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THE VEGETATIVE MORPHOLOGY OF THE RETICULATE-VEINED LILIIFLORAE*

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ABSTRACT

Conover, Margaret Howard (Botany Department, University of Massachusetts, Amherst, MA 01003) 1983. The vegetative morphology of the reticulate-veined Liliiflorae. Telopea 2(4): 401-412.—The Philesiaceae, Dioscoreaceae, Smilacaceae, and related families have traditionally been considered to be advanced within the Liliiflorae and most closely allied to the tribes Polygonateae and Uvularieae of the Liliaceae. Reticulate-veined leaves and climbing habit have been used to characterize the former families, but only a more rigorous analysis of their leaf morphology and growth habits will lead to an accurate appraisal of phylogenetic relationships within the Liliiflorae. The so-called reticulate-veined Liliiflorae are shown here to be climbing plants with indeterminate growth, proleptic branching, and spirally arranged, petiolate leaves that possess the following vascular and dermal characters: free vein endings, secondary veins which cross the intercostal panels, primary veins that do not always fuse apically, isodiametric and randomly arranged epidermal cells, stomates with fewer than 4 contact cells, and stomates oriented either transverse to the leaf axis or randomly. In these plants, the morphology of proximal portions of branches resembles the adult vegetative morphology of the parallel-veined allies in the Polygonateae and Uvularieae. This suggests that heterochrony may have been involved in the evolution of the Liliiflorae.

INTRODUCTION

Classically, the Smilacaceae, Philesiaceae, Dioscoreaceae, Stenomeridaceae, Stemonaceae, Trilliaceae and Taccaceae have been treated as advanced families of the Liliiflorae. Recently, however, some authors have expressed the opinion that these reticulate-veined taxa possess many characters that are primitive among the monocots (Burkill, 1960; Huber, 1969; Dahlgren and Clifford, 1981).

Unfortunately, efforts to use vegetative morphology to resolve this and other taxonomic questions have been limited by the fact that monocot leaf venation is still relatively poorly understood. It is not clear, for instance, what individual authors intend in their use of the term "reticulate". Does this refer to the occurrence of free vein-endings or to the random net-like arrangement of higher-order veins? Are these characters in any way comparable with those of reticulate-veined dicot leaves? Do leaves of the reticulate-veined Liliiflorae comply with Doyle's (1973) assertion that the longitudinal veins of all monocot leaves 1) are differentiated into more than one size class, 2) converge and fuse towards the leaf apex, and 3) are interconnected by transverse cross-veins? Does Stebbins' (1974) assertion that monocot leaves usually lack free vein-endings hold?

This research was undertaken in an attempt to adapt existing terms and concepts for dicot leaf architecture (Hickey, 1973, 1979) to the description of monocot leaves, in order to:

a) answer the questions posed above;
b) produce a survey of leaf-morphological characters in the reticulate-veined Lilliflorae and parallel-veined allies which may have taxonomic interest;

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c) discover any correlations between leaf architecture and other vegetative morphological characters, particularly those of epidermal patterns and growth habit;
d) establish whether a basis exists for comparing leaf architecture in the following three pairs of taxa: the reticulate-veined Liliiflorae and their parallel-veined allies, the reticulate-veined Liliiflorae and the dicots, the parallel-veined allies and the more typical Liliiflorae.

MATERIALS AND METHODS

One hundred and forty-one leaves of 98 species and 47 genera of reticulate-veined Liliiflorae and parallel-veined allies were selected from herbarium specimens and cleared in NaOH according to the technique of Hickey (1973). They were stained in safranin and mounted in Permount, between glass slides, or in polyester resin, between sheets of acetate film. Some were infiltrated with paraffin oil and left unmounted. Specimens were studied directly with a dissecting microscope. Data were collected in accordance with the outline of leaf-architectural characters produced by Hickey (1973, 1979). Whole leaves were photographed on a back-lit ground glass screen using Panatomic X film and a green filter. Higher-order venation was photographed, at a magnification of 20 X, using a Wild dissecting microscope and Panatomic X film. Prints were made on high-contrast photographic paper.

RESULTS

1. Leaf Architecture

The results from the survey of leaf architectural characters are listed in Table 1.

Table 1. Leaf venation characters in the reticulate-veined Liliiflorae and their parallel-veined allies. The number of species and specimens is indicated by values in square brackets [species-specimens]. Character states defined as in the accompanying key.

