STUDIES ON BIGELOWIA (ASTERACEAE), II. XYLARY COMPARISONS, WOODINESS, AND PAEDOMORPHOSIS

Loran C. Anderson *

MAJOR TRENDS IN XYLEM evolution discovered through the efforts of I. W. Bailey and his contemporaries have become generally accepted (see Carlquist, 1961; Esau, 1965; Fahn, 1967, for review). The apparent universality of the xylem trends has been of great comfort to systematists in their application of anatomic data to phylogenetic considerations. However, the concepts were developed by comparative studies, particularly among the Dicotyledoneae, in which the secondary xylem of woody shrubs and trees was used almost exclusively. This basis may provide an incomplete, perhaps biased, view of xylem evolution, as suggested by Carlquist (1962) in his study of juvenility in rosette trees and woody herbs. He concluded that woods from such growth forms may not be comparable to those from woody shrubs and trees. His further studies (1969a, 1969b, 1970a, 1970b) were directed toward understanding relationships between woody anatomy of herbaceous and woody species of angiosperms with special emphasis on insular forms. Cumbie (1963) reported in detail on cambial activity in *Hibiscus lasiocarpus*; nevertheless, little more has been done to compare continental herbaceous taxa with related woody ones.

The genus *Bigelowia* of the Astereae provides an excellent subject for such a study. These herbaceous rosette plants are frequently monocarpic (particularly so in the greenhouse), and appreciable amounts of secondary xylem are formed only in the caudex. The plants perennate through rhizomaty (in *B. nuttallii*) or produce offsets from the small caudices. (The caudex usually represents one year's growth; two or three growth rings develop only rarely.) Herbaceous forms in the Astereae are probably derived. Carlquist (1960) concluded his survey of the wood anatomy of the tribe with: "the evidence in Astereae, far from countering the well-established woody-to-herbaceous trend in dicots, seems to support it." Data on chromosome numbers reinforce that view (Raven, *et al.*, 1960; Solbrig, *et al.*, 1964, 1969). Near relatives of *Bigelowia* appear to be *Euthamia* and other woodier taxa in the *Haplopappus* alliance (Anderson, 1970); therefore, I used these plants to examine evolutionary trends in a phylad containing woody and herbaceous taxa.

MATERIALS AND METHODS

Living caudices and flowering stems of all taxa in the genus were collected in the field by me or supplied by R. K. Godfrey, S. B. Jones, O. Lakela, or

TABLE 1. Comparative xylary features from caudices of *Bigelowia*

Taxon and collection data	age of caudex, yrs.	caudex diameter, mm.	xylem radius, mm.	Vessel elements						Fibers		
				widest diameter, μ	average diameter, μ	average length, μ	average wall thickness, μ	range of pit diameters, μ	average number per group	average diameter, μ	average length, μ	average wall thickness, μ
B. NUTTALLII												
Anderson 3173, Brazos Co., Texas	1	3.02	0.88	24.6	18.0	48.3	3.2	3–5	2.9	13.3	221.4	4.4
Anderson 3089, Turner Co., Ga.	1	3.52	0.76	29.1	17.6	64.4	3.1	4–5	5.2	14.7	199.1	4.5
Godfrey 63191, Washington Co., Fla.	1	3.78	0.88	29.1	20.5	76.1	2.9	4–6	4.3	13.5	180.0	4.5
Thieret 25200, Vernon Par., La.	2	5.80	2.02	44.8	26.1	84.2	3.5	4–5	3.8	11.2	192.6	3.3
Thieret 25186, Natchitoches Par., La.	2	6.04	2.14	42.6	26.9	124.3	3.1	3–5	4.1	12.6	172.7	3.9
Anderson 3464, Pinellas Co., Fla.	2	8.00	2.75	67.2	31.4	141.3	4.2	4–5	4.1	17.8	362.1	5.1

B. NUDATA ssp. NUDATA

Jones 11071, Forrest Co., Miss.	1	4.28	1.01	33.6	23.4	77.0	2.6	5–7	2.7	14.4	274.4	3.8
Anderson 3088, Turner Co., Ga.	1	6.04	1.26	38.1	26.8	72.3	2.6	5–7	2.0	24.3	238.9	4.1
Anderson 3070, Wakulla Co., Fla.	1	4.78	1.13	38.1	23.5	86.3	2.1	5–10	2.4	19.6	193.6	3.7
Anderson 3263, Onslow Co., N.C.	2	6.12	2.12	44.8	27.6	118.7	2.3	5–8	2.3	15.1	286.7	3.5

B. NUDATA ssp. AUSTRALIS

Anderson 3471, Pinellas Co., Fla.	1	5.00	0.84	33.6	25.4	65.7	2.1	4–7	1.8	19.9	221.4	3.1
Lakela 30620 Collier Co., Fla.	1	7.30	1.26	47.0	28.9	79.2	2.0	4–7	2.1	20.3	271.4	2.5

J. W. Thieret, whose help is gratefully acknowledged. The larger caudices from each population sample were selected to insure greater xylem development. Material also was taken from the base of the flowering stem and just below the inflorescence for qualitative and quantitative comparisons with the caudex.

Tissues were preserved in FPA, softened in HF, and processed further to prepare slides for examination as in earlier studies (Anderson, 1963; Anderson & Reveal, 1966). Tabular data on cell sizes were obtained by averaging 50 measurements; vessel pit diameters were based on fewer measurements. Each entry in the tables represents a single plant, although more than one was processed for certain collections. Voucher specimens are deposited in the Kansas State University Herbarium (KSC). Additional information on morphology for most collections used in this study is found in Anderson (1970).

