SEEDLING MORPHOLOGY IN *CLEMATIS* (RANUNCULACEAE) AND ITS TAXONOMIC IMPLICATIONS

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ABSTRACT

Seeds of 58 species of *Clematis* and *Clematopsis* were obtained from a variety of sources, germinated, and their seedling and juvenile morphology observed. Two very distinctive patterns emerged, each consisting of a cluster of characters. In Type I seedlings, the eophylls are alternate and toothed. Hypocotyls are elongate (except in *Clematopsis*), elevating the cotyledons and apical bud above ground, and buds are lacking in the axils of the cotyledons. Such seedlings are similar to those found in related genera such as *Anemone*, and are found in *Clematis* in the infrageneric taxa *Clematis, Lasiantha, Connatae, Tubulosae, Atragene, Meclatis, Cheiropsis, Bebaeanthera, Naraveliopsis, Papuasicae*, and in the genus *Clematopsis*. In Type II seedlings, leaves are paired from the beginning, but the first 1 – 3 pairs are usually reduced to cataphylls. Leaves are generally entire, often becoming lobed or divided, but not toothed. Hypocotyls are short, keeping the cotyledon bases and the epicotyl at first subterranean. Buds are typically present in the axils of the cotyledons. Such seedlings are found in the infrageneric taxa *Crispae, Viticella, Patentes, Rectae*, and *Angustifoliae*. These differences in seedling morphology and some correlated characters suggest a fundamental split in the genus and a basis for a revised infrageneric classification.

RESUMEN

Semillas de 58 especie de *Clematis* y *Clematopsis* fueren obtenido de orígenes diversos, se germinó, y sus morfoligía juvenil se observió. Dos modelos distintos se manifestaron, cada uno consite en un grupo de varios caracteres. En las plantas de semilleros del Tipo Uno los cofilos son alternos y dentados. Los hipocotilos son alargados (con exclusión de *Clematopsis*), y elevan los cotiledones y la yema cimera sobre la tierra. Yemas son ausente de las axilas do los cotiledones. Plantas de seimlleros de este tipo son semejante a aquellas hallado en géneros relatados como *Anemone*. Se encuentran en las taxa infragenéricas *Clematis, Lasiantha, Connatae, Tubulosae, Atragene, Meclatis, Cheiropsis, Bebaeantebra, Naraveliopsis, Papuasicae*, de *Clematis* y en el género *Clematopsis*. En plantas de semilleros del Tipo II, todas hojas son opuestas, per las parea 1 – 3 son usualmente reduciendo a catáfilos. Las hojas son usualmente enteras, frecuentemente lobados pero no dentados. Hipocotilos son corto, y las bases de los cotiledones y la yema cimera se quedan subterráneo. Yemas se encuentran en las axilas de los cotiledones. Plantas de semilleros de este tipo se hallan en las taxa infrageréricas *Crispae, Viticella, Patentes, Rectae*, y *Angustifoliae*. Estas differencias morfológicas de las plantas de semilleros y algunes caracteres correlativos sugeron una división fundamental in el género y un fundamento para revisar la clasificación infragenérica.

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INTRODUCTION

The genus *Clematis* is a large and diverse genus of the presumedly archaic family Ranunculaceae. Found on every continent except Antarctica, the approximately 300 species of *Clematis* occur in nearly every climatic zone from the taiga to the equatorial tropics, and display a wide variety of both vegetative and floral forms. There has been no comprehensive revision of the genus since that of Kuntze (1885), but there have been recent efforts to develop a modern infrageneric classification. Authors have subdivided the genus in various ways (see Keener & Dennis, 1982, for a review), some dividing it into subgenera, others dividing it into sections. Tamura (1967) divided *Clematis* into 12 sections (Table 1) in the most comprehensive of recent classifications. His great familiarity with Asiatic Ranunculaceae allowed him to define fairly precisely various infrageneric taxa occurring in that region, but species from other regions, particularly Africa and New Zealand, are sometimes difficult to place in his system. Tamura did not attempt to group his sections into subgenera, perhaps feeling that there was insufficient basis for recognizing major divisions within the genus.

Keener and Dennis (1982), on the other hand, divided the native and naturalized North American species into four subgenera, drawing upon earlier subgeneric concepts. They did not attempt to incorporate the old world taxa into their system, or to further divide their subgenera into sections, etc., stating that a new world-wide monographic treatment would be needed in order to accomplish this. Thus, the reconciliation of Tamura's sectional classification with the subgeneric system of Keener and Dennis remains to be done.