		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Liliaceae												
Convalliarieae												
Convallaria	[1-2]	-e	5-7	a	ap	-	6	par	+	par	-	el-par
Reineckea	[1-1]	-e	3	p	ap	-	5	par	?	par	-	el-par
Speirantha	[1-1]	-e	5	p	ap	-	6	par	+	par	-	el-par
Liliaceae												
Polygonateae												
Clintonia	[2-2]	-e	5-7	a	ap	-	5	par	+	par	-	el-par
Disporopsis	[1-1]	-	5	a	ap	-	5	par	+	par	-	el-par
Disporum	[3-4]	-	5-7	a	ap	-	5-6	par	+	par	-	el-par
Prosartes	[5-7]	-	5-7	a	pr	+	5-6	par	+	ret	+ +	irr
Drymophila	[2-3]	-	5	a	pr	+	4	par	+	par	+ +	iso
Maianthemum	[2-2]	+	5	c	ap	+	6	par	+	par	-	el-par
Oligobotrya	[1-1]	-	7	a	ap	+	6	par	+	par	-	el-par
Polygonatum	[4-4]	-	5-7	a	pr	+	5-6	par	+	par	-	el-par
Smilacina	[1-1]	-	5-7	a	pr	+	5-6	par	+	par	-	el-par
Streptopus	[2-2]	-	5	a	ap	+	6	par	+	par	-	el-par
Liliaceae												
Uvularieae												
Gloriosa	[1-1]	-	?	a	ap	-	?	par	+	par	?	el-par
Kreysigia	[1-1]	-	5-7	a	pr	+	5	par	+	par	+	irr
Littonia	[1-1]	-	?	a	ap	-	?	par	+	par	?	el-par
Sandersonia	[1-1]	-e	5	a	ap	+	5	par	+	par	?	el-par
Schelhammera	[1-2]	-	5-7	a	ap	-	5-6	par	+	par	-	el-par
Tricyrtis	[5-5]	-e	7-9	a	pr	-	4-5	par	-	ret	-	irr
Uvularia	[1-2]	-	5	a	ap	-	5	par	+	par	-	el-par
Smilacaceae												
Heterosmilax	[1-1]	+	5	a-c	ap	+ +	6	pin	-	ret	+ +	irr
Smilax	[12-19]	+	5-7	a-c	pr	+ +	5-6	pin	-	ret	+ +	irr
Ripogonum	[4-7]	+	5	a	ap	+	5-6	pin	-	ret	+ +	irr

		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Philesiaceae												
Eustrephus	[1-4]	-	5-7	a	ap	-	5-6	par	+	par	-	el-par
Geitonoplesium	[1-2]	+	5	a	ap	-	4-5	par	+	par	-	el-par
Lapageria	[1-3]	+	5	a	pr	+ +	5	pin	-	ret	+ +	irr
Philageria	[1-1]	+	5	a	pr	+	5	pin	-	ret	+ +	irr
Philesia	[1-2]	+	3	a	ap	+	4	pin	-	ret	+ +	irr
Behnia	[1-2]	+	15	a	pr	+	2	pin	-	tra	+ +	el-tra
Luzuriaga	[4-8]	-	3-7	a	pr	-	2-4	par	+	par	+	el-par
Petermannia	[1-3]	+	5-7	a	ap	+ +	5-6	par	-	ret	+ +	irr
Alstroemeriaceae												
Alstroemeria	[1-1]	+	7	a	ap	+	5	par	+	par	-	el-par
Bomarea	[2-2]	+	5-7	a	ap	+	5	par	+	par	-	el-par
Dioscoreaceae												
Dioscorea	[10-10]	+	5-?	a-c	pr	+ +	5-6	pin	-	ret	+ +	irr
Rajania	[3-4]	+	5	a-c	pr	+ +	5	pin	-	ret	+ +	irr
Tamus	[1-2]	+	7	c	nc	+ +	5	pin	-	ret	+ +	irr
Stenomeridaceae												
Avetra	[1-1]	+	5-7	a	pr	+ +	6	pin	-	ret	+ +	irr
Stenomeris	[2-3]	+	9-?	c	pr	+ +	4	pin	-	tra	+	el-tra
Trichopus	[1-2]	+	5	a	pr	+	5	pin	-	ret	+ +	irr
Stemonaceae												
Croomia	[2-4]	+	7-9	a	pr	+ +	4	pin	-	tra	+ +	el-tra
Stemona	[5-5]	+	7-9	c	pr	+ +	2	pin	-	tra	+ +	el-tra
Stichoneuron	[1-2]	+	7-9	a	pr	+ +	4	pin	-	tra	+	el-tra
Trilliaceae												
Medeola	[1-2]	-	3-5	a	pr	+ +	4	pin	-	par	-	el-par
Paris	[4-4]	-	3-5	a	pr	+ +	4	pin	-	par	+	el-par
Scoliopus	[1-1]	-	7	p	ap	+	4	par	+	par	-	el-par
Trillium	[1-2]	-	3-5	a	ap	+ +	5	pin	-	par	-	el-par
Taccaceae												
Tacca	[3-6]	+	9-?	a	nc	+ +	5-7	pin	-	ret	+ +	irr