RESULTS

Xylem production in *Bigelowia* is not extensive; radial development apparently does not exceed 3 mm. Description of the woods (TABLE 1, FIGURES 1–12, and in the text) is based on study of the caudex. TABLE 2 compares tracheary elements from different regions of the plant body.

Vessels. Average diameter and length of vessel elements in *Bigelowia* are relatively smaller than in most Astereae (Anderson, 1963; Anderson & Reveal, 1966; Carlquist, 1960). The presence of vascular tracheids (practically indistinguishable from narrow vessel elements in transection) can aggravate determination of the average diameter; fortunately they are not common in *Bigelowia*. Most vessels are round in transection; angular ones (fairly typical for Astereae) are infrequent, particularly in *B. nudata*. The relation of wall thickness to diameter in vessels ranges from 11.5 to 17.7% in *B. nuttallii*; 8.3 to 11.1% in *B. nudata* ssp. *nudata*; and 6.9 to 8.3% in *B. nudata* ssp. *australis* (cf. TABLE 1).

The vessel elements all have simple perforation plates. Their end walls generally are transverse to somewhat oblique in orientation; a few of the narrower ones are caudate. Intervascular pits are alternate and have circular to elliptic borders (FIGURE 10); those of *B. nudata* ssp. *nudata* are particularly large for Astereae. Helical sculpture in vessel walls is absent or restricted to fine grooves in *Bigelowia*.

Amount of vessel grouping is varied in Astereae. *Bigelowia* vessels occur singly or in single radial chains (TABLE 1; FIGURES 1–5) as in *Euthamia leptocephala* (Anderson, 1963, as *Solidago leptocephala*). However, in *Chrysothamnus*, a group once thought to be part of *Bigelowia*, vessels are in large, tangentially spread clusters (often more than a dozen per cluster).

Libriform fibers. Dimensions of fibers in *Bigelowia* are most consistent with the average size for the tribe. The relation of wall thickness to fiber width is from 28.7 to 33.3% in *B. nuttallii*; 16.9 to 26.4% in *B. nudata* ssp. *nudata*; and 12.3 to 15.6% in *B. nudata* ssp. *australis*. In *Bigelowia*, fibers

are nonseptate; most retain active protoplasts, resulting in darker staining (FIGURES 7–9). Carlquist (1969a) reported nucleated, septate fibers in the lobelioids. Presence of living fibers, considered an evolutionary advance, may be associated with a reduced amount of axial parenchyma in the xylem (Esau, 1965) or may be an expression of xeromorphy (Fahn, 1964).

Fiber dimorphism with some fibers gelatinous occurs in some *Bigelowia* populations (more frequently in *B. nudata*). Gelatinous fibers can be determined from the amount of shrinkage in the secondary wall, differential staining, and lack of birefringence under polarized light. The gelatinous fibers are similar to the more typical wood fibers in all other ways (i.e., dimensions, original wall thickness, and living state).

Axial parenchyma. Paratracheal parenchyma is scanty and abaxially vasicentric, which is typical for Astereae and the family (Carlquist, 1960, 1966). Apotracheal parenchyma is present (weakly) as initial bands only in the *B. nuttallii* samples with growth rings (FIGURE 4).

Growth rings. Few caudices live more than a year, those that do, possess growth rings which are not strongly defined. Three years' growth in one caudex of my collection, *Anderson 3464*, is the greatest extent of wood found in the genus; other plants of that population had two years' growth (cf. TABLE 1). The wood is diffuse porous (FIGURES 3–5), and vessel diameter shows only slight fluctuation associated with annual ring formation. Fibers produced at the close of the first growing season, however, are noticeably smaller than those produced at the beginning of the second season. Quantitative and qualitative changes in the rays also accentuate the demarcation line (FIGURES 4, 12).

Wood rays. The very nature of the radial system seems to depend on a predisposition of the caudex to be annual or perennial. Differences between rays of one-year-old and two-year-old samples are striking. Such dichotomy also is evident in the general xylary growth pattern in the caudex (see below).

Rays of one-year-old caudices of all taxa always contain vascular traces to adventitious roots and basal leaves (FIGURES 6–8, 11). These rays possibly are merely extensions of gaps in the primary vascular system. Parenchyma surrounding the traces in the ray is loosely oriented, similar to the ground tissue of the pith, and mostly cuboidal to vertically elongated when seen in radial view. Transfusion cells (FIGURE 11) similar to those in *Brighamia* (Carlquist, 1962) are present. The vascular traces and associated parenchyma hardly seem products of the cambium. In a sense then, the wood could be termed rayless. Wood in rhizomes of *Bigelowia nuttallii* (the only species having them), including the single two-year-old rhizome found in *Anderson 3173* (FIGURE 5), is rayless. Rayless rhizomes have been reported for *Euthamia leptocephala* (Anderson, 1963).

