were described in Valerianaceae (Carlquist 1983), several Papaveraceae (Carlquist & Zona 1988 a) and Launaea of the Asteraceae (Carlquist 1988). More significantly, several types of vessel restriction can be seen in families that contain lianas, such as Convolvulaceae (Carlquist & Hanson 1991), Icacinaceae (Bailey & Howard 1941), and in two genera of Acanthaceae, Mendoncia and Thunbergia (Obaton 1960, Carlquist & Zona 1988 b). If one surveys the examples of vessel restriction patterns in lianas cited above, as well as patterns in Anredera, one often sees that the imperforate tracheary elements (mostly libriform fibers) tend to surround vessels, and that fiber-sheathed units of vessel groups are separated from each other by soft-walled parenchyma, either rays or axial parenchyma, or both. This suggests that fibrous tissue surrounded by soft-walled tissue serves in protecting vessels from torsion damage in lianas.

The vessels of A. baselloides are far more numerous per mm² (246–301) of transection than in most lianas because they are narrow and in much larger groups compared to the lianas sampled by Carlquist (1975), which average 19.1 per mm². The high number in A. baselloides would be lowered had rays and conjunctive tissue been included in the areas sampled, but the number would be halved, at most.

Another distinctive feature of some lianas shared by A. baselloides is the abrupt origin of wide rays. This phenomenon was illustrated in Aristolochia (Carlquist 1993).

In more 'typical' woody species, procumbent cells are much more abundant than upright or square cells in later-formed wood. In A. baselloides, procumbent cells are relatively less abundant, upright cells more abundant. This ray histology often characterizes phylads in which the ancestors were less woody (Carlquist 1988).

In general, cambial variants are comparatively more common in lianas and vines than in arboreal dicotyledons. The presence of successive cambia in Basellaceae might represent an adaptation to the habit rather than an indicator of phylogenetic relationship. However, one must take into account that there are several types of cambial variants other than successive cambia in Basellaceae.

Intraxylary phloem (phloem adjacent to bundles, at the periphery of the pith) is present in A. baselloides (Van Tieghem 1891). However, no cambial action related to intraxylary phloem could be detected. Cambia form adjacent to intraxylary phloem in Convolvulaceae (Carlquist & Hanson 1991) and Cucurbitaceae (Carlquist 1992) in species of lianoid habit. Intraxylary phloem potentially offers phloem strands in sites less likely to experience torsion than phloem strands at the periphery of a lianoid stem.

Pith strands of phloem in tubers of A. baselloides have cambial activity that produces both secondary xylem and secondary phloem. Scattered strands of xylem and phloem throughout the pith is a characteristic of tubers or tuberous roots such as potatoes and sweet potatoes (Metcalfe & Chalk 1950). Such strands potentially provide efficient input and withdrawal of photosynthates and water in a highly parenchymatous storage structure.

Initiation of phloem strands in axial parenchyma of A. baselloides is a structural feature not found in other Caryophyllales. Cambia eventually adjacent to them, apparently adding secondary phloem to the strand. These phloem strands qualify as interxylary phloem ('interxylary phloem' here denotes phloem within secondary xylem, but excludes phloem produced to the outside of a stem or root by successive cambia). The phloem strands of A. baselloides are much like those of

Figs. 13–16. Transections of Anredera baselloides. 13. Section of root-stem transition, to show intraxylary phloem strands (one labeled "ip") adjacent to the pith, which is crushed. 14–16. Sections from tuber. 14. Section of vascular tissue from main cylinder; interfascicular area shows the beginning of cambial action (ic) that will produce ray cells. 15–16. Vascular strands from pith of tuber. 15. Phloem strand to which a cambium (c) is adding secondary phloem. 16. Strand to which a cambium is adding both secondary xylem (center) and secondary phloem. Fig. 13, scale above Fig. 2; Fig.14–16, scale above Fig. 3.
another lianoid genus, *Coccinia* of Curcurbitaceae (CARLQUIST 1991). The intraxylary phloem strands in axial parenchyma in *A. baselloides* can be regarded as functionally similar to intraxylary phloem strands: dispersed strands of phloem in a stem are less likely to be damaged by torsion than are phloem strands at the periphery of the stems.

