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OBSERVATIONS ON THE VEGETATIVE ANATOMY OF
CREPIDIASTRUM AND *DENDROCACALIA*
(ASTERACEAE)

Sherwin Carlquist

INTRODUCTION

Although *Crepidiastrum* Nakai belongs to the tribe Lactuceae whereas *Dendrocacalia* Nakai is a member of Senecioneae, the two genera have been grouped here because both form woody species on offshore islands of Japan. As such, they provide material for further studies in wood anatomy and vegetative anatomy of Asteraceae; neither genus has been studied anatomically hitherto.

Crepidiastrum consists of about eight species in eastern Asia, from Korea through Japan (including the Bonin Islands) to Taiwan (Walker 1976). Most of these occur on rocky places near the sea (Ohwi 1965). *Crepidiastrum lanceolatum* (Houtt.) Nakai in the present study is representative of these. I collected it on limestone boulders (worn portions of uplifted coral reefs) near the shore on Iriomote, Ryukyu Islands. This species and other beach species are not truly woody; they are rosette perennials with succulent stems. Shoots with elongate internodes are sometimes produced, but the plant body as a whole may be deemed succulent rather than woody and the habit designated as a subshrub. Understanding of how this habit and texture relate to anatomy is one of the goals of this study. *Crepidiastrum ameristophyllum* (Koidz.) Nakai is a rosette shrub, sparsely branched and sometimes with a single stem (Fig. 5). The stem has a woody texture. *Crepidiastrum ameristophyllum* occurs on the summit ridge of Hahajima, Bonin Islands. This habitat is markedly unlike the seashore habitats of the other species. The summit of Hahajima is a humid cloud forest where periods of sunshine are limited. The marked difference in habit between *C. lanceolatum* and *C. ameristophyllum* invites comparison as a way of seeing how wood anatomy may shift with relation to habit. The fact that *C. ameristophyllum* is so restricted geographically, whereas the other species are more widely distributed and also so relatively uniform in their rosette-subshrub habit suggests that the habit of *C. ameristophyllum* might be derived from the habit of the other species. There are no cytological differences or other differences of an irreversible nature to give independent confirmation of the direction which has been followed in evolution of habit in this genus.

The distinctive habitats of *C. lanceolatum* and *C. ameristophyllum*, re-

spectively, also provide an interesting circumstance in which to investigate evolution of leaf anatomy with relation to habit.

The summit ridges of Hahajima are occupied not only by *Crepidiastrum ameristophyllum*, but also by *Dendrocacalia crepidifolia* Nakai, sole species of its genus. A rounded shrub to 5 m (Fig. 17), *Dendrocacalia* is common on these heights, whereas *C. ameristophyllum* is limited to a few areas of disturbed soil in the summit zone. Ways in which wood anatomy and leaf anatomy show a relationship to these habitats form a topic for investigation. Also, *Dendrocacalia* invites comparison to other Senecioneae with respect to wood anatomy.

Absence in this study of materials of species of *Crepidiastrum* other than *C. ameristophyllum* and *C. lanceolatum* is regrettable, although the diversity among the seashore species, to which *C. lanceolatum* belongs, is much less than the difference between those species and *C. ameristophyllum*.

The occurrence of scalariform or aberrant perforation plates in *Crepidiastrum ameristophyllum*, described below, is an interesting phenomenon because of the implications of both phylogenetic and ecologic dimensions as discussed in an accompanying paper (Carlquist 1983).

MATERIALS AND METHODS

Wood samples of *Crepidiastrum ameristophyllum* stems and roots were prepared by drying. These represent samples of optimal size for the species (stem ca. 2 cm in diameter). Wood samples of *Dendrocacalia crepidifolia* stems were prepared by drying. These represented both large stems (ca. 8 cm in diameter) and a stem about two years old (1 cm in diameter) in order that ontogenetic change in wood features could be studied.