Woods from perennial caudices have relatively greater ray development. However, very few of the rays have included vascular traces; most have none. The rays are multiseriate, averaging four to six cells in width
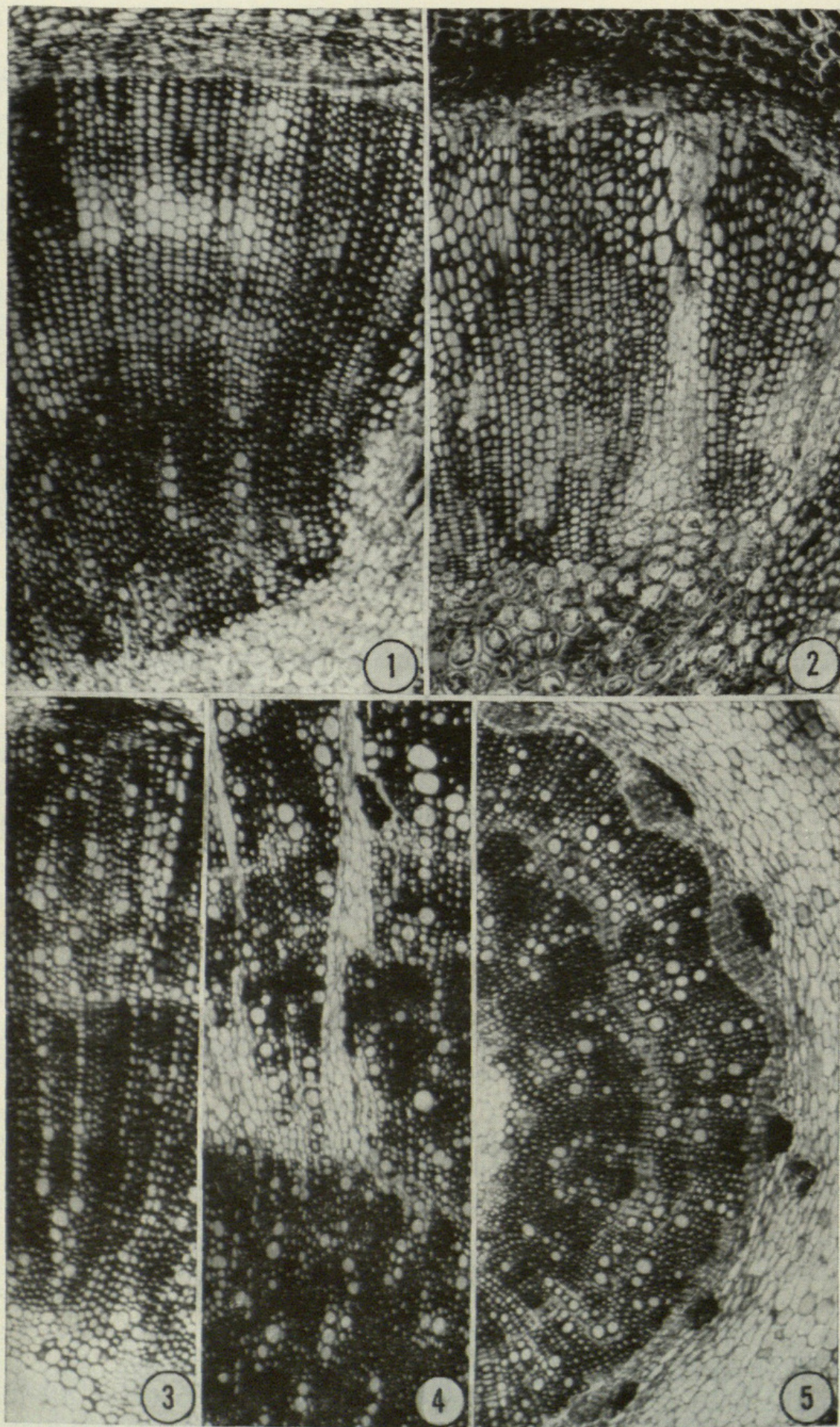
FIGURES 1–5. Transections of *Bigelowia*, pith toward base of page except in
FIGURE 5. 1, *B. nudata* ssp. *nudata* (*Anderson 3070*); 2, *B. nudata* ssp. *australis*,
caudex (*Lakela 30620*); 3, *B. nudata* ssp. *nudata*, two-year caudex (*Anderson
3263*); 4, *B. nuttallii*, two-year caudex (*Anderson 3464*), note absence of rays
in first year's xylem; 5, *B. nuttallii*, two-year rhizome (*Anderson 3173*). All,
× 83.
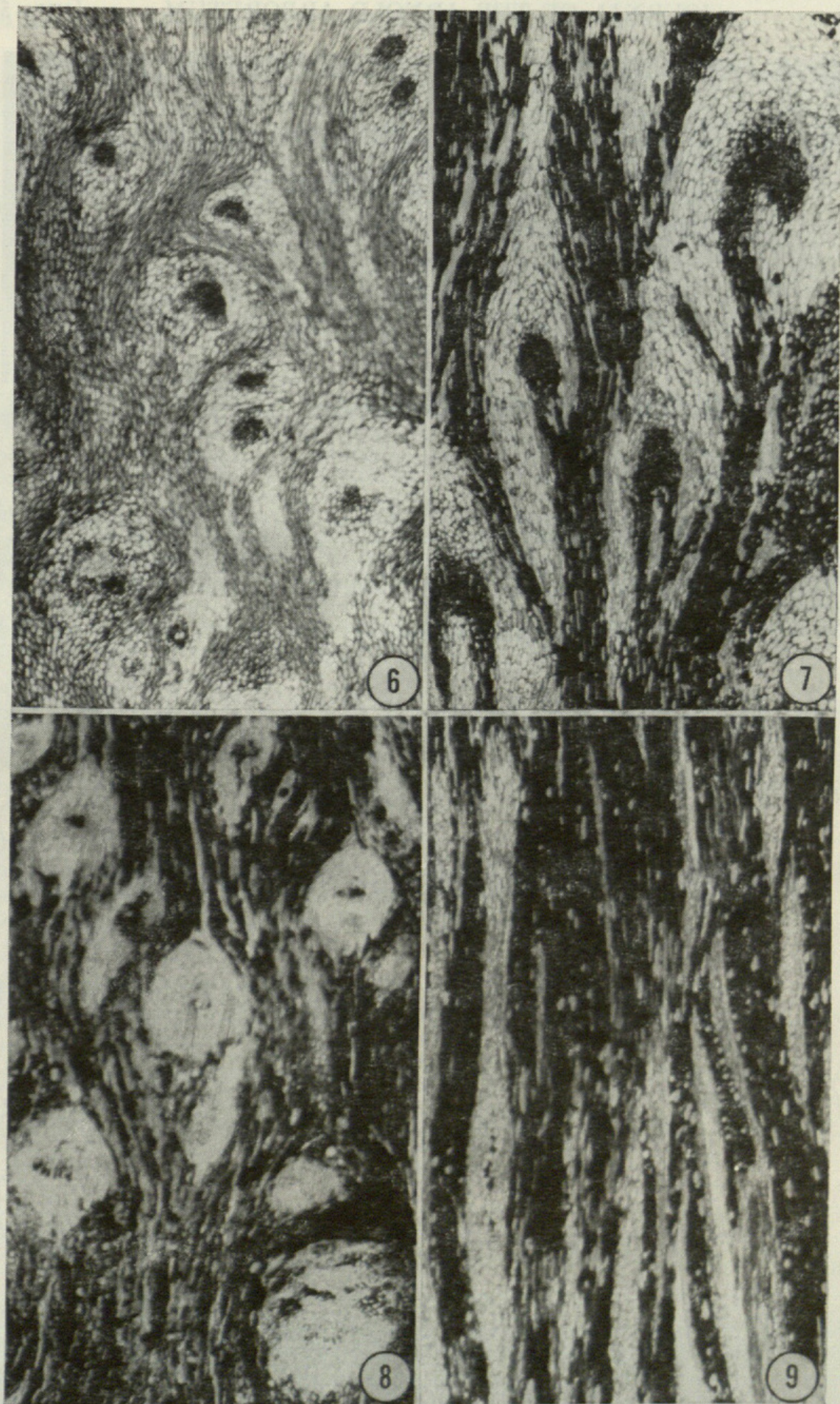
