WOOD ANATOMY OF SOME GENTIANACEAE: SYSTEMATIC AND ECOLOGICAL CONCLUSIONS

Sherwin Carlquist

INTRODUCTION

The present paper is contributed as part of a program of study of various sympetalous families of dicotyledons. Several phylogenists have shown renewed interest in attempting to delineate natural relationships and plausible groupings among these families. Wood anatomy does seem to offer some clues about affinity among the sympetalous families of dicotyledons.

The sympetalous (or "tubiflorous") families of dicotyledons have other features of interest with respect to study of wood anatomy. Because so many of these families are predominantly herbaceous, few studies on wood anatomy have been offered. Study of wood of predominantly herbaceous families has lagged behind study of wood of arboreal or even shrubby species. Not surprisingly, there has been no monograph on the woods of Gentianaceae. However, lack of studies on wood of Gentianaceae has been the result, in all likelihood, of the small number which are woody. To be sure, a few genera are woody throughout. Several species in both *Macrocarpaea* (Ewan 1947) and *Symbolanthus* (Macbride 1959) are shrubs or small trees ranging from 2 to 5 m in height. However, these two genera occur in tropical South America where they are usually not common, often in sparse populations in little-visited areas. The title of the present paper is intended to imply that the few species of the family for which I have collected wood samples do not represent a large sample of woody Gentianaceae. Other botanists in all likelihood will be able to assemble woods of other woody Gentianaceae. Eventually, wood of many of the shrubby or arboreal species of the family (and even subshrubby species) may be assembled, but that must result from the work of several collectors and will require a number of years.

The scarcity of material of woody Gentianaceae is evident from the fact that Metcalfe and Chalk (1950) discuss anatomy of the axis of Gentianaceae under the heading "Young Stem," with no section devoted to "Wood" as they do in many other families. Nevertheless, the observations offered by Metcalfe and Chalk represent the few published data on secondary xylem of the family thus far. Mennega (1980) has evidently seen wood of *Lisianthus*, rays of which she compares to those of *Retzia*, but she offers no further details on gentianaceous wood in her account of wood anatomy of Loganiaceae. Mennega's account of wood anatomy of Loganiaceae (sensu lato) does,

however, offer an excellent basis for comparison to the data on Gentianaceae below. Data on wood of *Ixanthus viscosus* Grisebach was briefly presented earlier (Carlquist 1974, p. 396).

The question as to whether Gentianaceae may be primitively herbaceous or woody is an interesting one, which the data of the present study may be useful in assessing.

The data offered here, however, are inadequate to use in commenting on interrelationships within the family. If Gentianaceae are divided into two subfamilies, Gentianoideae and Menyanthoideae, the genera of the present paper would belong to Gentianoideae. In the system of Gilg (1895), *Ixanthus* would fall in tribe Gentianeae subtribe Gentianinae. *Chelonanthus* and *Symbolanthus* would be included in the tribe Helieae.

Ixanthus viscosus, sole species of its endemic Canarian genus, is a perennial herb to 80 cm, woody at the base. It characterizes the laurel forest areas of Tenerife, Gran Canaria, La Palma, Gomera, and Hierro (Bramwell and Bramwell 1974). The specimen of *I. viscosus* was collected in shaded forests near El Bailadero, Tenerife. *Chelonanthus chelonoides* (L. f.) Gilg is a short-lived plant, woody at the base, which may reach 1 m in height; it ranges from Peru to Trinidad (Macbride 1959). The specimen in the present study was collected on a lateritic slope among weedy regrowth near an intact rain-forest area in the vicinity of Tocache Nuevo, Peru. The specimen of *Symbolanthus anomalus* (H.B.K.) Gilg is tentatively assigned to this species; it matches the technical features as given in the description given by Macbride, although the flower color differs somewhat. In the specimen collected, the flowers were bright green, prominently striped purple within. The plant was a shrub 2.5 m tall, growing in cloud-forest scrub with *Columellia* and *Siparuna* on the lower reaches of Wayna Picchu, a striking peak adjacent to the ruins of Macchu Picchu, Peru. The flowers of this specimen were slightly zygomorphic, and the pollen is in permanently united tetrads. These features qualify it for inclusion in *Symbolanthus* rather than *Macrocarpaea*. When more specimens of this genus have been collected, a more satisfying delineation of species will doubtless be developed.