The stems of *Crepidiastrum lanceolatum* collected were of maximal diameter (ca. 3 cm in diameter), at least five years old. These stems, as well as primary stems and leaves of all three species included in the present study were preserved in a 50% ethyl alcohol solution; this proved adequate for the histological details studied.

Sections of wood of *C. ameristophyllum* and *D. crepidifolia* were prepared by sectioning portions which had previously been boiled in water; sections were cut at 20 μ m on a sliding microtome. Wood macerations were prepared from wood samples boiled in water by treatment of portions in Jeffrey's fluid, followed by staining in safranin.

Wood of *C. lanceolatum* is quite soft in texture, and therefore old stems were infiltrated in a butyl alcohol series, embedded in paraffin, and sectioned on a rotary microtome. Leaves and primary stems of *Crepidiastrum* and *Dendrocacalia* were also embedded in paraffin and sectioned on a rotary microtome. Paraffin sections were stained with a safranin-fast green combination.

Specimens documenting the three collections studied are located in the herbarium of the Rancho Santa Ana Botanic Garden.

ANATOMICAL DESCRIPTIONS

Leaves.—*Crepidiastrum lanceolatum* (Carlquist 15679) (Fig. 1). Outer walls of epidermal cells 5–8 μm thick. Stomata on both adaxial and abaxial surfaces, ranunculaceous; stomata sunken below the level of adjacent epidermal cells. Cuticle present on both epidermal surfaces, 1–2 μm thick. Mesophyll 9–10 layers thick. Little differentiation into typical palisade and spongy cells present, only one layer palisadelike. All mesophyll layers relatively compact and with small intercellular spaces. No clear bundle sheath evident around smaller veins, although a bundle sheath present on larger veins (Fig. 1). Laticifers present adjacent to phloem of veins; no fibers associated with veins.

Crepidiastrum ameristophyllum (Carlquist 15768) (Fig. 6). Outer walls of epidermis about 3 μm thick. Stomata on abaxial surface of leaf only, ranunculaceous; stomata not sunken below the level of adjacent epidermal cells. Cuticle present on both epidermal surfaces, 0.5 μm or less thick. Mesophyll 8–10 layers thick, with no clear differentiation into palisade and spongy cells; only one layer at all similar to palisade. Laticifers present adjacent to phloem of bundles; no clear bundle sheath evident; no fibers adjacent to veins.

Dendrocacalia crepidifolia (Carlquist 15760). Epidermis with walls about 2 μm thick; discrete cuticle not observed (wall of epidermal cells probably impregnated with cutin). Stomata on abaxial surface only, ranunculaceous, not sunken below level of adjacent epidermal cells. About 14 layers of mesophyll present; of these, 1–2 are hypodermis with thin but cutinized walls. Chlorenchyma differentiated into 2–3 layers of palisade, 9–10 layers of spongy cells. Bundle sheath present on a single layer of cells on most veins. One (occasionally more than one) secretory canal present adjacent to phloem of most veins. No fibers observed on veins.

Primary stems and nodes.—Both species of *Crepidiastrum* studied agree in possessing pith bundles. These bundles are numerous and are scattered evenly throughout the pitch. About half of the bundles contain xylem as well as phloem; the remainder are phloic. Bundles which contain xylem are amphivasal. Numerous small phloem strands may be found in the cortex of the stem. Fibers are not present adjacent to phloem poles, but laticifers are. Collenchyma is present in the outer cortex.

The stem of *C. lanceolatum* studied had leaves with narrow bases; these leaf bases contain three veins which are related to trilacunar nodes. The stem of *C. ameristophyllum* studied had much larger leaf bases, in which seven veins, related to seven gaps in a multilacunar node, were present.