TABLE 1
Key to characters:

1. Petiole. + (present), - (absent), -e (absent, and leaf base encircling more than 180° of the stem).

2. Number of primary veins (range observed in leaves sampled).

3. Course of primary veins. a (acrodromous), p (parallelodromous), c (campylodromous).

4. Position of convergence of the most exmedial lateral veins, ap (at the apex of the leaf), pr (proximal to the leaf apex), nc (not convergent).

5. Acropetal weakening of primary veins.- (slight), + (pronounced), + + (very pronounced).

6. Number of vein orders (range observed in leaves sampled).

7. Course of secondary veins, (parallel or pinnate).

8. Do secondary veins enter the stele? + (yes), - (no).

9. Course of the higher vein orders: par (parallel) or tra (transverse to the leaf axis), or ret (with no predominant orientation).

10. Free-vein endings. - (absent), + (rare), + + (present).

11. Shape of areoles: irr (irregular), iso (isodiametric), el-par (elongate parallel to the leaf axis) or el-tra (elongate transverse to the leaf axis).

Leaf morphology of the reticulate-veined Liliiflorae and their parallel-veined allies is relatively uniform and unspecialized. Typically, leaves are 40-100 mm long, dorsiventral, simple and ovate, with entire margins and a narrow insertion at the node. Leaf length and shape are relatively variable. Petioles occur in many taxa (Character 1 of Table 1). Unlike the remainder of the Liliiflorae, these genera lack such predominantly monocotyledonous features as closed tubular leaf sheaths, radial

Vorläuferspitzen, ligules, and laminae that are unifacial, equitant, linear, plicate, or schizogenously divided.

The characteristic of dicot leaf venation that underlies Hickey's (1973, 1979) approach to its analysis and distinguishes it from that of fern and gymnosperm leaves, is the occurrence of several recognizable size classes of veins. This condition was found to be universal in the reticulate-veined Liliiflorae and parallel-veined allies (Character 6), facilitating the adaptation of Hickey's terminology and concepts for use with this group of monocots.

Primary veins, i.e., those that are the strongest in the leaf and of equal strength at their point of origin near the leaf base, are characterized, in the reticulate-veined Liliiflorae and parallel-veined allies, by the following features (see Fig. 1a, d).

1. There are 3 to 9 or more primary veins (Character 2), this variation often occurring within a single plant.
2. All primary veins are distinguishable in cross-section of the leaf base or petiole, and enter the stele discretely (Fig. 1c, f).
3. The greatest diameter of primary veins is less than 1% of the leaf width. Hence, they are classified as weak veins.
4. The midvein consists of a single vascular bundle and is not comparable with the multistranded costa found in many other monocots (Fig. 1c, f).
5. The course of primary veins is acrodromous, campylodromous (Fig. 1d), or parallelodromous (Fig. 1a; Character 3).
6. In any cross-section, each lateral primary vein is smaller in diameter, i.e., weaker, than its adjacent admedial primary.
7. Individual veins weaken acropetally (Character 5).
8. There is a strong tendency for primary veins to anastomose apically with one another (Fig. 1a, d).
9. This apical convergence follows a characteristic pattern: any given vein, at some point along the length of the leaf, curves towards and fuses only with the adjacent admedial vein. The adjacent exmedial vein, likewise curves and fuses, but always at a more proximal level. There is variation in the distance from the leaf tip at which this convergence occurs (Character 4).

The primary veins divide the leaf into intercostal panels. The course of the strongest veins within the panel, i.e., the secondary veins, may produce one of two distinct patterns (Character 7).

1) In some genera, secondary veins run parallel to the leaf axis, longitudinally bisecting the panel and running proximally through the leaf base into the stele (Character 8; Fig. 1a, c). Distally, these parallel secondaries fuse with adjacent primaries, but without affecting the basic pattern of primary vein convergence (Fig. 1a). Leaves of this type may be termed "parallel-veined".

2) In other genera, secondary veins arise from the admedial primary vein in a pinnate arrangement comparable with that observed in dicots (Character 7; Fig. 1d). These secondaries do not enter the stele proximally as in the previous example (Character 8; Fig. 1f). Distally, they may extend across the panel and fuse with the exmedial primary or they may ramify and end blindly. Leaves of this type may be termed "reticulate-veined".