FIGURES 6–9. Tangential sections of caudex. 6, *Bigelowia nudata* ssp. *nudata*, one-year-old sample (*Anderson 3070*) with vertical orientation of tracheary elements greatly distorted by large "rays"; 7, same from material of *B. nudata* ssp. *australis* (*Lakela 30620*); 8, same from material of *B. nuttallii* (*Godfrey 63191*); 9, two-year-old sample of *B. nuttallii* (*Anderson 3464*) with tall wood rays. All, × 32.
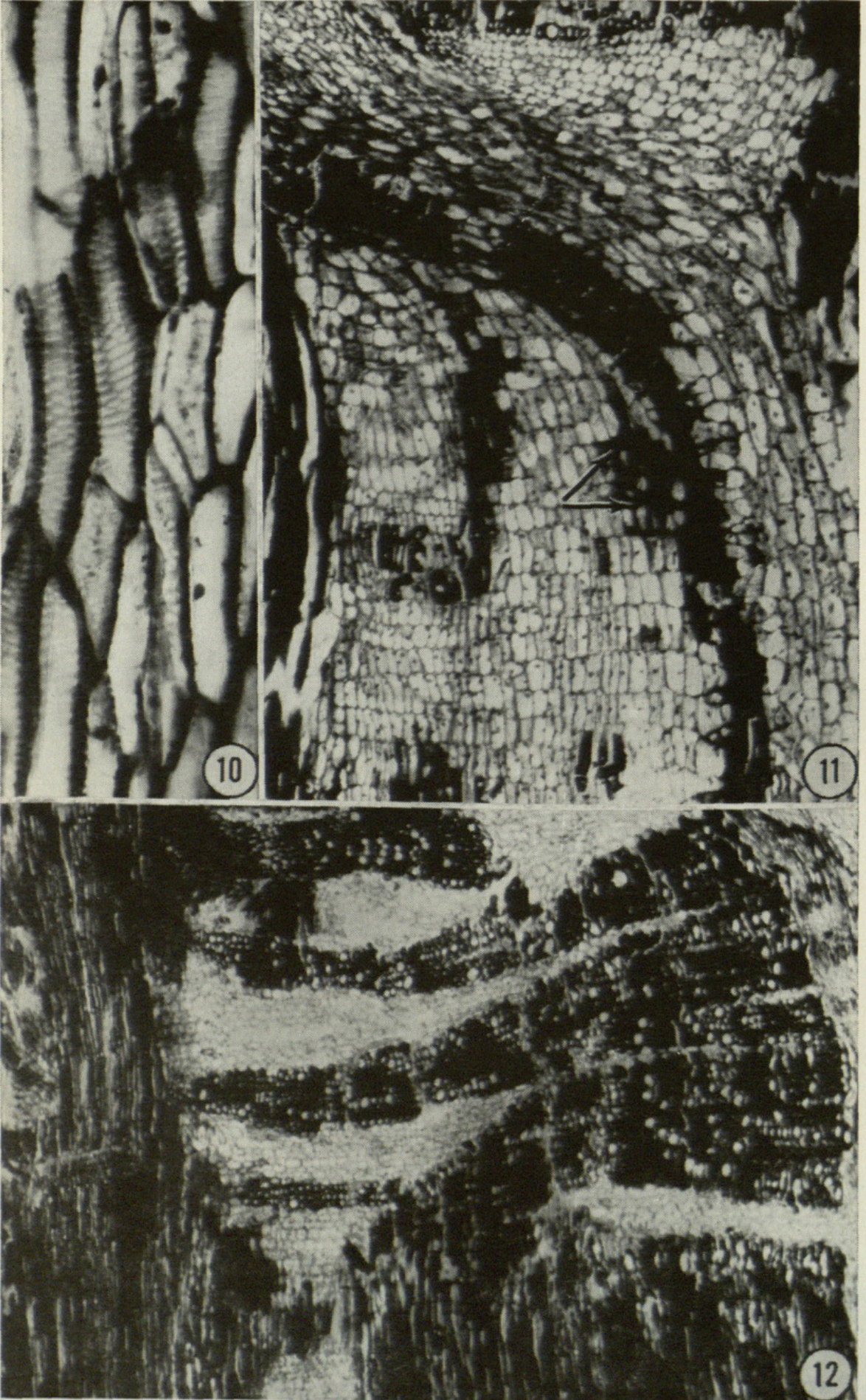
FIGURES 10–12. 10, *Bigelowia nudata* ssp. *australis*, vessel elements with large pits (*Lakela 30620*), × 200; 11, radial section of one-year-old caudex of *B. nuttallii* (*Anderson 3089*) with pith toward left side of page showing "ray" consisting of vertically oriented parenchyma, transfusion cells (arrows), and