The occurrence of successive cambia in *Anredera* is curious. In the stems of “*A. cordifolia*” and “*A. gracilis*” studied, successive cambia were not observed, but stems and roots available for those species were smaller than those for the large plant of *A. baselloides* described in detail in the present paper. Only a single circle of vascular tissue forms outside of the first vascular cylinder in *A. baselloides*, so that only one additional cambium event occurs in this material, and the amount of xylem and phloem produced by this additional cambial event is relatively small. The additional cambial action thus occurs late in the development of a stem or root, and therefore the fact that successive cambia have not previously been reported for Basellaceae is understandable.

The limited quantity of tissue formed by the outer cambium (which does not form a continuous cylinder around the stem, but occurs as a series of cambium plates separated by cortical parenchyma) and the late appearance of the outer cambium suggests that adaptation to the lianoid habit may not be the only relevant explanation. Rather, the products of additional cambial action in *A. baselloides* may be a mechanism for providing vascularization of relatively wide structures: the stem base and root in a mature plant of *A. baselloides* are appreciably thicker than the stem above the ground surface. These thicker stem and root portions in *A. baselloides* may serve in storage of water and photosynthates, and thus additional vascularization may relate to that function. Successive cambia in Caryophyllaceae are, with virtually no exceptions, restricted to roots (METCALFE & CHALK 1950, CARLQUIST 1995). This suggests a relationship to a storage function for vascular tissue produced by successive cambia in Caryophyllaceae.

**4.2. Relationship of Basellaceae**

The vessel element length of *A. baselloides* (means ranging between 184 μm and 206 μm) is shorter than that of the liana sample in CARLQUIST (1975): 334 μm. Vessel element length in lianas probably bears relatively little relationship to habit (CARLQUIST 1985), but more likely is an indicator of phyletic specialization, as hypothesized by BAILEY and TUPPER (1918). They found notably short vessel elements in species with storied cambia, and *A. baselloides* has a storied cambium. Short fusiform cambial initials and vague storying also occur in the related family Portulacaceae (CARLQUIST, submitted).

The presence of exclusively multiseriate rays in *A. baselloides* is interesting, because that condition characterizes virtually all Portulacaceae (CARLQUIST, submitted). The pitting of vessels in *A. baselloides* is also similar to that of Portulacaceae. However, the question is not whether rays like those of Basellaceae can be found in another family of Caryophyllales, but whether the phyletic status of this ray type is compatible with the cladistic results obtained thus far in the order. Multiseriate rays plus uniseriate rays, as found in Didiereaceae (RAUH & DITTMAR 1970), is commonly regarded as more primitive than presence of multiseriate rays only (KRIBS 1935). This conflicts with cladograms involving these families. DOWNIE & PALMER (1994a, 1994b) showed Portulacaceae and Basellaceae as sister groups of Didiereaceae. The trees of RETTIG et al. (1992) and MANHART & RETTIG (1994) place Basellaceae as a sister group to Didiereaceae, Cactaceae, and Portulacaceae. Rodman (1994) shows Basellaceae close to Didiereaceae, with Portucaeaceae as a sister to both.