Tamura's system emphasizes floral and inflorescence characters, as can be seen in Table 1. The best and most natural classification systems generally result, however, when a full range of characters from flower, fruit, seed, seedling, and vegetative shoots are employed. Study of additional characters, particularly vegetative characters, and perhaps also cytological and chemical characters, is therefore needed in this genus. A comprehensive new classification should reflect major lines of evolution at the subgeneric level, and link the sections, subsections, etc. in a hierarchical fashion.

In building up a collection of tropical and subtropical species of *Clematis* at the University of South Florida Botanical Garden, striking differences in seedling morphology and related vegetative features were noticed, suggesting that a survey of the genus would be worthwhile. Little has been recorded concerning seedling morphology in *Clematis*, despite the fact that numerous species have been cultivated over the past two centuries. Lubbock (1892) described and illustrated the seedlings of three species (*C. recta* L., *C. orientalis* L. (as *C. graveolens* Lindl.), and *C. (Atragene) alpina*

TABLE 1. Classification of the Clematis alliance according to Tamura 1956, 1967), with distinguishing characters as reported by Tamura; asterisk indicates taxa known to have Type II seedlings.

Genus CLEMATIS [leaves opposite, sepals valvate]
Section *Viorna* [sepals erect, often colored, stamen filaments hairy]
Subsection *Connatae* [woody vines, leaves toothed]
Subsection *Tubulosae* [erect semi-shrubs, leaves toothed]
*Subsection *Crispae* [perennial herbs or weak-stemmed vines, leaves entire]
Section *Bebaeanthera* [as in Viorna, but flowers fasciculate with new growth]
Section *Atragene* [flowers with stamen-derived "petals," leaves toothed]
Section *Meclatis* [sepals spreading to erect, mostly yellow to orange, stamen filaments hairy]
Subsection *Orientales* [flowers few to many in axillary or terminal clusters]
Subsection *Tanguticae* [single flowers terminating new shoots]
Section *Clematis* [sepals spreading, whitish, stamen filaments glabrous, leaves mostly toothed]
Subsection *Pierotianae* [flowers 3–3.5 cm diam., stamen filaments dilated downward]
Subsection *Vitalbae* [flowers < 3cm diam., stamen filaments filiform]
Subsection *Dioicae* [as above, but flowers mostly dioecious]
Subsection *Aristatae* [as above, but stamen connective projected]
Subsection *Papuasicae* [similar to above, difference in structure of panicle]
Subsection *Crassifoliae* [stamen filaments rugulose, leaves coriacious, entire]
*Subsection *Rectae* [anthers elongate; leaves entire]
*Subsection *Angustifoliae* [as above but flowers large, with 6 sepals]
Section *Cheiropsis* [flowers fasciculate with new growth, large, bisexual, sepals spreading]
Section *Lasiantha* [as above but flowers dioecious]
Section *Viticella* [flowers large, sepals spreading, colored, stamens glabrous, leaves entire]
Subsection *Floridae* [flowers solitary, axillary, subtended by two bracteoles, styles plumose]
*Subsection *Viticella* [as above, but styles short, not plumose]
*Section *Patentes* [as above but flowers from bud produced in fall]
Section *Pterocarpa* [achenes strongly compressed and winged, leaves entire]
Section *Fruticella* [woody shrubs with very small leaves]
Section *Naraveliopsis* [anther connectives much prolonged, similar to *Papuasicae*]
Genus **Archiclematis** [leaves alternate throughout, otherwise similar to *Connatae*]
Genus **Clematopsis** [flowers large, sepals imbricate, otherwise similar to *Connatae*]
Genus **Naravelia** [flowers with elongate, petal-like staminodes]

(L.) Miller). The seedling morphology of *C. recta* described by Lubbock agrees with the "Type II" morphology described in this paper, while that for *C. graveolens* and *C. alpina* agree with the "Type I" morphology described here. Erickson (1945) illustrated *C. fremontii* S. Watson var *riehlii* Erickson, and it agrees with "Type II."

This study was undertaken then in anticipation that unrecognized and overlooked vegetative features, such as those of the seedling, might provide clues to the major lines of evolution in the genus that are ambiguous when only floral features are used.

