Meclatis in *Clematis*:
Yellow flowering *Clematis* species

Systematic studies in *Clematis* L. (Ranunculaceae), inclusive of cultonomic aspects

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Clematis 'Bravo'

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CONTENTS

Stellingen behorende bij het proefschrift, getiteld: *Meclatis* in *Clematis*: Yellow flowering *Clematis* species - Systematic studies in *Clematis* L. (Ranunculaceae), inclusive of cultonomic aspects

I

Het onderscheid tussen houtige en kruidachtige *Clematis* soorten heeft tot dusver een goede interpretatie van de classificatie van het genus in de weg gestaan.

Dit proefschrift, hoofdstuk 1.

II

Het onderscheid tussen synflorescentie en inflorescentie is nuttig bij het beschrijven van planten; het veronachtzamen van dit onderscheid bemoeilijkt de interpretatie van bloemgestellen in genera als *Clematis*.

Troll, 1964, 1969.
Dit proefschrift, hoofdstuk 1.

III

Clematis is een goed genus om de hypothese te toetsen dat daar waar de grootste variatie gevonden wordt het ontstaansgebied is dan wel juist niet.

Dit proefschrift, hoofdstuk 1.

IV

De hier voorgestelde indeling van *Clematis* sect. *Meclatis* (Spach) Baillon maakt duidelijk dat de aanwezigheid van variatie nog niet onmiddellijk aanleiding moet zijn een nieuwe soort of een infraspecifiek taxon te beschrijven.

Dit proefschrift, hoofdstuk 2.

V

De pollenmorfologie van *Clematis* verdient systematische aandacht.

Dit proefschrift, hoofdstuk 2.

VI

Clematis is als genus van sierplanten buitengewoon interessant omdat de complete reeks van bloemkleuren er in voorkomt.

VII

Het feit dat er verwante niet-kruisbare planten naast kruisbare minder verwante soorten bestaan maakt het biologisch soortsbegrip onhoudbaar: een waarschuwing voor plantenveredelaars!

Dit proefschrift, hoofdstuk 1 en 5.

VIII

De cultivargroep als eenheid van classificatie is terug te voeren op 19de eeuwse tuinbouwkundige classificaties van sierplanten, waaronder de classificatie van toen in cultuur zijnde *Clematis*.

Dit proefschrift, hoofdstuk 3 en 4.

IX

De traditionele behandeling van kunstmatige hybrides in de plantensystematiek is een fundamentele misvatting van de mogelijkheden en de resultaten van de moderne plantenveredeling.

Dit proefschrift, hoofdstuk 3.

X

De introductie van het begrip culton was noodzakelijk om goede, flexibele classificaties van cultuurplanten met betrekking tot de betrokken eenheden (cultivar, cultivargroep) te ontwikkelen.

Hetterscheid & Brandenburg, 1995a, 1995b
Hetterscheid et al., 1996
Dit proefschrift, hoofdstuk 3.

XI

Dat voor cultuurplanten met behulp van botanische classificatiesystemen geen classificaties zijn te maken, valt af te leiden uit het feit dat er voor geen enkele belangrijke cultuurplant zo'n classificatie bestaat die algemeen is aanvaard.

Brandenburg & Schneider, 1988
Dit proefschrift, hoofdstuk 3.

XII

De studie van hemicyclische bloemen verdient meer aandacht van ontwikkelingsbiologen dan tot nu toe het geval is.

XIII

Genoomgrootte in termen van het aantal chromosomen per genoom kan nog steeds niet goed worden verklaard. De Ranunculaceae zijn in deze een goed 'proefkonijn' vanwege de verschillende, systematisch verspreide aantallen (x=6, 7 of 8) en de daarmee verband houdende chromosoommorfologie.

Dit proefschrift, hoofdstuk 2.

XIV

De huidige methodes van fylogenetische analyse hebben de plantensystematiek tot een wetenschappelijke discipline gemaakt met toetsbare hypotheses; de moleculaire biologie is een zeer krachtig hulpmiddel daarbij.

Dit proefschrift, hoofdstuk 5.

XV

Het is zorgwekkend dat de basis van de wereldvoedselvoorziening steeds meer afhankelijk wordt van steeds minder multinationale ondernemingen.

XVI

In de Westeuropese cultuur is geen plaats meer voor 'verliezers'; 'winners' en winst is wat er in het centrum van de aandacht staat. Dat daarmee ook de kunst van rouwen dan wel verliesverwerking verloren dreigt te gaan is echter geen winst maar echt verlies.

XVII

Rouwen is eerder kunst dan kunde.

XVIII

Anton Bruckner was behalve een begenadigd componist ook een zeer goed organist: dat hij als componist het orgel nooit uit het oog heeft verloren, blijkt uit het feit dat met name in zijn latere symfonieen (7-9) de rusten zo zijn gekozen dat de muziek langzaam wegebt: deze symfonieen komen dan ook het beste tot hun recht in grote kerken zoals de domkerk te Lübeck.

XIX

De zesde symfonie van Gustav Mahler heeft ten onrechte de bijnaam 'Tragische Symfonie' gekregen; echt tragisch in de uitvoeringspraktijk van deze symfonie is alleen dat een verkeerd gekozen tempo in de eerste 24 maten desastreus is voor de verdere uitvoering van de symfonie.

XX

Verkeer en verkeerd schelen maar één letter en dat kan helaas maar al te vaak op de openbare weg worden waargenomen.

0 PREFACE

In 1975, this *Clematis* study started as an experimental systematics project under supervision of Dr. R.A.H. Legro (Brandenburg, 1976, 1977a, 1977b). The aim of this study was to reveal the degree of relationship between *Clematis* species of (potential) economic importance and to overcome crossing barriers between them. This study was the continuation of earlier work by Barendrecht (1972). Barendrecht already indicated, that many cultivated *Clematis* species were assigned to species to which they either did not belong or with which they cannot be any longer solely linked because of repeated interspecific hybridization. This referred especially to the group of yellow-flowered species, initially indicated as *Clematis* ser. *Orientales* Prantl: e.g. *C. orientalis* L., as it was labelled in cultivation, showed remarkable differences to the wild plant.
The above project was later taken as the starting-point for an extended experimental systematics project to be carried out in the framework of the research programme of the then AU Dept. Taxonomy of Cultivated Plants and Weeds.

In the period 1978 - 1984, the research project was still focussed on the crossability potential of the species concerned. In this period, it became clear that *Clematis* is not a very suitable plant to be used in hybridization studies because of complex germination behaviour, slow growth to an adult flowering plant and large variation in flowering season per species. It was therefore decided to redefine the project in a more morphologic taxonomic way; the consequence of this being a large set of chromosome counts that can hardly be used for the new project. Also other data sets remained incomplete (pollen morphological and biochemical data).

In the period 1984 - 1987, the guidance of the project was laid in the hands of Prof. Van der Maesen and the project was largely focused on the systematics of yellow-flowered *Clematis* spp., as for these species a representative data set could be obtained. Besides that, data were collected to compile an international register for *Clematis* cultivars. The list of large-flowered *Clematis* cultivars has been completed up to 1991 and will be published separately.

The structure of this thesis reflects somewhat the direction of the evolution of both the evolution in thinking concerning this particular research project and my other personal development in systematics of cultivated plants, which was directed towards principles and concepts in classification of cultivated plants, and towards the development of an unequivocal nomenclature of cultivated plants, culminating in the development of the open classification concept, a plea for a consequent application of the cultivar group concept and the establishment of the culton concept (Brandenburg et al., 1982; Brandenburg, 1984, 1986a, 1986b; Brandenburg & Schneider, 1988; Hetterscheid & Brandenburg, 1995a, 1995b; Hetterscheid et al., 1996).

Chapter 1 deals with the genus as a whole surveying and analysing phylogenetically and biogeographically the classification of sections and subsections. The crossability data obtained between 16 species were analysed as well and viewed in the light of systematic evidence. Chapter 2 deals with the systematics of the *Clematis* sect. *Meclatis* (Spach) Baillon. Based on morphological characters this section has been analysed using multivariate and phylogenetic analysis methods and giving rise to a new classification of this thus far ambiguously classified section. The data were completed with distribution, cytological and pollen morphological data. Isozyme data were sampled incompletely to such an extent, that they only will be surveyed indicating their potential value but without any conclusive contribution as to this systematic analysis. Chapter 3 consists of a treatise of concepts in systematics of cultivated plants, needed to deal properly with cultivated *Clematis* in Chapter 4. Chapter 5 is the general discussion of the thesis particularly dealing with the fundamental problems brought up by this thesis and the possibilities for applications from this and similar research in plant systematics.

Completion of this thesis has been roughly done in three periods. In the period 1987 - 1991, the data were analyzed and the general set up of the thesis has been made. In 1993 and 1994 the first version of the thesis has been written and in 1999 the last one. The fact that it has taken so long is a matter of personal condition and my own responsibility. The fact that it has been finalized is largely due to a stimulating environment for which I am deeply grateful.

Many students of the small Department Taxonomy of Cultivated Plants and Weeds and later the Department of Plant Taxonomy have made important contributions to all systematic work on *Clematis* that if not directly relevant to this thesis was at least important for my thinking about it.

The late R.A.H. Legro made me enthusiastic for Clematis, the late Prof. J.H. van der Veen stimulated me to start with publishing my ideas on systematics of cultivated plants. Prof. L.J.L.D. van Griendsven, ir. C.A.A.A. Maenhout, dr. N.G. Hogenboom, dr. C.M. Colijn-Hooymans and dr. A.J. van Tunen respectively kept saying that I really should finalize this thesis.

I thank my colleagues in systematics of cultivated plants and economic botany in the Netherlands, Ronald van den Berg, Nynke Groendijk-Wilders, Mariet de Geus, Wilbert Hetterscheid, Marjan Boone for their numerous discussions and suggestions on various topics but especially for their patience with me when dealing with *Clematis*. Ruud van der Meijden introduced me into the field of floristics and we had a lot of discussions on the edge of both sides: systematics of cultivated plants and systematics of wild plants.

Jos van de Vooren was already involved in Clematis work long before I started as a student on the subject. Jos' open mind, innovative and unorthodox approach and strong support really kept me going. Besides that we spent a lot of time together which was indispensable. Anja van der Neut took a keen interest in *Clematis orientalis* and related species and made a major contribution to setting up the revision of *Clematis* sect. *Meclatis*. You both have always supported me both professionally and personally in such a way that I am still active in the fields of systematics of cultivated plants and economic botany that did not go at all without saying during the most recent period of my life.

I would like to commemorate all my friends for their interest in myself and this undertaking. All in my family who kept me on track to finalize this thesis I would like to thank. There were times that I made things difficult for you by not wanting to talk about it. Hanneke, we are both on track again and confident for the future. The fact that I still may talk about Clematis is significant for your interest in me and my undertakings. I admire your initiative to go into fashion and clothing design. Wouter, I am happy to see that you are studying sound engineering: keep cool, be happy and go for it!

1. HISTORICAL SURVEY OF CLASSIFICATION AND DELIMITATION OF THE GENUS *CLEMATIS* L.

1.1. Pre-Linnaean treatments of *Clematis*.

Etymologically, the word *Clematis* has been derived from κλημα (klèma), which means vine (Loudon, 1869). A Φΰτόν κληματειον (phyton klèmateion) is a vine, a climbing plant. According to Wittstein (1856), various climbing plants were indicated with *Clematis* in Dioscorides' herbals and mediaeval herbals based upon it:

> 'Κληματις Diosc. ist aber *Vinca minor* und eine andere κληματις desselben Schriftstellers ist warscheinlich *Polygonum convolvulus*; dahingegen stimmt κληματιτις Diosc. mit *Clematis cirrhosa* und eine andere κληματιτις Diosc. ist *Aristolochia baetica* (nicht *A. clematitis*).'

The names *Clematis* and *Clematitis* were used concurrently, the former being the Latinized form of Κληματις, the latter being the Latin transcription according to Backer (1936). This explanation only holds when κληματιτις has been used in Greek form derived from the Latin transcription. Both names remain concurrent until post-Linnaean classifications.

Θεόφραστος (Theophrastos) mentioned a wild vine in his Historia Naturalis (±320 BC) under the name ἀθραγένη (atragénè):

> 'They also say that a very good fire stick is made from the wood which some call traveller's joy: this is a tree like the vine or the 'wild vine', which, like these, climbs up trees (Hort, 1916, English translation of the Historia Plantarum, Book V, 6, 9).'

Theophrastos' classification was based on both medicinal or agronomic criteria and botanical characters. His work strongly influenced the botanical and medical literature till the 17th century. Herbals up to the 16th century are based on knowledge handed down from ancient times with as principal source various revised versions of Dioscorides' 1st century herbal (see Dioscorides et al., 1934), which was, however, inferior to Theophrastos' work by lack of his own botanical observations, and due to misinterpretations of some of the plants concerned. Only some later 16th and 17th century herbals consist of descriptions and data compiled by the authors themselves (e.g. Brunfels, 1530; Clusius, 1601; Fuchs, 1542; Lobelius, 1576). The name *Clematis* covered at that time a number of species that are still assigned to the genus, such as *C. recta* L., *C. vitalba* L. and *C. viticella* L., as well as a range of other plants, such as *Vinca* *minor* L. and *V. major* L. under the names *Clematis daphnoides* and *Clematis daphnoides major* respectively (Dodonaeus, 1583).

The main reason for incorporating *Clematis* spp. in herbals was their medicinal use. Especially *C. recta* was known in this respect. Van der Neut and Pfeiffer (1982) surveyed several Dutch herbals for medicinal uses of *Clematis*: puportedly diuretic and diaphoretic applications, expelling gall and phlegm, against various disorders and ischias could be cured with the plants. Moreover, Van der Neut and Pfeiffer (1982) mentioned that the young sprouts of *C. recta* and *C. viticella* were eaten as a vegetable. For *C. recta* this is remarkable, as this species is also mentioned as most effective in its medicinal characteristics. The medicinally effective chemical compounds are apparently absent in young sprouts. In contemporary ethnobotanic literature, mention is still made of young sprouts of various *Clematis* spp. eaten cooked as vegetable (Usher, 1974).

Clusius (1611) was one of the first to praise *C. viticella* as an ornamental. He especially mentioned the double-flowered form in this context.

Both Ray (1686, 1724) and Tournefort (1700, 1703) more or less established the genus concept (Stafleu, 1971; Stearn, 1957). Many Linnaean generic names are directly or indirectly derived from their publications. A third principal source of generic names for Linnaeus was Bauhin's *Pinax* (1623). Before 1736 already Ray and Tournefort frequently referred to Bauhin.

Already in the 17th and in the first half of the 18th century, there was some disagreement about which species should be assigned to the genus *Clematis*. Taking Linnaeus' *Species Plantarum*, ed. I (1753) as a starting-point, it is remarkable, that in this work *Atragene* was established as a separate genus, whereas in *Clematis* species were brought together, that were formerly assigned to another 'genus' *Flammula*, e.g. by Bauhin (1623) and Dillenius (1732). The species *C. cirrhosa* L., *C. crispa* L., *C. integrifolia* L., *C. vitalba* L., *C. viticella* L. were commonly assigned to *Clematis* or *Clematitis*, whereas *C. flammula* L., *C. recta* L. and *C. viorna* L. were variedly interpreted as belonging to either *Flammula* or *Clematis*. These different early opinions are the starting-point for the disagreement on generic delimitation of *Clematis* until this very day.

1.2. Classification of *Clematis* from Linnaeus onwards

Apart from separating *Atragene*, Linnaeus (1753) subdivided *Clematis* into two groups:

-	*_Scandentes_	1.	*C. viticella*
		2.	*C. viorna*
		3.	*C. crispa*
		4.	*C. orientalis*
		5.	*C. vitalba*
		6.	*C. cirrhosa*
		7.	*C. flammula*
	*_Erectae_	8.	*C. recta*
		9.	*C. integrifolia*

The status of the two groups remains unclear, as Linnaeus did not spend a word on them in his works on classification, nor in the various editions of the *Genera Plantarum*. As the format he used is principally designed to be an identification format, the two groups are to be regarded as informal indications (Stearn, 1957; Stafleu, 1971). However, the names are indicative enough.

In *Atragene*, Linnaeus distinguished:

1. *A. zeylanica* (= *Naravelia zeylanica* (L.) DC.),
2. *A. alpina* (= *C. alpina* (L.) Mill. p.p.),
3. *A. sibirica* (= *C. alpina* p.p.) and
4. *A. capensis* (= *Anemone capensis* (L.) Lam.).

Although some authors still recognize *Atragene* by the petaloid staminodia, the view of Miller (1768) to include *Atragene* in *Clematis*, is widely accepted.

Moench emphasized in Methodus Plantarum (1794) both number and form or structure of flower characters. Based on these characters, he defined several ‘classes’, among which Thalastemon (θαλαμος, thalamos, is receptacle, and στήμ ῶν, stèmoon, stamen) with `stamina receptaculo inserta'. He included the genera *Clematitis* and *Viticella* in this `class' as well as various other genera, now considered to belong to the Leguminosae, Liliaceae, Rosaceae and other families. He distinguished *Viticella* from *Clematitis* (= *Clematis*) by short-hairy styles and glabrous ovaries. He distinguished the following species:

- *Clematitis crispa*
- *Clematitis flava* (= *Clematis orientalis* L.)
- *Clematitis vitalba*
- *Clematitis integrifolia*
- *Viticella deltoidea* (= *Clematis viticella* L.)

With his generic names Moench[1] referred to pre-Linnaean *Clematitis* (Tournefort, 1700; 1703), and *Viticella* (Dillenius, 1732). Following the criteria for separating *Viticella* from *Clematitis*, it is remarkable that *Clematitis crispa* is not grouped under *Viticella*, as did Dillenius (1732 cited by Moench). The Moench system is inconsistent in its infrageneric classification of *Clematitis* and *Viticella* and has not found general acceptance. His classification scheme of `classes' did not survive either.

Persoon (1805) largely maintained the classification by Linnaeus, but extended it with species described meanwhile. His treatment of *Clematis* is the last one with a subdivision in Scandentes and Erectae, obviously meant as an informal subdivision. Quite remarkable is the placement of ** *Viorna* under *Atragene*, referring to species, later classified under the section *Cheiropsis* by De Candolle (1818). As he assigned the species *C. viorna* under *Clematis* * *Scandentes*, it is an obvious mistake. Persoon transferred some earlier described *Clematis* species to *Atragene*. These species (e.g. *C. florida* Murray ex Thunb.) occasionally produce petaloid staminodia, hence (semi-)double flowers.

A.P. De Candolle (1818) in his Regni Vegetabilis Systema Naturale had a broad view of *Clematis*. Within the tribe Clematideae, he distinguished only two genera: *Clematis*, inclusive of *Atragene*, and *Naravelia*, which Linnaeus (1753) assigned formerly to *Atragene*. De Candolle subdivided *Clematis* into 4 sections, based on inflorescence and fruit characters:

-	sect. *Flammula* DC.	achenes with barbate-plumose styles;
-	sect. *Viticella* (Moench) DC.	achenes with short, ± barbate styles;
-	sect. *Cheiropsis* DC.	an involucrum under the flower, achenes with barbate styles;

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[1] Although Moench variously spelled his name as Moench and Mönch, the standard author citation as compiled by Brummitt and Powell (1992) is followed (see also entries 6165 - 6169 in Stafleu and Cowan (1981)).

- sect. *Atragene* (L.) DC. numerous petals, achenes with barbate styles.

De Candolle regarded the corolla in the usual *Clematis* flowers as absent except in flowers of section *Atragene*.

Within section *Flammula*, he distinguished 5 informal groups (i.e. without indicating name and rank):

- § 1. many-branched, panicle-like synflorescences, pinnate leaves;
- § 2. many-branched, panicle-like synflorescences, ternate leaves;
- § 3. 3-flowered cymes, or terminally solitary flowers;
- § 4. solitary flowers, pinnate or ternate leaves;
- § 5. solitary flowers, simple leaves.

He attributed 85 species to *Clematis*, of which 70 were assigned to section *Flammula*.

De Candolle considered the genus *Naravelia* to be monotypic. The only species *N. zeylanica* was based on *Atragene zeylanica* L. The genus was distinguished from *Clematis* by having pinnatisect leaves with the basal pair of leaflets present and the other leaflets reduced to tendrils; the flower has the presence of staminodia in common with section *Atragene*. As there are also *Clematis* species, such as *C. afoliata* Buchanan, that show reduction of leaflets to tendrils, the separate status of *Naravelia* DC. may be doubted.

Spach (1839) proposed in his Histoire Naturelle des Végétaux a narrow delimitation of the genus *Clematis* and based this on earlier treatments of Moench (1794) and partly Reichenbach (1837), apart from references to pre-Linnaean literature. Within the tribe Clematideae, he distinguished many genera, which are now generally regarded to be sections of *Clematis*:

- *Atragene* L.	(=> sect. *Atragene* (L.) DC.);
- *Cheiropsis* (DC.) Spach	(=> sect. *Cheiropsis* DC.);
- *Viticella* Moench	(=> sect. *Viticella* (Moench) DC.);
- *Viorna* Rchb.	(campanulate flowers; the genus has been based on pre-Linnaean references, a.o. Dillenius (1732) by Reichenbach, 1837);
- *Meclatis* Spach	(the name being an anagram of *Clematis*, this genus has been established by Spach for yellow-flowered *Clematis* species and consisted of two species, *C. orientalis* L. and *C. glauca* Willd.);
- *Clematis* L.	(=> sect. *Flammula* DC.)

Within *Viorna* and *Clematis*, he distinguished sections:

Viorna

-	sect. *Euviorna* Spach	(woody climbers);
-	sect. *Viornium* Spach	(perennials).

Clematis

-	sect. *Vitalba* Spach	(woody climbers);
-	sect. *Flammula* Spach	(suffruticose ± climbers);
-	sect. *Aspidanthera* Spach	(woody climbers, anthers with an appendage).

Spach's classification - and therefore also the views of Moench and Reichenbach - has not been generally accepted, although his generic names play a role in modern classification of *Clematis* at the sectional level (*Meclatis*, *Viticella* and *Viorna*).

Loudon (1844, 1869) kept two genera within the tribe Clematideae: *Clematis* and *Atragene*; the tribe itself was distinguished in the Ranunculaceae by valvate or induplicate bud aestivation, evergreen or deciduous climbing habit and decussate leaf position. Within *Clematis* Loudon recognized 4 sections:

- *Flammula* DC.;
- *Viticella* (Moench) DC.;
- *Cheiropsis* DC.;
- *Anemoniflora* Loudon

Anemoniflora has not been maintained by later authors, but was reduced to the rank of series (*Montanae* C.K.Schneid.).

Within the tribe Clematideae, Bentham (1862) recognized two genera: *Clematis* and *Naravelia*. *Clematis* was subdivided into three sections:

- *Viticella* (Moench) DC.
- *Cheiropsis* DC.
- *Flammula* DC.

According to Bentham (1862), the characters distinguishing the Clematideae from the Anemoneae are the bud aestivation (valvate vs. imbricate) and the leaf position (decussate vs. scattered). Bentham estimated that there were 100 species within *Clematis*.

In the period 1867-1869 Baillon published his Histoire des Plantes. In volume 1 (1867) he described many morphological features of the flower within Clematideae. For *Clematis* he focussed on flower bud aestivation, dehiscence of anthers and transient forms between androecium and perianth. He largely enhanced the classification by De Candolle (1818), but added his own observations and references. Baillon subdivided *Clematis* into seven sections:

- *Atragene* (L.) DC.
- *Naravelia* (L.) DC.; the section was regarded as derived from *Atragene*.
- *Cheiropsis* DC.
- *Meclatis* (Spach) Baill.
- *Viorna* (Rchb.) Baill.; syn. *Muralta* Adans. ex Endl.
- *Viticella* (Moench) DC.
- *Flammula* DC.

Kuntze (1885) wrote a monograph on the genus *Clematis*, in which he combined detailed observations with a rather peculiar classification. His infrageneric classification seems partially to have been derived from Linnaeus', although he did not state it explicitly. His informal classification, i.e. without stating any rank, is as follows:

a. *Scandentes* (woody plants or subshrubs climbing with ranking petiolules);
    1. *Scandentes eperulatae* (flowering branches developing at the young growth);
    2. *Scandentes perulatae* (mostly reduced, flowering branches developing from buds at the last years growth);
b.(=) 3. *Escandentes* (non-climbing perennials, subshrubs or shrubs; b=a3 indicating that these plants are regarded to be derived from the *Scandentes*).

He tried to interpret all species as derived from *C. vitalba*, which as an exercise is worthwhile doing, but he failed to pinpoint consequences, as is in essence the intention of modern phylogenetic analysis.