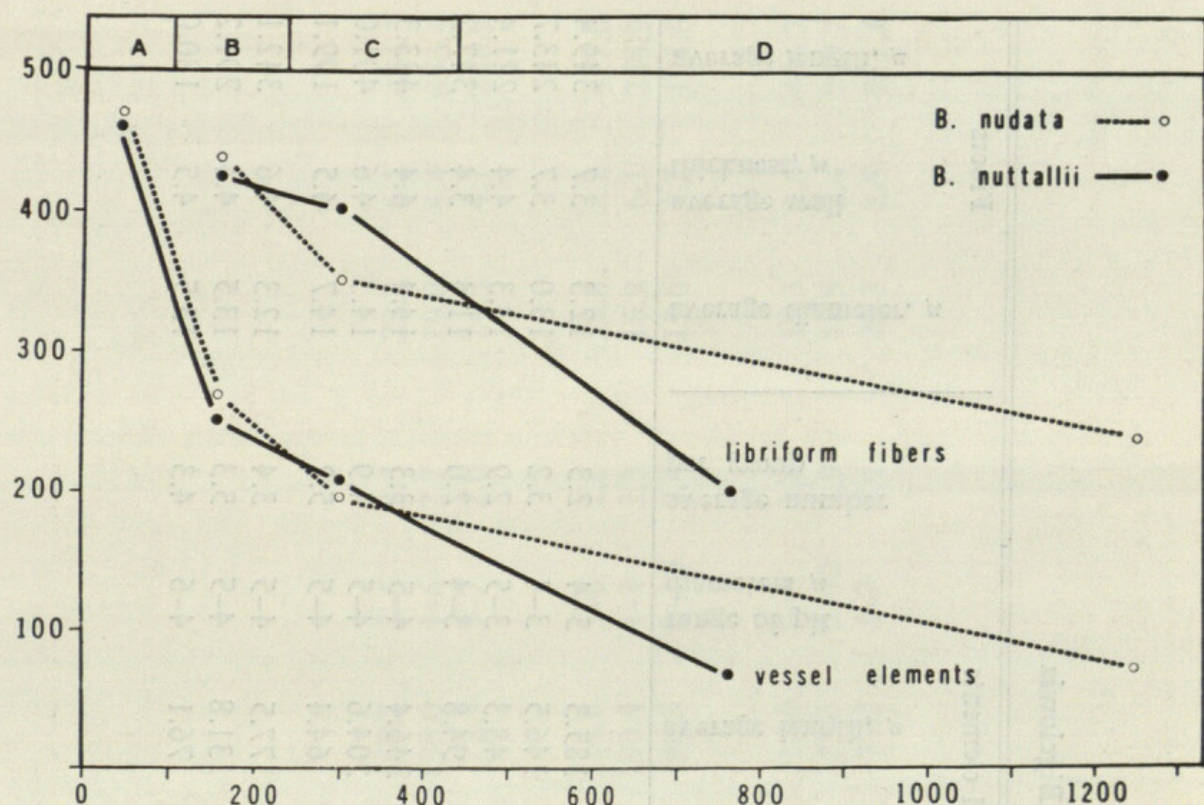
FIGURE 13. Comparison of average tracheary element lengths from different zones of the same plant. Ordinate, cell length in microns; abscissa, radial distance from center of stem or caudex in microns. Zone A, metaxylem of upper stem (fibers absent); B, secondary xylem of upper stem; C, secondary xylem of lower region of aërial stem; D, secondary xylem of caudex. Plants studied, *Anderson 3088* (*Bigelowia nudata*) and *Anderson 3089* (*B. nuttallii*), were growing within a few meters of one another. *B. nuttallii* was on shallow, dry soil of sandstone outcrops; whereas *B. nudata* was in a depression filled with peat moss at the margin of the outcrop.