MATERIALS AND METHODS

Efforts were made to obtain seed of species representing all recognized infrageneric taxa in *Clematis* and of several closely related genera, following

the classification of Tamura (1967, see Table 1). According to Tamura, three genera, *Archiclematis, Clematopsis*, and *Naravelia*, are distinct from *Clematis*, but closely related. Each has been included in it by various previous authors. Therefore, they have been considered in this study, although I thus far have only obtained seed of *Clematopsis*. Altogether, Tamura's smallest units (subsections and undivided sections), plus the three related genera, make 26 initial units for systematic study.

Seedlings of 58 species, representing 20 of these 26 units (Table 2) were observed. Seeds were obtained from a variety of sources, including botanical gardens, commercial seed companies, and private collectors. Seeds of native Florida species and some others were collected by the author. Seed from cultivated sources frequently prove to be misidentified or of dubious or mixed ancestry. Therefore, great care has been taken to assure that the material reported upon has been accurately identified. Identity of all specimens is being verified as the plants become mature, and specimens whose identity or infrageneric placement is still uncertain are not included.

Seeds were germinated in a greenhouse at the USF Botanical Garden, some only after stratification and/or a long period of dormancy. Many plants were later transferred to an outdoor experimental plot. All accessions were photographed after the first leaf appeared and often at later stages. Seedlings of many species were preserved and examined under a dissecting microscope. Voucher specimens and photographs are being made as each specimen blooms for the first time.

TABLE 2. Species examined (all cultivated at USF Botanical Garden).

Name	*Taxon*	*Type*	*USF Acc. #*
C. addisonii Britton	Crispae	II	87-40
C. alpina Miller	Atragene	I	87-41
C. apiifolia DC.	Vitalbae	I	82-22
C. aristata R. Br.	Aristatae	I	87-57
C. baldwinii Torrey & A. Gray	Crispae	II	86-25
C. barbellata Edgew.	Bebaeanthera	I	87-139
C. brachiata Ker.-Gawl	Vitalbae	I	87-2
C. buchaniana DC.	Connatae	I	87-104
C. campanuliflora Brot.	Viticella	II	87-33
C. catesbyana Pursh	Dioicae	I	85-9, 86-35
C. chinensis Osbeck	Rectae	II	88-2
C. chrysocoma Franchet	Cheiropsis	I	87-48

TABLE 2 (Continued)

C. cirrhosa L.	Cheiropsis	I	87-5
C. crispa L.	Crispae	II	85-2
C. denticulata Vell.	Dioicae	I	87-79
C. drummondii Torrey & A. Gray	Dioicae	I	87-34
C. filamentosa Dunn	Naraveliopsis	I	87-58
C. flammula L.	Rectae	II	87-121
C. fusca Turcz.	Crispae	II	87-122
C. gentianoides DC.	Aristatae	I	86-28
C. glaucophylla Small	Crispae	II	87-136
C. grata Wallich	Vitalbae	I	87-105
C. heracleifolia DC.	Tubulosae	I	87-53
C. hexapetala Pall.	Angustifoliae	II	87-71
C. hirsutissima Pursh	Crispae	II	86-30
C. integrifolia L.	Crispae	II	85-3
C. intricata Bunge	Meclatis	I	87-70
C. kirilowii Maxim.	Rectae	II	87-76
C. lasiantha Nutt.	Lasiantha	I	87-7
C. leschenaultiana DC.	Connatae	I	87-66
C. ligusticifolia Nutt.	Dioicae	I	87-4, 86-32
C. macropetala Ledeb.	Atragene	I	86-33
C. mandshurica Rupr.	Rectae	II	87-124
C. microphylla DC.	?	?	87-43, 87-55
C. napaulensis DC.	Bebaeanthera	I	87-106
C. orientalis L.	Meclatis	I	86-33
C. orientalis "ladakhiana"	Meclatis	I	87-107
C. papuasica Merr. & Perry	Papuasicae	I	89-1
C. patens Morr. & Decne	Patentes	II	87-140
C. peterae Hand.-Mazz.	Vitalbae	I	87-50
C. pierotii Miquel	Pierotianae	I	86-37
C. pitcheri Sargent	Crispae	II	88-33
C. ranunculoides Franchet	Connatae	I	87-49
C. recta L.	Rectae	II	86-39
C. rehderiana Craib	Meclatis	I	88-24
C. reticulata Walter	Crispae	II	85-7
C. serratifolia Rehder	Meclatis	I	87-125
C. tangutica Korsh	Meclatis	I	87-73
C. terniflora DC. (as C. paniculata)	Rectae	II	85-6
C. terniflora DC.	Rectae	II	85-8
C. texensis Buckley	Crispae	II	87-38, 87-78
C. viorna L.	Crispae	II	88-32, 87-39
C. vitalba L.	Vitalbae	I	86-1a, 86-42
C. viticella L.	Viticella	II	88-39
CLEMATOPSIS			
C. villosa DC.		I	86-45
C. scabiosifolia Viguier & Perrier var. kirkii	Oliver	I	86-47
C. anethifolia Hook.		I	88-42