Fig. 1–4. Sections of *Crepidiastrum lanceolatum* (Carlquist 15679).—1. Leaf transection, midvein at upper right, upper epidermis at left.—2–4. Sections of secondary xylem.—2. Transection, showing two growth rings.—3. Portion of tangential section, illustrating a strand of interxylary phloem.—4. Portion of transverse section; a strand of interxylary phloem near center. (Fig. 1, 3, 4, magnification scale above Fig. 1 [divisions = 10 μ m]; Fig. 2, scale above Fig. 2 [divisions = 10 μ m].)

While the larger sheathing leaf bases of the *C. ameristophyllum* material might well be expected have more numerous veins than the *C. lanceolatum* material, in which leaf bases were narrower, variation in vein number and therefore nodal type is to be expected based on wideness of leaf base.

The stem of *Dendrocacalia crepidifolia* has a cylinder of bundles, with no pith bundles. Fibers are present as bundle caps on some bundles. Secretory canals are present adjacent to phloem of some bundles. The cortex is largely composed of cells grading from lacunar collenchyma near the outside to ordinary parenchyma near the cylinder of bundles. Nodes are multilacunar; five traces related to five gaps occurred in the material studied.

Secondary xylem.—*Crepidiastrum lanceolatum* (Carlquist 15679), stem (Fig. 2–4, 16). Growth rings evident (Fig. 2), most often as latewood poorer in fibers than earlywood. Vessels angular to round in transection. Mean vessel diameter 36.5 μm . Mean number of vessels per mm^2 , 362. Mean number of vessels per group = 3.2. Vessels mostly arranged in radial chains. Mean vessel wall thickness, 4 μm . Mean vessel-element length, 416 μm . Lateral wall pitting of vessels essentially scalariform (Fig. 16), although more properly termed pseudoscalariform because of probable derivation from alternate pits much widened laterally. Perforation plates simple. Axial xylem composed largely of axial parenchyma, with libriform fibers present in annual bands. Mean libriform fiber diameter at widest point, 21 μm . Mean libriform fiber wall thickness, 2 μm . Libriform fiber length not determined because of paucity. Axial parenchyma type not separable from the abundant zones of parenchyma. The abundant axial parenchyma also merges imperceptibly into upright ray cells, so that limits of rays are not visible and therefore dimensions cannot be determined. For the same reason, uniseriate rays are rarely discernible. Ray cell walls are thin walled and nonlignified (Fig. 3). Strands of interxylary phloem present in a few places in older secondary xylem (Fig. 2, 3, 4). These strands of phloem do not occur in the most recent year's secondary xylem, and evidently are developed by means of subdivision of files of axial parenchyma cells. Wood not storied.

Crepidiastrum ameristophyllum (Carlquist 15768), stem (Fig. 7, 8, 9–15). Growth rings absent (Fig. 7). Vessels chiefly circular in outline in transection. Mean vessel diameter 35 μm . Mean number of vessels per mm^2 , 47. Mean number of vessels per group = 1.3. Vessels arranged in radial rows (Fig. 7). Mean vessel wall thickness, 2.3 μm . Mean vessel-element length, 145 μm . Lateral wall pitting of vessels alternate (Fig. 9, 11–15). Perforation plates simple or variously scalariform; scalariform plates common (about 20% of perforation plates), most with 2–4 bars (Fig. 9–15), some with bars running tangentially rather than radially (Fig. 9), some with bars arranged in a networklike fashion (Fig. 14). Mean libriform fiber length, 355 μm . Mean diameter of libriform fibers at widest point, 20 μm . Mean libriform fiber wall thickness, 25 μm (Fig. 9). Axial parenchyma vasicentric, forming a sheath

Fig. 5–8. *Crepidiastrum ameristophyllum* (Carlquist 15768).—5. Habit of plant 1.2 m tall, summit of Chibusayama, Hahajima, Bonin Islands.—6. Transection of leaf, upper epidermis at left.—7–8. Sections of secondary xylem of stem.—7. Transection; virtually no growth ring activity present.—8. Tangential section; erect cells predominate in rays. (Fig. 6, magnification scale above Fig. 1; Fig. 7, 8, scale above Fig. 2.)