The distribution of this character, that is, of secondary vein course, or, more precisely, of entry of secondary veins into the stele, is found to correspond closely to taxonomic groupings. Parallel-veined leaves occur in 24 genera, including the entire Polygonateae, Convallarieae, Alstroemeriaceae, 3 genera of the Philesiaceae, 6 of the 7 genera of the Uvularieae, and the genus *Scoliopus* of the Trilliaceae. Reticulate-veined leaves occur in 22 of the genera surveyed, characterizing the families Smilacaceae, Dioscoreaceae, Stenomeridaceae, Stemonaceae, Trilliaceae, Taccaceae, 5 genera of the Philesiaceae, and the genus *Tricyrtis* of the Uvularieae.

The course of tertiary and higher-order veins is largely correlated with that of secondary veins (Character 9).

1) In those genera with parallel secondaries, higher-order vein course is also parallel (Fig. 1b). Each tertiary vein longitudinally bisects the panel between secondaries, each quaternary vein longitudinally bisects the panel between tertiaries, and so forth. Some or all of the vein orders may enter the stele proximally. Distally they fuse with adjacent veins of lower order (Fig. 1a).

2) In those genera with pinnate secondary veins, tertiary and higher-order veins are truly reticulate (Fig. 1e), arising, usually at right angles, from a vein of lower order and either fusing with another vein distally or ramifying. The course of these veins may be random, or with a predominant orientation at a given angle to the leaf axis. Like the secondaries, they do not enter the stele.

The course of the finest veins of the leaf, here termed "ultimate veinlets", also correlates with the course of secondary veins.

1) Ultimate venation of parallel-veined leaves is in the form of unbranched, transverse commissural veinlets (Fig. 1b). Free vein endings are usually absent (Character 10). The areoles are rectangular in shape, oriented parallel to the leaf axis (Character 11).

2) Those genera with pinnate secondary veins exhibit ramifying veinlets with free vein endings (Fig. 1e). The areoles are usually isodiametric or of incompletely closed meshes with no predominant orientation (Character 11).

The correlation of secondary vein course with other leaf-architectural characters is illustrated in Table 2 (Characters 1-7), where the frequency of several character states is recorded for groups established on the basis of the entry of secondary veins into the stele. Leaves with pinnate secondaries usually possess petioles, and a stronger acropetal weakening and more gradual apical convergence of primary veins than seen in parallel-veined leaves.

2. Epidermal Morphology

In order to document variation in epidermal patterns, several characters, both developmental and mature, were recorded for 39 genera. The extent of correlation between dermal and vascular patterns is illustrated in Table 2 (Characters 8-13), and its taxonomic significance summarized below.

The parallel-veined genera have elongate epidermal cells arranged in distinct files (Fig. 2a), while the reticulate-veined Liliiflorae have predominantly isodiametric, randomly arranged epidermal cells (Fig. 2c).

Stomates of the reticulate-veined Liliiflorae and parallel-veined allies, unlike those of many monocot leaves, are usually restricted to one, usually the abaxial, surface of the lamina (Fig. 2b, d). Subsidiary cells are entirely absent here and, with the exception of the genus *Ripogonum,* development of the stomatal complex is perigenous. The number of contact cells which each stomate has at maturity appears to be taxonomically significant. It is developmentally determined by the initial number of sides of the meristemoid (3 or 4), and by further divisions of neighbour cells.

Table 2. Correlation between characters of leaf architecture, leaf epidermal patterns, and growth habit, with the course of secondary veins in 46 genera of the reticulate-veined Liliiflorae and parallel-veined allies. Values represent the number of genera with each combination of characters. Chi square and p were calculated from a 2 x 2 contingency test.