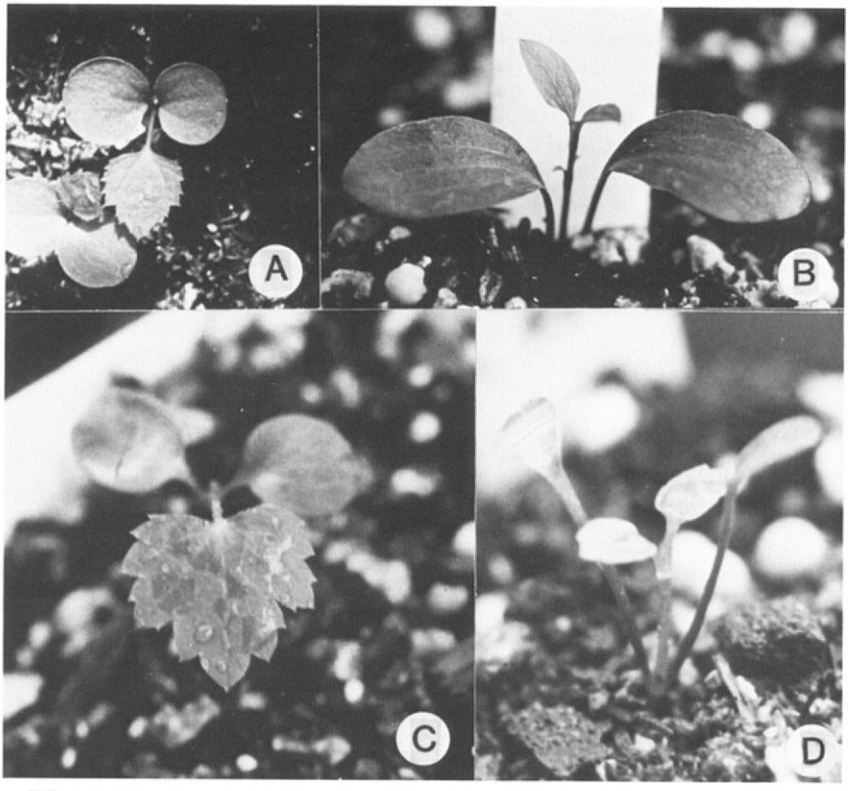

FIG. 1. Seedling types. A. Type I seedling of *Clematis heracleifolia* DC. B. Type II seedling of *Clematis crispa* L. C. Type I seedling of *Clematis cateshyana* Pursh. D. Type II seedling of *Clematis terniflora* DC.

RESULTS

The specimens studied fall into two major categories with respect to four distinct sets of characters involving not only seedling morphology, but also aspects of the adult foliage and the achenes. The features associated with each type of seedling are summarized in Table 3, and discussed in detail below. A summary of Tamura's taxa falling into the two categories, along with the taxa that have not yet been studied is presented in Table 4.

1. Seedling phyllotaxy

In Type I seedlings (Figure 1A,C), the first several eophylls (seedling leaves) are alternate, and closely spaced, forming a small rosette at the apex of the hypocotyl. This alternate phyllotaxy later gives way to the opposite

phyllotaxy typical of the adult plants, usually at the time that internodal elongation begins. This may happen as early as the third and fourth leaves in some taxa, but in *Connatae* and *Clematopsis*, leaves may remain alternate throughout the first juvenile shoot. The genus *Archiclematis* has been segregated from *Clematis* on the basis of its permanently alternate phyllotaxy. In section *Meclatis*, the first eophyll is typically followed quickly by a second eophyll without internodal elongation, giving the appearance of opposite or subopposite leaves. Internodal elongation in *Meclatis* begins after 2 or 3 eophylls, while the leaves are still alternate.