MATERIALS AND METHODS

Wood samples of the three species studied were prepared by drying; bark was removed to facilitate drying and to prevent moulding. Because *Ixanthus* possesses interxylary phloem, liquid preservation would have been preferable, but walls of these cells remained integral even though cellular contents disappeared (Fig. 10, 11). All Gentianaceae have intraxylary phloem (Metcalfe and Chalk 1950), and liquid preservation would doubtless have aided study of that also, but walls were well retained even so (Fig. 9).

Wood of all species was boiled in water, stored in 50% ethyl alcohol, and

sectioned on a sliding microtome. No softening was necessary. Wood of *Ixanthus viscosus* was stained with safranin alone; wood of *Chelonanthus chelonoides* and *Symbolanthus anomalus* was stained in safranin and counterstained with fast green.

Macerations were prepared with Jeffrey's Fluid and stained with safranin. Means for quantitative features are based on 25 measurements except where structures (e.g., rays in *Ixanthus*) were too infrequent.

All wood samples are vouchered by herbarium specimens located in the herbarium of the Rancho Santa Ana Botanic Garden.

ANATOMICAL DESCRIPTIONS

Chelonanthus chelonoides, Carlquist 7124 (Fig. 1–2).—Growth rings absent, but vessels diminished in diameter during cessation of growth of secondary xylem at time of flowering (Fig. 1, top). Vessels round in transection. Mean vessel diameter, 38 μm. Vessels in radial chains (Fig. 1). Mean number of vessels per group, 1.96. Mean number of vessels per mm^2 of transection = 84. Mean vessel-element length, 427 μm. Mean vessel wall thickness, 1.1 μm. Perforation plates simple. Lateral wall pitting of vessels wholly of alternate pits, oval in shape, about 4 μm × 5 μm, pit apertures elliptical. Some fibriform vessel elements present. Imperforate tracheary elements are all fiber-tracheids by virtue of the much reduced circular pit borders (about 1 μm in diameter); pit apertures slitlike. Mean fiber-tracheid diameter at widest point, 25 μm. Mean length of fiber-tracheids, 5.7 μm. Mean fiber-tracheid wall thickness, 2.3 μm. Axial parenchyma vasicentric scanty, usually in strands of two (less frequently three) cells. Rays uniseriate and biseriate, uniseriate rays more frequent than biseriate rays (Fig. 2). Mean biseriate ray height, 701 μm. Mean biseriate ray width, 27 μm. Mean uniseriate ray height, 268 μm. All ray cells are basically upright (Fig. 2), square cells present only by subdivision. Ray cells with moderately thin, lignified walls bearing simple pits. Wood nonstoried. No amorphous deposits or crystals seen. Interxylary phloem absent.