Kuntze defined species as broadly as possible, so he combined many species known at the time. Although he made some rather peculiar combinations, based on insufficient material, studying some of these mergers is worthwhile. He was, by doing so, really the first *Clematis* author who deviated from the traditional typological taxonomic treatment and who dared to interpret infraspecific variation. He was, however, inconsequent in dealing with variation by creating exhaustive infraspecific classifications, which are strictly hierarchical in the sense that the broader the infraspecific variation he described the more extensive his hierarchical classification was. His treatment was not accepted by later authors. Furthermore, his implicit stating of infraspecific ranks was cumbersome. As an example, his treatment of *C. orientalis* is presented below (ranks interpreted by the present author):

- *C. orientalis* L.
  - subsp. *α normalis*
    - var. 1. *flava* (Moench) Kuntze
    - var. 2. *daurica* (Pers.) Kuntze
      - subvar. a. *persoonii* Kuntze
      - subvar. b. *thomsonii* Kuntze
      - subvar. c. *dyeri* (Clarke) Kuntze
    - var. 3. *albida* (Klotzsch) Kuntze
      - subvar. a. *obtusifolia* Hook.f. & Thomson
      - subvar. b. *massoniana* (DC.) Kuntze
      - subvar. c. *vulgaris* (Trautv.) Kuntze
      - subvar. d. *angustifolia* (Ledeb.) Kuntze
      - subvar. e. *fasciculata* Kuntze
  - subsp. *β graveolens* (Lindl.) Kuntze
    - var. 1. *lindleyana* Kuntze
    - var. 2. *hookeriana* Kuntze
    - var. 3. *aitchisonii* Kuntze
    - var. 4. *subtripinnata* Kuntze
  - subsp. *γ thunbergii* (Steud.) Kuntze
    - var. 2. *lutea* (Jacquem.) Kuntze
    - var. 3. *intricata* (Bunge) Kuntze
    - var. 4. *glabrescens* Kuntze
    - var. 5. *pauciflora* Kuntze
  - subsp. *δ brachiata* (Thunb.) Kuntze
    - var. 2. *subglabra* Kuntze
  - subsp. *ε wightiana* (Wall.) Kuntze
    - var. 1. *typica*
      - subvar. a. *glaucescens* (Fresen.) Kuntze
      - subvar. b. *inciso-dentata* (Rich.) Kuntze
    - var. 2. *longecaudata* (Ledeb.) Kuntze
    - var. 3. *pseudobuchananiana* Kuntze
    - var. 4. *hoffmanni* Vatke ex Kuntze
  - subsp. *ζ simensis* (Fresen.) Kuntze
    - var. 2. *brevifoliola* Kuntze
    - var. 3. *longifoliola* Kuntze

Further examination of the above classificaton of *C. orientalis* will learn that it is a mixture of true *C. orientalis* and allied species on the one hand with species that are misclassified for various reasons on the other hand (see Chapter 2).

Prantl (1888) was one of the first authors, who tried to classify the genus *Clematis* both by considering all available morphological characters, and by interpreting the polarity of character states. This resulted in the following classification:

Clematis L.
- sect. *Pseudanemone* Prantl
    - ser. *Spatulifoliae* Prantl
    - ser. *Villosae* Prantl
- sect. *Viorna* (Rchb.) Prantl
    - ser. *Crispae* Prantl
    - ser. *Tubulosae* Decne.
    - ser. *Atragenae* Prantl
    - ser. *Cirrhosae* Prantl
- sect. *Viticella* (Moench) DC. emend.
    - ser. *Euviticellae* Prantl
    - ser. *Floridae* Prantl
- sect. *Flammula* DC. emend.
    - ser. *Rectae* Prantl
    - ser. *Vitalbae* Prantl
        - subser. *Euvitalbae* Prantl
        - subser. *Saxicolae* Prantl
        - subser. *Dioicae* Prantl
        - subser. *Hexapetalae* Prantl
    - ser. *Aristatae* Prantl
    - ser. *Orientales* Prantl
- sect. *Naravelia* (DC.) Prantl emend.

The rank of series as currently applied has been derived from Prantl's 'Gruppe'. In references antedating Prantl his names for series have, however, variedly been considered to be either subsection or series names, see e.g. Tamura (1968a, 1987). Prantl formulated the hypothesis that the original forms of *Clematis*, i.e. those forms most similar to the genus *Anemone* L., were to be found in the Palaeotropics. The section *Pseudanemone* should be most similar to this group and is indeed restricted to the Palaeotropics, having its distribution area in Africa. Section *Naravelia* was regarded as an early diverging section. Section *Flammula* originated in the Palaeotropics, but has dispersed all over the world, except for the polar regions. Section *Viorna* originated and remained restricted to the Northern Hemisphere, whereas ser. *Atragene* has dispersed to subarctic and mountainous regions and ser. *Cirrhosae* settled in the Mediterranean. Section *Viticella* originated in Central and Eastern Asia. It now also occurs in the Mediterranean area.

As to the higher classification of *Clematis* within the Ranunculaceae, Prantl stressed that there are no particular reasons why there should be a separate tribe Clematideae DC. Although predominantly present, the valvate aestivation of flower buds is not a unique character and the structure of the inflorescence and fruit is similar to *Anemone*. The only distinguishing character is the decussate leaf position. Prantl regarded *Clematis* as belonging to the tribe Anemoneae.

Both Prantl's classification and his phylogenetic hypothesis contain some inconsistencies, but were the base of modern *Clematis* classification.

Koehne (1893) followed Prantl's classification of *Clematis*:

- sect. *Flammula* DC.
    - ser. *Vitalbae* Prantl
    - ser. *Orientales* Prantl

- sect. *Viticella* (Moench) DC.

- sect. *Viorna* (Rchb.) Prantl
    - subsect. *Euviorna* Koehne
    - subsect. *Connatae* Koehne
    - subsect. *Escandentes* Koehne
    - subsect. *Atragene* (L.) Koehne

It is remarkable that he subdivided the section *Flammula* in series, whereas he erected subsections in section *Viorna* without any argument. Furthermore, *Atragene* was reduced to the rank of subsection contrary to the view, still adopted by some current authors, that it should be a separate genus. Anyhow, Koehne clearly denoted ranks in his classification.

Hooker (1837) showed a plate of a specimen assigned to a then newly recognized genus *Clematopsis* Bojer ex Hook., but produced no description. Hutchinson (1920) presented a first survey of that genus, separated from *Clematis* mainly on its flower bud aestivation, being imbricate instead of induplicative. *Clematopsis* is more or less similar to Prantl's section *Pseudanemone*. Brummitt (1976) and Raynal (1978) presented the most recent survey of *Clematopsis*. Tamura (1987) again included *Clematopsis* in *Clematis*.

In his Manual of Cultivated Trees and Shrubs (1974 2nd ed. 12th pr.; first published in 1923), Rehder classified the *Clematis* species, important in cultivation. He partly followed Prantl (1888), Koehne (1893), and Schneider's (1904) Illustriertes Handbuch der Laubholzkunde:

Clematis L.
- sect. *Flammula* DC.
    - ser. *Vitalbae* Prantl
    - ser. *Rectae* Prantl
    - ser. *Orientales* Prantl
    - ser. *Montanae* C.K.Schneid.
- sect. *Atragene* (L.) DC.
- sect. *Viticella* (Moench) DC.
- sect. *Viorna* (Rchb.) Prantl
    - ser. *Cirrhosae* Prantl
    - ser. *Crispae* Prantl
    - ser. *Connatae* (Koehne) Rehder
    - ser. *Tubulosae* Dcne.

Tamura (1968a) published an extensive classification of the Ranunculaceae, based on phylogenetic considerations, as final part of a series of publications on the phylogenetic value of characters within this family. Within the tribe Anemoneae he distinguished three subtribes, including the Clematidinae, as defined by Lotsy (1911):

> 'Die Clematidinae weichen von allen anderen Gruppen der Anemoneae durch gewöhnliche faltig-klappige Aestivation des Kelches und gegenständige Blätter ab. Es sind 4 bis mehrere kronblattartige Kelchblätter vorhanden, nur die Untergattung *Atragene* hat lineare Korollenblätter, den andern fehlt die Korolle. Die Frucht ist eine Nuß, oft wie bei *Pulsatilla* mit auswachsendem federförmigen Griffel.'

Within the Clematidinae, Tamura initally maintained 4 genera: *Archiclematis* Tamura, *Clematis* L., *Clematopsis* Bojer ex Hook., and *Naravelia* DC., although the principal distinguishing tribal characters, flower bud aestivation and leaf position, were no constant character states. Tamura classified *Clematis* into 12 sections and distinguished 15 subsections:

Clematis
- sect. *Viorna* (Rchb.) Prantl
    - subsect. *Viorna* (Rchb.) Tamura
    - subsect. *Connatae* Koehne
    - subsect. *Crispae* (Prantl) Tamura
- sect. *Bebaeanthera* Edgew. (*Paratragene* Tamura)
- sect. *Atragene* (L.) DC.
- sect. *Meclatis* (Spach) Baill.
    - subsect. *Orientales* (Prantl) C.K.Schneid.
    - subsect. *Tanguticae* C.K.Schneid.

- sect. *Clematis*
    - subsect. *Pierotianae* (Tamura) Tamura
    - subsect. *Vitalbae* Tamura
    - subsect. *Dioicae* (Prantl) Tamura
    - subsect. *Aristatae* (Prantl) Tamura
    - subsect. *Papuasicae* H.Eichler
    - subsect. *Crassifoliae* (Tamura) Tamura
    - subsect. *Rectae* (Prantl) Tamura
    - subsect. *Angustifoliae* Tamura
- sect. *Cheiropsis* DC.
- sect. *Lasiantha* Tamura
- sect. *Viticella* (Moench) DC.
    - subsect. *Floridae* (Prantl) Tamura
    - subsect. *Viticella*
- sect. *Patentes* Tamura
- sect. *Pterocarpa* Tamura
- sect. *Fruticella* Tamura
- sect. *Naraveliopsis* Hand.-Mazz.

In 1987, Tamura modified his classification considerably:

Clematis

- subgen. *Campanella* Tamura
    - sect. *Campanella* Tamura
    - sect. *Tubulosae* (Decne.) Kitag.
    - sect. *Bebaeanthera* Edgew.
    - sect. *Atragene* (L.) DC.
    - sect. *Meclatis* (Spach) Baill.
        - subsect. *Orientales* (Prantl) C.K.Schneid.
        - subsect. *Tanguticae* C.K.Schneid.
    - sect. *Pseudanemone* Prantl
- subgen. *Viorna* (Rchb.) Tamura
- subgen. *Clematis*
    - sect. *Clematis*
        - subsect. *Clematis*
        - subsect. *Pierotianae* (Tamura) Tamura
        - subsect. *Dioicae* (Prantl) Tamura
    - sect. *Cheiropsis* DC.
    - sect. *Lasiantha* Tamura
    - sect. *Aspidanthera* Spach
    - sect. *Naraveliopsis* Hand.-Mazz.
- subgen. *Flammula* (DC.) Peterm.
    - sect. *Flammula* DC.
        - subsect. *Rectae* (Prantl) Tamura
            - ser. *Rectae* Prantl

        ser. *Uncinatae* Tamura
      subsect. *Angustifoliae* Tamura
      subsect. *Crassifoliae* (Tamura) Tamura
   sect. *Pterocarpa* Tamura
   sect. *Viticella* (Moench) DC.
      subsect. *Floridae* (Prantl) Tamura
      subsect. *Patentes* Tamura
   sect. *Fruticella* Tamura

Compared to his earlier classification in 1968, Tamura now introduced the subgenus rank. Subgenus *Campanella* is newly defined and based on the new section *Campanella*. One of the subgenera, *Viorna*, is just an upgraded section. Others, subgenus *Clematis* and subgenus *Flammula*, are new combinations of earlier described sections. As this classification shows some inconsistencies and is more cumbersome. the classification of 1968 has been chosen as starting-point for further examination.

1.3. Phylogenetic analysis of the genus *Clematis*

In order to judge the integrity of the genus, cladistic analyses have been carried out, based on morphological characters of subdivisions of *Clematis* and of related genera (1.3.1.), and analysis of the global distribution of *Clematis* (1.3.2.). It is preferable to carry out this type of analysis with scores of characters. By them, it is also possible to judge the integrity of the subdivisions of a genus. The databases built, however, were based on integral data for the subdivisions themselves as they were defined by Prantl (1888) and Tamura (1968a). This restricts the possibility to draw detailed conclusions from the analysis, but globally provides insight on variation patterns in the genus, both with regard to its distribution (Barton, 1989; Cox, 1990; Cracraft, 1975; Humphries, 1979; Humphries et al., 1988; Nelson & Platnick, 1981; Raven & Axelrod, 1974; Rosen, 1975, 1978; Schuster, 1976; Thorne, 1978, 1983; Wiley, 1975, 1977, 1978, 1979a, 1979b, 1979c, 1980, 1981; Wulff, 1950; Zandee & Roos, 1987) and to its overall variation (Ax, 1985; Bremer & Wanntorp, 1978, 1981; Brooks et al., 1984; Brooks & Wiley, 1985; Eldredge, 1985, 1989; Eldredge & Cracraft, 1980; Estabrook, 1972, 1978; Funk & Brooks, 1990; Hennig, 1950, 1965, 1966; Humphries & Funk, 1984; Loconte & Stephenson, 1990, 1991; Minelli, 1993; Nelson, 1978, 1979, Queiros &

Donoghue, 1990a, 1990b; Sluiman, 1985; Sober, 1975, 1983, 1984, 1988; Stevens, 1991; Stuessy, 1990; Wiley, 1981).

1.3.1. *Cladistic analysis of subdivisions of* ***Clematis*** *and of related genera*

As to the delimitation of the genus *Clematis*, there are many unresolved issues. A number of taxa, often described as separate genera, have been included in the genus s.l., such as *Atragene* (Linnaeus, 1753, vs. Miller, 1768), *Naravelia* (De Candolle, 1818, vs. Prantl, 1888), *Clematopsis* (Prantl, 1888, vs. Bojer ex Hooker, 1837 / Hutchinson, 1920), *Meclatis* (Spach, 1839, vs. all other authors after him), *Viorna* (Reichenbach, 1837, vs. De Candolle, 1818), *Viticella* (Moench, 1794, vs. De Candolle, 1818) and *Archiclematis* (Tamura, 1968a, 1970 vs. e.g. Rehder, 1974) are included. Whether or not *Clematis* can be considered as a monophyletic genus is the main criterium to decide upon its delimitation. In the modern view on botanical classification, monophyly is considered to be a strict condition for real systematic entities. As Farris (1991; cf. Farris, 1974; Platnick, 1977) put it:

> 'Monophyly can be defined (though not recognized) without reference to character evidence only because monophyletic groups have real and independent historical existence. Paraphyletic and polyphyletic groups have no such existence; they are nothing but the characters by which they are delimited. Without characters, paraphyly and polyphyly mean nothing. It is the reality of monophyletic groups that ultimately distinguishes phylogenetic systematics from syncretistic taxonomies'.

Prantl's (1888) and Tamura's (1968a) classifications have been chosen for phylogenetic analysis, as these classifications are relatively recent and widely accepted. A data set was constructed based on their respective publications. As these publications differ in their usage of descriptive characters, the data sets also slightly differ. Tables 1.1 and 1.5 survey the used characters for both analyses. Tables 1.2 and 1.6 present the two data matrices. The data sets were analysed by Hennig86 release 1.5 (Farris, 1988), using mhennig and bb for branch swapping. The cladograms thus obtained were subjected to successive weighting using the consistency index of characters as weighting criterium (Carpenter, 1988; Farris, 1969, 1989). A strict consensus tree, using Farris'nelsen algorithm, was constructed, if several equally parsimonious trees were obtained from the analysis. This tree gives an impression of the information content of the used data set (the degree of homoplasy) and visualizes uncertain steps in the tree (Anderberg & Tehler, 1990; Miyamoto, 1985).

In the case of Prantl (1888), the tribe Anemoneae (*Anemone* s.l. and *Clematis* s.l.) was included in the data matrix to get a better sight on the bordercases of the involved genera. The results are presented in figures 1.1, 1.2 and 1.3. As in all produced trees the section *Homalocarpus* seems to be the sister group of *Clematis*, the analysis has also been carried out with *Anemone* section *Homalocarpus* as outgroup, the results being presented in figure 1.4.

Table 1.1. Character set for Prantl's classification of the Anemoneae, used in phylogenetic analysis with Hennig86.

Character		character states		
1	Habitus	perennial **1**	subshrub **2**	shrub **3**
2	Leaf	simple **1**	composite **2**	
3	Leaf	palmately nerved **1**	pinnately nerved **2**	
4	Leaf	scattered **1**	alternate **2**	decussate **3**
5	Leaf	irregularly serrate/dentate **1**	serrate **2**	lobed **3**
		entire **4**		
6	Leaf	pilose **1**	nerves pilose underneath **2**	
		glabrous **3**		
7	Leaf	herbaceous **1**	pergamentaceous **2**	coriaceous **3**
8	Leaf	tendrils absent **1**	present **2**	
9	Bracts	free **1**	± fused **2**	involucral **3**
10	Infl.	simple cymae **1**	composite cymae **2**	fasciculate **3**
		heterotactic **4**	solitary fls. **5**	
11	Infl.	flowering on the young wood **1**	flowering on the old wood **2**	
12	Flower	flat, erect **1**	broadly campanulate **2**	campanulate **3**
		tubulose, urceolate **4**		
13	Flower	hermaphrodite **1**	unisexual **2**	dioecious **3**
14	Tepal	n=4 **1**	n=5 **2**	n≥6 **3**
15	Tepal	herbaceous **1**	coriaceous **2**	fleshy **3**
16	Tepal	ovate **1**	rhomboid **2**	obovate **3**
17	Tepal	imbricate **1**	valvate **2**	
18	Tepal	villose at margins, glabrous **1**	ditto, but pilose inside **2**	
		ditto, but pilose outside **3**		
19	Tepal	acute **1**	acuminate **2**	mucronate **3**
20	Staminodia	absent **1**	incidentally present **2**	present **3**
		present, petaloid **4**		
21	Filament	filiform **1**	dilatate **2**	rugulose **3**
22	Filament	glabrous **1**	ciliate **2**	
23	Anther	shorter **1**	as long as **2**	longer than filament **3**
24	Anther	connective not elongate **1**		elongate **2**
25	Ovary	ovate **1**	rhomboid **2**	
26	Ovary	ovules 2-4 **1**	ovules 1 **2**	
27	Fruit	ovate **1**	rhomboid **2**	
		rhomboid, dorsiventrally costate **3**		fleshy **4**
28	Fruit	glabrous **1**	pilose **2**	villose **3**
29	Fruit	style not elongate **1**	2× elongate **2**	>2× elongate **3**

Table 1.2. Data matrix for Prantl's classification (1888) of the tribe Anemoneae.

Character no ▸ ▾ Subdivisions	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Anemonanthea	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Eriocephalus	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1
Pulsatilloides	1	2	1	1	1	1	1	1	3	5	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1
Homalocarpus	1	2	1	1	1	1	1	1	1	3	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1
Hepatica	1	1	1	1	3	3	1	1	3	1	1	1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Barneoudia	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Knowltonia	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	4	1	1	1	1	1	1	4	1	1
Preonanthus	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	3	1	1	1	2	1	1	1	1	1	3	3
Campanaria	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	3	1	3	1	2	1	1	1	1	1	3	3
Spatulifolia	1	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	2
Villosae	1	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	2
Crispae	2	2	2	3	3	2	2	1	1	1	1	3	1	1	3	2	2	2	1	1	2	2	1	1	2	1	3	1	2
Tubulosae	1	2	2	3	1	1	1	1	1	2	1	4	1	1	1	1	2	2	1	1	2	2	1	1	2	1	3	1	2
Atragene	3	2	1	3	2	2	1	1	1	3	2	3	1	1	1	3	2	1	1	4	2	2	1	1	1	1	1	2	3
Cirrhosae	3	2	2	3	3	1	1	1	1	3	2	3	1	1	1	3	2	1	1	1	1	1	1	1	2	1	2	1	1
Euviticellae	3	2	2	3	3	2	1	1	1	4	1	1	1	1	1	2	2	1	2	1	2	1	1	1	2	1	3	1	2
Floridae	3	2	2	3	3	1	1	1	1	4	2	1	1	3	1	2	2	1	1	1	2	1	1	1	2	1	3	1	2
Rectae	1	2	2	3	4	1	1	1	1	4	1	1	1	1	1	3	2	1	2	1	2	1	1	1	2	1	3	1	2
Euvitalbae	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	3	2	2	2	1	2	2	1	1	2	1	2	1	1
Saxicolae	3	2	2	3	3	1	1	1	1	2	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	1	2	1	1
Dioicae	3	2	2	3	3	1	1	1	1	4	1	1	2	1	1	1	2	1	2	1	2	2	1	1	2	1	2	1	2
Hexapetalae	3	2	2	3	3	1	1	1	1	4	1	1	2	3	1	1	2	1	1	3	2	1	1	1	2	1	2	1	1
Aristatae	3	2	2	3	1	1	1	1	1	4	1	1	2	1	1	1	2	1	2	1	2	2	1	2	2	1	2	1	2
Orientales	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	1	1	1	2	2
Wightianae	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	3	1	1	2	2	1	1	2	1	2	2	2
Naravelia	3	2	2	3	1	1	1	2	1	2	1	1	1	1	1	1	2	3	1	2	1	1	2	2	1	1	1	1	1

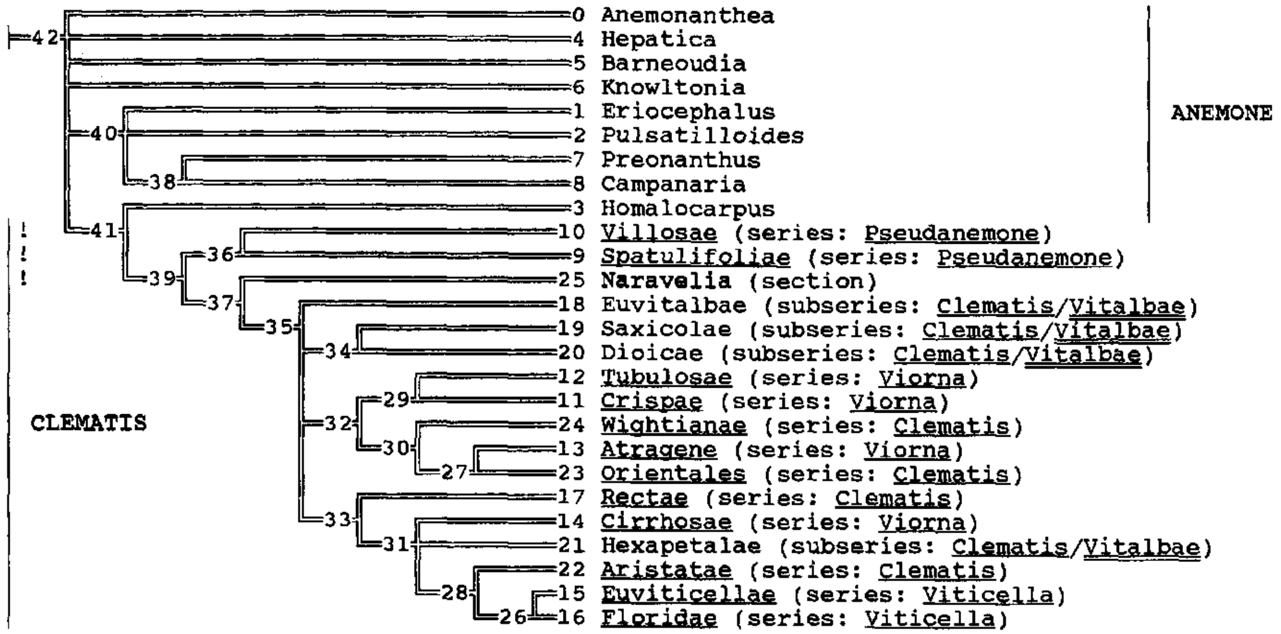


Figure 1.1. Cladogram based on Prantl's classification (1888) of the tribe Anemoneae (characters unweighted).

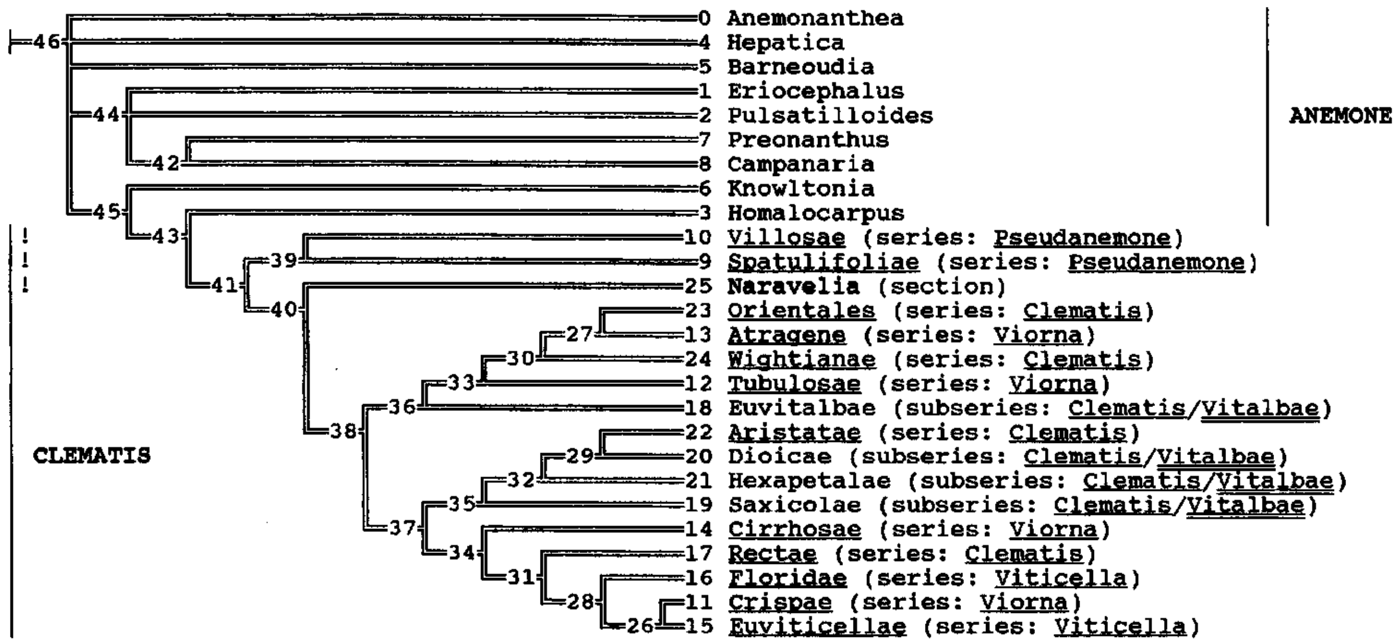


Figure 1.2. One of four cladograms based on Prantl's classification (1888) of the tribe Anemoneae after repeated successive weighting of characters, using Farris' consistency algorithm.