Type II seedlings (Figure 1B,D, 2L) contrast strongly in that leaves are opposite from the beginning, and several sets of paired cataphylls are produced before any leaflike eophylls are produced. Internodal elongation is present from the beginning also, even during the catophyll stage, except that the first pair of catophylls may be produced immediately above the cotyledons (e.g. in *Clematis crispa* L.).

TABLE 3. Characters distinguishing Type I from Type II *Clematis*.

Character	*Type I*	*Type II*
Phyllotaxy of seedling	alternate	opposite
Hypocotyl	mostly elongate (except in *Clematopsis*)	suppressed
Initial shoot	condensed rosette	elongate
Cataphylls	absent	several pairs present
Eophyll margin	toothed	entire
Adult foliage	most often toothed and membranous, or entire and glossy-coriaceous	often lobed or dissected but not toothed, mostly membranous
Regenerative buds	in aerial leaf axils or (in *Clematopsis*) in subterranean axils of rosette eophylls	in subterranean axils of cotyledons and some cataphylls
Growth form	woody vines or shrubs; many rooting at aerial nodes	perennial erect herbs, weak-stemmed vines or sometimes woody vines; these regenerating from subterranean buds
Achenes	laterally compressed, but narrow, turgid	broad, very flat

2. Eophyll and leaf morphology.

In Type I seedlings, leaf shape varies considerably (Figure 2C – K), but eophylls are typically broad, sometimes 3-lobed, with small veins diverging from the peripheral region and terminating in marginal teeth. This pattern usually persists in the adult foliage, and most of the taxa with Type I seedlings have conspicuously dentate foliage throughout the plant. In Section *Meclatis* the first eophylls are narrow and little-toothed (typically entire to irregularly 1-toothed — Figure 2I,J), but subsequent leaves are dentate. Section *Atragene*, considered a distinct genus by some authors, differs from the common form only in that the first eophylls are deeply divided (Figure 2C).

In Type II seedlings, The first eophylls (after the cataphylls) are mostly elliptic-ovate and entire, although in *C. terniflora* the first eophylls are sometimes 3-lobed at the tip (Figure 1D). Adult foliage may be variously divided and lobed but never toothed as in Type I species.

3. Cotyledon, hypocotyl orientation, and habit.

In the terminology of Duke and Polhill (1981) most Type I seedlings are phaneroepigeal, i.e. the cotyledons and epicotyl are elevated above ground by an elongate hypocotyl. As adults, Type I plants are mostly woody vines, or in subsection *Tubulosae*, suffrutescent shrubs. Branching can occur only from aerial nodes above the hypocotyl. Many species, however, readily form adventitious roots when aerial shoots touch the ground, and can spread quite rampantly in this way.

In the three species of *Clematopsis* examined, which otherwise have all the characteristics of Type I species, the cotyledons emerge from the ground, but the hypocotyl does not elongate and the cotyledon bases, and initially the epicotyl, remain below ground (phanerohypogeal). Several eophylls are produced without internodal elongation, forming a small rosette, and these subterranean nodes form a rootcrown with buds that can repeatedly regenerate the plant if the top dies off due to drought, fire or normal seasonal cycles.

Type II seedlings are all hypogeal, as the hypocotyl does not elongate, although the blades of the cotyledons may emerge (phanerohypogeal). In this one respect they are similar to the species of *Clematopsis* mentioned above. However, in Type II plants, an elongate shoot is produced directly, without formation of a rosette. Regenerative buds are produced in the axils of the cotyledons and some of the lowest cataphylls.

The predominant growth form in Type II *Clematis*, at least in subsections *Crispae* and *Angustifoliae*, and in *Clematis recta*, is a perennial herb or weak-stemmed vine, in which stems die back to the ground each winter. The

underground rootcrown established by the seedlings allows for repeated renewal of the plant in successive growing seasons. Other taxa with Type II seedlings, such as *Clematis terniflora* and several of its Eurasian relatives in section *Rectae*, along with the sections *Viticella* and *Patentes* have persistent