Characters	**Course of secondary veins** not entering the stele (reticulated-veined)	 entering the stele (parallel -veined)	*total number of genera*	χ^2	p
	(Number of genera)				
1) Petiole:					
present	18	4			
absent	4	20	46	16.19	<.001
2) Acropetal and lateral weakening of primary veins:					
pronounced	21	12			
not pronounced	1	12	46	10.21	<.01
3) Apical convergence of primary veins:					
below leaf apex (gradual)	17	6			
near leaf apex (abrupt)	5	18	46	9.83	<.01
4) Course of secondary veins:					
pinnate	20	0			
parallel	2	24	46	34.04	<.001
5) Course of higher vein orders:					
reticulate	19	1			
parallel	3	23	46	24.44	<.001
6) Areole shape:					
isodiametric or irregular	19	3			
elongate parallel to axis	3	21	46	21.34	<.001
7) Free vein endings:					
present	19	4			
absent	3	17	43	16.04	<.001
8) Adaxial epidermal cell shape:					
isodiametric	19	1			
elongate	2	17	39	24.68	<.001
9) Adaxial cell files:					
absent	20	4			
present	1	14	39	18.85	<.001
10) Adaxial anticlinal cell walls:					
sinuous	9	5			
straight or curved	12	13	39	.41	.520
11) Stomatal orientation:					
random	13	0			
regular	8	18	39	14.04	<.01
12) Stomatal orientation:					
not parallel to leaf axis	15	0			
parallel to leaf axis	6	18	39	17.98	<.001
13) Number of contact cells:					
fewer than 4	14	0			
4 or more	7	18	39	15.93	<.001
14) Aerial axes:					
climbing	11	5			
not climbing	9	19	44	4.12	<.05

15) Aerial axes:					
indeterminate	9	4			
determinate	10	20	43	4.71	<.05
16) Branching:					
proleptic	9	4			
absent or sylleptic	7	19	39	7.82	<.05
17) Phyllotaxy:					
not distichous	8	2			
always distichous	3	15	28	7.17	<.01
18) Aerial shoots:					
evergreen	5	6			
herbaceous	8	16	35	0.10	.755

Stomates of the parallel-veined genera studied here, like most other monocots, have four or more contact cells (Fig. 2b), while those of the reticulate-veined Liliiflorae often have fewer (Fig. 2d). The second stomatal character of taxonomic significance is that of orientation. Stomates of the parallel-veined allies are oriented strictly parallel to the leaf axis (Fig. 2b), while those of the reticulate-veined Liliiflorae are generally randomly oriented with a tendency to be perpendicular to the leaf axis (Fig. 2d). Epidermal characters found to be unrelated to leaf venation include sinuosity of anticlinal walls, stomatal density, stomatal index, epidermal cell size, guard cell length, and ratio of epidermal and guard cell lengths.

3. Growth habit

Whole living plants of 43 genera and 52 species of the reticulate-veined Liliiflorae and their allies were observed in their native habitats or in cultivation. This analysis established the existence of correlations between several features of growth habit and leaf architecture (See Table 2, Characters 14-18). Parallel-veined genera are usually rosette plants or caulescent non-climbers. The rosette habit is distinguished by leaves borne at ground level, on a short shoot at the apex of a rhizome, as in most monocot herbs. No aerial leaf-bearing axis is apparent in the vegetative condition. Growth is determinate. The caulescent non-climbers, in contrast, bear leaves on aerial but determinate long shoots. Branching, which seldom occurs, is usually sylleptic, and phyllotaxy is distichous. These plants are largely herbaceous perennials, the overwintering parts consisting of a rhizome with large subterranean buds bearing relatively well-developed leaves packed tightly together. In spring, internodes of the caulescent form expand rapidly into a long shoot, while those of the rosette plants fail to elongate.

The reticulate-veined Liliiflorae are largely climbers with indeterminate, proleptically branched long shoots. Although the foliage leaves of these genera are spirally arranged or opposite, the lower, or juvenile nodes bear, in distichous phyllotaxy, small cataphylls with stem-encircling leaf bases, parallel veins and parallel stomates. Many of these plants are evergreen climbers with small dormant axillary buds containing relatively unexpanded young leaves. Growth of these leaves does not occur until elongation of internodes is nearly complete.

DISCUSSION

One of the aims of this research has been to seek comparisons between leaves of the reticulate-veined Liliiflorae and parallel-veined allies and of both monocots and dicots. The most obvious point of comparison is between the parallel-veined allies and the more typical monocots. In venation and morphology, leaves of the 24 parallel-veined genera investigated here resemble bifacial, linear leaves of the remainder of the Liliiflorae and other monocots, differing primarily in shape and in the absence of an encircling leaf base.