Table 1.3. Character states of ancestors as indicated in the cladogram of figure 1.2. (successive weighting).

Characters▸ **▾ Ancestors**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
26	3	2	2	3	3	2	1	1	1	4	1	1	1	1	1	2	2	1	1	1	2	1	1	1	2	☒	3	1	2
27	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	1	☒	1	2	2
28	3	2	2	3	3	1	1	1	1	4	1	1	1	1	1	2	2	1	1	1	2	1	1	1	2	☒	3	1	2
29	3	2	2	3	3	1	1	1	1	4	1	1	2	1	1	1	2	1	2	1	2	2	1	1	2	☒	2	1	2
30	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	2	☒	2	2	2
31	3	2	2	3	3	1	1	1	1	4	1	1	1	1	1	3	2	1	1	1	2	1	1	1	2	☒	3	1	1
32	3	2	2	3	3	1	1	1	1	4	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	☒	2	1	1
33	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	2	☒	2	1	2
34	3	2	2	3	3	1	1	1	1	23	1	1	1	1	1	3	2	1	1	1	2	1	1	1	2	☒	2	1	1
35	3	2	2	3	3	1	1	1	1	24	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	☒	2	1	1
36	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	2	☒	2	1	1
37	3	2	2	3	3	1	1	1	1	24	1	1	1	1	1	1	2	1	1	1	2	1	1	1	2	☒	2	1	1
38	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	2	1	1	1	2	☒	2	1	1
39	1	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	☒	2	1	2
40	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	☒	2	1	1
41	1	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	☒	2	1	1
42	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	3	1	1	1	2	1	1	1	☒	1	3	3
43	1	2	1	1	1	1	1	1	1	12	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	☒	2	1	1
44	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	☒	1	3	1
45	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	☒	12	1	1
46	1	2	1	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	☒	1	1	1

By having a consistency index of 0, there are no expressed character states for character 26. Weighting codes for characters (char. - weight): 1 - 4; 2 - 10; 3 - 4; 4 - 10; 5 - 4; 6 - 3; 7 - 10; 8 - 10; 9 - 10; 10 - 3; 11 - 0; 12 - 0; 13 - 4; 14 - 10; 15 - 10; 16 - 3; 17 - 10; 18 - 1; 19 - 0; 20 - 0; 21 - 4; 22 - 1; 23 - 0; 24 - 0; 25 - 4; 26 - 10; 27 - 3; 28 - 10; and 29 - 2.

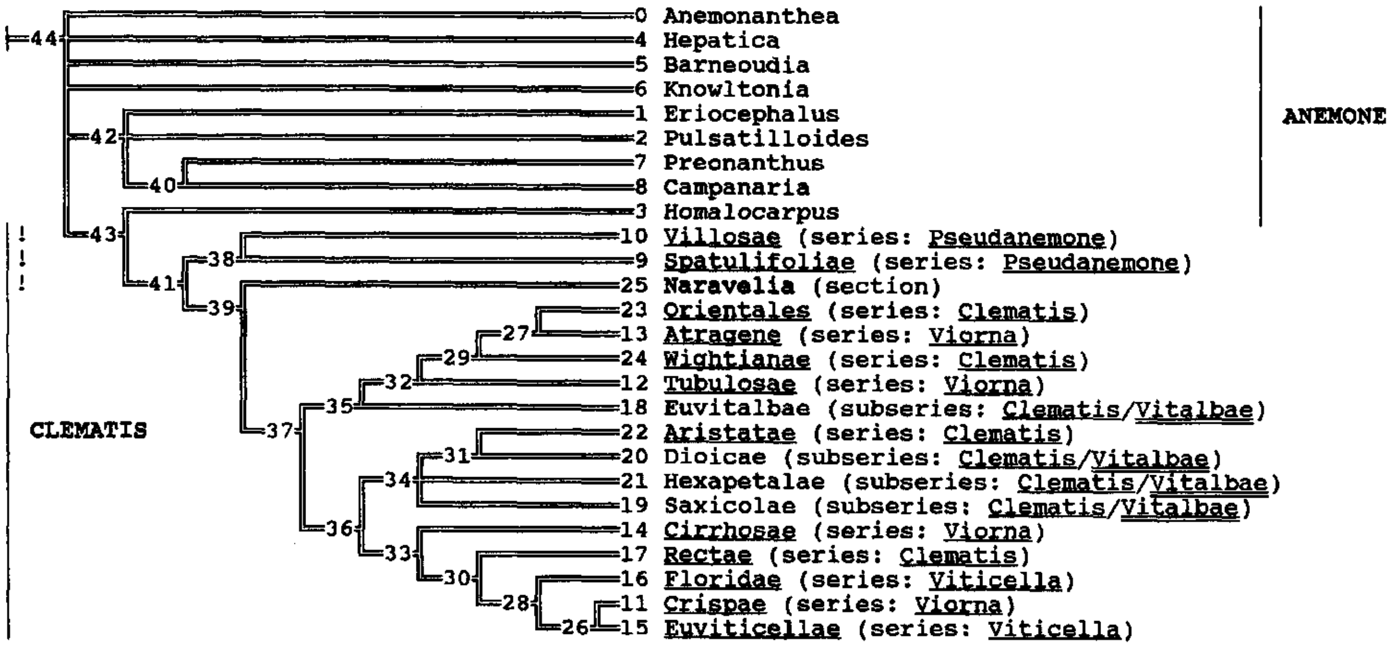


Figure 1.3. Strict consensus tree based on Prantl's classification (1888), using Farris' nelsen algorithm after successive weighting of characters.

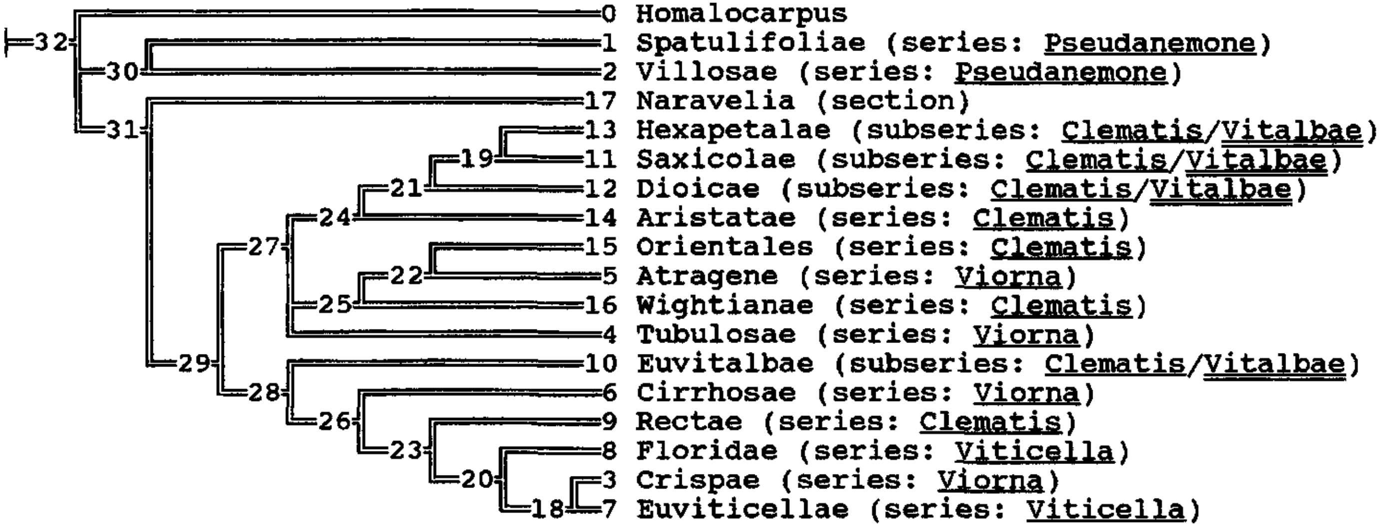


Figure 1.4. A cladogram based on Prantl's classification (1888) with *Anemone* sect. *Homalocarpus* as outgroup after successive weighting using Farris' consistency algorithm. This cladogram was the single outcome and hence similar to the strict consensus tree.

Table 1.4. Character states of ancestors as indicated in the cladogram of figure 1.4. (successive weighting).

Characters▸ ▾ Ancestors	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
18	3	☒	2	3	3	2	1	1	☒	4	1	1	1	1	1	2	2	1	1	1	2	1	1	1	2	☒	3	1	2
19	3	☒	2	3	3	1	1	1	☒	4	1	1	2	1	1	1	2	1	1	1	2	1	1	1	2	☒	2	1	1
20	3	☒	2	3	3	1	1	1	☒	4	1	1	1	1	1	2	2	1	1	1	2	1	1	1	2	☒	3	1	2
21	3	☒	2	3	3	1	1	1	☒	4	1	1	2	1	1	1	2	1	12	1	2	2	1	1	2	☒	2	1	2
22	3	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	1	2	1	1	1	2	2	1	1	1	☒	1	2	2
23	3	☒	2	3	3	1	1	1	☒	4	1	1	1	1	1	3	2	1	1	1	2	1	1	1	2	☒	3	1	1
24	3	☒	2	3	1	1	1	1	☒	4	1	1	2	1	1	1	2	1	12	1	2	2	1	1	2	☒	2	1	2
25	3	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	2	2
26	3	☒	2	3	3	1	1	1	☒	23	1	1	1	1	1	3	2	1	1	1	2	1	1	1	2	☒	2	1	1
27	3	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	1	2
28	3	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	3	2	1	1	1	2	12	1	1	2	☒	2	1	1
29	3	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	1	2	1	1	1	2	12	1	1	2	☒	2	1	1
30	1	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	☒	2	1	2
31	3	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	1	2	1	1	1	1	12	1	1	1	☒	2	1	1
32	1	☒	2	3	1	1	1	1	☒	2	1	1	1	1	1	1	1	1	1	1	1	12	1	1	1	☒	2	1	1

By having a consistency index of 0, there are no expressed character states for characters 2, 9 and 26. Weighting codes for characters (char. - weight): 1 - 2; 2 - 10; 3 - 0; 4 - 10; 5 - 4; 6 - 2; 7 - 10; 8 - 10; 9 - 10; 10 - 1; 11 - 0; 12 - 0; 13 - 10; 14 - 0; 15 - 10; 16 - 10; 17 - 10; 18 - 0; 19 - 0; 20 - 0; 21 - 3; 22 - 0; 23 - 0; 24 - 0; 25 - 4; 26 - 10; 27 - 3; 28 - 10; and 29 - 2.

From the data matrix based on Prantl's classification, four cladograms have been constructed (figures 1.1, 1.2, 1.3 and 1.4). The first one (characters unweighted) shows four multifurcate forks, indicating question marks on character statements of the ancestor concerned. The second cladogram (characters weighted) only shows multifurcations at the basis of the cladogram within the scope of *Anemone*, making clear that the classification of this genus by Prantl is highly artificial. The tree characteristics (tree length 261, consistency index 69, retention index 88) shows that there is considerable incongruence in the data set. Table 1.3 shows multiple statements for four hypothetical ancestors at character 10 (inflorescence structure) and for one ancestor at character 27 (achene morphology), thus indicating that character state expression is left undetermined. Furthermore, the data set has been restricted by the weighting procedure by eliminating characters with either a low consistency index, or no variation: Characters 11, 12, 19, 20, 23, 24 and 26 are left out by weight 0. The third cladogram, the strict consensus tree, (figure 1.3) supports the modest information content, especially with regard to *Anemone*: the basal multifurcate fork has increased with one branch, whereas the other multifurcate fork has not been dissolved, thus demonstrating the uncertainty about ancestral character states. If one takes into account that in other classifications section *Pseudanemone* is the separate genus *Clematopsis* and section *Naravelia* is recognized as a separate genus, the cladogram shows *Clematopsis* as monophyletic at the series level. *Naravelia* is monotypic. The remainder of *Clematis* (sensu Prantl) is monophyletic as well, having as apparent synapomorphies dilatate filaments and rhomboid achenes. Considering *Clematis* sensu Prantl as a whole, synapomorphies are pinnately nerved leaves, decussate leaf position, tepal number 4, and rhomboid achenes. In other classifications this implies that these synapomorphies are valid for the entire tribe Clematideae.

As in all equally parsimonious cladograms *Anemone* section *Homalocarpus* adjoins *Clematis*, the data set was restricted to *Clematis* sensu Prantl and section *Homalocarpus*. The resulting cladogram (characters weighted) is presented in figure 1.4. Considering section *Pseudanemone* as a separate genus (*Clematopsis*), only the valvate bud aestivation appears to be a synapomorphy for *Clematis* and *Naravelia*, the latter separated by leaf tendrils and appendages at the anthers. The tree length of 169 steps and the many characters with either a consistency index 0 or weight 0 (2, 3, 9, 11, 12, 14, 18, 19, 20, 22, 23, 24 and 26) indicate that the information content of this set is low and that detailed conclusions are not possible. The remaining character with a multiple statement at one ancestral node is character 10 (inflorescence structure). The evolutionary history of *Clematis* can only be clarified after a detailed analysis of inflorescence structure and flower characteristics.

Although the information content of the data set concerned is rather low, some conclusions may be drawn:

- Section *Clematis* and its series *Vitalbae* appear to be polyphyletic;
- The same holds for the section *Viorna*, although this cannot be a strong statement regarding the fact that *Atragene* is mostly classified as section. The position of the series *Tubulosae* has to be further ascertained, being also related in classifications to sections *Clematis* and *Flammula* (see Tamura, 1987);
- The section *Viticella* looks paraphyletic, in this respect the species of the series *Crispae* have to be analysed.

Taking into account the treatment by Tamura (1968a), the subtribe Clematidinae sensu Tamura (i.e. Clematidinae as defined by Lotsy (1911)) was included, especially to consider whether the separate genera *Archiclematis*, *Clematopsis* and *Naravelia* are interposed between sections or subsections of the genus *Clematis* sensu Tamura. The results are presented in figures 1.5, 1.6 and 1.7.

Table 1.5. Character set for Tamura's classification of the Clematideae with *Anemone* as outgroup, used in phylogenetic analysis with Hennig86.

Character		character states		
1	Habit	perennial **1**	subshrub **2**	shrub **3**
2	Leaf	simple **1**	composite **2**	
3	Leaf	palmately nerved **1**	pinnately nerved **2**	
4	Leaf	scattered **1**	alternate **2**	decussate **3**
5	Leaf	irregularly serrate/dentate **1**	serrate **2**	lobed **3**
		entire **4**		
6	Leaf	pilose **1**	nerves pilose underneath **2**	
		glabrous **3**		
7	Leaf	herbaceous **1**	pergamentaceous **2**	coriaceous **3**
8	Leaf	tendril absent **1**	present **2**	
9	Bracts	free **1**	fused **2**	
10	Infl.	simple cymes **1**	composite cymes **2**	fasciculate **3**
		heterotactic **4**	solitary fls. **5**	
11	Infl.	flowering on the young wood **1**		flowering on the old wood **2**
12	Flower	flat, erect **1**	broadly campanulate **2**	campanulate **3**
		tubulose, urceolate **4**		
13	Flower	hermaphrodite **1**	unisexual **2**	dioecious **3**
14	Tepal	n=4 **1**	n=5 **2**	n≥6 **3**
15	Tepal	herbaceous **1**	coriaceous **2**	fleshy **3**
16	Tepal	ovate **1**	rhomboid **2**	obovate **3**
17	Tepal	imbricate **1**	valvate **2**	
18	Tepal	villose at margins, glabrous **1**		ditto, but pilose inside **2**
		ditto, but pilose outside **3**		
19	Tepal	acute **1**	acuminate **2**	mucronate **3**
20	Staminodia	absent **1**	occasionally present **2**	present **3**
		present, petaloid **4**		
21	Filament	filiform **1**	dilatate **2**	rugulose **3**
22	Filament	glabrous **1**	ciliate **2**	
23	Anther	shorter **1**	as long as **2**	longer than filament **3**
24	Anther	connective not elongate **1**		elongate **2**
25	Ovary	ovate **1**	rhomboid **2**	
26	Ovary	ovules 2-4 **1**	ovules 1 **2**	
27	Fruit	ovate **1**	rhomboid **2**	
		rhomboid, dorsiventrally costate **3**		fleshy **4**
28	Fruit	style not elongate **1**	2× elongate **2**	>2× elongate **3**

Table 1.6. Data matrix based on Tamura's classification (1968a)

Characters ▸ **▾ Subdivisions**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
Anemone	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Archiclematis	3	1	2	2	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
Clematopsis	1	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1	1
Naravelia	3	2	2	3	1	1	1	2	1	2	1	1	1	1	1	1	2	3	1	3	1	1	2	2	1	1	1	1
Viorna	2	2	2	3	3	2	2	1	1	1	1	3	1	1	2	1	2	2	1	1	2	2	1	1	2	1	2	2
Connatae	2	2	2	3	3	2	2	1	1	1	1	3	1	1	3	1	2	2	1	1	2	2	1	1	1	1	1	2
Crispae	2	2	2	3	3	2	2	1	1	1	1	2	1	1	1	2	2	1	1	1	2	2	1	1	2	1	3	2
Bebaeanthera	3	2	2	3	1	1	1	1	1	3	2	2	1	1	1	3	2	1	2	1	2	2	1	1	2	1	2	2
Atragene	3	2	1	3	2	2	1	1	1	3	2	2	1	1	1	1	2	1	1	4	2	2	1	1	1	1	1	3
Orientales	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	1	1	1	2
Tanguticae	3	2	2	3	1	1	1	1	1	5	1	2	1	1	1	1	2	2	1	1	2	2	1	1	1	1	1	2
Pierotianae	3	2	2	3	1	2	1	1	1	1	1	1	1	1	1	1	2	1	2	1	2	2	1	1	2	1	2	3
Vitalbae	3	2	2	3	1	1	1	1	1	2	1	1	1	1	1	3	2	2	2	1	2	2	1	1	2	1	2	1
Dioicae	3	2	2	3	1	1	1	1	1	4	1	1	2	1	1	1	2	1	2	1	2	2	1	1	2	1	2	2
Aristatae	3	2	2	3	1	1	1	1	1	4	1	1	2	1	1	1	2	1	2	1	2	2	1	2	2	1	2	2
Papuasicae	3	2	2	3	1	2	3	1	1	4	1	1	2	1	1	1	2	1	1	1	2	2	1	2	2	1	2	2
Crassifiliae	3	2	2	3	4	3	3	1	1	4	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2	1	2	2
Rectae	1	2	2	3	4	1	1	1	1	4	1	1	1	1	1	1	2	1	1	1	1	1	1	1	2	1	3	1
Angustifoliae	1	2	2	3	4	1	1	1	1	4	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1
Cheiropsis	3	2	2	3	1	1	1	1	2	3	2	1	1	1	1	3	2	2	2	1	1	1	1	1	2	1	2	1
Lasiantha	3	2	2	3	1	1	1	1	1	3	2	1	3	1	1	2	2	2	2	1	1	1	1	1	2	1	2	1
Floridae	3	2	2	3	3	1	1	1	1	1	2	1	1	2	1	2	2	1	2	2	2	1	1	1	2	1	3	2
Viticella	3	2	2	3	3	2	1	1	1	4	1	1	1	1	1	2	2	1	2	1	2	1	2	1	2	1	3	2
Patentes	3	2	2	3	4	2	1	1	1	1	2	1	1	3	1	2	2	1	2	1	2	1	1	1	2	1	3	2
Pterocarpa	3	2	2	3	1	1	1	1	1	1	1	1	1	1	1	3	2	1	2	1	1	1	1	1	2	1	3	2
Fruticella	3	1	2	3	2	1	1	1	1	2	1	1	1	1	3	2	2	1	2	1	2	1	1	1	2	1	3	1
Naraveliopsis	3	2	2	3	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	2	1	1	2	2	1	2	1

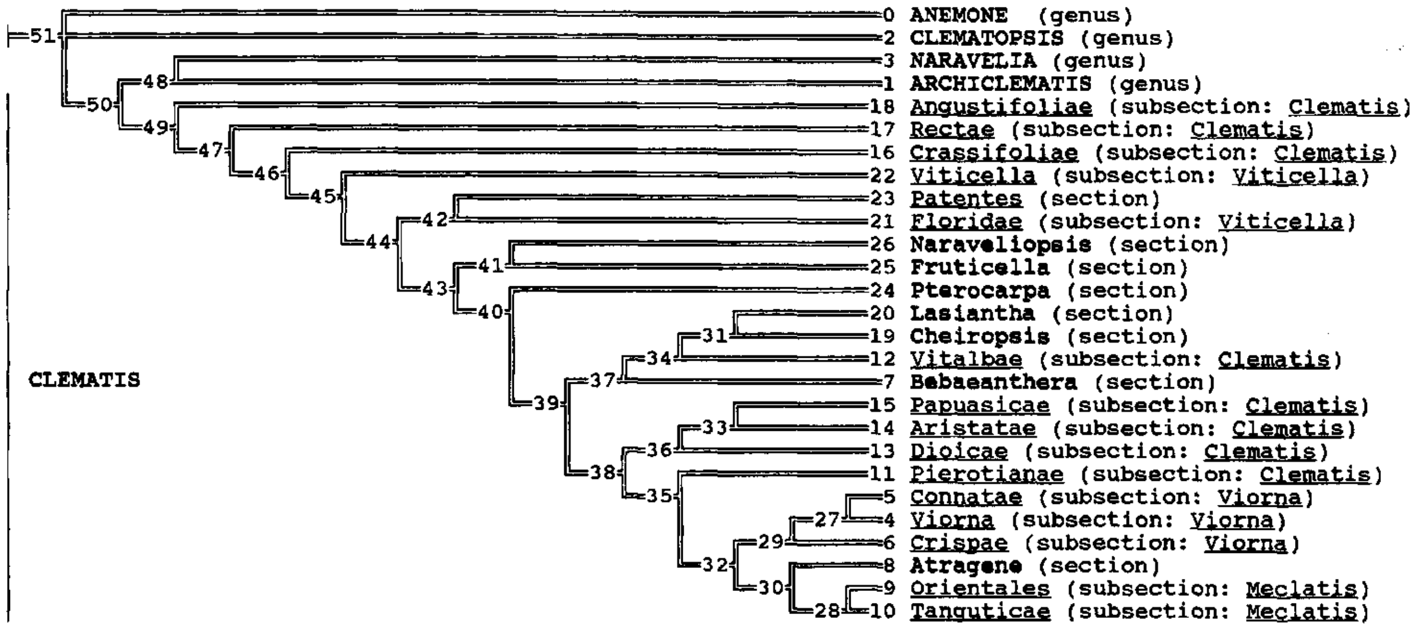


Figure 1.5. Cladogram of Tamura's classification (1968a) of the subtribe Clematidinae (characters unweighted).

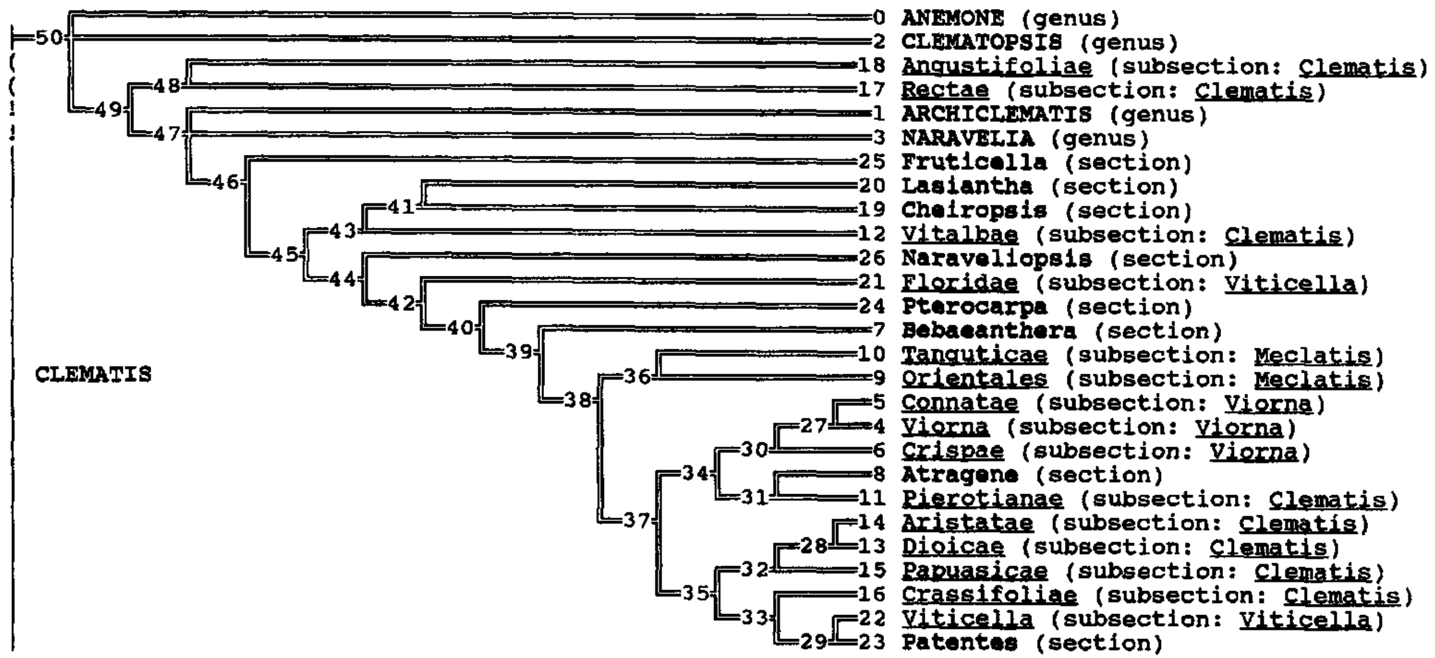


Figure 1.6. One of eight cladograms based on Tamura's classification (1968a) after successive weighting of characters.