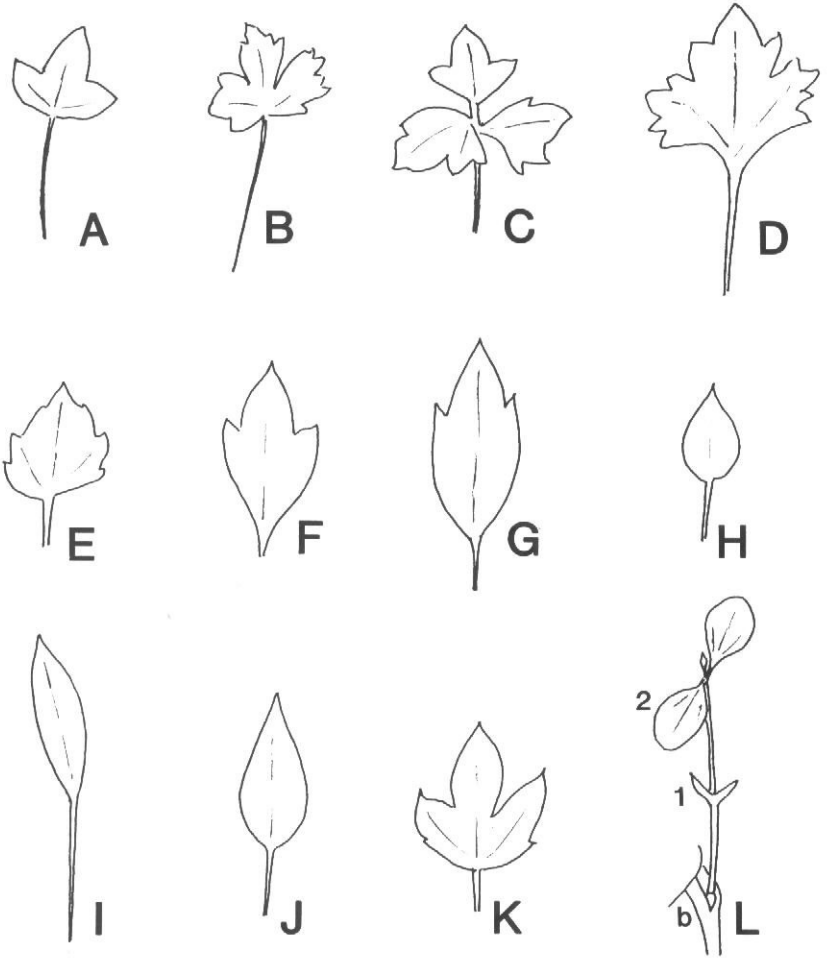

FIG. 2. Variation in first seedling leaf, including outgroup comparisons with *Anemone* (A,B); A-K represent Type I seedlings, L is Type II. A. *Anemone pulsatilla* L. (*Pulsatilla vulgaris* Miller). B. *Anemone berlandieri* Pritzel. C. *Clematis* (*Atragene*) *alpina* Miller. D. *Clematis chrysocoma* Franchet. E. *Clematopsis villosa* DC. F. *Clematis papuasica* Merrill & Perry. G. *Clematis gentianoides* DC. H. *Clematis filamentosa* Dunn. I. *Clematis orientalis* L. J. *Clematis tangutica* Korsh. K. *Clematis microphylla* DC. (one of two opposite leaves). L. *Clematis fusca* Turcz. (first and second pair of leaves are numbered; "b" indicates position of buds in axils of cotyledons).

TABLE 4. Summary of Tamura's (1967) infrageneric taxa displaying Type I and Type II morphologies.

Type I	*Type II*	*Undetermined*
Vitalbae	Crispae	Crassifoliae (prob. I)
Pierotinae	Rectae (Eurasian group)	Rectae (tropical Asian) (prob. I)
Dioicae	Viticella	Fruticella (?)
Bebaeanthera	Patentes	Pterocarpa (prob. II)
Lasiantha	Angustifoliae	Floridae (prob. II)
Cheiropsis		Naravelia (prob. I)
Aristatae		Archiclematis (prob. I)
Naraveliopsis		
Papuasica		
Connatae		
Tubulosae		
Meclatis		
Atragene		
Clematopsis		

woody stems, but even in well-established plants, new shoots can arise from the subterranean buds at the base of the original shoot.

There is a strong trend toward cryptohypogeal germination in this group, in which the cotyledons remain within the seedcoat below ground. The specimens studied of *Clematis viorna, reticulata, fusca, texensis, pitcheri, glaucophylla,* and *patens* were cryptohypogeal, while *C. integrifolia, crispa, baldwinii, terniflora, hexapetala* and *kirilowii* were phanerohypogeal.