(FIGURES 4, 9), and ranging from 0.6 to 1.5 mm. tall (the taller ones being in *B. nuttallii*). Ray parenchyma is predominantly procumbent (FIGURE 12) rather than being vertically oriented as are most ray cells of one-year-old caudices (FIGURE 11). New rays, initiated at the beginning of each successive year of growth (FIGURES 2, 14), are wider in the spring wood than in summer wood. The propensity for raylessness in *Bigelowia* woods is also suggested by the increased production of rays after the initial year's growth in the perennial caudices. The ontogenetic relationships between early rayless wood and later wood, in which rays had developed, was noted by Barghoorn (1941).

GROWTH PATTERNS

Study of growth forms should involve measurement of variability in tracheary elements among different organs of the plant and also determi-

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vascular trace, × 80; 12, radial section of three-year-old caudex of *B. nuttallii* (*Anderson 3464*) showing absence of wood rays in initial year's xylem (left) and their increased abundance in each subsequent growth ring, rays composed of predominantly procumbent cells, × 40.

TABLE 2. Xylem data from different tissues in Bigelowia

Taxon collection	sample	sample diameter, mm.	xylem radius, mm.	Vessel elements widest diameter, μ	average diameter, μ	average wall thickness, μ	average length, μ	range of pit diameters μ	average number per group	Fibers average diameter, μ	average wall thickness, μ	average length, μ
B. NUTTALLII												
Anderson 3173	high stem	1.38	0.20	30.2	22.1	2.4	185.3	3–4	2.3	12.3	3.7	349.4
	low stem	2.22	0.40	31.4	23.5	3.1	146.5	3–4	3.2	13.0	3.7	243.7
	caudex	3.02	0.88	24.6	18.0	3.2	48.3	3–5	2.9	13.3	4.4	221.4
	rhizome	1.93	0.52	38.1	27.1	3.1	94.8	3–4	2.0	11.4	3.4	347.2
Anderson 3089	high stem	1.50	0.14	40.3	30.6	3.4	246.4	4–5	3.3	14.4	4.4	423.3
	low stem	2.00	0.19	38.1	23.4	3.4	204.6	4–5	4.9	14.3	4.6	401.0
	caudex	3.52	0.76	29.1	17.6	3.1	64.4	4–5	5.2	14.7	4.5	199.1
Godfrey 63191	high stem	1.80	0.32	44.8	30.2	3.0	177.5	4–5	3.4	12.3	4.6	342.1
	low stem	1.92	0.38	29.1	21.3	2.9	131.8	4–5	5.3	13.5	4.4	291.2
	caudex	3.78	0.88	29.1	20.5	2.9	76.1	4–6	4.3	13.5	4.5	180.0

B. NUDATA ssp. NUDATA

Anderson 3088											
	high stem	1.68	0.14	44.8	30.5	2.2	267.7	3–6	2.3	23.3	6.1	434.3
	low stem	2.50	0.24	47.0	31.9	2.3	198.0	4–6	2.7	19.0	4.4	353.4
	caudex	6.04	1.26	38.1	26.8	2.6	72.3	5–7	2.0	24.3	4.1	238.9
Anderson 3070	high stem	0.85	0.11	35.8	26.4	2.1	314.8	5–6	2.2	15.8	3.2	417.0
	low stem	1.90	0.30	44.2	31.4	2.5	190.4	4–8	2.3	18.9	6.1	256.9
	caudex	4.78	1.13	38.1	23.5	2.1	86.3	5–10	2.4	19.6	3.7	193.6

B. NUDATA ssp. AUSTRALIS

Lakela 30620	high stem	2.52	0.19	44.8	35.0	2.4	313.6	5–9	1.8	16.3	3.6	436.7
	low stem	3.58	0.60	35.9	26.1	2.6	189.3	5–10	1.9	18.5	2.4	297.7
	caudex	7.30	1.26	47.0	28.9	2.0	79.2	4–7	2.1	20.3	2.5	271.4

nation of patterns of change in element length during growth in a given organ. Variability among different organs or plant regions is tabulated in TABLE 2. Growth patterns, as depicted by average tracheary element lengths in different plant zones, are shown for *Bigelowia nuttallii* and *B. nudata* in FIGURE 13; patterns of change during growth in element length in the caudex are shown in FIGURE 14.

Considerable dissimilarity might be expected in tracheary elements from different regions of the plant when their ontogeny and environment are examined. The aërial (flowering) stem grows rapidly in a single season and is in a more xeric environment than the caudex or rhizome. The high stem (cf. TABLE 2), just below the branches of the inflorescence, has limited cambial activity; the secondary xylem (zone B of FIGURE 13), less abundant than the primary xylem, contains vessel elements and fibers, fibers being absent in the primary xylem (zone A, FIGURE 13). The low stem zone, arbitrarily taken 2 cm. above the caudex has little secondary xylem (zone C, FIGURE 13), but more than does the high stem. The caudex grows more slowly and accumulates the greatest amount of xylem in the plant (zone D, FIGURE 13). The rhizome of *Anderson 3173* (FIGURE 5) has wider vessels but narrower fibers than do other plant regions. In all taxa, vessel members from the aërial stems are generally wider and longer than those of the caudices, whereas fibers are narrower but longer. Vessel wall thickness is rather uniform throughout different zones of the same plant, although the vessels of the caudices, being narrower, have relatively thicker walls.

The assumption that the caudex is more or less predestined to be either annual or perennial is reinforced in the growth patterns of the secondary xylem of both species (FIGURE 14). The fusiform cambial initials of the annual samples and, consequently, the vessel elements they produce become progressively shorter during the growing season. Note that shortening is not so pronounced in the caudices of *Anderson 3088* and *Anderson 3089* (FIGURE 14) as in the different zones of the same plants (FIGURE 13). Cambial initials and vessel elements of the two-year-old caudices in FIGURE 14, on the contrary, become successively longer during the first growing season, and the trend is continued in the second season. In all samples studied, the terminal growth of the two-year-old caudices contained longer vessel elements than did the one-year-old caudices (TABLE 1). Libriform fibers do not necessarily indicate the size of the cambial initials that produce them because fibers exhibit varying amounts of intrusive growth during differentiation and maturation.