Table 1.7. Character states of ancestors as indicated in the cladogram of figure 1.7. (successive weighting).

Characters ▸ ▾ Ancestors	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
27	2	2	2	3	3	2	2	☒	1	1	1	3	1	1	12	1	2	2	1	1	2	2	1	1	2	☒	2	2
28	3	2	2	3	1	1	1	☒	1	4	1	1	2	1	1	1	2	1	2	1	2	2	1	12	2	☒	2	2
29	3	2	2	3	4	2	1	☒	1	4	1	1	1	1	1	2	2	1	2	1	2	1	1	1	2	☒	2	2
30	2	2	2	3	3	2	2	☒	1	1	1	12	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	2
31	3	2	2	3	1	2	1	☒	1	1	1	12	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	3
32	3	2	2	3	1	2	1	☒	1	4	1	1	2	1	1	1	2	1	1	1	2	2	1	12	2	☒	2	2
33	3	2	2	3	4	2	1	☒	1	4	1	1	1	1	1	1	2	1	1	1	2	1	1	1	2	☒	2	2
34	3	2	2	3	1	2	1	☒	1	1	1	12	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	2
35	3	2	2	3	1	2	1	☒	1	4	1	1	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	2
36	3	2	2	3	1	1	1	☒	1	12	1	12	1	1	1	1	2	2	1	1	2	2	1	1	2	☒	1	2
37	3	2	2	3	1	2	1	☒	1	1	1	12	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	2
38	3	2	2	3	1	1	1	☒	1	1	1	12	1	1	1	1	2	1	1	1	2	2	1	1	2	☒	2	2
39	3	2	2	3	1	1	1	☒	1	1	1	12	1	1	1	3	2	1	2	1	2	2	1	1	2	☒	2	2
40	3	2	2	3	1	1	1	☒	1	1	1	1	1	1	1	3	2	1	2	1	2	1	1	1	2	☒	2	2
41	3	2	2	3	1	1	1	☒	1	3	1	1	1	1	1	23	2	2	2	1	2	1	1	1	2	☒	2	1
42	3	2	2	3	1	1	1	☒	1	1	1	1	1	1	1	2	2	1	2	1	2	1	1	1	2	☒	2	2
43	3	2	2	3	1	1	1	☒	1	2	1	1	1	1	1	23	2	2	2	1	2	1	1	1	2	☒	2	1
44	3	2	2	3	1	1	1	☒	1	1	1	1	1	1	1	2	2	1	2	1	2	1	1	1	2	☒	2	1
45	3	2	2	3	1	1	1	☒	1	2	1	1	1	1	1	2	2	1	2	1	2	1	1	1	2	☒	2	1
46	3	2	2	3	1	1	1	☒	1	2	1	1	1	1	1	2	2	1	2	1	2	1	1	1	2	☒	12	1
47	3	2	2	3	1	1	1	☒	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	☒	1	1
48	1	2	2	3	4	1	1	☒	1	4	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	☒	1	1
49	1	2	2	3	1	1	1	☒	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	☒	1	1
50	1	2	1	3	1	1	1	☒	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	☒	1	1

By having a consistency index of 0, there are no expressed character states for characters 8 and 26. Weighting codes for characters (char. - weight): 1 - 10; 2 - 0; 3 - 2; 4 - 10; 5 - 2; 6 - 5; 7 - 4; 8 - 10; 9 - 10; 10 - 3; 11 - 0; 12 - 1; 13 - 10; 14 - 0; 15 - 0; 16 - 1; 17 - 10; 18 - 2; 19 - 0; 20 - 0; 21 - 1; 22 - 1; 23 - 10; 24 - 0; 25 - 1; 26 - 10; 27 - 1; and 28 - 10.

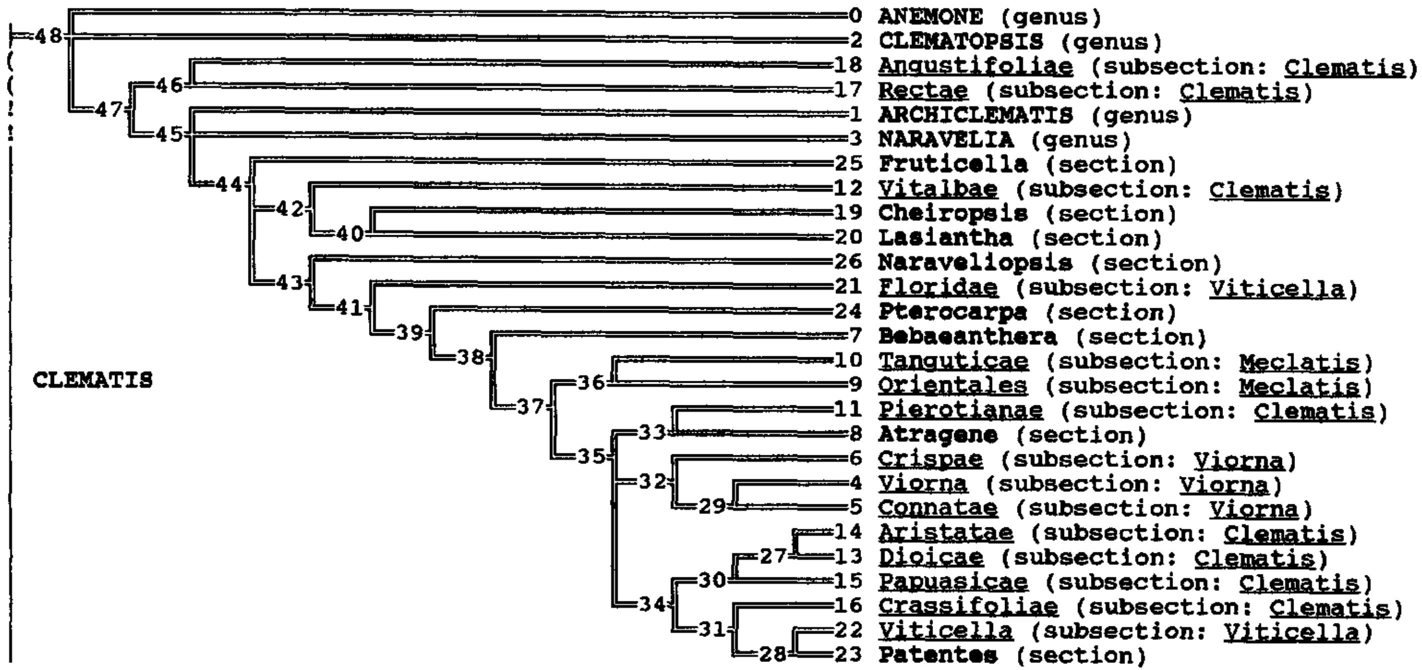


Figure 1.7. Strict consensus tree based on Tamura's classification (1968a) , using Farris' nelsen algorithm after successive weighting of characters.

From the data matrix of Tamura's classification, three cladograms are presented (figures 1.5, 1.6 and 1.7). Although the first one (characters unweighted) seems to make clear, that *Clematis* is well separated from the other genera *Anemone*, *Archiclematis*, *Clematopsis* and *Naravelia*, the second cladogram makes clear that such a conclusion is not justified by the data, at least as far as *Archiclematis* and *Naravelia* are concerned. With a tree length of 219, a consistency index of 72 and a retention index of 83, there is a lot of incongruence within the data set. Table 1.7. supports this showing the character states of hypothetical ancestors with many multiple statements at certain characters (10, 12, 15, 16, 24 and 27; 15 and 24 excluded from the cladogram by weight 0). Character 12 (gross flower morphology) in particular is a dissolving character, and similarly character 16 (tepal morphology). Looking at characters, the data set would be greatly improved by analysing the *Clematis* inflorescence structure per species (Tobe, 1979, 1980d; Troll, 1964, 1969; Weberling, 1981). Thus far, only fragmented information is present. The same holds for other flower characters, especially those concerning morphology, texture and venation of tepals, and nectar leaves. As to vegetative characters, the growth habit viz. the growth model should be analysed in more detail per species, as the relation between herbaceous, suffruticose and woody species is not solved, and neither is the presence or absence of the climbing capacity (Baillon, 1867; Bell, 1974; Decamps, 1975, 1976, 1979; Hallé et al., 1978; Jeannoda-Robinson, 1977; Sterckx, 1897; Tomlinson, 1984). However, this cladogram reveals that only *Clematopsis* may be maintained as a separate genus, and that it seems logical to include *Archiclematis* and *Naravelia* in *Clematis*. Pinnately nerved leaves and valvate/induplicate bud aestivation are then synapomorphies for *Clematis*, including *Archiclematis* and *Naravelia*. The decussate leaf position is a synapomorphy, shared by *Clematis* and *Clematopsis*, and the pinnately nerved leaf is an autapomorphy for both *Clematis* and *Clematopsis*. The decussate leaf position is therefore the only remaining character to distinguish the tribe Clematideae according to this data set, but, especially with respect to *Naravelia*, decisions whether or not to include these genera in *Clematis* have to wait until further data become available.

Bearing in mind the modest information content of the data set, some conclusions concerning classification can be drawn:

- The section *Clematis* is polyphyletic; the conclusion agrees with the one from the analysis of Prantl's classification.

- The section *Viticella* is polyphyletic; the conclusion disagrees with the results by analysing Prantl's classification provided that Prantl's classification is rather paraphyletic than polyphyletic.
- Subdividing the section *Meclatis* into the subsections *Orientales* and *Tanguticae* is dubious, as the distinguishing characters (inflorescence structure [10] and gross flower morphology [12]) cause a multiple statement in character states for their hypothetical ancestor (see further Chapter 2).
- The section *Viorna* seems to be monophyletic, but this disagrees with the analysis of Prantl's classification.
- Maintaining *Archiclematis* and *Naravelia* as separate genera is dubious; inclusion in *Clematis* seems to be more appropriate.

Although groups of convenience are also present in Tamura's classification, the number of monophyletic groups increased (figure 1.7). The section *Clematis* turned out to be polyphyletic here also and the section *Viticella* is to be regarded either as paraphyletic or as polyphyletic. The characters number of tepals, flowering on the young or old wood and the presence of staminodia have been used to determine the relative position of series within the section *Viticella*. From observations in the cultivated assortment of *Clematis* cultivars it is obvious that precisely these characters are very weak and not as decisive as Tamura supposed. Furthermore, as species delimitation within the section *Viticella* is only gradual (Brandenburg and van de Vooren, 1986, 1988a), there are strong reasons not to maintain an infrasectional, supraspecific classification within this section.

As in Tamura's classification the section *Viorna* has been restricted in its delimitation compared to Prantl's classification (*Cirrhosae* and *Atragene* are considered separate sections), *Viorna* sensu Tamura is a monophyletic group.

The only remaining polyphyletic section is section *Clematis* which indeed shows many divergent traits (perennials vs. shrubs; sex polymorphisms; various flower and fruit characters). As it is circumscribed in literature up to and including Tamura, this section has to be regarded as a 'rest group' in all classifications. The subsections of *Clematis* sect. *Clematis* in Tamura's system (1968a) consist of restricted sets of affiliated species. As such they should be considered as real entities as result of the evolutionary history of *Clematis* and therefore equally ranked: they have to be regarded as true sections. The subsections of the section *Meclatis* are clearly sister groups, as distinguished by Tamura, but looking at the species level (for more details Chapter 2) the distinguishing characters appear to be gradually changing over these subsections. Since similar reasons apply to the section *Viticella* not to maintain subsections, they will not be maintained in the section *Meclatis* either. For the time being, the subsections of *Viorna* are preliminary maintained, since they have not been subjected to detailed study in this investigation.

The resulting sectional classification of *Clematis* is:

Clematis L.

- sect. *Angustifoliae* (Prantl) Brandenburg comb. nov.
- sect. *Aristatae* (Prantl) Brandenburg comb. nov.
- sect. *Atragene* (L.) DC.
- sect. *Bebaeanthera* Edgew. (*Paratragene* Tamura)
- sect. *Cheiropsis* DC.
- sect. *Clematis* (ser. *Vitalbae* Prantl)
- sect. *Crassifoliae* (Tamura) Brandenburg comb. nov.
- sect. *Dioicae* (Prantl) Brandenburg comb. nov.
- sect. *Fruticella* (Tamura) Brandenburg comb. nov.
- sect. *Lasiantha* (Tamura) Brandenburg comb. nov.
- sect. *Meclatis* (Spach) Baill.
- sect. *Papuasicae* (H.Eichler) Brandenburg comb. nov.
- sect. *Naraveliopsis* (Hand.-Mazz.) Brandenburg comb. nov.
- sect. *Pierotianae* (Tamura) Brandenburg comb. nov.
- sect. *Pterocarpa* (Tamura) Brandenburg comb. nov.
- sect. *Rectae* (Prantl) Brandenburg comb. nov.
- sect. *Viorna* (Rchb.) Prantl
    subsect. *Viorna*
    subsect. *Connatae* Koehne
    subsect. *Crispae* (Prantl) Tamura
- sect. *Viticella* (Moench) DC.

This classification has been used for the analysis in section 1.3.2 on the biogeography of *Clematis*.

1.3.2. *Biogeography of **Clematis***

The large diversity within *Clematis* has been interpreted variously: The number of species to be accepted is largely dependent on the interpretation of distribution patterns within the genus.

According to current views on the evolution of flowering plants, Ranunculean plants are considered by a.o. Stebbins (1950, 1974) and Takhtajan (1969, 1980, 1991) to constitute the more primitive plant groups among the Angiospermae. Their distribution is cosmopolitan except for polar regions; they occur in all climatic regions, although most abundantly in the temperate zone of the Northern Hemisphere; they occur both in montane regions and plains, in woodlands and open vegetation. In some characters, such as wood anatomy, leaf venation and flower structure, they express character state combinations, that reflect their origin at the divergence between Monocotyledons and Dicotyledons (Dahlgren and Bremer, 1985). They also show a large differentation of flower types, although the basic phenomenon of hemicycly is typical throughout the family (Brouland, 1935; Eyde, 1975; Leppik, 1964; Meicenheimer, 1978; Tobe, 1976a, 1976b, 1980a, 1980b, 1980c, 1980d). There is some palaeobotanical evidence for the above. Krassilov et al. (1983) found in Siberia in Albian deposits fossil remains of bisexual flowers which reflect the general flower structure of Ranunculaceae or Paeoniaceae (flattened receptacle, with 3-5 follicles and remains of both perianth and androecium (Batten, 1984).

Clematis shows many primitive features in comparison to other genera of the family: the basic type of flower structure (without specialized nectar leaves; Prantl, 1888), the basic type of metacentric and submetacentric chromosomes (Gregory, 1941). It also shows some advanced characters, expressed in the majority of its species: decussate leaf position (Haccius, 1942) and the woody performance of stems and branches of the majority of its representatives, this state is considered to be derived by comparison with the stem anatomy of related herbaceous plants (Smith, 1928; Sterckx, 1897; Tepfer, 1960).

Due to its relatively long evolutionary history, *Clematis* shows particular distribution patterns as to sections, which have to be understood in terms of the origin and movement of continents, and in terms of dispersal mechanisms. Geographic distribution of representatives of the sections *Atragene*, *Meclatis*, *Viorna* and *Viticella* are presented in figure 1.8.

The section *Atragene* is largely confined to the montane regions of Northern and Central Europe, Northern and Central Asia and North America. Species of the section occurs in many disjunct areas. Representatives from North America resemble the European ones to such an extent that uniting them pairwise into one species has to be considered, the distinguishing characters not being constant in expression. This is in line with the movements of continents in the past (Eurasia and North America having once been fused), as can be seen in figure 1.9.

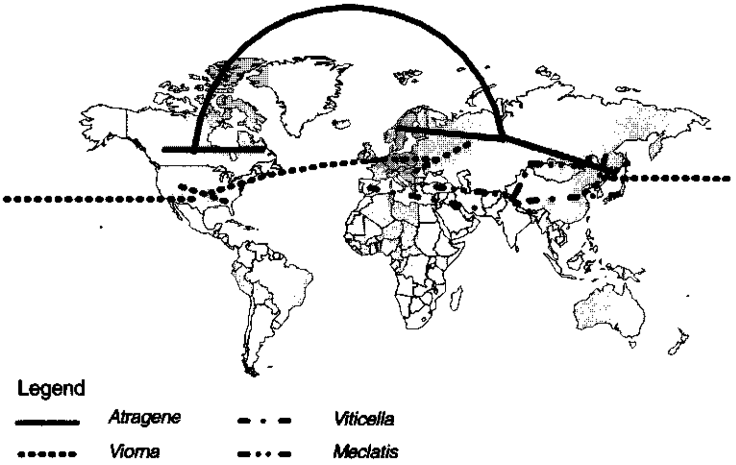


Figure 1.8. Geographic distribution trends in *Clematis* classication for 4 sections. Further explanation in text.

The section *Meclatis* is dispersed from Turkey to Korea along mountain chains and in the montane region of the Himalayas and Tibet (for details see figure 2.1). Representatives of this section are present in some adjacent areas (Himalaya, Kashmir, Tibet), but also in disjunct areas (Korea). This fact and their mutual genetical affinity combined with differences between populations, that are only minor, make plausible that there is a restricted number of variable species and not 10 or more (cf. 1.4 and Chapter 2).

The section *Viorna* is largely confined to the USA and Mexico apart from only a few taxa in Europe and the Far East. The occurrence of representatives of this section in the eastern and western extremes of Eurasia must have formed one area with the *Viorna* distribution in North America, because the Eurasian counterparts have their parallel species in North America (e.g. *C. integrifolia* L. vs. *C. ochroleuca* Aiton; *C. fusca* Turcz. vs. *C. pitcheri* Torr. & A.Gray a.o.).

The section *Viticella* has its representatives in two separate areas:

- Mediterranean area (*C. viticella* L. subsp. *viticella*), inclusive of the Portuguese Atlantic region (*C. viticella* subsp. *campaniflora* (Brot. Font Quer ex O. Bolòs and Vigo);
- Eastern China / Japan (*C. florida* Murray ex Thunb.; *C. patens* C.Morren and Decne.).

Although interspecific hybridization between these species has given rise to many large-flowered cultivars, it does not seem to occur spontaneously and is hampered by various isolating mechanisms (see 1.4.). In both regions species of this section have overlapping areas, but because of differing flowering times and a differential ecological preference they appear to be well isolated. This section is restricted to Eurasia and has no counterpart in North America, or we should find such a counterpart among representatives of the section *Viorna*.

It is worthwhile looking at the distribution of the various subdivisions of the genus over continents or parts of continents. The results of this are presented in table 1.9, and figures 1.10, 1.11 and 1.12. For this survey the classification of Tamura (1968a) was modified: the section *Patentes*, and the subsections *Floridae* and *Viticella* were combined into section *Viticella*, and the subsections *Orientales* and *Tanguticae* were combined into the section *Meclatis*. The rationale of these decisions has been discussed in 1.3.1.

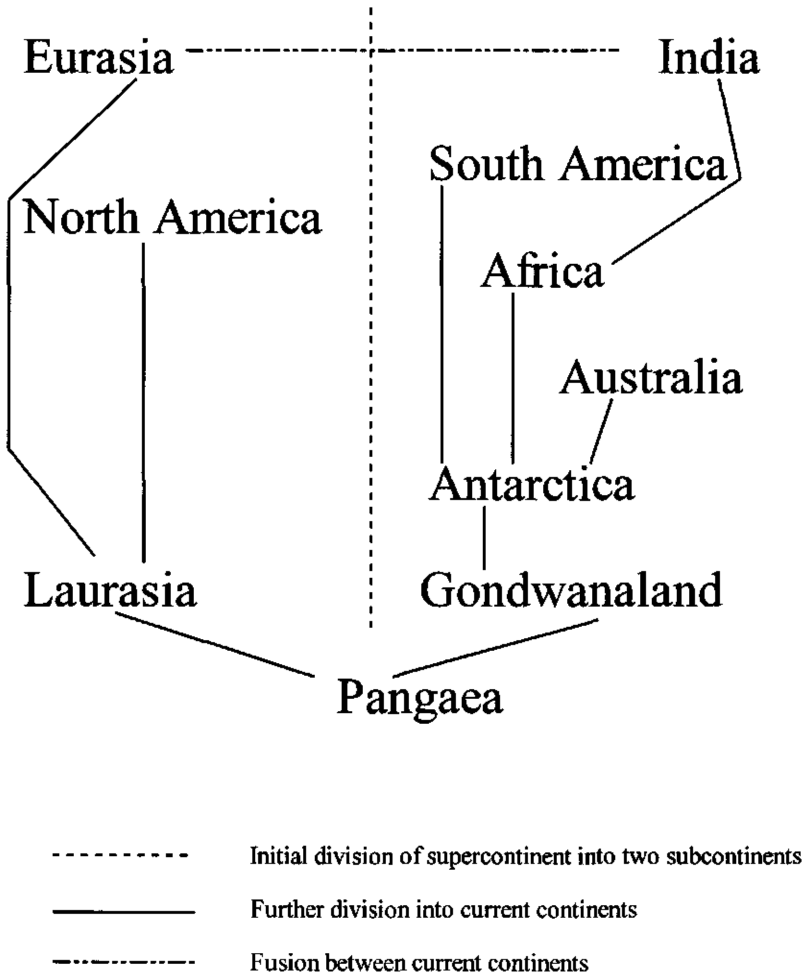


Figure 1.9. Schematical presentation of continental shifts in the past.

Table 1.8. Presence or absence of *Clematis* sections and subsections as recognized here.