4. Achene shape.

Achenes in Type I taxa, although laterally compressed, tend to be small and turgid, while those in Type II taxa tend to be very broad and flat, and often have a conspicuously thickened rim.

Of all the specimens examined, just one appears to be intermediate between Type I and Type II seedlings. Specimens of *Clematis microphylla* DC from Australia have seedlings with an elongate hypocotyl, with the eophylls strongly 3-lobed and toothed. Eophylls are paired from the beginning, however, and there are buds in the axils of the cotyledons, the internodes are elongate after the first pair of leaves, and the achenes are broad and flat. Whether this species is phylogenetically intermediate between the two types or represents convergence or reversal in some characters remains to be elucidated through further study.

DISCUSSION

This survey of seedling morphology and correlated characters of the foliage and achenes reveals two well-defined patterns in *Clematis* (Table 3), suggesting a fundamental and natural division in the genus that could provide the basis for clearly defined subgenera. Taxonomic division of the genus along Type I and Type II lines (Table 4) would, however, require a radical departure from the traditional system of Tamura (1967), which was based primarily on floral characters (Table 1). It would cut across Tamura's two largest sections, *Clematis* and *Viorna*, and require a regrouping of the smaller sections.

Traditionally, section *Clematis* is defined as having numerous, small, upright flowers, usually produced in complex dichasial panicles, and with thin, spreading, whitish sepals (true petals are lacking in the genus) and glabrous stamens. Section or subgenus *Viorna*, on the other hand, is characterized by relatively large, generally nodding, urn-shaped flowers with rather thick, colored, erect sepals and hairy stamen filaments, and which are either solitary or in few-flowered inflorescence units. Both sections, however, contain subgroups with Type I and Type II morphologies (Table 1). The smaller sections are mostly distinguished on the basis of minor variation from one of these two patterns, and most likely will not be found to contain more than one seedling type.

Adherence to the traditional system of classification (Table 1) would require the interpretation that the rather extended set of specialized Type II vegetative characters, including fundamental differences in embryonic development, evolved independently several times, presumably in response to similar ecological conditions. The alternate system, based on a division between Type I and Type II seedling morphology, requires the interpretation that similar floral types, particularly small white flowers produced in masses, have evolved at least twice in the genus, in response to a common pollination strategy.

Which of these two alternatives most likely reflects the actual phylogeny of the genus, and should therefore serve as the basis for an infrageneric classification? The most parsimonious alternative is the latter one, i.e. a primary division along the lines of seedling morphology, with later radiation and convergence of pollination types. The changes involved in seedling morphology are complex, involving many changes in the shape, venation and phyllotaxy of the embryonic leaves, and in the growth pattern of the seedling axis. The changes required to shift pollination strategies are by contrast rather simple: increased branching of the inflorescence, reduction in size and pigmentation of the flowers, and loss of hairs on the stamen filaments. Similar shifts have occurred in many plant families.

Some additional information can be interjected at this point. Data on historical hybridization within the genus, although somewhat scant, supports the natural division of *Clematis* along Type I and Type II lines. This genus has been popular in horticulture for several centuries and many hybrids have been made. As far as can be gathered from the horticultural literature, however, no hybrids have ever been made between Type I and Type II taxa, even those having similar looking flowers and placed traditionally in the same section. On the other hand hybrids have been made between species with small white flowers and species with large colored flowers placed traditionally in different sections, but sharing the same seedling and vegetative morphology. Notable are the crosses between Type I taxa *Vitalbae* (section *Clematis)* and *Tubulosae* (section*Viorna*), between Type II taxa *Rectae* (section *Clematis*) and *Crispae* (section *Viorna*), and between *Rectae* and section *Viticella* (also Type II) (Table 5). Many of the most popular garden hybrids arose from crosses among the various large-flowered Type II taxa that are placed in separate sections in Tamura's system. Multiple attempts by the author at hybridization between*Clematis terniflora* DC (Type II) and the superficially similar *C. cateshyana* Pursh (Type I), which are traditionally placed in the same section, caused initiation of achenes, but these all aborted after a few weeks.