DISCUSSION

Trends in xylem evolution in Asteraceae seem rather closely controlled by environmental factors and paedomorphosis, i.e., shifts in wood anatomy related to change in lengths of cambial initials (Carlquist, 1966). Discussion of these factors is an appropriate prelude to taxonomic considerations.
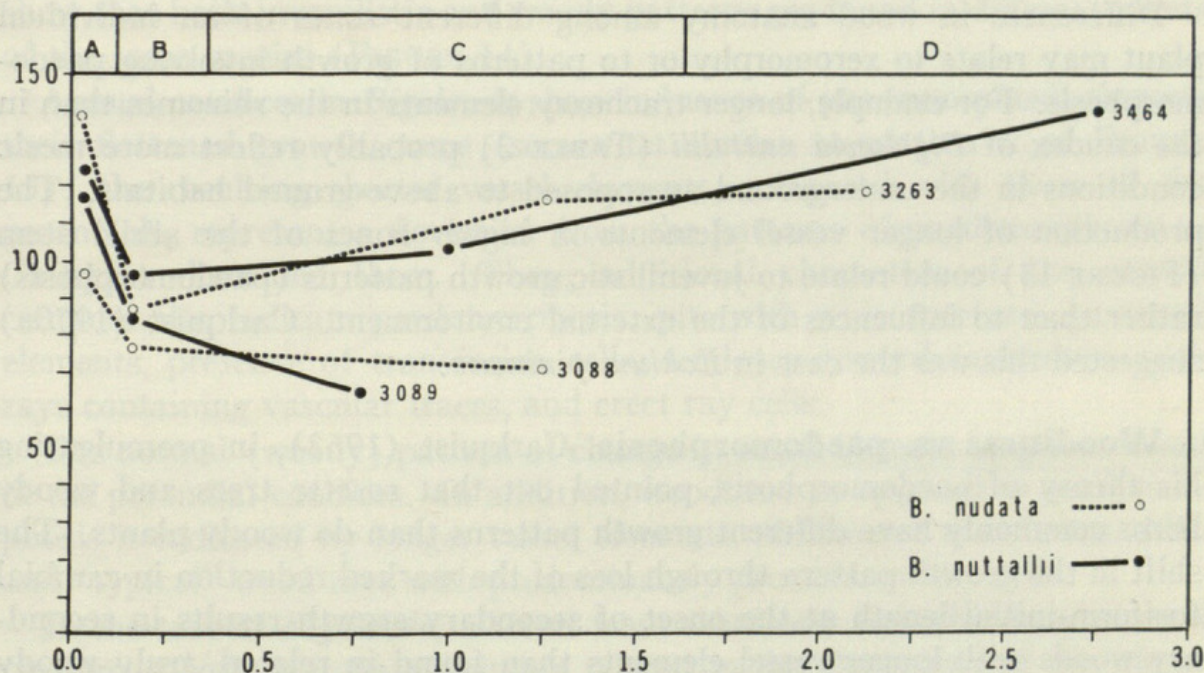
FIGURE 14. Average vessel element length from different positions within the caudex. Ordinate, element length in microns; abscissa, distance from caudex center in millimeters. Zone A, metaxylem; B, first-formed secondary xylem; C, last-formed secondary xylem of first year's growth (total growth for some); D, last-formed xylem of second year's growth. Note shift in growth pattern between annual and perennial caudices during first year's growth.

Ecological anatomy. Fragmentary observations on the ecology of *Bigelowia* (Harper, 1911; Anderson, 1970) indicate that the general environments of the taxa are similar. The range of *B. nuttallii* extends farther west (into Texas) than the range of *B. nudata.* (That western zone is somewhat warmer and drier, as suggested from mean annual temperature and rainfall data.) The species are closely sympatric at one locality in Florida (Harper, 1911) and at scattered stations in southern Georgia, where they differ in habitat preferences. The soils on rock outcrops where *B. nuttallii* grows are usually reddish-brown sandy loams with little organic matter (0.5–2.5%) and low cation exchange capacity. Soils where *B. nudata* grows are usually gray sandy loams with more organic matter (2.0–5.0%) and greater cation exchange capacity.

The sunny, open sites where *Bigelowia nuttallii* grows on shallow, better-drained soils are definitely more xeric than those where *B. nudata* grows. Considerable xeromorphy is shown in root and leaf anatomy (Anderson, unpublished) of *B. nuttallii* and is reflected in these anatomical features of the wood: 1) narrow, frequently short vessel elements with thick walls and narrow pits; 2) a number of vessels per group; 3) a number of vascular tracheids; and 4) narrow, short fibers with thick walls. The greater amount of living fibers might also reflect xeromorphism when compared to that of *B. nudata*, but the taller wood rays in the perennial caudices certainly do not. Helical sculpture on vessel walls tends to be more abundant or elaborate in xerophytic composites (Carlquist, 1966), but no taxa of *Bigelowia* have much helical sculpture.

Differences in wood anatomy among different zones of an individual plant may relate to xeromorphy or to patterns of growth involving paedomorphosis. For example, longer tracheary elements in the rhizomes than in the caudex of *Bigelowia nuttallii* (TABLE 2) probably reflect more mesic conditions in the underground as opposed to above-ground habitats. The production of longer vessel elements in higher zones of the aërial stem (FIGURE 13) could relate to juvenilistic growth patterns (paedomorphosis) rather than to influences of the external environment. Carlquist (1970a) suggested this was the case in *Echium pininana*.