Fig. 9-16. Details of vessels from sections of secondary xylem of stem of *Crepidiastrum*.—9-15. *C. ameristophyllum* (Carlquist 15768).—9. Two vessels from radial section, showing near-scalariform perforation plates with few bars.—10. Two vessels from a transection, showing bars running in a tangential rather than radial direction (ray at right serves for orientation).—11-15. Perforation plates from vessels in radial sections, showing various modifications of scalariform conditions.—16. *C. lanceolatum* (Carlquist 15679), lateral wall of vessel from tangential section. (Magnification scale for all above Fig. 9 [divisions = 10 μ m].)

Fig. 17–21. *Dendrocacalia crepidifolia* (Carlquist 15760).—17. Habit of shrub 2 m tall near summit of Chibusayama, Hahajima, Bonin Islands.—18–21. Sections of secondary xylem of stem.—18–19. Sections from the periphery of larger stem.—18. Transection; bands of parenchyma above.—19. Tangential section; parenchyma (left) and libriform fibers (center, right) markedly storied.—20. Tangential section from young stem; parenchyma (left) more clearly storied than libriform fibers (right).—21. Vessel wall from radial section of smaller stem; grooves interconnecting pit apertures visible. (Fig. 18–20. Scale above Fig. 2; Fig. 21, scale above Fig. 9.)

1–2 cells wide around vessels or vessel groups. Rays multiseriate or uniseriate (Fig. 8), multiseriate rays somewhat more common than uniseriate rays. Mean height of multiseriate rays, 341 μm . Mean height of uniseriate rays, 77 μm . Ray cells square to erect, erect ray cells more common. Ray cell walls moderately thick (ca. 2 μm) but lignified. Wood not storied.

Crepidiastrum ameristophyllum (Carlquist 15768), root: wood identical with that of stem except for features given herewith. Mean vessel diameter, 35 μm . Mean number of vessels per mm^2 , 80. Mean number of vessels per group, 1.8. Mean vessel wall thickness, 2.3 μm . Mean vessel-element length, 219 μm . Mean libriform fiber length, 402 μm . Mean diameter of libriform fibers at widest point, 18 μm . Mean wall thickness of libriform fibers, 2.5 μm . Mean height of uniseriate rays, 83 μm . Mean height multiseriate rays, 494 μm .

Dendrocacalia crepidifolia (Carlquist 15760). Older stem (Fig. 18–19). Growth rings absent, although bands of axial parenchyma appear on a non-annual basis (Fig. 18, top). Mean vessel diameter, 60 μm . Mean number of vessels per mm^2 = 24. Mean number of vessels per group, 2.1. Vessels grouped chiefly in radial rows. Mean vessel wall thickness, 3.5 μm . Mean vessel-element length, 254 μm . Lateral walls of vessels with alternate pits, but apertures of pits interconnected into short grooves (Fig. 21). Perforation plates simple. Mean libriform fiber length, 489 μm . Mean diameter of libriform fibers at widest point, 28 μm . Mean libriform fiber wall thickness 4.6 μm . Axial parenchyma vasicentric scanty. Axial parenchyma derived from fiber dimorphism (cf. Carlquist 1958a) present in a few bands (Fig. 18, top; Fig. 19, left). Axial parenchyma of bands mostly not subdivided, some cells in strands of two; vasicentric axial parenchyma in strands of 2–4 cells, mostly 2–3. Rays multiseriate exclusively (Fig. 19). Mean multiseriate ray height, 1656 μm . Mean width of multiseriate rays at widest point, 7.8 cells. Ray cells procumbent, a few cells present as sheathing cells of rays (Fig. 19). Libriform fibers and parenchyma of bands storied (Fig. 19).