The homology between leaves of the reticulate-veined Liliiflorae and their parallel-veined allies is also supported by the similarity in their morphology, including courses of the primary veins. The major difference between the two groups is the difference in courses of the secondary veins. The distinction between the two forms is not absolute, and intermediate conditions exist in *Tricyrtis* and *Petermannia.*

The validity of homologizing secondary veins of parallel-veined monocot leaves with those of reticulate-veined leaves has been questioned by Hickey and Peterson (1978). Their argument against designating vein order has been based upon the observation that parallel veins vary in strength until they overlap those of another thickness, thus making unambiguous identification of vein order impossible. However, since in the parallel-veined leaves studied here, each successive vein order is closed distally by fusion with veins of lower order and since each vein longitudinally bisects each panel, it is possible to read the venation of the leaf tip basipetally, as a dendrogram, with successive vein orders appearing at each level of anastomosis (Fig. 1a). Similarly, at the base of the leaf, higher-order veins anastomose at a point above that of the lower-order veins. Thus, it is possible to use patterns of apical and basal fusion to identify vein orders unambiguously in all the parallel-veined genera studied here. The numbered vein orders thus arrived at correspond closely to the lettered subsets used by Hickey and Peterson (1978) to designate veins of different strength in parallel-veined monocot leaves (primary veins are equivalent to the A series, secondaries to the B series, and so forth), although discrepancies may arise where veins are not distinguishable on size alone. Hickey and Peterson's terminology is especially appropriate for the description of fossil leaf fragments and, until the degree of universality of these patterns of apical and basal fusion is known, it remains more generally applicable than the concepts proposed here.

The grounds for comparing leaves of the reticulate-veined Liliiflorae with other reticulate-veined leaves, i.e. those of dicots, are not so easily shown. Past attempts to compare monocot and dicot leaf blades have been based on studies of monocot leaves that were morphologically very distinct from those of dicots in being strongly linear or unifacial, or in having a distinct leaf sheath, ligule or radial tip. None of these features is present in the reticulate-veined Liliiflorae, and leaf morphology otherwise resembles that of dicotyledons. Higher vein orders are fundamentally identical in both groups (Pray, 1963) and secondary veins run similar courses. Although the primary veins of most reticulate-veined Liliiflorae exhibit the apical convergence which is suggested by Doyle (1973) to be characteristic of monocots, this does not occur in *Tamus* and is poorly expressed in some others. In addition, there are, among primitive dicots (including Amborellaceae, Hernandiaceae, Lauraceae, Piperales, Aristolochiales and Coriariaceae), many taxa with primary venation similar to that of *Tamus* and other reticulate-veined Liliiflorae (see Hickey and Wolfe, 1975). Since this research has produced no argument against comparing leaf architecture of the reticulate-veined Liliiflorae with that of dicots, it is possible that the continuum of leaf architectural characters observed here reflects a phylogenetic character series linking typical monocot leaves to those of dicots.

The importance of this series of leaf-architectural characters is confirmed by the observed correlations with epidermal patterns and growth habit. The parallel-veined genera studied here share with the more typical Liliiflorae not only features of leaf architecture, but other vegetative characters such as parallel stomates, elongate epidermal cells, and a non-climbing habit. The reticulate-veined Liliiflorae, on the other hand, share the following with dicots: randomly oriented stomates, isodiametric epidermal cells, a form of growth habit found in many Magnoliidae, and proleptic branching, the latter an especially rare character among monocots.

The suggestion that the monocot leaf blade is homologous to that of dicots is made in the face of numerous arguments, both historical and modern, that the monocot lamina represents some other part of the leaf, e.g., the petiole or the leaf base, which has expanded secondarily (Arber 1925; Kaplan 1970, 1973, 1975). It should be remembered, however, that most of these theories were motivated by the need to interpret unifacial monocot leaves and that the plants investigated, e.g. *Sagittaria, Acorus,* and *Acacia,* can by no means be considered as primitive.

Although it is certainly possible that the reticulate-veined leaf blades described here represent organs derived from such unifacial leaves, the lack of direct evidence for convergent evolution makes the more parsimonious hypothesis preferable.

This character series, furthermore, suggests a mechanism for the evolution of vegetative morphology of the typical Liliiflorae. Doyle and Hickey (1974) have proposed that the dicot lamina arose from a reduced leaf through the activity of a newly evolved plate meristem. They also present, as the earliest monocot leaf, the fossil, *Acaciaeaphyllum,* which in habit and leaf venation resembles *Luzuriaga* more than it does any other extant monocot. It is suggested here that, like *Luzuriaga* and *Philesia,* the original monocots, were proleptically branched, shrubby plants lacking true rhizomes. Their small leaves could have expanded through newly evolved plate meristem activity to produce the broad laminae of the reticulate-veined Liliiflorae. This origin of the monocotyledonous growth habit from that of plants like *Philesia* was first proposed by Hallier (1912).

It was noted above that the reticulate-veined Liliiflorae often exhibit a heteroblastic leaf-series with juvenile leaves taking the form of small, distichous, parallel-veined, ensheathing scale leaves with parallel stomates. If the growth of such plants were to become determinate at a point just above the juvenile leaves, a neotenous plant with vegetative morphology resembling that of the caulescent non-climbers would result. Tomlinson's (1966) suggestion that neoteny is responsible for distichous shoots in the Commelinaceae is an argument analogous to the one proposed here.