Woodiness vs. **paedomorphosis.** Carlquist (1962), in promulgating his theory of paedomorphosis, pointed out that rosette trees and woody herbs commonly have different growth patterns than do woody plants. The shift in the growth pattern through loss of the marked reduction in cambial fusiform-initial length at the onset of secondary growth results in secondary woods with longer vessel elements than found in related, truly woody plants (FIGURE 15, adapted from Carlquist, 1966).
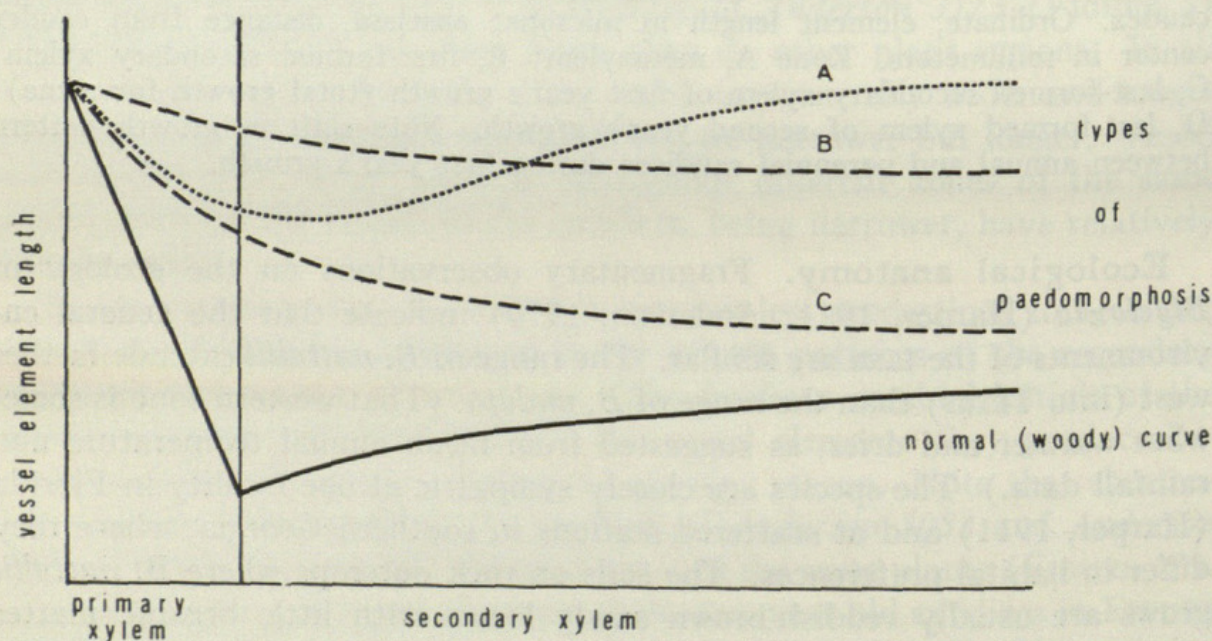

FIGURE 15. Patterns of change in average vessel element length during growth of plant (adapted from Carlquist, 1966).

Such patterns are discomforting to phylogenists. Woody plants, being *generally* more primitive, *generally* have longer cambial initials and, thereby, longer vessel elements than do related, less woody plants. Yet through paedomorphosis, a derived herbaceous plant might have longer vessel elements than related more woody taxa.

Carlquist (1962) suggested that woods influenced by paedomorphosis cannot be compared with those from woody plants because "phylesis both toward and away from herbaceousness would involve juvenile expressions, so these could not be used as criteria of one ancestry or the other." *If* this proves universally true, then woods of woody and herbaceous members of a genus cannot be compared. However, these studies in *Bigelowia*

show that both juvenilistic and woody patterns are found in different plants of the same species (FIGURE 14).

Annual caudices in *Bigelowia* show influence of paedomorphosis through their flattened growth curve (somewhat similar to pattern C of FIGURE 15); the resulting shorter vessel elements, compared with those of the perennials, represent a deviation from the patterns of paedomorphosis as Carlquist described them. These additional characters of the annual caudices also indicate paedomorphosis: pits with wide apertures on vessel elements, presence of transfusion cells, tendency toward raylessness with rays containing vascular traces, and erect ray cells.

The normal (woody) pattern of change in vessel element length is found in the perennial caudices. In addition, woodiness as opposed to paedomorphosis is indicated by longer vessel elements, absence of transfusion cells, and "typical" wood rays with predominantly procumbent ray cells.

In the case of *Bigelowia*, a trend from woodiness to herbaceousness and paedomorphosis is apparent and is related to the shortening of the life of the caudex.

Phylogenetic considerations. *Bigelowia nuttallii* and *B. nudata* are closely related; artificial, sterile hybrids between the species have been produced (Anderson, unpublished). If one species were to be considered more primitive, based on data from wood anatomy, it would be *B. nuttallii* which has generally longer vessel elements (even though probably shortened through xeromorphism); also, a greater number of perennials have been found in that species.

Woodiness may appropriately be designated a primitive feature for *Bigelowia*, as apparently it is for the tribe (Carlquist, 1960). *Euthamia* has been suggested as a close relative of *Bigelowia* (Anderson, 1970). Patterns of change in vessel element length during growth have been determined for plants of *E. graminifolia* and *E. leptocephala* (Anderson, unpublished); interestingly, both have a normal (woody) growth curve.

More than a quarter of a century ago, Tippo (1946), in discussing the role of wood anatomy in phylogeny, stated:

> The next logical development which may
> be expected in this field of endeavor
> is a series of exploratory investiga-
> tions of the herbaceous Dicotyledons
> whose purpose will be not only to
> uncover new phylogenetic sequences, but
> to extend the lines of specialization
> already established into the relatively
> virgin territory. There is every reason
> to suppose that the trends already defined
> will be found to prevail in the secondary
> wood of the herbs, and there is also some
> basis for belief that similar sequences
> will be unearthed in the primary xylem.

Knowledge of wood anatomy in herbaceous plants is still so limited that we do not know how universal paedomorphosis is or what other patterns may be found. Certainly they will not parallel the trends already established for woody dicots, as Tippo supposed they would.

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DIVISION OF BIOLOGY
KANSAS STATE UNIVERSITY
MANHATTAN, KANSAS 66506