Dendrocacalia crepidifolia (Carlquist 15760), young branch (Fig. 20–21): wood identical to wood of old stem except for features herewith. Mean vessel diameter, 50 μm . Mean number of vessels per mm^2 , 22. Mean number of vessels per group = 2.0. Mean vessel wall thickness, 2 μm . Mean vessel-element length, 220 μm . Mean libriform fiber length, 504 μm . Mean libriform fiber diameter at widest point, 26 μm . Mean wall thickness of libriform fibers, 3 μm . Mean height of multiseriate rays, 1117 μm . Mean width of multiseriate rays, 6.1 cells. Libriform fibers indistinctly storied (Fig. 20), although parenchyma cells of bands clearly storied (Fig. 20, left).

CONCLUSIONS

Leaf anatomy.—The leaf anatomy of *Crepidiastrum lanceolatum* contrasts with that of *C. ameristophyllum* in ways correlated with the habitats of the

two species. The leaf of *C. lanceolatum* is amphistomatal. Because this species grows on coral rocks, its leaves receive bright illumination from below even though they tend to be borne horizontally. The fact that mesophyll in this species is not clearly differentiated into palisade and other (spongy) chlorenchyma types prevents one from designating the leaf as clearly isolateral despite its amphistomatal condition. Xeromorphic features of the leaf of *C. lanceolatum* include sunken stomata, greater thickness of epidermal walls (as compared to *C. ameristophyllum*), more compact chlorenchyma with smaller air spaces, and a slightly greater leaf thickness. The leaf anatomy obviously matches the contrasting habitats of the two species, respectively. This reinforces the obvious difference in leaf size: the leaves of *C. ameristophyllum* are mesomorphic in having appreciably larger dimensions compared with the leaves of the seashore species.

The leaves of *Dendrocacalia* are likewise mesomorphic in their dimensions. The occurrence in *Dendrocacalia* leaves of secretory canals is not unexpected in view of the distribution of secretory canals in the family (e.g., Col 1899). The occurrence of hypodermis in leaves of *Dendrocacalia* may be exceptional for Asteraceae as a whole. However, hypodermis in leaves of Asteraceae has been reported in genera which occur in humid (but probably bright) tropical areas, such as *Petrobium* and *Oparanthus* (Carlquist 1957) or various of the Mutisieae from the Guayana highlands of Venezuela (Carlquist 1958b).

Anatomy of stems and nodes.—The primary stems of *Crepidiastrum* are noteworthy in presence of pith bundles. Pith bundles, while unusual in Asteraceae as a whole, have been reported from a scattering of genera, including some in the tribe Lactuceae (Metcalfe and Chalk 1950). The occurrence of multilacunar nodes in *Crepidiastrum ameristophyllum* and *Dendrocacalia crepidifolia* relates to leaf size in these two taxa. In turn, leaf size in these two shrubs is probably related, as mentioned above, to a habitat where humidity is high and cloud cover frequent, so that overheating of leaves is unlikely to occur.

Wood anatomy.—The difference between *Crepidiastrum ameristophyllum* and *C. lanceolatum* with respect to parenchymatization is quite evident, as comparison of Fig. 2 and 7 reveals. This is a demonstration of succulence related to the rosette habit versus woodiness as related to the shrub habit. Moreover, the ease with which a transition from one to the other has occurred is evident, judging from the coexistence of the two in the same genus.

The presence of phloem strands in older secondary xylem of *C. lanceolatum* is quite distinctive; such interxylary phloem has not been reported in Lactuceae before. In three genera of the tribe Inuleae, *Elytropappus*, *Metalaisia*, and *Phaenocoma*, Adamson (1934) has reported interxylary phloem. However, in these three genera the pattern is not like that of *Crepidiastrum*;

rather, those genera have cambia which produce cork to the outside and xylem containing interxylary phloem strands to the inside. In this respect, the three genera of Inuleae show more resemblance to *Stylidium* (Carlquist 1981) than to *Crepidiastrum*.