The rosette habit could have evolved from that of the caulescent non-climbers through further neoteny; internode elongation being delayed relative to leaf expansion and eventually ceasing to occur. Thus, the vegetative morphology of the reticulate-veined Liliiflorae and parallel-veined allies could represent the condition of those ancestral monocots which evolved directly into the rhizomatous rosette plants so common among the Liliiflorae and which Stebbins (1974) considers to be primitive in the monocots.

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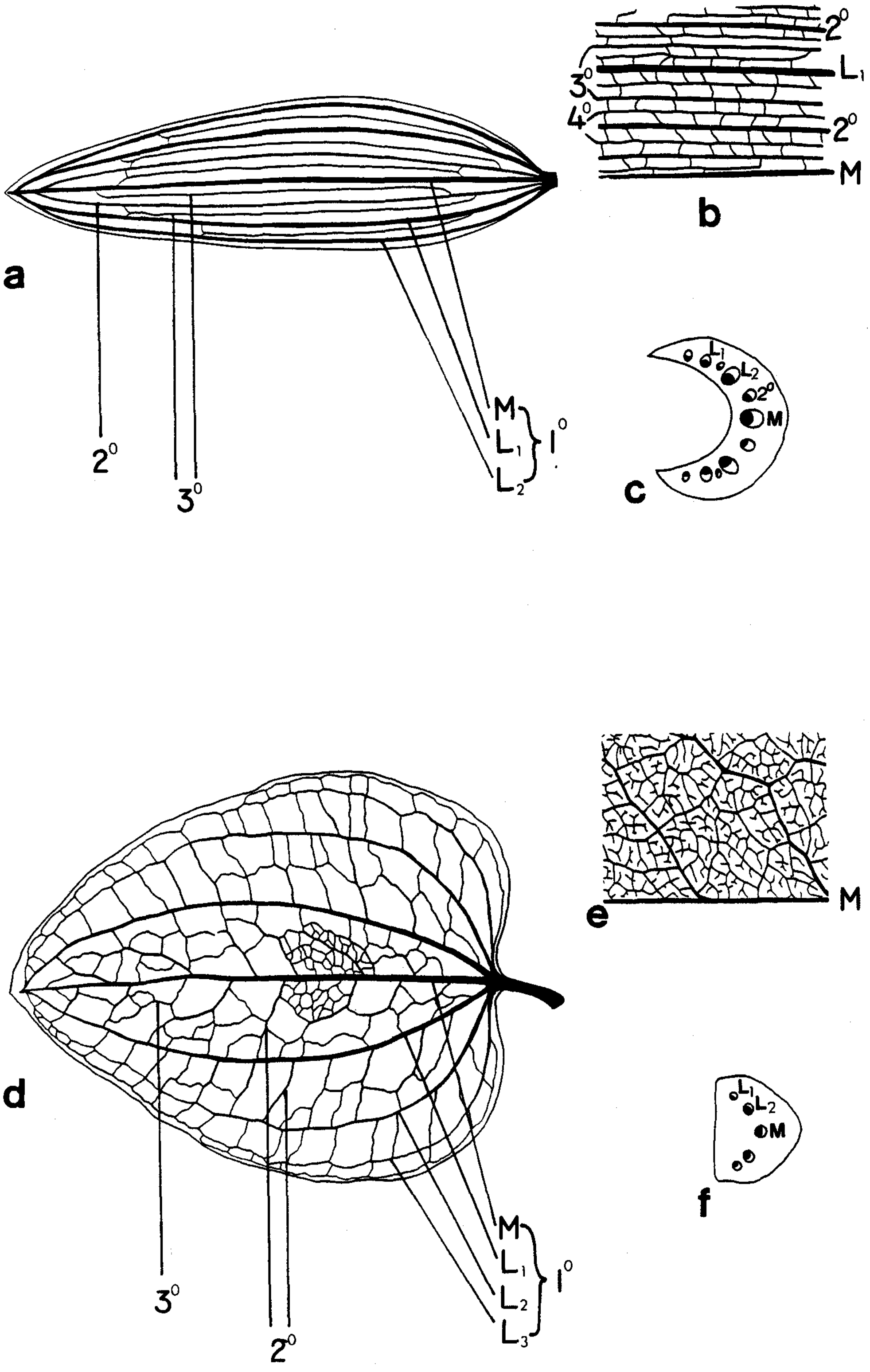
Figure 1. Models of leaf venation patterns in the reticulate-veined Liliiflorae and parallel-veined allies. M, L_1, L_2, etc., represent the midvein and adjacent lateral primary veins. Secondary and tertiary veins are indicated by "2°" and "3°".