Area number▸ ▾Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**TOTAL**	**15**	**16**	**17**	**subdivisions acronyms**
Viorna	1	1	1	0	0	1	0	1	1	0	0	0	1	0	**7**	1	0	0	**vio**
Connatae	0	1	1	1	1	1	0	0	0	0	0	0	0	0	**5**	1	0	0	**con**
Crispae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**	1	0	0	**cri**
Bebaeanthera	0	1	1	1	1	1	0	0	0	0	0	0	0	0	**5**	1	0	0	**beb**
Atragene	1	0	1	0	0	1	0	1	0	0	0	0	1	0	**5**	1	0	0	**atr**
Meclatis	1	1	1	1	0	1	0	1	0	0	0	0	0	0	**6**	1	0	0	**ori**
Pierotanae	0	0	0	0	1	1	0	0	0	1	1	0	0	0	**4**	1	1	0	**pie**
Vitalbae	1	1	1	1	1	1	1	1	0	0	0	0	1	0	**9**	1	1	0	**vit**
Dioicae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	**2**	1	1	0	**dio**
Aristatae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**	0	1	0	**ari**
Papuasicae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**	0	1	0	**pap**
Crassifoliae	0	0	0	0	0	1	0	0	0	1	1	1	0	0	**4**	1	1	0	**cra**
Rectae	1	1	1	1	0	1	1	1	1	0	0	0	0	0	**8**	1	1	0	**rec**
Angustifoliae	1	0	1	0	0	0	0	1	0	0	0	0	0	0	**3**	1	0	0	**ang**
Cheiropsis	1	1	1	1	0	1	1	0	0	0	0	0	0	0	**6**	1	1	0	**che**
Lasiantha	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**	1	0	0	**las**
Viticella	1	1	0	0	0	1	0	0	1	0	0	0	0	0	**4**	1	0	0	**vii**
Pterocarpa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**	1	0	0	**pte**
Fruticella	0	0	0	1	0	1	0	1	0	0	0	0	0	0	**3**	1	0	0	**fru**
Naraveliopsis	0	0	0	0	0	1	0	0	0	1	1	0	0	0	**3**	1	0	0	**nar**
Archiclematis	0	0	0	1	0	1	0	0	0	0	1	0	0	0	**3**	1	0	0	**arc**
Clematopsis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**	0	1	0	**cle**
Naravelia	0	0	0	0	0	0	0	0	0	1	1	0	0	0	**2**	1	0	0	**naa**
TOTAL	**8**	**8**	**9**	**8**	**4**	**15**	**4**	**7**	**3**	**4**	**6**	**2**	**6**	**1**		**20**	**9**	**0**	
Area acronyms	**eur**	**me**	**ca**	**him**	**ind**	**chi**	**afr**	**sib**	**jap**	**ich**	**ina**	**anz**	**nca**	**sa**		**la**	**go**	**pg**	

Legend:

pg	Pangaea	**ind**	India	**anz**	Australia/New Zealand
la	Laurasia	**chi**	China	**nca**	North and Central America
go	Gondwanaland	**afr**	Africa	**sa**	South America
eur	Europe (incl. Eur. Russia)	**sib**	Siberia/Mongolia/Manchuria		
me	Mediterranean area / Middle East	**jap**	Japan		
ca	Central Asia	**ich**	Indochina		
him	Himalayan area/Kashmir/Tibet	**ina**	Indonesian archipelago		

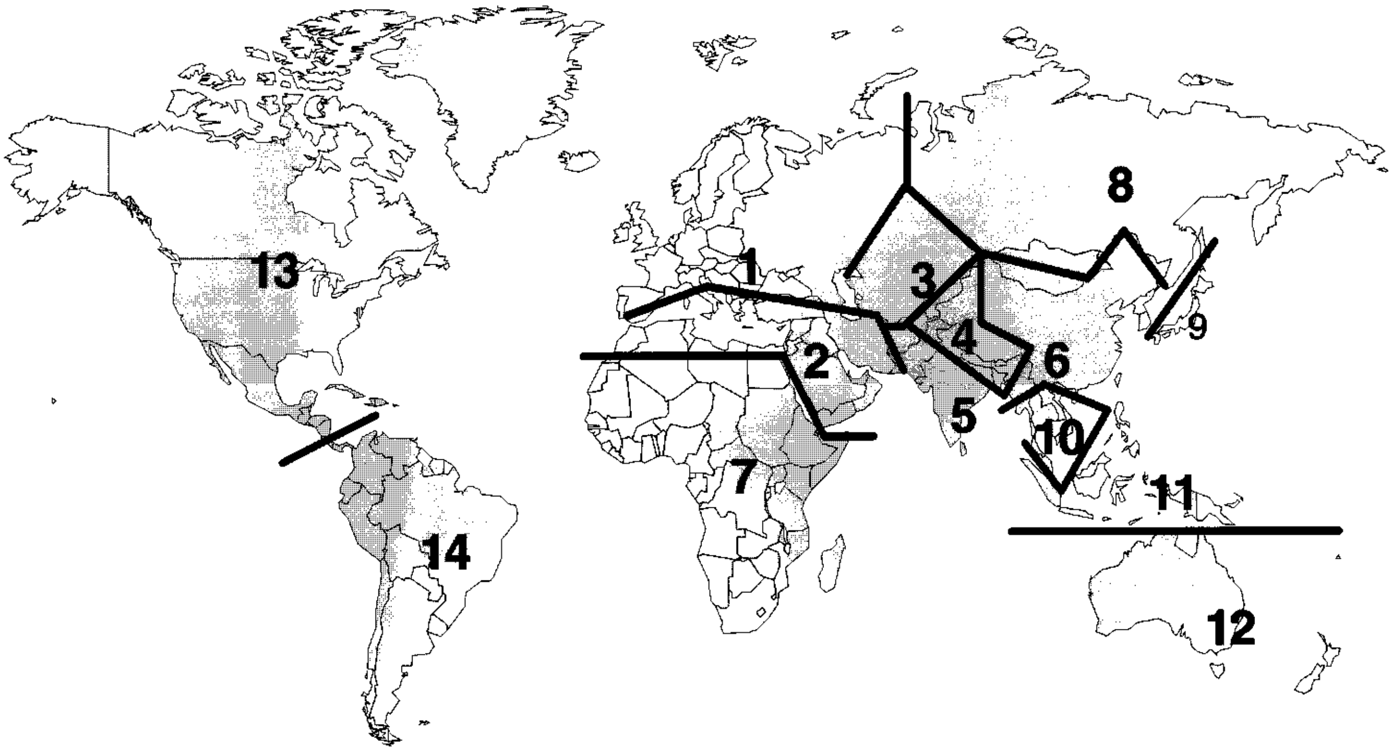


Figure 1.10. Global regions as recognized here. For explanation of numbers, see table 1.8.

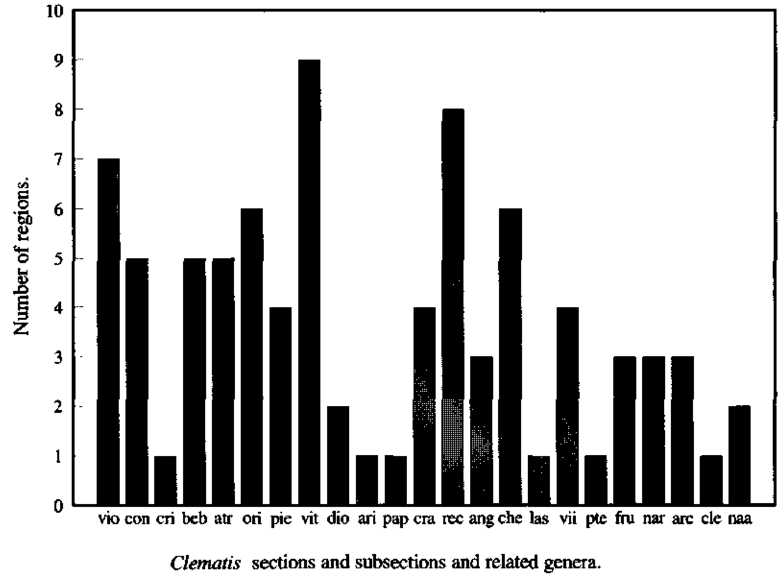


Figure 1.11. Distribution of taxa over regions.
For explanation of taxon acronyms, see table 1.8.

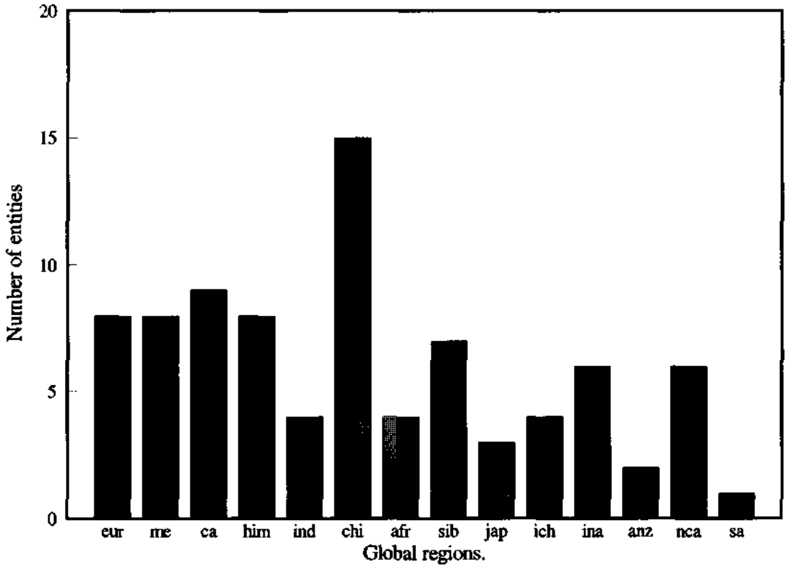


Figure 1.12. Distribution of taxa over regions 2.
For acronyms of regions, see table 1.8.

Abundance in variation is indicative for the origin of taxa; two attitudes conflicting in part have been summarized by Wiley (1981):

- The region in which the most abundant variation is present is the likely centre of origin of the taxon concerned; the most primitive representatives are to be found in other marginal areas (Croizat, 1962, 1964; Croizat et al, 1974; Nelson & Platnick, 1981);
- The region in which the most abundant variation is present is the centre of origin and primitive forms of the taxon concerned have been maintained there, whereas more derived forms have dispersed to other areas; this is the essence of what is formulated by Hennig (1966) as the progression rule (Cracraft, 1975).

To see whether current distribution of *Clematis* divulges more information on origins, the distribution data of table 1.8 were subjected to further analysis using Hennig86. The analysis was performed twice: one with the taxa and their distribution over global regions; one with global regions and the abundance of occurring taxa. The first approach facilitates the comparison with cladograms of section 1.3.1., especially those of figure 1.5, 1.6 and 1.7. There are four equally parsimonious trees after successive weighting with *Archiclematis* or with *Clematopsis* as outgroups, respectively. In both cases the strict consensus trees showing the question marks of the results by multifurcate forks are presented in figure 1.13. The outgroups were chosen as inspired by Tamura (1970), who postulated *Archiclematis alternata* as ancestor for *Clematis* and as gleaned from Hutchinson (1920), who considered *Clematopsis* a primitive genus of the tribe Clematideae because it shares characters with both *Anemone* (bud aestivation) and *Clematis* (leaf position). Consequently, the analysis of distribution data per global region has been carried out with Laurasia and Gondwanaland as outgroups respectively; moreover there is one added with Pangaea as outgroup with a postulated zero distribution. Pangaea with a postulated one distribution has also been tested. According to Nelson and Platnick (1981), the one distribution starts from the assumption that *Clematis* is already present in its ancestral, undifferentiated form. Being undifferentiated and all current subdivisions of the genus are derived from the ancestral form, it has been scored one over all current subdivisions of the genus as to be present. The zero distribution does not consider derivation from the ancestral form and states the current subdivisions of *Clematis* as being absent in Pangaea. The one distribution results in a less parsimonious cladogram after successive weighting and is not presented.

After successive weighting, in all three cases a single most parsimonious cladogram resulted from the analysis.

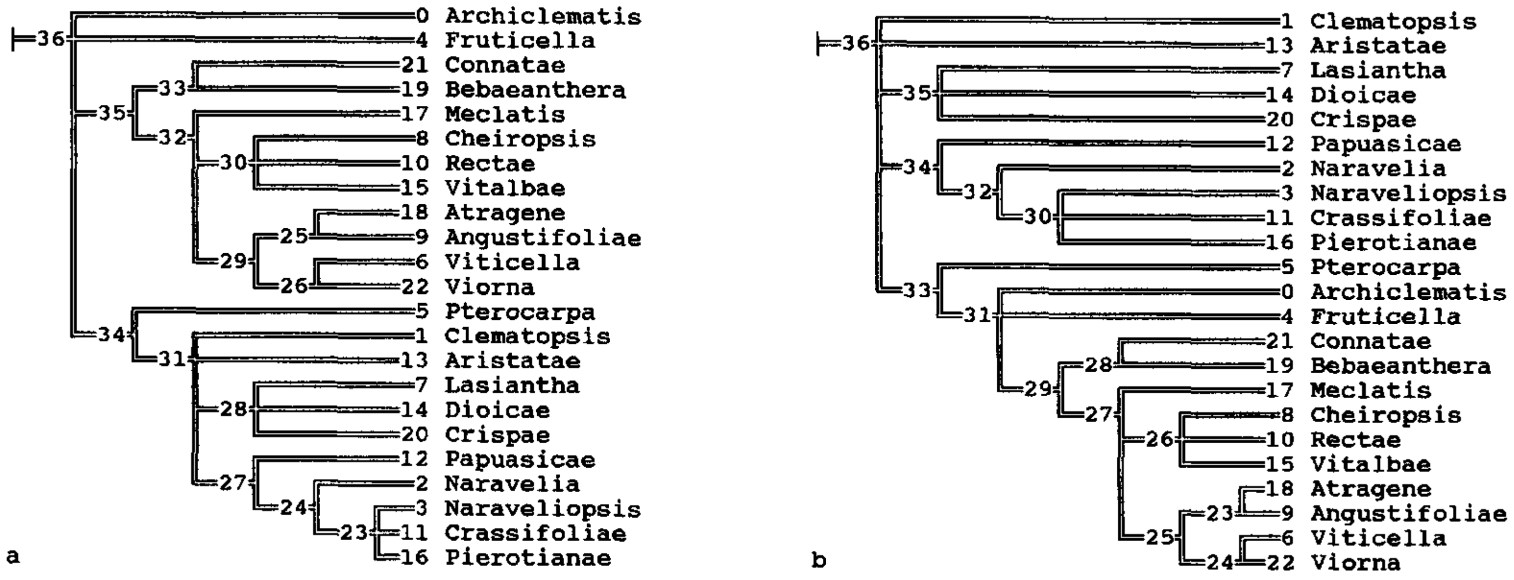


Figure 1.13. Strict consensus trees of 4 trees (89 steps), using the distribution data of taxonomic units of table 1.8. after successive weighting with Farris' consistency algorithm and nelsen algorithm respectively.

a. with *Archiclematis* as outgroup.

b. with *Clematopsis* as outgroup.

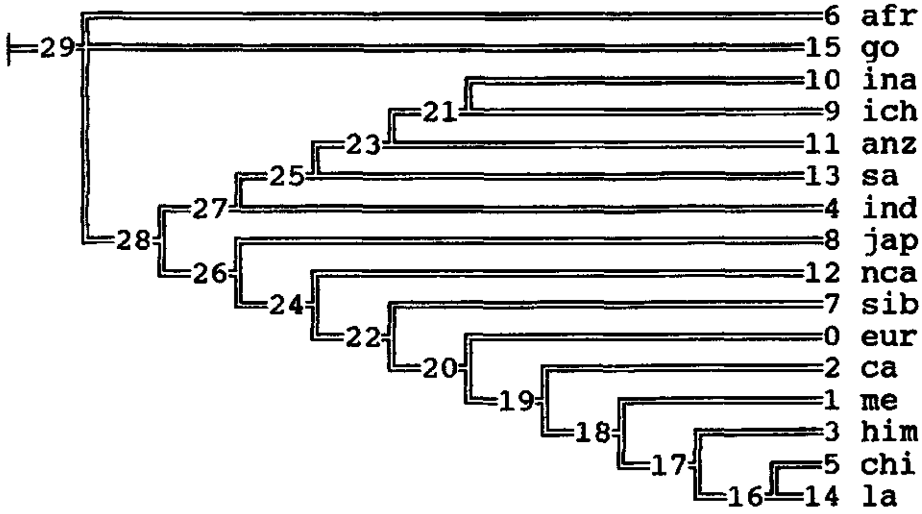


Figure 1.14. Area cladogram of areas and taxa listed in table 1.10. after successive weighting with Gondwanaland as outgroup; weights and states of distributional nodes listed in table 1.9.

Table 1.9. Character states of distribution nodes as indicated in the cladogram of figure 1.14 (successive weighting).

Taxa▸ ▾ Distribution	vio	con	cri	beb	atr	ori	pie	vit	dio	ari	pap	cra	rec	ang	che	las	vii	pte	fru	nar	arc	cle	naa
16	1	1	0	1	1	1	1	1	0	0	0	1	1	0	1	0	1	1	1	1	1	0	0
17	1	1	0	1	01	1	0	1	0	0	0	0	1	0	1	0	01	0	1	0	1	0	0
18	1	1	0	1	01	1	0	1	0	0	0	0	1	0	1	0	01	0	0	0	0	0	0
19	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0
20	1	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1
22	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
24	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0

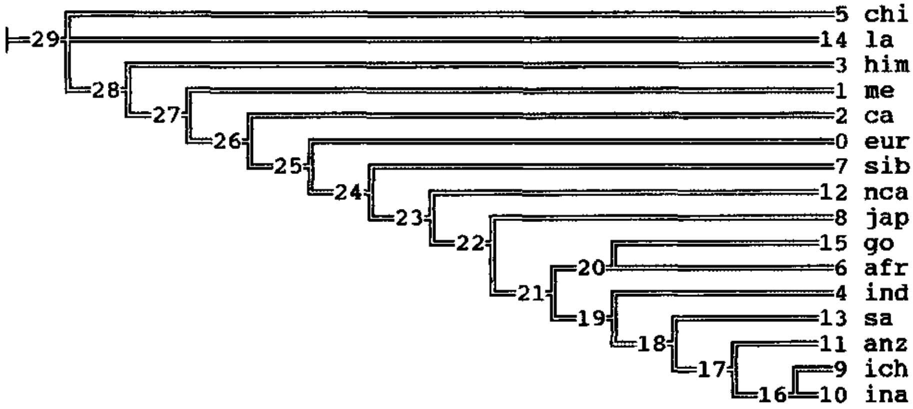


Figure 1.15. Area cladogram of areas and taxa listed in table 1.8. after successive weighting with Laurasia as outgroup; weights and states of distributional nodes listed in table 1.10.

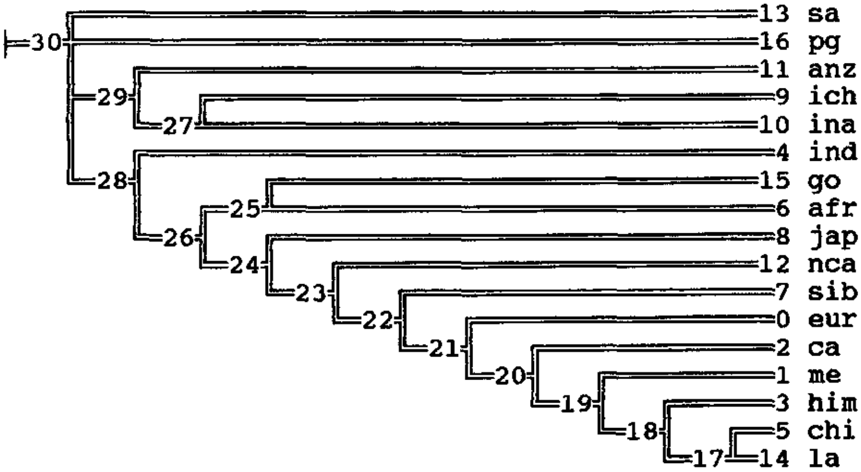


Figure 1.16. Area cladogram of areas and taxa listed in table. 1.8. after successive weighting with Pangaea as outgroup; weights and states of distributional nodes listed in table 1.11.

Table 1.10. Character states of distribution nodes as indicated in the cladogram of figure 1.15 (successive weighting).

Taxa▸ ▾Distribution	vio	con	cri	beb	atr	orf	pie	vit	dio	ari	pap	cra	rec	ang	che	las	vii	pte	fru	nar	arc	cle	naa
16	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1
17	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
21	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
22	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
23	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
24	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
25	1	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0
26	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0
27	1	1	0	1	01	1	0	1	0	0	0	0	1	0	1	0	01	0	0	0	0	0	0
28	1	1	0	1	01	1	0	1	0	0	0	0	1	0	1	0	01	0	1	0	1	0	0
29	1	1	0	1	1	1	1	1	0	0	0	1	1	0	1	0	1	1	1	1	1	0	0

Legend: la = outgroup. Weighting codes for entities (ent. - weight): 1 - 4; 2 - 4; 3 - 0; 4 - 4; 5 - 2; 6 - 10; 7 - 1; 8 - 3; 9 - 0; 10 - 0; 11 - 0; 12 - 2; 13 - 4; 14 - 1; 15 - 4; 16 - 0; 17 - 0; 18 - 10; 19 - 3; 20 - 3; 21 - 3; 22 - 10; 23 - 2.
For abbreviations of entities, see table 1.8.

Table 1.11. Character states of distribution nodes as indicated in the cladogram of figure 1.16 (successive weighting).

Taxa▸ ▾ Distribution	vio	con	cri	beb	atr	ori	pie	vit	dio	ari	pap	cra	rec	ang	che	las	vii	pte	fru	nar	arc	cle	naa
17	1	1	0	1	1	1	1	1	0	0	0	1	1	0	1	0	1	1	1	1	1	0	0
18	1	1	0	1	01	1	0	1	0	0	0	0	1	0	1	0	01	0	1	0	1	0	0
19	1	1	0	1	01	1	0	1	0	0	0	0	1	0	1	0	01	0	0	0	0	0	0
20	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0
21	1	0	0	0	1	1	0	1	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0
22	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
23	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
24	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
26	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1
28	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Legend: pg = outgroup. Weighting codes for entities (ent. - weight): 1 - 4; 2 - 4; 3 - 0; 4 - 4; 5 - 2; 6 - 10; 7 - 1; 8 - 3; 9 - 0; 10 - 0; 11 - 0; 12 - 2; 13 - 4; 14 - 1; 15 - 4; 16 - 0; 17 - 0; 18 - 10; 19 - 3; 20 - 3; 21 - 3; 22 - 10; 23 - 2.
For abbreviations of entities, see table 1.8.

When comparing both strict consensus trees of figure 1.13, it appears that they mutually agree. The best presentation is therefore dependent on further details. From figure 1.11, it appears that some sections are widespread, whereas others are endemic and confined to a restricted area. The region of most abundant variation is no doubt China, but this variation does not include many endemics, while both primitive and advanced parts of the genus (and related genera) are represented here (Tamura, 1970). On the other hand, many endemic subdivisions, sharing remarkable characters, such as dioecy, occur in Africa, South America, Indochina and Australia. With *Clematopsis* distributed in Africa and the viewpoint of Prantl (1888) that *Clematis* is supposed to have originated in the palaeotropics, this is in favour of a development from an origin in Gondwanaland. The area cladogram of figure 1.14 is in agreement with this hypothesis, as is but to a lesser extent that of figure 1.16, whereas the area cladogram of figure 1.15. is not fully in agreement with the hypothesis of Tamura (1970), *Archiclematis* being the ancestor of *Clematis* with its distribution in China and Indochina.

As the analysis has been carried out at the level of subdivisions of *Clematis* with consideration of related genera, but without consideration of the number of species involved per subdivision, no firm conclusion can be drawn, except that combination of continental movements (see figure 1.9.; Krutzsch, 1989) and current distribution patterns of *Clematis* subdivisions and related genera points in the direction of a Gondwanaland origin. This agrees with *Clematopsis* as progenitor, its African distribution and the proportion of endemic entities still in Gondwanic continents. The Malaysian connection is still a link to the other hypothesis. On the other hand when the idea of centres of origin is not adhered to, it is possible to indicate areas of endemism: Africa, Australia, and China and North America, which is more or less in agreement with the palaeobotanic findings of Krassilov et al. (1983).

Further analysis based on both species descriptions and distribution data is needed to reach a conclusion and to test the two hypotheses summarized by Wiley (1981). China is the area of most abundant variation looking at the number of present subdivisions of *Clematis*. Following Croizat (1962, 1964), Croizat et al. (1974) and Nelson & Platnick (1981), this still does not exclude *Clematopsis* from being the postulated ancestor of *Clematis*. In case one adheres to the progression rule (Crisci & Stuessy, 1980; Hennig, 1966; Cracraft, 1975), China should be the centre of origin, while there is a problem in finding a most primitive form, as *Archiclematis* occurs outside this area.

1.4. **Interspecific crosses in *Clematis***

From horticultural literature it is generally known that most of the current *Clematis* assortment originated from many interspecific crosses of which the most important ones had already been made in the 19th century (Moore & Jackman, 1872). Since these crosses were carried out by chance, hardly any insight was gained in the genetic breeding potential of *Clematis* species. The hybridization experiments, reported here, were carried out to reveal potential interspecific relationships and to evaluate hybridization data in the light of systematic research.

1.4.1. *Introduction to the experiment*

To characterize relationships between *Clematis* species, a diallel hybridization scheme was carried out. Species were selected either by their availability in the Wageningen *Clematis* collection or by their importance for *Clematis* cultivation. Seed set and, in some cases, pollen tube growth were scored. In a restricted number of crosses also the progeny populations were observed. The complex germination behaviour of most *Clematis* species precluded further extension of these experiments. The germination behaviour as present in most *Clematis* species has been described in literature (Barton, 1967; Blair, 1959; Kinzel, 1913; Niethammer, 1928). A double seed dormancy mechanism, with temperature and light as suggested important factors, prevents seed germination for a period of one or two years:

- the morphologically mature seed contains an immature embryo and is surrounded by an impermeable fruit wall;
- after the first winter season, the fruit wall has been weathered to such an extent that it becomes permeable and the embryo starts to develop in the following season, but is not capable to germinate;
- after a second winter, seeds germinate, but sometimes two such cycles are required.

1.4.2. *Material and methods*

By designing the diallel interspecific hybridization experiment, Rehder's (1974) classification was taken as a starting-point. This reference is a good representation of the horticultural taxonomic treatment of taxa important as ornamental and mainly follows the classification of

Prantl (1888):

Section	Series	Species used
Viorna Rchb.		
	Crispae Prantl	*C. integrifolia* L.
	Tubulosae Decne.	*C. heracleifolia* DC.
	Connatae Koehne	
	Cirrhosae Prantl	*C. cirrhosa* L.
Atragene (L.) DC.		*C. alpina* (L.) Mill.
		C. macropetala Ledeb.
Viticella (Moench) DC.		*C. campaniflora* Brot.
		C. viticella L.
		C. patens C.Morren et Decne.
Flammula DC.	Montanae C.K.Schneid.	*C. montana* Buch.-Ham. ex DC.
	Rectae Prantl	*C. recta* L.
	Vitalbae Prantl	*C. vitalba* L.
	Orientales Prantl	*C. orientalis* L.
		C. glauca Willd.
		C. serratifolia Rehder
		C. tangutica (Maxim.) Korsh.

We used populations from natural provenances or S_1-populations, except for *C. macropetala* and *C. patens*. During the experiment, populations from natural provenances of *C. macropetala* have not been available to us, and of *C. patens* we had an often reproduced, but originally natural population at our disposal.