Based on the data presented here, the following phylogenetic scenario for *Clematis* is suggested: Type I seedling characters and related morphology represent the ancestral or plesiomorphic condition, as they occur in related genera such as *Anemone* (Figure 2A,B). The ancestral population of *Clematis* therefore had Type I seedlings, coarsely toothed foliage, and flowers with large, colored, erect to spreading sepals and hairy stamens. These early *Clematis* were essentially like many members of the modern subsection *Connatae*. An early lineage developed Type II characters, apparently in response to strongly seasonal climates. These characters included the suppression of hypocotyl elongation, the resulting hypogeal germination, and the regenerating rootcrown. Within both Type I and Type II lineages, one or more groups shifted, in parallel, to small, more numerous, white flowers with glabrous stamens, adapting to a rather common and successful pollination syndrome. Other Type I and Type II groups retained the ancestral type of flower.

TAXONOMIC CONCLUSIONS

Although considerable study is still needed before a complete new infrageneric classification can be developed for *Clematis*, the system of subgenera employed by Keener and Dennis (1982) and earlier workers can be supported and extended to the old world taxa defined by Tamura (1956,

TABLE 5. Historic hybrids among infrageneric taxa.

Type I × Type I
Vitalbae × Tubulosae (*C.* × jouiniana C. K. Schneider, fide Hortus Third, 1976)
Vitalbae × Tubulosae (*C.* × takedana Makino, fide Ohwi, 1965)
Type II × Type II
Viticella × Crispae (*C.* × *eriostemon* Decne., fide Hortus Third, 1976)
Viticella × Crispae (*C.* × *cylindrica* Sims, fide Kuntze, 1885)
Viticella × Florida (*C.* × *jackmanii* T. Moore, fide Hortus Third, 1976)
Florida × Crispae (*C.* × *durandii* Durand, fide Kuntze, 1885 and Hortus Third, 1976)
Florida × Patentes (*C.* × *lawsoniana* T. Moore & Jackmann, fide Hortus Third, 1976))
Crispae × Rectae (*C.* × *aromatica* Lenne & Koch, fide Kuntze, 1885 and Hortus Third 1976)
Rectae × Viticella (*C.* × *violacea* A.P. DeCandolle, fide Kuntze, 1885)
Rectae × Viticella (*C.* × *rubromarginata*, fide Lloyd 1965)

1967), with the following specific modifications suggested by the current data:

1. Type I taxa include the type species (*Clematis vitalba* L.) of subgenus *Clematis* sensu Keener and Dennis, and therefore Type I characters can be considered definitive for subgenus *Clematis*.

2. Type II taxa include the type species (*Clematis viorna* L.) of subgenus *Viorna* sensu Keener & Dennis (and genus *Coriflora* Weber 1982), and therefore Type II characters should be considered definitive for subgenus *Viorna*.

3. Part of subsection *Rectae* (the two series, *Rectae* and *Chinenses*, defined by Tamura in 1956) should be transferred from subgenus *Clematis* to subgenus *Viorna*. The remaining series in subsection *Rectae* (series *Crassifoliae*, *Meyenianae*, and *Uncinatae*) need further study, but based on the shape of their achenes and rather different foliage, most likely will be excluded from *Rectae*.

4. Subsection *Angustifoliae* should be included under subgenus *Viorna*. It differs very little from subsection *Rectae*.

5. Tamura's subsections *Connatae* and *Tubulosae* of his section *Viorna* should be transferred to subgenus *Clematis*.

6. Subgenus *Viticella* (Moench) Keener & Dennis should be reconsidered. It shows much affinity with other Type II taxa, and probably should be included as a section under *Viorna*.

7. Subgenus *Atragene* should be reconsidered. It has Type I seedling morphology and differs from subgenus *Clematis* only in the usual presence

of petal-like staminodes. It possibly should be included as a section under subgenus *Clematis*.

8. *Clematopsis* has been excluded from *Clematis* in the past primarily because of its broad, imbricate sepals, which contrast with the valvate sepals of *Clematis*. Otherwise, it has the characteristics of the genus *Clematis* and fits in with the old world complex of Type I taxa. Thorough study of the African *Clematis* is needed in order to determine the appropriate status for this taxon.

Placement of other sections, and formal infrageneric reorganization of *Clematis*, is deferred pending more complete studies. Recognition of the two major phyletic lines in the genus, should, however, make it easier to proceed with revisionary and phylogenetic studies. It is recommended that future uses of the subgeneric taxa *Clematis* and *Viorna* reflect the changes outlined here.

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