Symbolanthus anomalus, Carlquist 7330 (Fig. 3–5).—Growth rings absent. Vessels round as seen in transection. Mean vessel diameter, 43 μm. Vessels often in radial chains (Fig. 4). Mean number of vessels per group, 1.81. Mean number of vessels per mm^2 of transection = 31. Mean vessel-element length, 317 μm. Mean vessel wall thickness, 2.1 μm. Perforation plates simple. Lateral wall pitting of vessels consists of alternate oval pits about 4 μm × 5 μm in diameter with narrow elliptical apertures the same length as the pit cavities. Fibriform vessels elements very infrequent. Imperforate tracheary elements are fiber-tracheids by virtue of small circular pit borders (1–1.5 μm in diameter); pit apertures slitlike (Fig. 3). Mean fiber-tracheid diameter at widest point, 28 μm. Mean fiber-tracheid length, 480
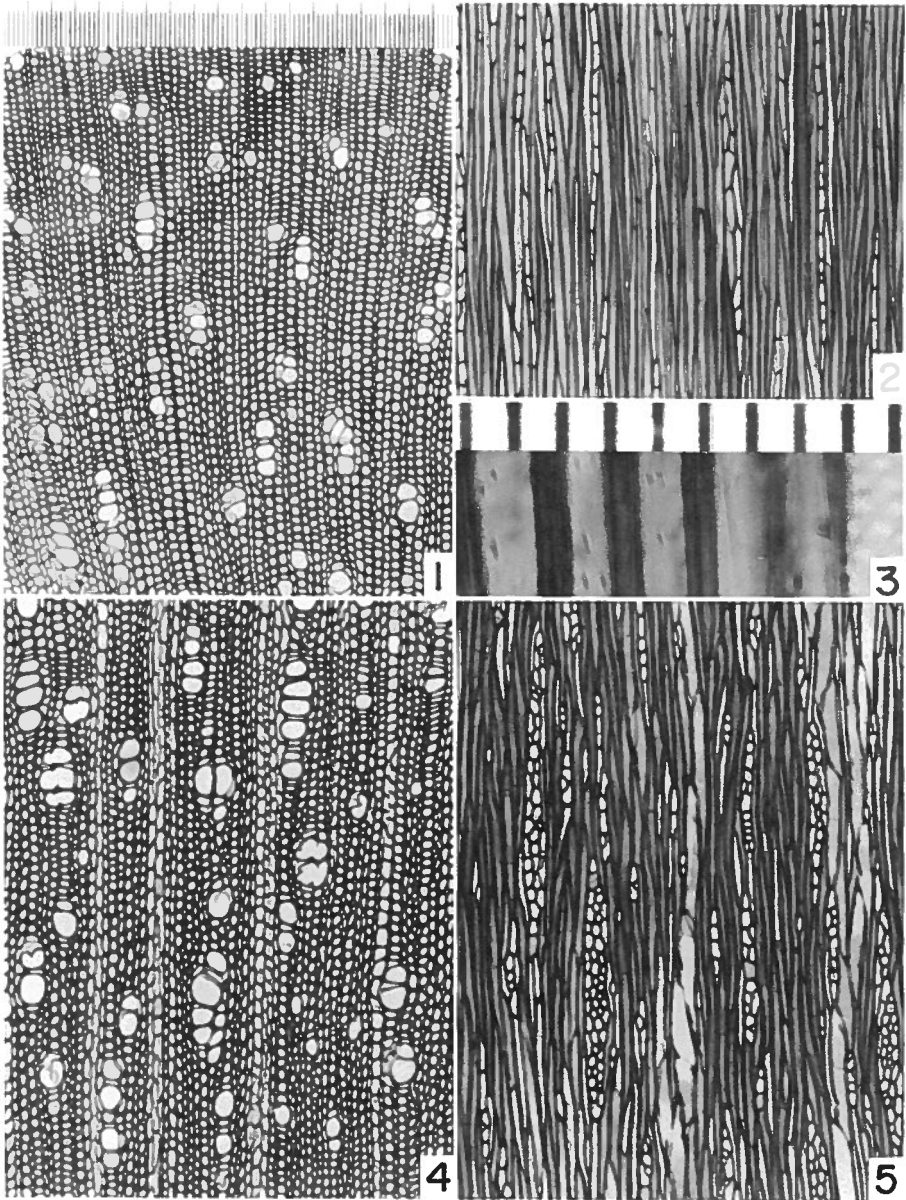
Fig. 1–5. Wood sections of Gentianaceae.— 1–2. *Chelonanthus chelonoides (Carlquist 7124).*— 1. Transection; top of section represents wood at periphery of stem in a plant in flowering condition, showing narrowing of vessels.— 2. Tangential section. Uniseriate rays predominate, ray cells are all upright.— 3–5. *Symbolanthus anomalus (Carlquist 7330).*—3. Fiber-tracheids from a radial section; slitlike pit apertures visible, left.— 4. Transection; vessels tend to be in

μm. Mean fiber-tracheid wall thickness, 2.5 μm. Axial parenchyma vasicentric scanty, usually in strands of two (less frequently three). Rays uniseriate and multiseriate. Multiseriate rays slightly more frequent than uniseriate rays (Fig. 5). Mean height of multiseriate rays, 431 μm. Mean width of multiseriate rays 3.4 cells or 54 μm at widest point. Mean height uniseriate rays, 95 μm (most about two cells high). Upright, square, and procumbent cells about equally frequent. Ray cells moderately thin walled, with lignified walls bearing simple pits. Wood nonstoried. No amorphous deposits or crystals observed.