Crosses were made during the period 1978 - 1983 in the greenhouse to avoid contamination by adverse weather conditions and to prevent uncontrolled cross-pollination. From 1 September to 1 May there was additional lighting with incandescent light to ensure an effective daylength of 14 hrs. Under these conditions plants continued to grow and flowered during the period March / April, enabling crosses between early winter- and spring-flowering species and summer-flowering species. In order to verify pollen quality under these conditions, pollen samples were checked for vitality by in vitro germinating in van Tieghem cells, in a hanging drop of 12.5% saccharose, 10% Brewbaker medium and 0.2% agar solution. Pollen samples with a germination percentage less than 50% were excluded from the hybridization programme. Pollen samples maintained more than 50% germination percentage by storage at 5 °C in a vacuum exsiccator for up to 105 days, which appeared to be sufficient to overcome various gaps in flowering period. Crosses in the period from 1981 - 1983 were made for this diallel hybridization scheme; from 1978 until 1981 only incidental crosses were made to optimise the technique of artificial hybridization in *Clematis*, and to verify certain hybridizations made or supposed by *Clematis* nurseries in the past and not dealt with here further.

Flowers were emasculated at the mature bud stage, just before the tepals stretch and spread out, or in the case of tubular or urceolate flowers, when the corolla opens at the apex. The stage for removal of the anthers appeared to be crucial, as early removal damages the stigmas and renders them non-functional. When the tepals are already spreading, the outer stamens already dehisce their pollen. During the spreading tepal stage emasculation is convenient, but use of the flowers is not advisable for crossing despite protandry. Self-compatibility to various degrees and the hemicyclic nature makes selfing likely at that stage. Pollination followed immediately throughout the day.

In profusely flowering accessions, crosses were carried out on several flowers of the same plant. Seed set was averaged per flower. Some flowers were used to analyse the pollen tube growth. In selected cases, seeds were sown to test viability and to observe progenies.

Pollen tube growth was observed by epifluorescence microscopy. The preparations were made according to the method by Kho and Baër (1968) with some modifications:

- Collect flowers 3-7 days after pollination, depending on weather conditions (up to 10 days after pollination good slides can be prepared).
- Removal of pistils from the receptacle; pistils were soaked in a Herr solution to clear tissues. In case of *Clematis* pistils pellucidity is absolutely necessary because of the pubescence of styles and ovaries. Composition of the Herr (1971) solution:

- lactic acid 85%	2 parts
- chloric hydrate	2 parts
- phenole	2 parts
- xylol	1 part
- clove oil	2 parts

- Rinse 2× in ethanol or xylol and 1× in demineralized water.

- Macerate pistils in 1N NaOH at 60°C during 1½-3hrs at 60°C.
- Rinse with demineralized water, transfer to anilin-blue stain solution and incubate during 20-24 hrs. Composition of the stain solution:
    - 7 g $K_3PO_4.3H_2O$
    - 1 g Anilin-blue (Merck, Anilinblau W.S. C.1, nr. 42755)
    - 1 l demineralized water
- Squash pistils slightly in glycerol and mount slides with Canada-balsam; store slides dark and cool.

Observations were made with a Zeiss epifluorescence microscope with the excitation / barrier filter combination 02. Photographs were made with a M63 Camera system. Pollen tube growth is shown by yellow fluorescence of callose along pollen tubes.

The number of seeds obtained after hybridization was counted. Of each interspecific combination a selection of crosses was then put to germinate. As seed dormancy in *Clematis* may last two years, the seeds were sown in seed trays. If there was no germination at once, these trays were left alone for half a year in a cool (5-10°C) and dark place, then the trays were placed at room temperature 20°C for two months. When there was still no germination some of the seeds were taken out to examine whether there was an embryo and if so to determine the developmental stage of the embryo. If the checks were positive, the trays with the remaining seeds were left cool again for half a year. After the second period, the seeds should germinate, which some did to varying degrees. F_1's were observed to judge their performance.

1.4.3. *Results and discussion*

This section deals with the results of the hybridization experiments in three paragraphs. The first paragraph is dealing with seed set and eventual offspring of the hybridization experiments; the second paragraph with the pollen-pistil relationships in the interspecific hybridizations; and the third paragraph consists of a discussion of both earlier sections.

1.4.3.1. Seed set and offspring of diallel and other crosses

Within the framework of the diallel hybridization scheme, interspecific crosses were examined for seed set characteristics, results are shown in table 1.12 and figures 1.17, 1.18 and 1.19.

Table 1.12. Seed set and number of pollinations in diallel interspecific crosses 1981 - 1983.

♂ ▸ ▾ ♀	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. *C. tangutica*	418 / 4	264 / 5	79 / 5	8 / 2	104 / 1	0 / 6	0 / 4	20 / 5	41 / 1	101 / 4	1 / 3	5 / 6	185 / 4	0 / 3	195 / 3
2. *C. orientalis*	18 / 6	170 /12	256 / 8	108 / 3	4 / 4	0 / 2	4 / 4	0 / 2	40 / 3	0 / 4	0 / 2	0 / 3	0 / 2	44 / 2	0 / 2
3. *C. vernayi*	151 / 8	274 / 2	568 /15	12 / 5	0 / 3	0 / 4	0 / 4	0 / 3	0 / 3	0 / 4	0 / 6	0 / 5	0 / 4	0 / 3	0 / 4
4. *C. serratifolia*	0 / 3	497 / 5	1 / 2	514 / 2	4 / 4	6 / 3	36 / 4	2 / 1	1 / 3	1 / 2	3 / 2	20 / 2	30 / 2	16 / 4	5 / 2
5. *C. vitalba*	4 / 2	0 / 1	13 / 2	0 / 1	0 / 1	0 / 1	68 / 2	0 / 1	3 / 2	8 / 4	0 / 3	0 / 1	0 / 1	0 / 1	0 / 1
6. *C. montana*	0 / 2	0 / 1	0 / 1	- / -	0 / 1	208 /16	2 / 4	0 / 2	8 / 3	1 /15	1 / 5	1 / 5	0 / 2	4 / 2	0 / 5
7. *C. recta*	0 / 3	0 / 1	0 / 5	- / -	0 / 1	0 / 4	26 / 6	0 / 1	0 / 2	0 / 2	0 / 2	1 / 1	9 / 2	40 / 5	0 / 3
8. *C. campaniflora*	2 / 3	1 / 1	5 / 5	- / -	0 / 2	2 / 2	5 / 3	13 / 4	14 / 5	19 / 4	20 / 4	0 / 2	0 / 2	0 / 3	2 / 2
9. *C. viticella*	0 / 2	0 / 2	0 / 4	0 / 4	1 / 2	0 / 3	0 / 5	45 / 7	15 / 8	15 / 5	2 / 1	1 / 4	0 / 3	7 / 5	0 / 4
10. *C. patens*	0 / 1	0 / 1	0 / 2	- / -	0 / 1	6 /13	51 / 3	0 / 1	23 / 3	252 /17	0 / 4	17 / 2	- / -	43 / 1	8 / 5
11. *C. alpina*	0 / 2	0 / 2	0 / 3	0 / 1	0 / 2	0 / 2	0 / 4	0 / 2	2 / 3	0 / 8	0 / 2	0 / 4	0 / 1	0 / 2	0 / 2
12. *C. pitcheri*	0 / 3	0 / 2	0 / 2	0 / 6	0 / 1	0 / 3	5 / 2	0 / 1	43 / 3	6 / 5	1 / 2	50 / 2	1 / 1	24 / 2	1 / 2
13. *C. heracleifolia*	6 / 1	13 / 1	71 / 2	42 / 1	- / -	3 / 1	0 / 1	- / -	2 / 1	0 / 1	0 / 1	- / -	- / -	7 / 1	11 / 2
14. *C. integrifolia*	0 / 2	11 / 3	0 / 2	57 / 4	29 / 3	0 / 3	22 / 5	0 / 3	7 / 2	0 / 4	0 / 3	28 / 5	22 / 6	21 / 5	0 / 3
15. *C. cirrhosa*	0 / 3	3 / 3	1 / 3	0 / 1	0 / 1	0 / 3	0 / 3	0 / 1	0 / 2	116 / 6	0 / 3	0 / 2	0 / 2	16 / 2	3 / 5

From table 1.12 a survey of seed set by pollination per species was calculated (figure 1.17), and seed set on mother plants (figure 1.18), and corrected for the number of crosses per combination in figure 1.20 and table 1.13.

Table 1.13. Interspecific crosses of *Clematis* species. Female and male contribution per species in seeds/cross.

Column number ▸ ▾ ***Clematis* species**	**1**	**2**	**3**	**4**
1. *C. tangutica*	25.4	19.3	13.6	4.5
2. *C. orientalis*	10.9	10.1	26.2	30.4
3. *C. vernayi*	12.9	6.9	16.3	9.3
4. *C. serratifolia*	27.7	16.0	24.7	8.1
5. *C. vitalba*	4.0	4.2	5.3	5.5
6. *C. montana*	3.5	0.4	3.4	0.4
7. *C. recta*	2.0	1.6	4.1	4.0
8. *C. campaniflora*	2.0	1.8	2.4	2.2
9. *C. viticella*	1.5	1.4	4.5	5.1
10. *C. patens*	7.4	4.0	6.1	3.9
11. *C. alpina*	0.1	0.1	0.7	0.7
12. *C. pitcheri*	3.5	2.3	2.8	1.7
13. *C. heracleifolia*	13.3	11.9	8.3	7.7
14. *C. integrifolia*	3.7	3.7	5.4	5.6
15. *C. cirrhosa*	3.5	4.0	5.0	5.6

Legend of column numbers:

1	Female contribution within and between species
2	Female contribution between species
3	Male contribution within and between species
4	Male contribution between species

The first two columns per species are to be compared with figure 1.17; the last two with those in figure 1.18. The relatively large number of seeds per cross for *C. tangutica*, *C. orientalis*, *C. vernayi* and *C. serratifolia* implies more genetic affinity between these species than between one of them and any of the others of the diallel. On the other hand the nearly zero success in crosses with *C. alpina* does not imply that this species is completely isolated, as for both the female and male contribution there is no difference between "within and between" and "between" species. One may expect that "within and between" at least equals "between" species for both the female and male contribution. This effect was general except for in *C. orientalis*. This species had a better male performance for "between" than for "within and between" species. This may be an indication for an incompatibility mechanism in this species, so in 1986 extra pollinations were carried out. On the other hand, *C. montana* has already shown to have a self-incompatibility mechanism (Brandenburg, 1984a), but apparently also a relatively poor capacity for cross-fertilization in comparison with other species involved.

A relative contribution female/male per species was calculated to judge the barrier vs. penetration capacity of each species (figure 1.19; Hogenboom, 1973). In a balanced situation (i.e. barrier capacity = penetration capacity) the quotient equals 1. The quotient of *C. tangutica* is remarkably high and attracted further investigation. It is caused by relatively large amounts of seeds produced from crosses with *C. vitalba*, *C. patens*, *C. heracleifolia* and *C. cirrhosa* as pollen parent. A sample of the obtained F_1-seeds were grown and seedlings appeared to be exact copies of the initial mother parent, whereas the F_2-progenies behaved like a S_1 of the motherplant (this S_1 was sown alongside the F_2 of the interspecific cross), thus indicating that no hybridization had taken place. These results, except for *C. vitalba*, were checked and confirmed by epifluorescence of pollen tubes on *C. tangutica* stigmas. This phenomenon, adventive embryony, is not observed in other interspecific combinations. Interspecific combinations with *C. heracleifolia*, *C. integrifolia* and *C. cirrhosa* as mother led to seed set, but seeds were non-viable. Seeds, taken from seed populations that did not germinate at all, were dissected and it turned out that the embryo was lacking. Whether or not there was an aborted embryo could not be verified anymore. Therefore, it cannot be concluded from these experiments that fruit development could be parthenocarpous. By pollinating large-flowered *Clematis* cultivars with nearly non-viable pollen in isolation bags, and the resulting empty achenes, it is known that parthenocarpous fruit development does occur in *Clematis*. However, interspecific hybrids of *C. heracleifolia* and *C. integrifolia* are reported under the name *C.* ×*jouiniana* C.K.Schneid. Hybrid progeny from *C. heracleifolia* and *C. vitalba* has been reported, of which the cultivar *C.* 'Mrs. Robert Brydon' is still in cultivation and indeed shows intermediate characteristics. Mainly based on crosses between *C. integrifolia* and *C. viticella*, several cultivars have been raised from the 19th century onward; for instance *C.*

was already reported in 1852 and is still in cultivation. In order to establish nomenclatural stability around this group of cultivars, the *Clematis* Diversifolia Group was circumscribed as cultivar group (Brandenburg and van de Vooren, 1988b).

From these experiments, a cross polygon has been constructed (figure 1.21). This shows that most species involved in the hybridization programme are genetically isolated. The rough seed set data hence can easily be misleading by the phenomenon of fruit development due to parthenocarpy or adventive embryony (as is observed for *C. tangutica*).

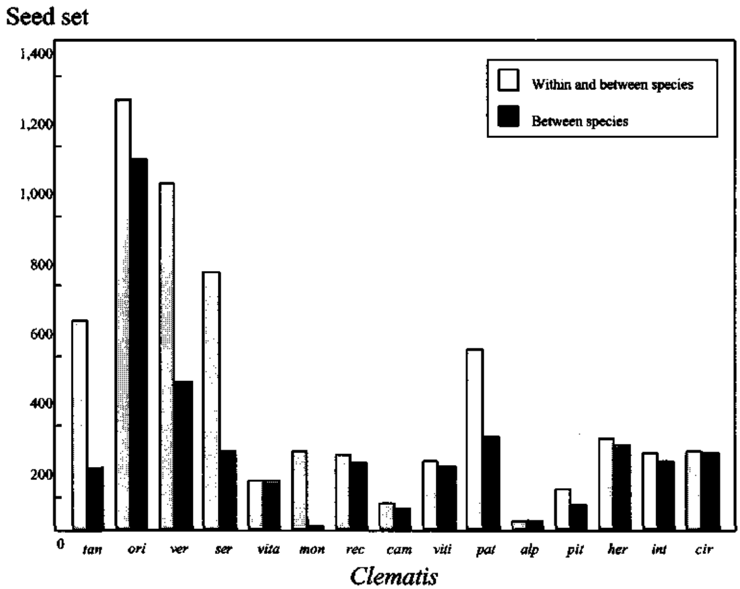


Figure 1.17. Interspecific crosses of *Clematis* species: seed set by pollination per species; for abbreviations, see figure 1.21.

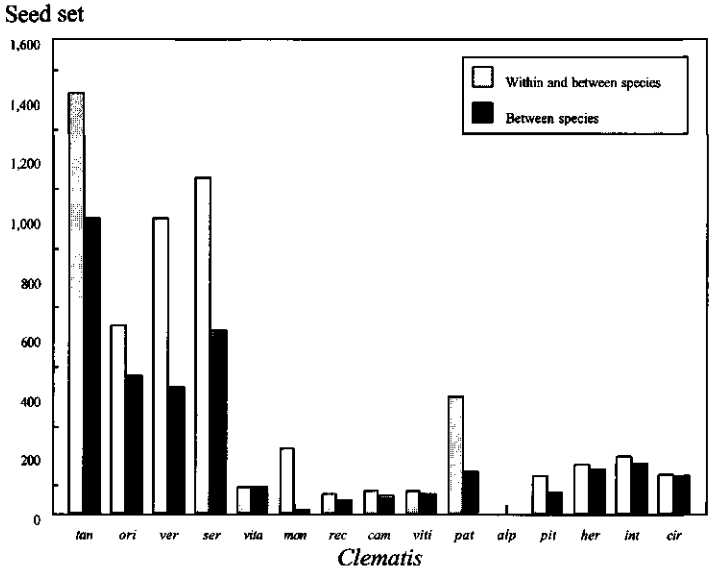


Figure 1.18. Interspecific crosses of *Clematis* species: seed set on mother plants; for abbreviations, see figure 1.21.

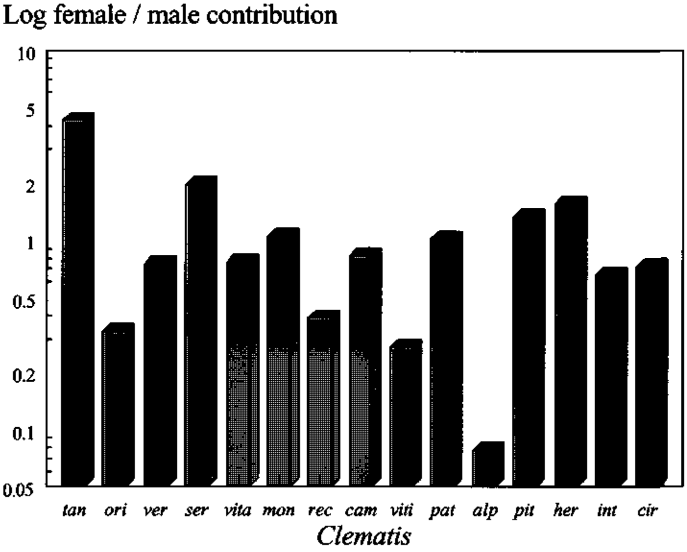


Figure 1.19. Interspecific crosses of *Clematis* species: relative contribution female/male per species; for abbreviations, see figure 1.21.

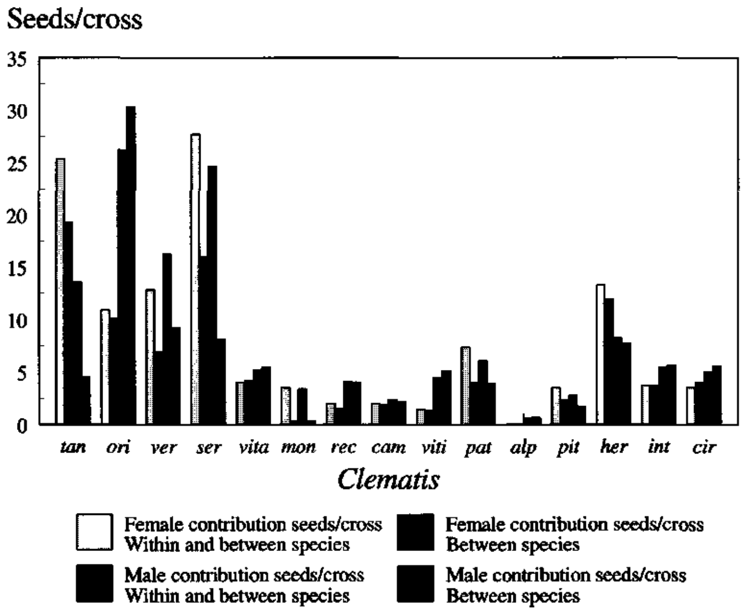


Figure 1.20. Interspecific crosses of *Clematis* species: female and male contribution per species in seeds per cross; for abbreviations, see figure 1.21.

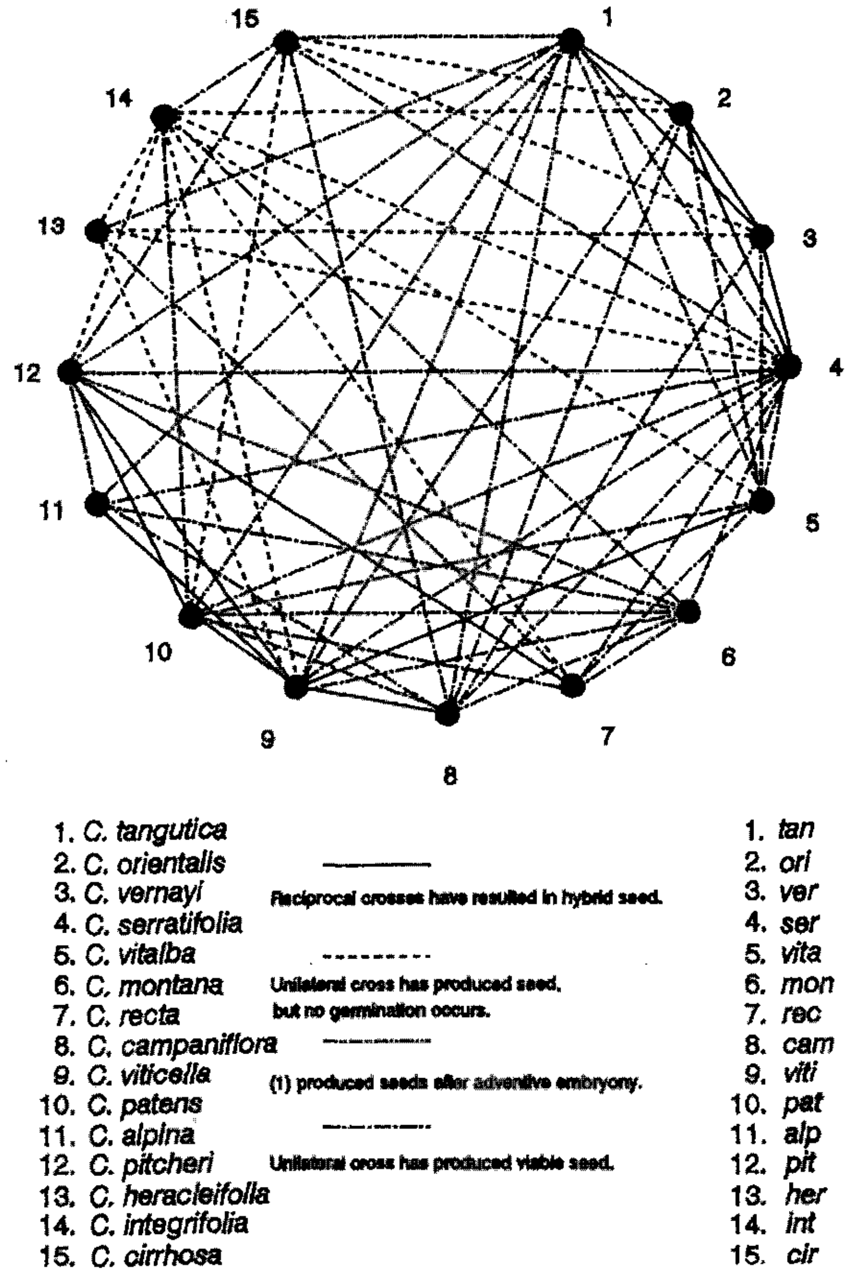


Figure 1.21. Interspecific crosses in *Clematis*: cross polygon of involved species.

1.4.3.2. Pollen tube growth experiments

Hogenboom (1973) introduced the term incongruity in order to approach mechanisms of interpopulational divergence. Although interpopulational relations are subject to biosystematics research, and hybrid inviability is of interest to evolutionary research (Coyne, 1974), up to now the term incongruity has hardly been used in biosystematics. According to Hogenboom (1975), at least two mechanisms for non-functioning in pistil-pollen relationships occur:

- incompatibility: preventing or disturbing the functioning of the relationships, although the potential for functioning of both pollen and pistil is complete;
- incongruity: non-functioning due to incompleteness of the relationship; genic systems of both partners do not fully fit together.

In an incongruent combination the penetration capacity of the pollen is too restricted compared with barrier capacity of the pistil, for whatever reason. Incongruity is coherent with evolutionary divergence between populations, whereas incompatibility is a result of a positive selection pressure within populations, favouring genes that prevent self-fertilization. Nowadays, breeding progammes have been developed which make use of incongruity in order to obtain F_1 hybrids (Hogenboom, 1979b).

Although the concept of incongruity has proved to be useful, there are still controversies with respect to the need for distinction between incompatibility and incongruity (Hermsen and Sawicka, 1979; Hogenboom, 1979a; Pandey, 1979). Working with *Nicotiana* L., Pandey (1979) stated that S-gene polymorphism has been developed by evolutionary processes, thus leading in the first place to interspecific incompatibility, and in the second place to infraspecific incompatibility. Comparing Hogenboom's concept of incongruity with Pandey's hypothesis, Hermsen and Sawicka (1979) came to the conclusion that interspecific relationships are more simply and more widely explained by means of incongruity, than by means of complex S-gene polymorphism. Although some effects like pollen-tube growth inhibition can be caused by both incompatibility as well as incongruity, many phenomena (pistil length vs. maximum pollen tube growth, or pollen unable to stick on alien stigma lobes) may only be explained by the concept of incongruity (Hogenboom, 1983b). The same concept is applicable to related fields of intimate relationships (Hogenboom, 1983a).

Within the framework of the diallel hybridization scheme, interspecific crosses were examined by epifluorescence microscopy, the results of which are to be found in table 1.14. Only for some combinations pollen tube growth was observed by UV microscopy. This was due both to the restricted amount of available flowers and to labour intensity of this work. For the section *Meclatis*, table 1.15 shows the results and observations on resulting F_1 plants.

Table 1.14. Results of pollen tube growth in combinations of the *Clematis* interspecific diallel.