a. Parallel-veined leaf, with 5 primary veins fusing near the leaf tip, x 1. Secondary veins longitudinally bisect the intercostal panels and fuse with primary veins near the tip, but without disrupting the fundamental pattern of primary vein convergence. Proximally, they enter the stele. Tertiary veins bisect the panels between secondary veins. The point at which they fuse apically is proximal to that for secondary veins. **b.** Higher-order venation of parallel-veined leaf, x 5. Tertiary and quaternary veins also run parallel and bisect intercostal panels between lower-order veins. Ultimate veinlets are transverse and unbranched. Free vein endings are absent and areoles are elongate parallel to the leaf axis. **c.** Cross section through the petiole of parallel-veined leaf, x 25. Both primary and secondary veins are present and appear to enter the stele. **d.** Reticulate-veined leaf, with 7 primary veins showing pronounced acropetal and lateral weakening, x 1. Secondary veins are pinnate. Tertiary veins are reticulate. **e.** Higher-order venation of reticulate-veined leaf, x 5. Tertiary and quaternary veins are reticulate. Ultimate veinlets are randomly oriented and branched. Free vein endings are present and areoles are irregular in shape and size. **f.** Cross-section through the petiole of reticulate-veined leaf, x 25; only primary veins enter the stele.


a
2°
3°
M
L1
L2
1°
b
2°
L1
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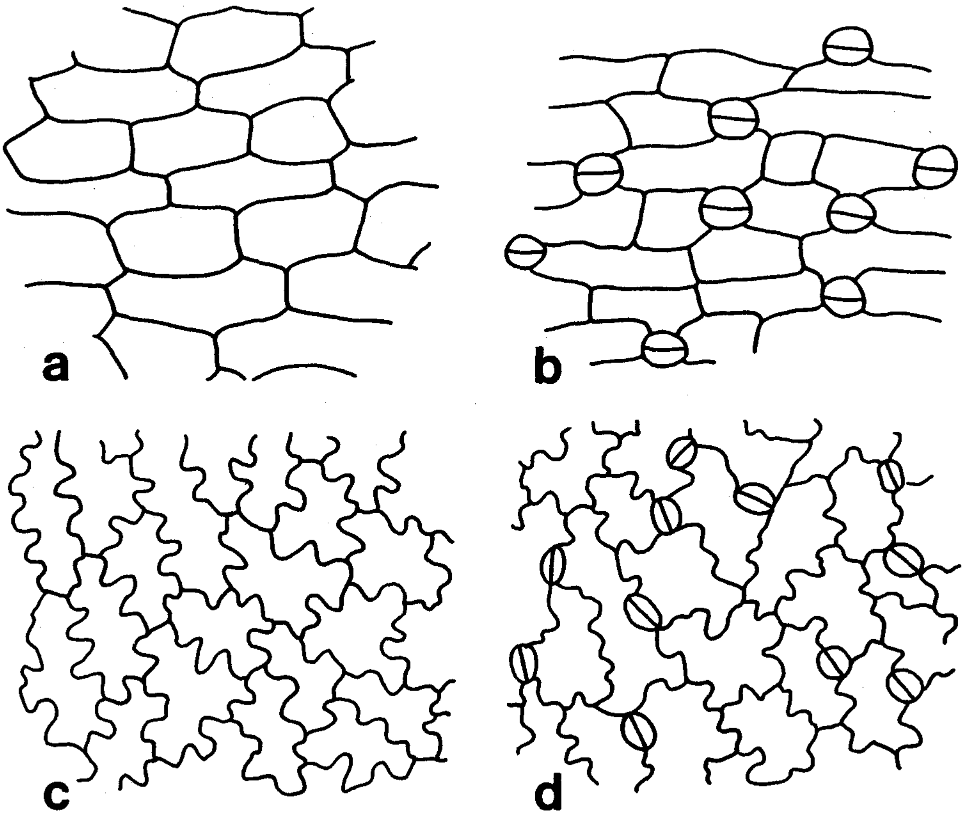

Figure 2. Epidermal features of the reticulate-veined Liliiflorae and parallel-veined allies. (Apex of leaf towards the left of the page.) a. Adaxial epidermis of parallel-veined leaf. b. Abaxial epidermis of parallel-veined leaf. c. Adaxial epidermis of reticulate-veined leaf. d. Abaxial epidermis of reticulate-veined leaf.