Ixanthus viscosus, Carlquist 2068 (Fig. 6–11).—Growth rings present (Fig. 6), vessels and libriform fibers narrower in latewood. Strands of interxylary phloem are common in earlywood, much less frequent in the remainder of each growth ring. Vessels angular to round in transection, the narrow more nearly angular. Mean diameter of identifiable vessels, 26 μm. Vessels in radial rows (Fig. 6, 8). Mean number of identifiable vessels per group, 3.30. Mean number of identifiable vessels per mm² of transection = 340. Mean vessel-element length, 415 μm. Mean vessel wall thickness, 2.3 μm. Perforation plates simple (Fig. 8) or a few fringed by a strand of lignified wall material. A few double perforation plates seen. Some very small perforation plates are pitlike in appearance. Lateral wall pitting of vessels consists of circular alternate pits about 4 μm in diameter, with apertures widely elliptical, about the same length as the diameter of the pit cavity. Numerous fibriform vessel elements present; perhaps the majority of vessel elements are fibriform. Imperforate tracheary elements are considered libriform fibers here because no pit borders could be discerned. Pit apertures of libriform fibers narrowly slitlike. Mean diameter of libriform fibers at widest point, 24 μm. Libriform fibers often square in transection (Fig. 10, 11). Mean length of libriform fibers, 516 μm. Mean wall thickness of libriform fibers, 2.3 μm. Axial parenchyma vasicentric scanty, typically in strands of two cells. Rays relatively infrequent (Fig. 7), wood rayless in earlier portions. Uniseriate rays more common than biseriate rays. Extremely few rays wider than two cells at widest point. Mean height biseriate rays, 289 μm. Mean width of biseriate rays at widest point, 35 μm. Mean height of uniseriate rays, 198 μm. Ray cells mostly upright; a very few square cells present, and procumbent cells are present by subdivision of upright cells only. Ray cells moderately thin walled, cell walls lignified and bearing simple pits. Wood nonstoried. No amorphous deposits or crystals seen. Interxylary phloem cells larger than