♂ ▸ ▾ ♀	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. *C. tangutica*	B	D	E	D	-	-	D	C/D	-	E/F	-	D	B	D	C/D
2. *C. orientalis*	D	D	C/D	G	C/D	-	F/G	-	G/H	-	-	C/G*	D	C/G*-	D
3. *C. vernayi*	C/G*	D	H	F/G	-	D	C/D	-	-	A	D	C/D	C/D	-	-
4. *C. serratifolia*	A/G*	C/D	G	E	C/D	-	E	-	E/G*	-	D	D/E	A/?	-	A/D
5. *C. vitalba*	A/D	-	-	-	-	-	G	-	G	G	-	-	-	-	-
6. *C. montana*	-	-	A/G*	-	-	B/C/G*	-	E	G	G	D	E/G*	-	-	-
7. *C. recta*	D/E	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8. *C. campaniflora*	B	-	B	-	A	-	B	-	H	E	-	-	-	E	-
9. *C. viticella*	-	-	-	D	D	-	-	H	-	?	-	-	-	F	-
10. *C. patens*	-	-	-	-	-	-	F/G*	-	-	-	-	-	-	-	-
11. *C. alpina*	E/G*C/	-	-	-	-	-	F/G*	-	-	-	-	-	-	-	-
12. *C. pitcheri*	C/D	-	-	-	-	C/D	-	E	-	-	-	-	-	-	C
13. *C. heracleifolia*	-	-	-	-	-	-	G	-	-	-	-	D	-	E/G*/H	-
14. *C. integrifolia*	-	E	-	D/G*	-	-	-	-	-	E	-	D	G	-	-
15. *C. cirrhosa*	-	G	-	-	-	F/G	-	-	-	G	-	E/G*	E	-	B

Legend: see table 1.15.

Table 1.15. Epifluorescence microscopy of pollen tube growth in infrasectional crosses 1985 in the section *Meclatis* (Spach) Baill. and characterization of resulting seedling populations.

♂ ▸ ▾ ♀	**1**	**2**	**3**	**4**
1. *C. tangutica*	B a	D a	E a	D a
2. *C. orientalis*	D ab	D b	C/D bc	G b
3. *C. vernayi*	C/G* c	D bc	H c	F/G cd
4. *C. serratifolia*	A/G* -	C/D b	G (d)	E d

Legend

A - Pollen tube growth inhibition on stigma papillae surface; no germination of pollen;
B - Pollen germinates incompletely; if germinating pollen tube growth is inhibited in stigma or style;
C - Pollen tube growth is inhibited in stigma;
D - Pollen tube growth is inhibited in the upper half of the style;
E - Pollen tube growth is inhibited in the basal half of the style;
F - Pollen tube growth is inhibited in the apex of the ovary;
G - Pollen tube growth is not reaching the egg by confused growth in the ovary ending up in a knot of pollen tubes;
G* - Variable reactions among which reaction G;
H - Pollen tube growth is normal and leading to fertilization.
? - Results ambiguous.
a - Plants are similar to *C. tangutica*;
b - Plants are similar to *C. orientalis*;
c - Plants are similar to *C. vernayi*;
d - Plants are similar to *C. serratifolia*;
(d) - Just one plant similar to *C. serratifolia*;
ab - Plants are intermediate between *C. tangutica* and *C. orientalis*; etc. for bc and cd.

Table 1.15 shows that despite of the presence of various forms of pollen tube inhibition, there was still considerable seed set, in all cases producing seedling populations. Therefore, in addition to the diallel hybridization programme, in 1986 extra crosses between species of the section *Meclatis* were made to obtain a detailed characterization of infrasectional hybridization behaviour, and to find out whether there are differences between provenances within species. Results are presented in table 1.16.

Table 1.16. Epifluorescence microscopy of pollen tube growth in infrasectional crosses 1986 in the section *Meclatis* (Spach) Baill. and characterization of resulting seedling populations.

♂ ▸ ▾ ♀	**1**	**2**	**3**	**4**
1. *C. tangutica*	B/H a	G/H a/ab	E/G/H c	G -
2. *C. orientalis*	G/H ab	A/G/H b	G/H bc	G/H -
3. *C. vernayi*	G/H c	G/H bc	H c	G/H -
4. *C. serratifolia*	B/C -	G/H -	B/C -	H -

Legend: see table 1.15. Different codes indicate different accessions.

Comparison of tables 1.15 and 1.16 shows that with regard to pollen tube growth the accessions used in 1986 were generally more productive in combinations. Furthermore, as fertilization was succesful in those combinations with *C. tangutica* as female parent, and the offspring is quite similar to *C. tangutica*, *C. tangutica* possesses more dominant alleles in relation to the other species of the section *Meclatis*, although adventive embryony cannot be excluded completely (F_2-populations have not been screened in all cases). *C. serratifolia* appeared to be most isolated from the other *Meclatis* species. With both *C. tangutica* and *C. vernayi* as pollen parents fertilization did not take place, whereas between the three other species fertilization was occasional and reciprocal (figure 1.23). So differences between accessions are important in selecting parents for plant breeding programmes.

Apart from the diallel scheme, some other interspecific crosses were made between putative related species, such as *C. chrysocoma* Franch. with *C. montana* and *C. ispahanica*

Boiss. with *C. orientalis*. Results of pollen tube growth in combinations between *C. montana* and *C. chrysocoma* are presented in table 1.17.

Table 1.17. Epifluorescence microscopy of pollen tube growth in crosses within and between the species *C. montana* and *C. chrysocoma*.

♂ ▸ ▾ ♀	1	2
1. *C. montana*	B/C/G*/H	G/H
2. *C. chrysocoma*	C/D/G*	B/C/G*/H

Legend: see table 1.15. Different codes indicate different accessions.

The results with *C. montana* and *C. chrysocoma* show that self-incompatibility and incongruity reactions may coincide in the same complex of related species. Both *C. montana* and *C. chrysocoma* show variable pollen tube growth behaviour. In selfings the pollen tube was inhibited in the stigma (figure 1.22); in infraspecific crosses the phenomena vary from inhibition in the stigma to complete fertilization. Reciprocal crosses between both species are reciprocally different: *C. montana* as mother plant shows fertilization, whereas the reciprocal combination shows all patterns of pollen tube inhibition.

The results of crosses between *C. ispahanica* and species of the section *Meclatis* are presented in table 1.18.

Table 1.18. Epifluorescence microscopy of pollen tube growth with *C. ispahanica* as receptive parent and various species of the section *Meclatis* as pollen parent.

♂ ► ▼ ♀	1	2	3	4
1. C. *ispahanica*	B/H	D/G*	G/H	D/G*

Legend
pollen parent:
1. *C. ispahanica*
2. *C. tangutica*
3. *C. orientalis*
4. *C. vernayi*

Legend: see table 1.15. Different codes indicate different accessions.

C. ispahanica is a poorly known species, which is regularly confused with *C. orientalis*, being distinguished by its suffruticose habit. In two combinations, but not with *C. orientalis*, fertilization was observed; resulting seeds failed to germinate. The embryos, present in the seeds when sown, apparently aborted.

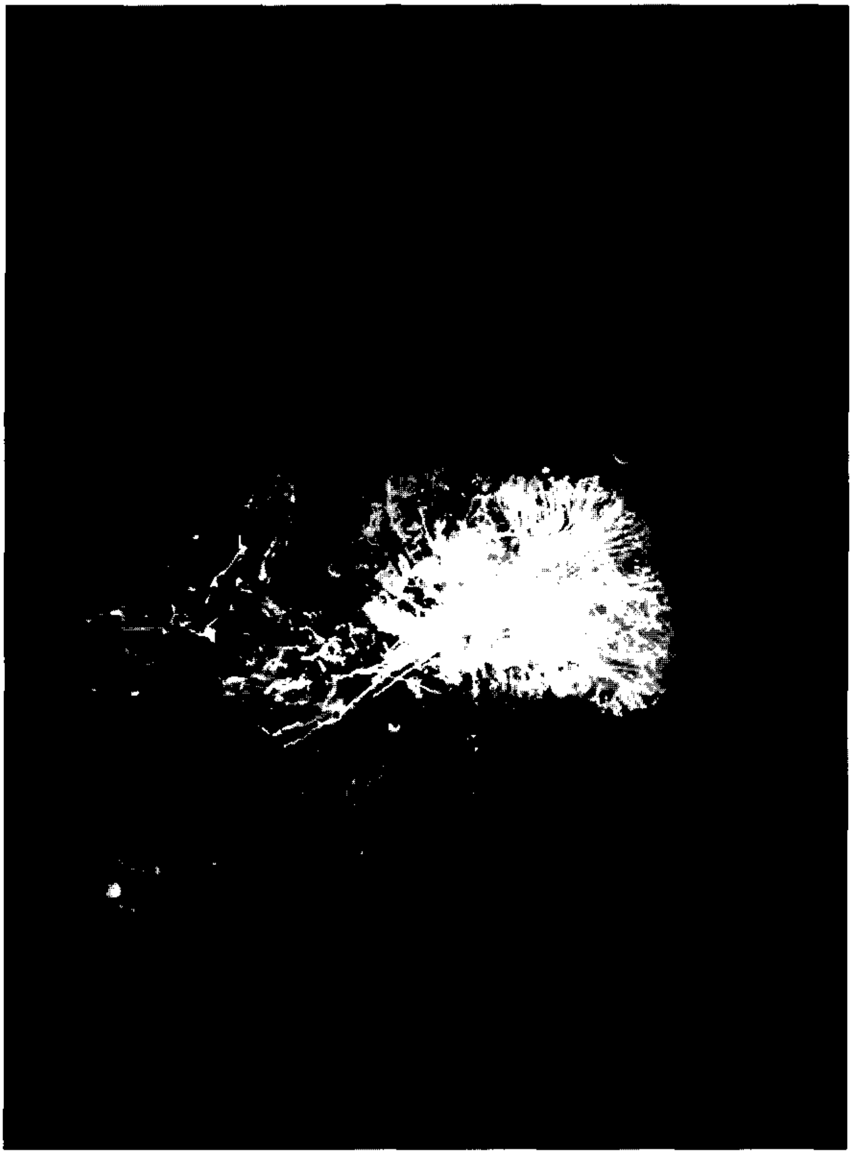
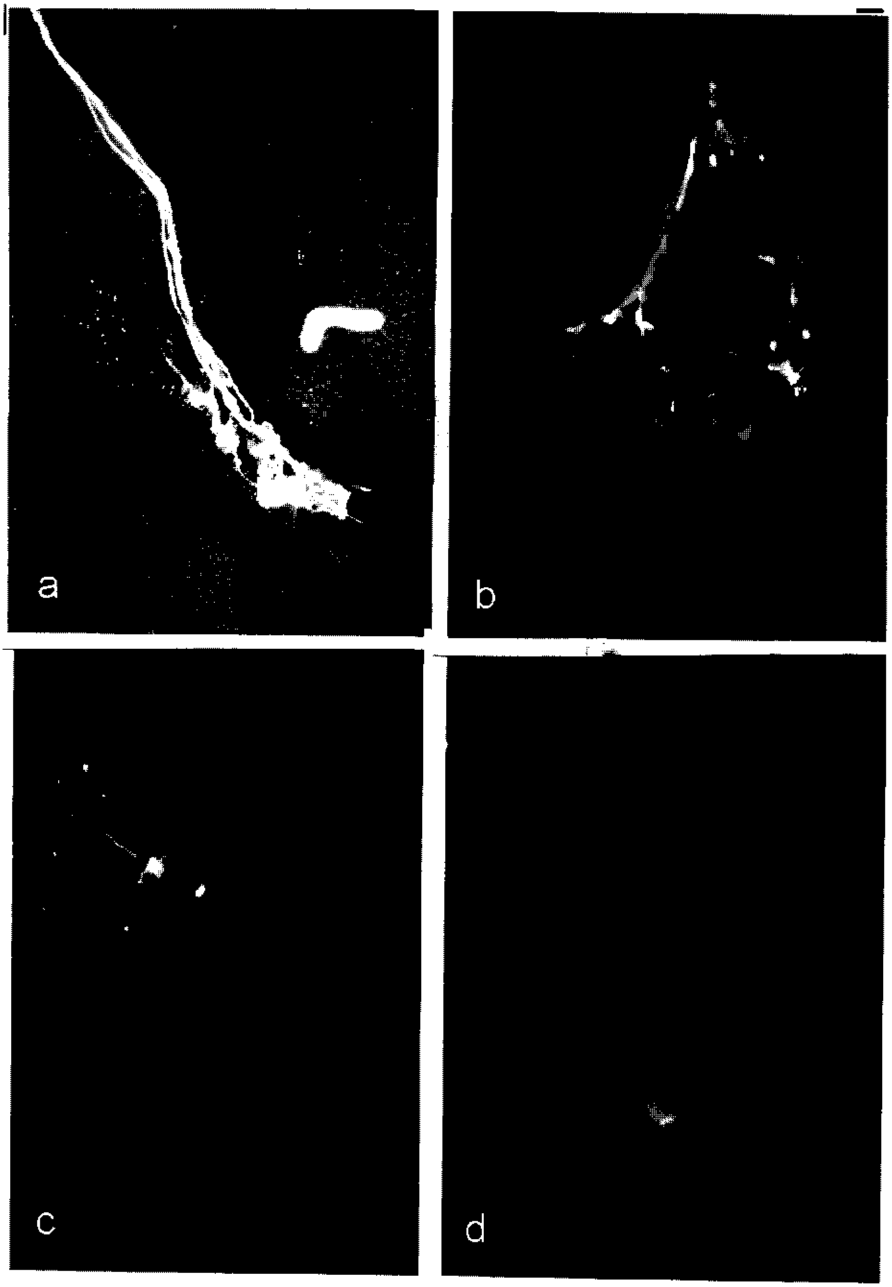


Figure 1.22. Pollen tube growth inhibition as self-incompatibility reaction. *C. montana* self-pollinated. The pollen tubes are inhibited in the stigma.


a
b
c
d


f
g1
h1
e
g2
h2


i
j
k
l

Figure 1.23. Various patterns of pollen tube growth in relation to incongruity as seen by epifluorescence microscopy.

Interspecific crosses:

a. *C. montana* × *C. chrysocoma*: vigorous pollen tube growth, but pollen tube becomes uncoordinated in growth when approaching the ovary;
b. *C. montana* × *C. chrysocoma*: same as a.;
c. *C. montana* × *C. chrysocoma*: pollen tube growth inhibited when approaching the ovary;
d. *C. chrysocoma* × *C. montana*: pollen tube growth normal, leading to fertilization;
e. *C. viticella* × *C. integrifolia*: pollen tube growth normal, leading to fertilization;
f. *C. integrifolia* × *C. viticella*: pollen tube growth inhibited in the style;
g. C. viticella × *C. campaniflora*: pollen tube growth normal, leading to fertilization;
h. *C. campaniflora* × *C. viticella*: pollen tube growth normal, leading to fertilization;
i. *C. orientalis* × *C. tibetana* subsp. *vernayi*: pollen tube growth normal, leading to fertilization;
j. *C. tibetana* subsp. *vernayi* × *C. orientalis*: pollen tube growth normal, leading to fertilization;
k. *C. tibetana* subsp. *vernayi* × *C. tibetana* subsp. *tangutica*: pollen tube growth normal, leading to fertilization;
l. *C. tibetana* subsp. *tangutica* × *C. tibetana* subsp. *vernayi*: pollen tube growth normal, leading to fertilization.

1.4.3.3. Discussion and conclusions

Between *Clematis* species an incongruity system is operating as well as an incompatibility system within species, as already shown earlier (Brandenburg, 1984a). According to Brewbaker (1957), pollen tube growth inhibition at the surface of or just inside the stigma is an indication for the gametophytic system of trinucleate species. East (1940) classified several Ranunculean species in this category. Very complex self-incompatibility systems are reported in *Ranunculus acris* L. by Lundquist et al. (1973). From the not very pronounced system of self-incompatibility in Ranunculaceae with trends present both in Monocotyledones and Dicotyledones, De Nettancourt (1977) concluded that there must have been a common ancestral system of self-incompatibility for the Angiospermae before the diversification into Monocotyledones and Dicotyledones.

With respect to interspecific hybridization various phenomena of impeded penetration have been observed:

- pollen not germinating on the stigma surface and if some grains germinate the tubes are inhibited in stigma or style;
- inhibition of pollen tubes just below the stigma;
- inhibition of pollen tubes at various places in the style;
- pollen tubes forming a kind of haustorium in the neighbourhood of the egg but not in it.

These phenomena are not fully similar in reciprocal combinations, as can be learned from table 1.14. In table 1.15 progeny data and epifluorescence data of table 1.14 were combined for *Meclatis*. They do not agree with each other. The additional crosses in 1986 show that there is variation between accessions of different provenances: the disagreement between data of table 1.15 finds its explanation in the variation between populations of different provenances as to their crossability. Similar results are known from other plant groups, such as between *Brassica oleracea* L. and related species (Snogerup, 1980), *Cucumis melo* L., *Cucumis sativus* L. and related species (Kho et al., 1980; Kroon et al., 1980; Ramachandran et al., 1983), and *Lycopersicon esculentum* Mill. and related species (Rick, 1950, 1995; Rick et al., 1979). This crossability behaviour in combination with distribution areas makes necessary further thought on species concepts as to *Clematis.*

1.4.4. *Speciation and species concepts in **Clematis***

In order to study biosystematic relationships between species, two aspects of research are important:

- to gather genetic information on interspecific barriers;
- to obtain ecological information on the adaptive abilities of the taxa concerned.

The combination of these two types of information, leading to a genecological approach of species, has proven to be a good starting-point in botanical classification (Anderson, 1949; Briggs & Walters, 1984; Camp, 1951; Camp & Gilly, 1943; Clausen, 1951; Clausen et al., 1940, 1947, 1948; De Wet, 1981; Grant, 1971; Hogenboom, 1973; Pickersgill, 1981; Stebbins, 1950; Valentine, 1975).

Species definitions are subject to much discussion in taxonomy. Wagner (1984) presented a rather cumbersome but practical definition:

> 'Species is a convenient taxonomic category that defines a unit of organismic diversity in a given time frame and composed of individual organisms that resemble one another in all or most of their structural and functional characters, that reproduce true by any means, sexual or asexual, and constitute a distinct phylogenetic line that differs consistently and persistently from populations of other species in gaps in character state combinations including geographical, ecological, morphological, anatomical, cytological, chemical, and genetic, the character states of number and kind ordinarily used for species discrimination in the same and related genera, and if partially or wholly sympatric and coexistent with related species in the same habitats, unable to cross or, if able to cross, able to maintain the special distinctions.'

The species in this sense is a multidimensional entity, that can be interpreted in three main ways:

- a genetical unit, which forms an adaptive complex;
- an ecological unit, in which genetic information can freely be interchanged within the framework of a certain response to an environment;
- an evolutionary unit (and so of a certain descent to be regarded as an independent lineage) in time and space, which forms an adaptive complex in which genetic information can freely be interchanged.

At first sight, the three approaches seem to be similar, but they quite differ in their way of analysis.

The genetical approach, which is largely based on the interpretation of genomic differences (behaviour, structure and number of chromosomes) makes all other diagnostic characters used in plant systematics dependent on such differences and leads to complicated classification schemes, as can be seen from treatments in grass systematics (Dewey, 1984; Estes & Tyrl, 1982; Löve, 1982; Raven, 1975; Sakamura, 1918; Tateoka, 1960; Wenzel & Hemleben, 1982).

Ecological studies have revealed systematic variation related with abiotic and biotic factors in the ecosystem. The results of these are meaningful, if combined with data concerning the reproductive strategy of the plants concerned and their genetic background.

In the evolutionary approach, the direction of evolution or the development of the variation of a certain plant group has to be derived from data sets of current plant collections. Using morphological data, extracted from literature, this was done for *Clematis* and dealt with in 1.3.1. In this approach the response of the genetic variation in a population to the environment is implicitly dealt with by taken into account the distribution data of the taxa concerned. In this respect hybridization has caused many problems in phylogenetic data sets, as the OTU's were supposed to be independent lineages. Funk (1985) and Wagner (1980, 1983) adressed the problem, but did not solve it.

In an attempt to solve the lack of consistency in species' definitions, Kornet (1993) established the concept of composite species starting from three main approaches of species:

- the morphological species - dependent on version of approach -, based on either morphological similarities or shared unique character states (Adanson, 1763; Nixon and Wheeler, 1990; Wagner, 1984);
- the biological species, based on interbreeding ability of individuals and - dependent on version of approach - either potential or real (Dobzhansky, 1935; Mayr, 1940, 1976, 1978, 1982);
- the internodal species, based on common membership of the genealogical network between two permanent splitting events or a splitting event and an extinction event (Hennig, 1966; Kornet, 1993; Nixon and Wheeler, 1990).

The composite species concept by Kornet (1993) is defined as follows:

`A composite species is the set of all organisms belonging to an originator internodon, and all organisms belonging to any of its descendant internodons, excluding further originator internodons and their descendant internodons'; internodons being the equivalent of internodal species in the sense of Nixon and Wheeler (1990) and the originator internodon being `an internodon distinguished by having some quality Q' and quality Q being `the property of an internodon within the life span of which a character state becomes fixed'.

The composite species concept is not tested for its general applicability thus far. Especially, its consequences for hybridization, when occurring, are compelling for further study. The composite species concept has as consequence that hybridization between species cannot occur spontaneously, or else species thought to be separate have to be combined. The results under 1.4. are obtained by artificial hybridization, starting from thoughts around the biological species concept and evolutionary considerations assigned to that (Dobzhansky, 1935; Lotsy, 1916; Solbrich, 1968) and therefore say something about genetic relatedness rather than about species'border-line cases bearing the composite species concept in mind. They may, however, be helpful in formulating hypotheses on how species have evolved from each other as one of the consequences of the composite species concept is that new species branches off from existing species and that reticulate variation patterns may exist (Wanntorp, 1983) rather than that an ancestral complex splits into two new species (Kornet, 1993).

1.5. Description of the genus *Clematis*

1.5.1. *Growth habit*

Clematis is rather polymorphic in growth habit. The predominant habit within the Ranunculaceae is the single stemmed perennial, of which the seasonal growth is ended by one terminal flower or an inflorescence, whereas the next year's growth develops from geophytic side axes or rhizomes. This growth type is prevailing in most *Anemone* species and in several *Clematis* species, such as *C. integrifolia*. The branching pattern of the rhizome is similar for all *Clematis* species. The degree of woodiness, or persistence to the next growth season, and the degree of branching of aboveground parts in subsequent years are the varying factors on the above theme. Some species die back to the ground and are perennial herbs. Others die back to the basal, woody, overground parts, whereas the development of the rhizome warrants sufficient number of new axes; they form subshrubs, such as *C. texensis* Buckley. The woody type of this habit shows no real difference between vegetative and generative side axes; they form vigorous, woody climbers, such as *C. vitalba*. Other woody plants within *Clematis* show two types of aboveground stems:

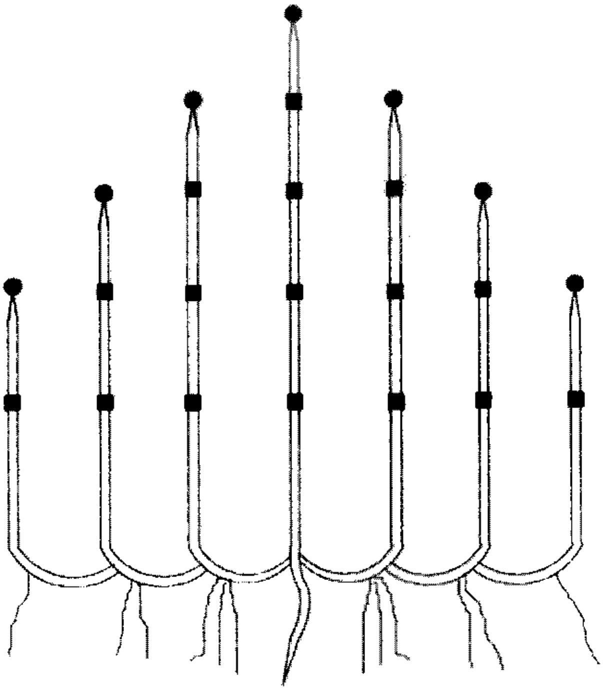
- vegetative stems developing from the rhizome or basal aboveground nodes;
- generative stems developing from higher nodes and ending up either in synflorescences consisting of several axillary and (composite) cymes, or in (composite) cymes, or one solitary flower; these stems die back after the growth season.

This type is represented by *C. viticella*. An extreme of this model is that these generative stems are very much reduced, and flowering occurs in the next growth season in the axils of the one years growth, as in *C. alpina* and *C. montana*. Hallé et al. (1978), Tomlinson (1984) and Jeannoda-Robinson (1977) have made descriptions of growth models of woody plants and perennials. *Clematis* largely fits the model of Tomlinson. This model starts from a rhythmic annual growth of a rhizome with roots at the basal nodes. The rhizome ends in an upright stem with foliar nodes and finally nodes combining foliage and inflorescences. Cremers (1973, 1974, 1975) made clear that there may well be separate growth models for climbing plants, as they have sometimes a growth habit intermediate between those of woody and herbaceous plants.

Moreover, rhizome organization has to be considered in relation with the vegetative spread of the plants (Bell, 1974).

The growth forms are exemplified with photographs of *C. integrifolia*, *C. heracleifolia* and a schematic presentation of Tomlinson's growth model in figure 1.24.