The presence of scalariform perforation plates (with various degrees of modification) in a sizeable proportion of perforation plates of *Crepidiastrum ameristophyllum* vessel elements requires interpretation. One possible explanation applicable to *C. ameristophyllum* is given in the case of *Patrinia villosa* Juss. in an accompanying paper (Carlquist 1983). According to the data of Bierhorst and Zamora (1965), certain Lactuceae have scalariform perforation plates in primary xylem. Through paedomorphosis, this primary xylem pattern might be protracted into the secondary xylem. Such juvenilism can be deemed likely because the stems of *C. ameristophyllum* never exceed two to three centimeters in diameter. Scalariform perforation plates are not of negative selective value in this species because it grows in humid mesic sites where flow of large volumes of water per unit time may never occur; if rapid transpiration and therefore flow of large volumes of water occurred, selection for simple perforation plates would be expected to occur. Consequently, a juvenile perforation plate pattern is spread into secondary xylem, where simple perforation plates (in accordance with the almost universal occurrence of simple plates in wood of the family) would ordinarily be expected. Simple perforation plates do occur without exception in wood of *C. lanceolatum*, which occurs in more xeric sites. Modified scalariform perforation plates in secondary xylem of other Lactuceae have been reported in the case of *Dendroseris* sect. *Phoenicoseris* (Carlquist 1960). These are insular species of moist forest, a habitat much like that where *C. ameristophyllum* grows. One may note that the scalariform perforation plates of *C. ameristophyllum* are often much modified, with bars running in tangential directions (Fig. 10) rather than in radial orientation frequently. This argues in favor of a juvenilistic overlay concept in the secondary xylem rather than the alternative idea, a phylogenetic retention of scalariform perforation plates as a feature inherited from ancestors in which scalariform perforation plates were present in all secondary xylem vessels. The reader may have noted that the lateral wall pitting of vessels in *C. ameristophyllum* is alternate, not pseudoscalariform, as one might expect of vessels juvenilistic in all respects. However, the shrubby habit of *C. ameristophyllum* probably does place selective pressure on mechanical strength of vessel elements as well as libriform fibers, and alternate circular bordered pits represent a configuration of maximal strength. On the other hand, the lateral walls of vessels in *C. lanceolatum* bear pseudoscalariform pits (Fig. 16). This pitting, considered a juvenilistic feature (Carlquist 1962a), has been protracted into secondary xylem in *C. lanceolatum* because, in my interpretation, selection for mechanical strength is lowered in succulent forms. This interpretation has been

offered earlier for plants with similar growth forms (Carlquist 1975). Thus, the role paedomorphosis plays in the secondary xylem is not an inflexible one, but species which show paedomorphosis will show various degrees and kinds of retention of juvenile features depending on the selective value of any given feature in any particular species.

The woods of *Crepidiastrum* and *Dendrocacalia* invite ecological interpretation on account of the distinctive habitats they occupy. The index I have termed Mesomorphy earlier (Carlquist 1977) can be used to compare these woods. The Mesomorphy value for *Crepidiastrum lanceolatum* is 42; that of *C. ameristophyllum* is 109 (stem) or 95 (root). Thus, the wood of *C. ameristophyllum* does seem to reflect the more mesic habitat of that species as compared to *C. lanceolatum*. The difference in figures between root and stem of *C. ameristophyllum* are negligible and can be considered statistically the same. The wood of *Dendrocacalia crepidifolia* has a Mesomorphy value of 493 (small stem) or 630 (large stem), figures remarkably high, even for Asteraceae. Although *C. ameristophyllum* is geographically in the same area as *D. crepidifolia*, *C. ameristophyllum* is in more open, unstable areas whereas *D. crepidifolia* is in intact cloud forest. The large size of *Dendrocacalia* plants (compared to plants of *Crepidiastrum*) means that *Dendrocacalia* roots probably tap deeper soil levels which are perpetually moist, whereas the shallower soil levels in which *C. ameristophyllum* roots grow very likely fluctuate more in moisture content. Thus, the high Mesomorphy value of *D. crepidifolia* compared to *C. ameristophyllum* is understandable.