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radial rows.—5. Tangential section. Multiseriate rays with procumbent cells are frequent. (Fig. 1–2, 4–5, magnification scale above Fig. 1 [finest divisions = 10 μm]. Fig. 3, scale above Fig. 3 [divisions = 10 μm].)
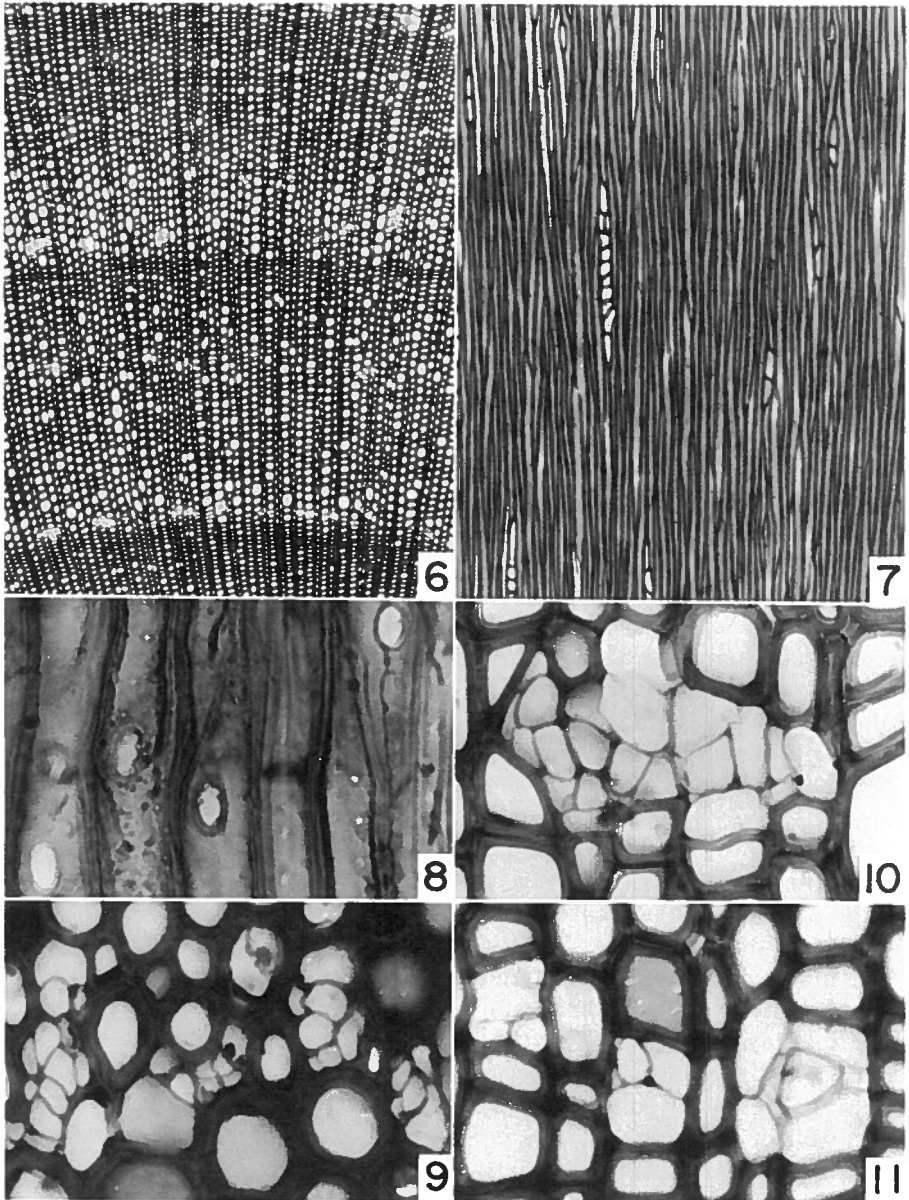
Fig. 6–11.   Wood sections of *Ixanthus viscosus* (*Carlquist 2068*).—6. Transection, showing two growth rings; interxylary phloem strands are predominantly in earlywood.—7. Tangential section; rays are few, mostly uniseriate.—8. Perforation plates from fibriform vessels as seen in a radial section.—9. Intraxylary phloem (pith below, xylem above) from stem transection.— 10. Interxylary phloem from stem transection, numerous phloem cells forming a group roughly

intraxylary phloem cells (compare Fig. 9 to Fig. 10, 11). Interxylary phloem strands numerous and scattered, the larger oval in transection. Interxylary phloem strands range in size from a pair of cells (sieve-tube element plus companion cell) to several such cells (Fig. 11) or larger groups of phloem cells (Fig. 10).

The narrow fibriform vessel elements of *Ixanthus viscosus* are only a little wider than the libriform fibers and are difficult to identify in transection. Fibriform vessel elements are very abundant in *Ixanthus,* predominating over typical vessel elements. Because of difficulty in identifying vessel elements in transections of wood of *Ixanthus,* the number of vessels per mm^2 is doubtless larger than indicated above, and the number of vessels per group may also be larger than recorded. Mean vessel diameter may actually be smaller than recorded, because some cells identified as libriform fibers in transection may actually bear perforation plates.

SYSTEMATIC CONCLUSIONS

Wood anatomy of Gentianaceae is characterized by vessels round in transection (rarely square where very small), the vessels in radial chains. Perforation plates are simple. Lateral wall pitting of vessels consists of alternate oval pits with elliptical apertures about the same length as the pit cavity diameter. Imperforate tracheary elements are fiber-tracheids with vestigial borders or else are libriform fibers. Axial parenchyma is vasicentric scanty, in strands of two or three cells. Wood may be rayless at first (apparent raylessness reported by Metcalfe and Chalk in *Blackstonia, Centaurium, Exacum,* and *Gentiana*). Rays where present are predominantly uniseriate or, in larger stems (*Symbolanthus anomalus*) multiseriate rays are equally frequent. Ray cells are upright except in the larger stems (*Symbolanthus anomalus*). The widening of rays and the increase in the proportion of procumbent cells with age are ontogenetic trends identified by Barghoorn (1941a) in wood of dicotyledons at large. He also noted that woods rayless at first may acquire rays during the growth of the stem (Barghoorn 1941b). Intraxylary phloem has been reported in all Gentianaceae studied to date (Metcalfe and Chalk 1950). They have reported interxylary phloem (small strands of sieve tubes) in *Blackstonia, Geniostemon, Gentiana, Nemotheca, Schultesia,* and *Swertia.* In the present study, *Ixanthus* was shown to have interxylary phloem. Wood of Gentianaceae is nonstoried and lacks crystals.