The role of successive cambia is of great interest in the systematics and phylogeny of Caryophyllales. The assumption is generally made (e.g., RODMAN 1994) that absence of successive cambia precedes presence of successive cambia. Basellaceae are generally placed in a suborder of Caryophyllales, Portulacineae (CRONQUIST & THORNE 1994), which consists of Basellaceae, Cactaceae, Didiereaceae, Hectorellaceae, and Portulacaceae. The results of RODMAN et al. (1984) and Rodman (1994) showed a clade corresponding to Portulacineae as defined above, with the exception that Aizoaceae appear in this clade in a basal position. Aizoaceae have successive cambia, whereas Cactaceae, Didiereaceae, Hectorellaceae, and Portulacaceae lack them. If the cladogram of Rodman (1994) represented the true phylogeny of these families, one would trace Caryophyllales from the outgroups Polygonaceae and Plumbaginaceae, which lack successive cambia except in Aegialitis (CARLQUIST & BOGGs 1996), a genus not usually considered basal in Plumbaginaceae (PAX 1891, THORNE 1992). Thus, successive cambia would have been invented in the order prior to Stegnospermaceae, a family that is placed basally in most cladograms of Caryophyllales. From this stock, successive cambia would have to be lost prior to origin of all of the clades in the order except that leading to Aizoaceae and lost prior to origin of Cactaceae and Portulacaceae, yet reinvented prior to origin of Basellaceae. The possible placement of character state changes in successive cambium presence on phylogenetic trees along with changes in other anatomical features will be shown graphically on trees in a concluding paper of this series.
The above imaginary sequences call attention to the problems of interpretation of successive cambia in Caryophyllales. As compared to other orders, relatively numerous families of Caryophyllales have successive cambia (Aizoaceae, Amaranthaceae, Basellaceae, Chenopodiaceae, Nyctaginaceae, Stegnospermaceae, and some Caryophyllaceae and Phytolaccaceae and segregates of Phytolaccaceae); the families in which successive cambia do not occur include Achatocarpaceae, Cactaceae, Didieriaceae, Hectorellaceae, and Portalulaceae (Balford 1965, Bedell 1980, Cronquist 1995, Esau & Cheadle 1969, Gibson 1994, Horak 1981, Michaelisell 1979, Wheat 1977). Cambial variants are reported in Barbeuia, Petiveria, Rivina, and possibly Agdestis by Pfeiffer (1926), and these genera need additional investigation. The distribution of successive cambia in Caryophyllales is not congruent with proposed phylogenies except for the pairing of Amaranthaceae and Chenopodiaceae, regardless of whose phylogenies are considered. The phylogenies are not necessarily incorrect. The distribution of successive cambia may involve developmental factors. For example, successive cambia appear quite late in Basellaceae. In the branches of Stegnosperma, successive cambia appear relatively tardily compared to their appearance in stems of other caryophyllalean families (Horak 1981). A similar situation occurs in Menispermae, in which most genera have been reported to have more than one cambium, but no successive cambia have yet been reported in some genera of that family (Metcalf & Chalk 1950). Most wood samples of Menispermae are not basal stems of maximal diameter, so that we do not know whether successive cambia might eventually appear in genera of Menispermae for which they have not yet been reported. Perhaps the genetic information required for formation of successive cambia originated early in the order Caryophyllales, but relatively minor genetic changes might be needed to activate, inhibit, or delay formation of successive cambia. When more wood and stem data on other families of Caryophyllales have been accumulated in the present series of papers, an attempt will be made to re-examine the systematic distribution, the diversity in types, and the phylogenetic status of successive cambia.

References


FLORA (1999) 194
Gibson, A. C. (1978): Rayless secondary xylem of Halo-
Heidelberg, pp. 45–74.
Horak, K. E. (1981): Anomalous secondary thickening in
Stegnosperma (Phytolaccaceae). Bot. Gaz. (Crawfords-
ville) 142: 545–549.
IAWA Committee on Nomenclature (1964): Multilingual
glossary of terms used in wood anatomy. Verlagsbuch-
anstalt Konkordia, Winterthur.
rays of dicotyledons. Bot. Gaz. (Crawfordsville) 96:
547–557.
data. In: Behnke, H.-D., & Mabry, T. J. (eds.): Caryo-
235–246.
Metcalfe, C. R., & Chalk, L. (1950): Anatomy of the dico-
Mikesell, J. E. (1979): Anomalous secondary thickening in
Nowicke, J. M. (1994): Pollen morphology and exine ultra-
167–221.
— (1996): Pollen morphology, exine structure and the rela-
tionships of Basellaceae and Didiereaceae to Portulaca-
Obaton, M. (1960): Les laines ligneuses à structure anormale
Bot., sér. 12, 1: 111–220.
secondary growth in some vascular plants. In: Puri, V.
et al. (eds.): Biology of the land plants. Sarita Prakashan,
Meerut, India, pp. 100–109.
(eds.): Die natürlichen Pflanzenfamilien IV (1). Verlag
Pfeiffer, H. (1926): Das abnorme Dickenwachstum. In:
Linsbauer, K. (ed.): Handbuch der Pflanzenanatomie
an Didiereaceae. 3. Teil. Vergleichend anatomische Unter-
suchungen an den Sproßachsen und den Dornen der
Didiereaceae. Sitzungsber. Heidelberger Akad. Wiss.,
logeney of the Caryophyllales – gene sequence data.
Taxon 41: 201–209.
—, Oliver, M. K., Nakamura, R. R., McClammer, J. U., &
tion, Harvard University, Cambridge, Massachusetts.
Thorne, R. F. (1992): Classification and geography of
H. (eds.): Die natürlichen Pflanzenfamilien. Ed. 2, 16e:
Van Tiegheim, P. (1891): Sur les tubes criblés extraliberiens
et les vaisseaux extralibreux J. de Bot. 5: 117–128.
Wheat, D. (1977): Successive cambial in the stem of Phytol-