The Mesomorphy value of *D. crepidifolia* shows increase with age of a stem; outer wood is more mesomorphic than inner wood. This is apparent not merely in vessel diameter, but in vessel-element length also. This trend with age of stems can be found not merely in this species, but in dicotyledons at large. The reason is not obscure. The Mesomorphy index, reflecting increase in vessel diameter as it does, reflects increased transpiration in that feature. Thus, the Mesomorphic index would be expected to advance as plants increase in height (foliage exposed to sunlight more) and roots lengthen (sources of water less subject to fluctuation available). Changes in wood of *Dendrocacalia* with age also include widening of rays; this is a common tendency in dicotyledon woods, as noted by Barghoorn (1941) and subsequent authors.

Increase in storiness with age, observed in *Dendrocacalia crepidifolia*, is to be expected in view of Bailey's (1923) account of storied cambium. In its storied cambium and wide multiseriate rays, the wood of *Dendrocacalia crepidifolia* closely matches that of other Senecioneae, such as *Senecio ecuadoriensis* Hieron. and *S. huntii* F. Meull. (Carlquist 1962b). This pattern is probably common in Senecioneae and resemblance of any pair of taxa should not necessarily be taken as indicative of close relationship.

LITERATURE CITED

- Adamson, R. S. 1934. Anomalous secondary thickening in Compositae. *Ann. Bot. (London)* 48:505-514.
- Bailey, I. W. 1923. The cambium and its derivative tissues. IV. The increase in girth of the cambium. *Amer. J. Bot.* 10:499-509.
- Barghoorn, E. S. 1941. The ontogenetic and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. *Amer. J. Bot.* 28:273-282.
- Bierhorst, D. W., and P. M. Zamora. 1965. Primary xylem elements and element associations of angiosperms. *Amer. J. Bot.* 52:657-710.
- Carlquist, S. 1957. The genus *Fitchia* (Compositae). *Univ. Calif. Publ. Bot.* 29:1-144.
- . 1958a. Wood anatomy of Heliantheae (Compositae). *Trop. Woods* 108:1-30.
- . 1958b. Anatomy of Guayana Mutisieae. Part II. *Mem. N.Y. Bot. Gard.* 10:157-184.
- . 1960. Wood anatomy of Cichorieae (Compositae). *Trop. Woods* 112:65-91.
- . 1962a. Wood anatomy of Senecioneae (Compositae). *Aliso* 5:123-146.
- . 1962b. A theory of paedomorphosis in dicotyledonous woods. *Phytomorphology* 12:30-45.
- . 1975. Ecological strategies of xylem evolution. *Univ. of Calif. Press, Berkeley, Los Angeles and London.* 259 p.
- . 1977. Wood anatomy of Onagraceae: additional species and concepts. *Ann. Missouri Bot. Gard.* 64:627-637.
- . 1981. Types of cambial activity and wood anatomy of *Stylidium* (Stylidiaceae). *Amer. J. Bot.* 68:778-785.
- . 1983. Wood anatomy of Calyceraceae and Valerianaceae, with comments on aberrant perforation plates in predominantly herbaceous groups of dicotyledons. *Aliso* 10:413-425.
- Col, M. A. 1899. Recherches sur l'appareil secreteur interne des Composées. *J. Bot. (Morot)* 13:234-252.
- Metcalf, C. R., and L. Chalk. 1950. *Anatomy of the dicotyledons.* The Clarendon Press, Oxford. 1500 p.
- Ohwi, J. 1965. *Flora of Japan* (ed. F. G. Meyer and E. H. Walker). Smithsonian Institution, Washington, D.C. 1067 p.
- Walker, E. H. 1976. *Flora of Okinawa and the southern Ryukyu Islands.* Smithsonian Institution Press, Washington, D.C. 1159 p.

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