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oval in outline.—11. Three strands of interxylary phloem from a stem transection; the smallest (left) consists of only one sieve tube element and one companion cell. Above the strand of phloem, center, may be seen the cross-wall of an axial parenchyma strand. (Fig. 6–7, magnification scale above Fig. 1. Fig. 8–11, scale above Fig. 3.)

The vessel-element/imperforate tracheary-element ratio ("V/F" of Mennega 1980) is a little lower here than in the bulk of Loganiaceae studied by Mennega.

All of the features above may be found in Loganiaceae, where they can be described as common or even modal in that family (Metcalfe and Chalk 1950; Mennega 1980) except for raylessness. The congruence between wood anatomy of Gentianaceae and that of Loganiaceae is close enough so that comparison with a wider range of dicotyledon families seems superfluous at this point. Systematists seem in very close agreement regarding the relationships of Gentianaceae with other families. The order Gentianales usually is held to consist of Gentianaceae, Loganiaceae, Apocynaceae, Asclepiadaceae, Oleaceae, and Buddlejaceae.

The presence of fibriform vessel elements in *Ixanthus* and, to a lesser extent, *Chelonanthus* does not seem a feature indicative of relationship. Fibriform vessel elements may occur in various groups of dicotyledons such as Hydrophyllaceae (Carlquist et al. 1983) and Passifloraceae (Woodworth 1935; Ayensu and Stern 1964).

The occurrence of intraxylary and interxylary phloem in Gentianaceae does not indicate a relationship with Onagraceae, which also has both of these (Carlquist 1975), or to other myrtalean families. Intraxylary and interxylary phloem have a physiological significance, and have been independently invented in Myrtales and Gentianales. In both groups, intraxylary phloem is widespread but interxylary phloem more limited in distribution: Onagraceae is typical in this regard. Intraxylary phloem can be regarded as a kind of morphological precursor for interxylary phloem; the latter may or may not occur, depending on various factors, particularly the physiological nature of the plant (Carlquist 1975).

ECOLOGICAL CONCLUSIONS

The tendency for vessels to be narrower toward the end of xylem accumulation in *Chelonanthus chelonoides* has obvious correlations. Flowering of the plant at this time signals an end to xylem accumulation and the xeric quality denoted by narrower vessels may be expected because flowering of short-lived perennials (or annuals) tends to occur at the end of a growing season when less water is available than it is during the period when vegetative growth and transpiration are greatest.

The growth rings of *Ixanthus* relate to the temperate climate in which that genus exists. The climate of the Canary Islands is moderate by virtue of being insular, but the laurel forest areas where *Ixanthus* occurs experience winter cold as well as a fluctuation between winter rainfall and summer drought. The most noteworthy feature of *Ixanthus* growth rings is the occurrence of interxylary phloem strands almost exclusively in earlywood. This

may have a physiological significance. Rapid mobilization of photosynthates for rapid growth or flowering is cited as a probable correlation with occurrence of interxylary phloem in Onagraceae (Carlquist 1975); Onagraceae with steady growth and continuous flowering tend to lack interxylary phloem. This correlation may hold in Gentianaceae as well. Growth and flowering are highly seasonal in *Ixanthus* but nonseasonal in *Chelonanthus* and *Symbolanthus,* both of which lack interxylary phloem.

The very narrow vessels of *Ixanthus* betoken a more temperate habitat with periods of drought or frost as compared with the uniformly mild and wet climates of the habitats where *Chelonanthus* and *Symbolanthus* grow.

If one calculated a ratio, Mesomorphy (Carlquist 1977), one obtains the figure 32 for *Ixanthus viscosus,* 192 for *Chelonanthus chelonoides,* and 440 for *Symbolanthus anomalus.* These figures seem to correlate closely with the habitats of these species as described in the Introduction. The fact that these values do correlate closely with habitats indicates that leaves are not a primary water-management tool in these species, with wood playing a comparatively small role. Rather, the leaves are drought-deciduous in *Ixanthus* and in other Gentianaceae, so that the nature of wood structure does become important for maintaining the integrity of the water-conducting system. If Mesomorphy values correlate well with known habitat, wood structure is probably directly related to the nature of the water economy of the plant. If the Mesomorphy value differs from that which might be expected in a particular habitat, that fact is *predictive*: it indicates one should look for duration or structure of leaves, presence of succulence, etc., as factors which are important mediating devices in the water-management system.

HABIT OF GENTIANACEAE

Does wood give any indication as to whether Gentianaceae have a woody ancestry or an herbaceous ancestry? The present sample is too small to be decisive. However, one can call attention to the lack of rays in *Ixanthus* and other Gentianaceae, and to the predominance of upright cells in rays of *Ixanthus* and *Chelonanthus.* A high frequency of erect ray cells characterizes wood of predominantly herbaceous groups (Carlquist 1962). Raylessness seems to be present in some herbaceous groups which are in the process of becoming secondarily woody (Carlquist 1970). In these cases, raylessness may represent a way of converting a maximum of xylem to mechanical tissue and thereby achieving a greater stature in an evolutionarily rapid way. *Ixanthus* may well be secondarily woody, using this feature as indicative. However, the wood of *Symbolanthus anomalus* described here shows no indication of any herbaceousness in structure. Judging from its ray histology in particular, a woody habit might have been primitive in Gentianaceae. In any family such as Gentianaceae where herbs with various degrees of wood-

iness are frequent, fluctuation toward woodiness and away from woodiness may both take place several times independently. Thus even if one hypothesizes a woody ancestry for the family, some genera in the family could be secondarily woody.

LITERATURE CITED

Ayensu, E. S., and W. L. Stern. 1964. Systematic anatomy and ontogeny of the stem in Passifloraceae. Contrib. U.S. Nat. Herb. 34:45–73.

Barghoorn, E. S. 1941a. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. Amer. J. Bot. 28:273–282.

———. 1941b. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. III. The elimination of rays. Bull. Torrey Bot. Club 68:317–325.

Bramwell, D., and Z. I. Bramwell. 1974. Wild flowers of the Canary Islands. Stanley Thornes, Ltd., London and Burford. 261 p.

Carlquist, S. 1962. A theory of paedomorphosis in dicotyledonous woods. Phytomorphology 12:30–45.

———. 1970. Wood anatomy of insular species of *Plantago* and the problem of raylessness. Bull. Torrey Bot. Club 97:353–361.

———. 1974. Island biology. Columbia University Press, New York. 660 p.

———. 1975. Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. Ann. Missouri Bot. Gard. 62:386–424.

———. 1977. Wood anatomy of Onagraceae: additional species and concepts. Ann. Missouri Bot. Gard. 64:627–637.

———, V. M. Eckhart, and D. C. Michener. 1983. Wood anatomy of Hydrophyllaceae. I. *Eriodictyon*. Aliso 10:397–412.

Ewan, J. 1947. A revision of *Macrocarpaea*, a neotropical genus of shrubby gentians. Contrib. U.S. Nat. Herb. 29:209–249.

Gilg, E. 1895. Gentianaceae. *In* A. Engler and K. Prantl [eds.], Die natürlichen Pflanzenfamilien IV(2):50–108. Verlag von Wilhelm Engelmann, Leipzig.

Macbride, J. F. 1959. Gentianaceae. *In* J. F. Macbride [ed.], Flora of Peru. Field Museum of Natural History, Bot. Ser. 13(5:1):270–363.

Mennega, A. M. W. 1980. Anatomy of the secondary xylem. *In* A. J. M. Leeuwenberg [ed.], Die natürlichen Pflanzenfamilien, ed. 2, 28bI:112–161. Duncker & Humblot, Berlin.

Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford. 1500 p.

Woodworth, R. H. 1935. Fibriform vessel members in the Passifloraceae. Tropical Woods 41:8–16.

Rancho Santa Ana Botanic Garden, Claremont, California 91711, and Department of Biology, Pomona College, Claremont, California 91711.

Footnote