Especially in woody climbers, the distinction between typical growth forms in *Clematis* is only gradual, as can be seen from species such as *C. patens*. Prantl (1888) already described the coherence of apparently different growth forms.



a Model of Tomlinson

● Nodes with foliage and inflorescences

■ Nodes with foliage

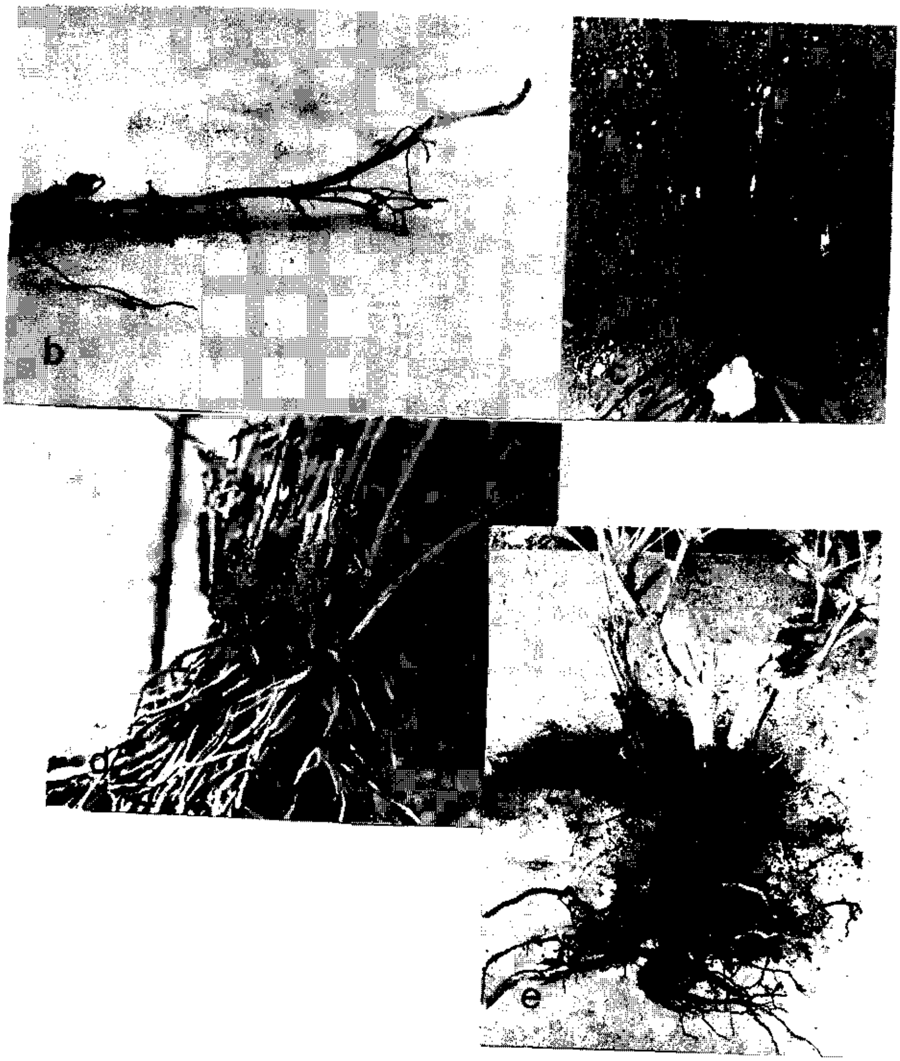


Figure 1.24. Basic growth habit of *Clematis*.
a. Tomlinson's growth model; b., c., d. *C. integrifolia*; e. *C. heracleifolia*.
(Photographs: Jos van de Vooren)

1.5.2. *Leaves*

Leaf morphology in *Clematis* is very variable, ranging from simple to ternately or pinnately composed leaves. Simple leaves occur only in some perennials, such as *C. integrifolia*, whereas consequent ternate, or biternate leaves occur in some woody climbers, such as *C. columbiana* Torr. & A.Gray and *C. alpina* respectively.

In most *Clematis* spp., the one basic leaf morphology varies considerably between individual plants, and shows moreover effects of position within individuals, such as reduction of lower leaves (these may even be simple), and gradual change to bracts, bracteoles and bracteolules.

Kuntze (1885) remarked that it is sometimes impossible to describe composite *Clematis* leaves with the usual descriptive terminology. Many *Clematis* spp., such as *C. flammula*, bear leaves of which the basal leaflets of the first order are again subdivided one to several times, whereas toward the top they are just simple, with intermediate variously lobed forms in between. Such leaves he termed flammuliform.

In perennial *Clematis* spp., the one-year old rhizomes, and later their geophytic side axes, bear much reduced scaly and simple leaves. The lateral branches, bearing the inflorescences, develop from the rhizome axils.

1.5.3. *Synflorescence and inflorescence*

The basic structure of the *Clematis* inflorescence is the cyme (figure 1.25a), mostly borne axillary along a young shoot and bearing bracteoles and bracteolules, which look like reduced leaves. In *Clematis* spp. with multiple compound leaves, bracts are similar to leaflets of the first order, bracteoles to leaflets of the second order and bracteolules to leaflets of the third order. In some species, however, bracteolules are reduced to minor scales, which disappear soon after flower buds open.

In some *Clematis* species with solitary, axillary flowers, the basic cymose structure of the inflorescence can be recognized from flower stalks, bearing bracteoles at the place where the peduncle ends and the pedicel commences (figure 1.25b). In these cases, the inflorescence may sometimes bear two or three flowers, thus showing the original pattern of the inflorescence.

In other *Clematis* species, such as *C. orientalis*, the inflorescence is a composite cyme, i.e. a cyme of which the side branches and the top branch form again partial or entire cymes (figure 1.25c). This can be repeated several times, leading to clusters of flowers.

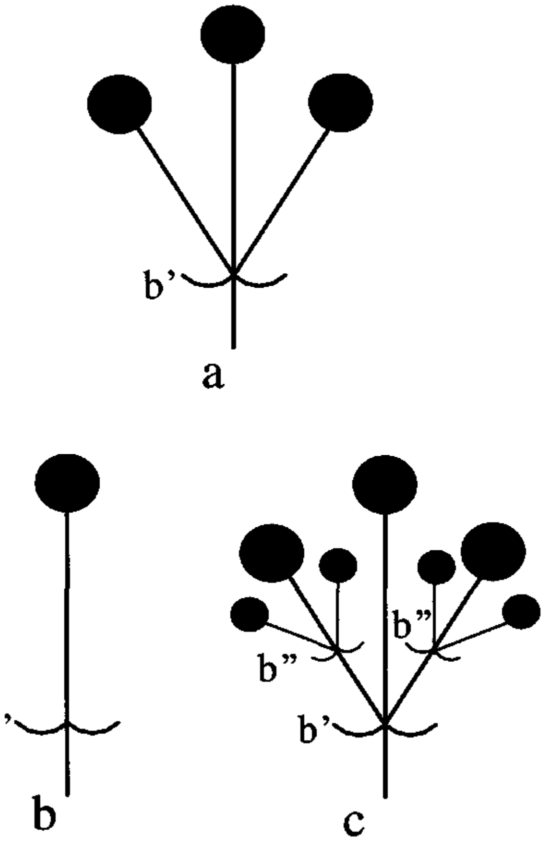
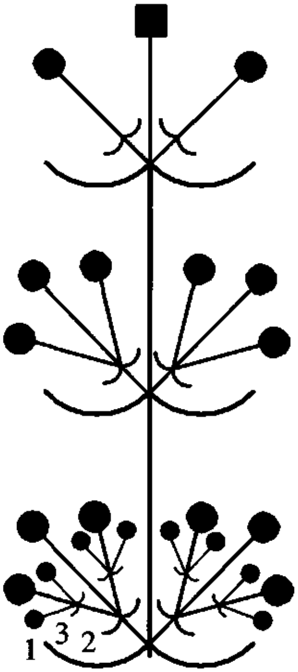


Figure 1.25. Schematic presentation of *Clematis* inflorescences.

a. dichasium ground plan.
b. reduced dichasium: solitary flower
c. multiple dichasium
b'. bracteole
b". bracteolule

Troll (1964) used the term synflorescence for flowering branches, that are characterized by a gradual transition from vegetative growth to inflorescence structures. In various plants, this appears to be a pragmatic approach. In Compositae, for example, the inflorescence is always a flower head (capitulum), surrounded by an involucrum, but the synflorescence may vary greatly in size and shape. As a rule, in all cases of derived, inflorescence structures description of the synflorescence is worthwhile considering. In plants with gradual transition from vegetative to flowering branches, the description of the synflorescence adds to the understanding of the plant morphology. In Cruciferae, for instance, the inflorescence is always a raceme, but if we look at the total of racemes and their position, synflorescences are either absent or greatly vary also in size and structure. The same holds for Ranunculaceae. In *Clematis*, some species bear thyrsoid synflorescences, of which the inflorescence properly remains determinate, based on the cymose structures, whereas the synflorescence has an undeterminate character, acting more or less as a raceme. The characterization of the synflorescence structure, being thyrsoid instead of being a real thyrsus, is to be justified by the fact that the top structure is in fact either determinate, being a terminal cyme that is much reduced and bears often aborted flower buds, or undeterminate, being a terminal cyme which partially or wholly changes over to vegetative growth ending by a vegetative bud as the start of next year's growth.

The confusion about inflorescence structure has much troubled *Clematis* literature, ranging from the misapplication of terms, such as bracts, bracteoles and bracteolules, to the misinterpretation of flowering branches by various authors (Baillon, 1867; Prantl, 1888; Tamura, 1968a). The importance of a consistent terminology in this respect, is the more evident as a *Clematis* cultivar group classification, principally based on habit, synflorescence and inflorescence morphology exists since more than a century (Moore & Jackman, 1872; Brandenburg & van de Vooren, 1988a; Brandenburg, 1989a).



■ either flower or vegetative bud for next season's growth

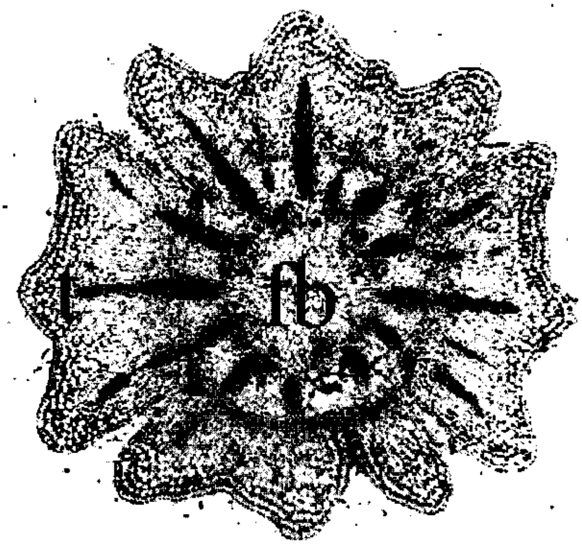
● flower
1 bract
2 bracteole
3 bracteolule

Figure 1.26. Schematic presentation of *Clematis* synflorescences.

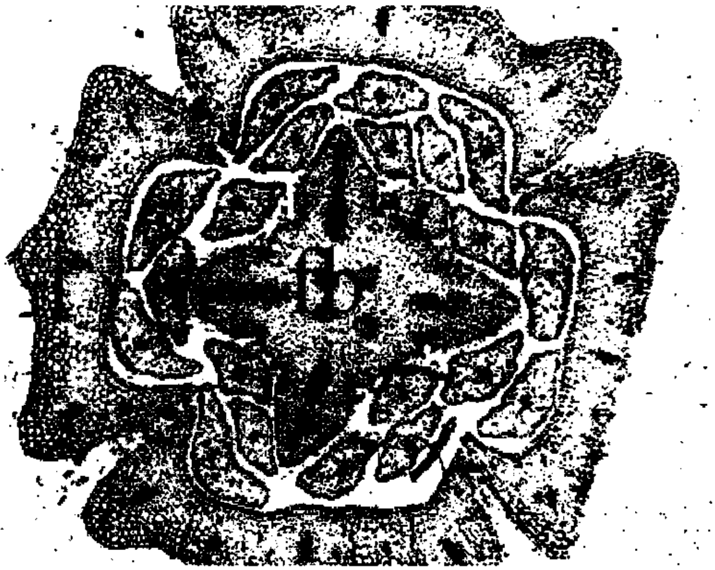
1.5.4. *Flower*

At first sight, *Clematis* flowers seem to have a simple structure without specialized organs. Normally the flower is hemicyclic, in having an undifferentiated, ± cyclic perianth, an androecium consisting of numerous spirally arranged stamens, and a gynoecium of numerous spirally arranged apocarpous pistils, each pistil forming an achene (Schöffel, 1932). *Clematis* has this flower morphology in common with the other genera of the tribe Anemoneae. It can be considered as the first variant of the most primitive structure of the flower (Dilcher & Crane, 1984; Kosuge & Tamura, 1989; Raßner, 1931; Trapl, 1912). The distinctive character is that the *Clematis* flower has two whorls in its perianth in lieu of the decussate leaf position. A series of transect slides of the flower development of *C. campaniflora* by Ackermans (1983; figure 1.27) demonstrates this, using the approach by Meicenheimer (1978, 1979) and the anatomical dissection technique by Tobe (1976, 1980a, 1980b). The presence of two whorls cannot always clearly be recognized in the arrangement of nectar leaves - if present, as is in section *Atragene*. In the androecium and the gynoecium, the presence of two whorls can only be deduced in part from the above mentioned series of slides by comparing relative positions and dimensions of stamens and pistils respectively. Comparison of the results by Ackermans, Meicenheimer and Tobe reveals the agreement of Ackermans and Tobe that two whorls in the flower arrangement of *Clematis* could be shown as opposite in *Ranunculus* L., analysed by Meicenheimer. Apart from his anatomical work, Ackermans separated flower parts per flower of several *Clematis* species and mounted them on paper in the existing order showing the relation between position and dimension of flower parts. Comparing flower parts in this way proved the presence of two whorls in the flower arrangement of *Clematis*, irrespective of the species concerned.

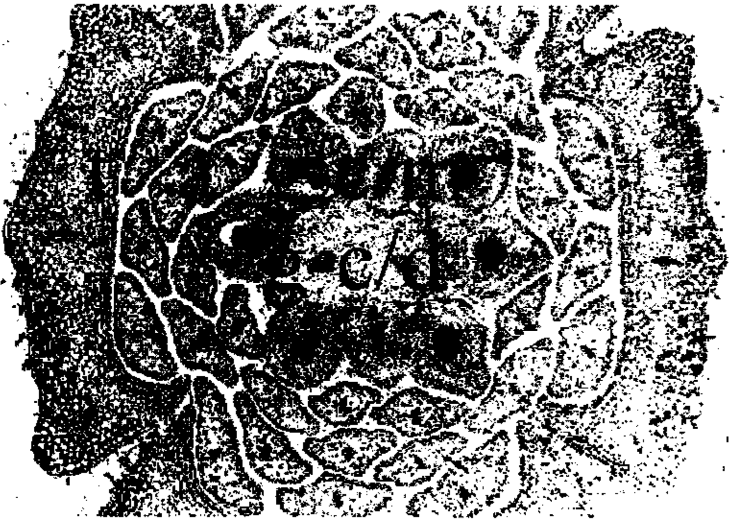
Van Heel (1981, 1983) studied the formation of free carpels, typical for *Clematis*.



a



b



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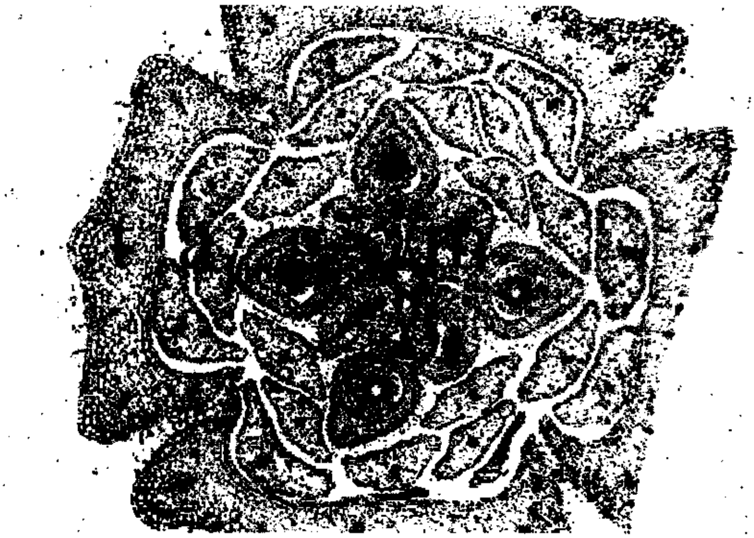


d

Figure 1.27. Excerpt of a series of transsections of flowers of *C. campaniflora*. Legend:

a young bud, tepals developed (tepals + floral base)
b mature bud, transection at base (tepals + androecium + floral base)
c immature bud (tepals + androecium + gynoecium + ovules developing)
d same bud as b, but transection in the middle of the bud (tepals + androecium + gynoecium + ovules mature)

fb - floral base; t - tepals; a - androecium; g-c/d - gynoecium / carpels developing; g-c/m - gynoecium / carpels mature; o - ovule.

(Photographs: Guy Ackermans)

Prantl (1888) analysed the floral morphology of the Ranunculaceae from - as he put it - a phylogenetic point of view:

> 'Es dürfte zunächst zugegeben werden, dass bei einer Anzahl von Gattungen (wenigstens in ihren größeren Artenzahl) überhaupt nur ein einfaches Perigon vorhanden ist, das keine Sonderung in Kelch und Krone erfährt, das auch weder als Kelch noch als Krone zu bezeichnen ist, weil eben kein Grund zu der Annahme vorliegt, dass der andere dieser beiden Perigonteile wiederum verschwunden sei' (p. 15).

For Ranunculaceae, Prantl settled for the following basic flower structures outside the androecium:

1a. Simple petaloid perianth, nectar leaves (Honigblätter) absent: a.o. the majority of *Anemone* and *Clematis* species;
1b. Periant with differentiated calyx and corolla, nectar leaves absent: a.o. *Anemone* § *Knowltonia*;
2a. Simple perianth, either tending towards corollar, or towards calycious perfomance,
    α nectar leaves present: a.o. *Clematis zeylanica*;
    β staminodia present: a.o. *Clematis* § *Atragene*;
2b. Perianth with differentiated calyx and corolla, nectar leaves present.

Prantl made a distinction between nectary and the term nectar leaf, introduced by him:

- Only nectar secreting tissue is indicated with nectarium; such tissue may be localized on any flower parts, such as stamens in *Clematis* § *Viorna*; whereas
- nectar leaves are leafy organs with as main function nectar secretion; nectar leaves are supposed to be derived from stamens after losing their reproduction function.

Within the Ranunculaceae, nectaria occur on normal stamens (*Clematis* § *Viorna*); on nectar leaves (most Ranunculaceae; Werth, 1941); and on ovaries (*Caltha* and most *Trollius* spp.; Prantl, 1888). Their location shows up by treating filaments with Fehlings reagens, as *Clematis* nectar largely consists of disaccharides (Daumann and Slavikova, 1968). Clematis flowers are not very specialized in pollinators (Knuth, 1898, 1904).

1.5.4.1 Perianth

Tepals usually 4, but in some species 5-10 or more, petaloid, aestivation valvate, induplicate or with age sometimes imbricate (Godley, 1977). Tepal position is distichous, each pair has similarly shaped tepals. With regard to venation, three largely parallel main veins are connected by reticulate minor veins. Shape and size of tepal margin outside the main veins vary dependent on bud aestivation. In some sections, such as *Viticella*, there is an extended margin (figure 1.28b), whereas in others the margin is just reduced to a villose margin outside the lateral veins (figure 1.28c).

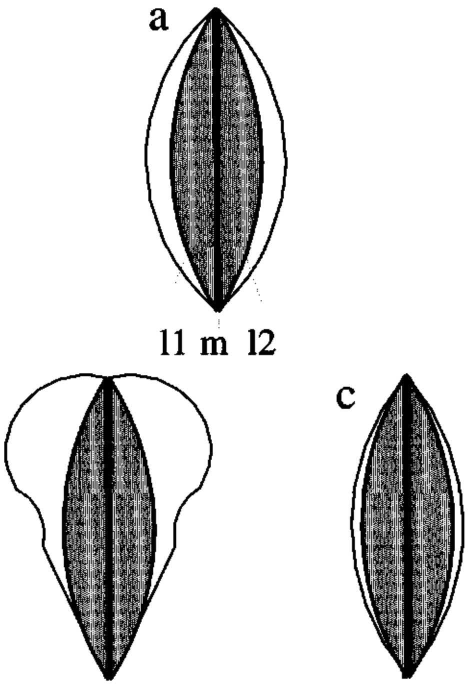


Figure 1.28. Polymorphism in *Clematis* tepal morphology.

a. basal shape of tepal.
b. tepal with showy margins beside the veins.
c. tepal with hardly any margin (mostly lanate) beside the lateral veins (l1 and l2).
m. midrib.
l1. left lateral vein.
l2. right lateral vein.

The apex of tepals is mostly acuminate to acute and sometimes mucronate. The hairiness of the outer and inner side of tepals may vary individually within species, although in the bud stage the margin is at least pilose, mostly villose.

1.5.4.2. Nectar leaves

Nectar leaves are not characteristic for *Clematis* as a whole, but for certain sections of the genus, such as *Atragene*. Their shape and size (figure 1.29) may vary from almost petaloid organs to non-functional stamens of which the filaments are strongly dilatate, as e.g. in section *Naravelia* and in some *Atragene* species. In other sections, some species show a strong tendency towards the development of staminodia, which are essentially not different from nectar leaves, thus leading to double-flowered forms. In some species, this tendency is expressed so frequently, that after their introduction to Europe, such forms were originally supposed to be the wild type form. This was the case with *Clematis florida* Thunb. ex Murray.

Apart from a strong midrib, the venation of nectar leaves is largely reticulate. The nectaries are located on and along the midrib of those leaves (Heyting et al., 1980).

1.5.4.3. Stamens

Stamens are numerous, positioned in two whorls at the flower base, the whorls gradually developing from either the perianth or the whorls of nectar leaves. However, due to the spiral-like structure of the flower, there is no fixed number of stamens per flower, in this respect there are considerable differences between *Clematis* species: *C. viticella* has an average of 60 stamens per flower, whereas *C. alpina* and *C. montana* have an average of 130 stamens per flower.

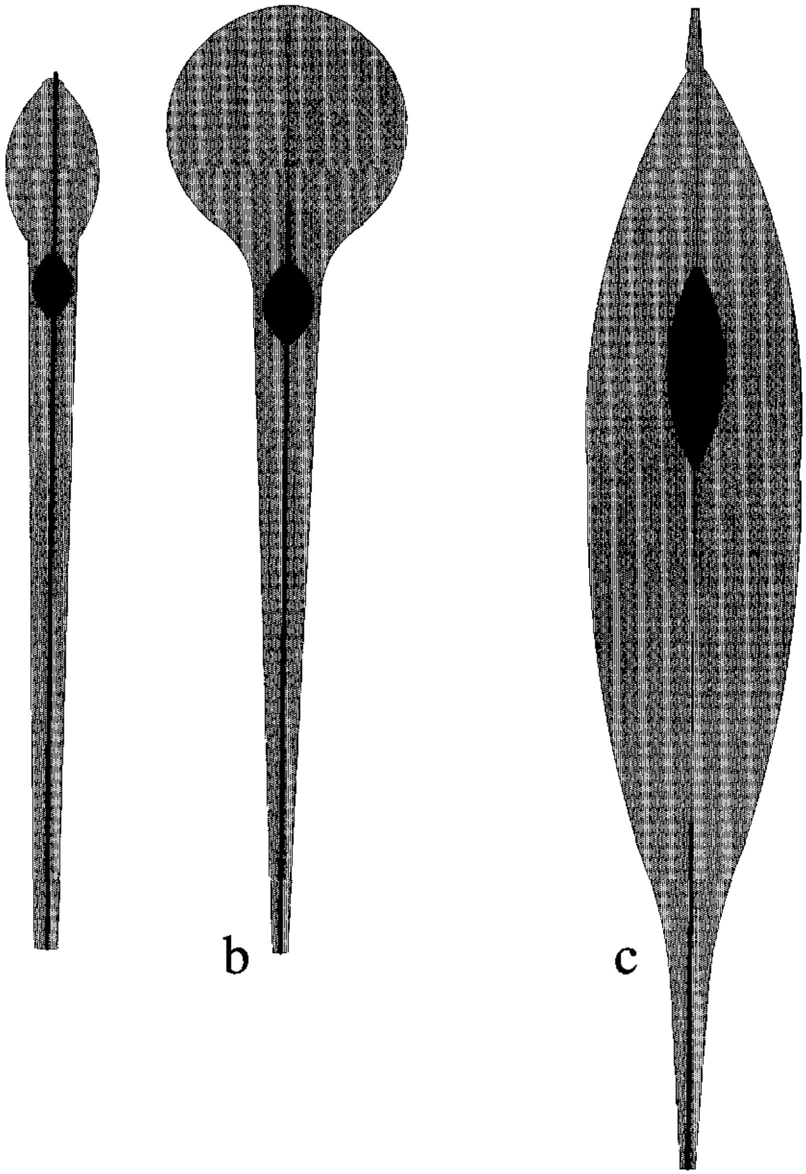


Figure 1.29. Polymorphism in nectar leaves of *Clematis* flowers. Black dots mark the ventral location of nectaria (Heyting et al., 1980).

a. Staminodial nectar leaf; staminal derivation is still easily recognized.

b. Spatulate nectar leaf; filament part is still recognizable.

c. Petaloid nectar leaf; the staminal derivation is only to be deduced by forms transitional to functional stamens

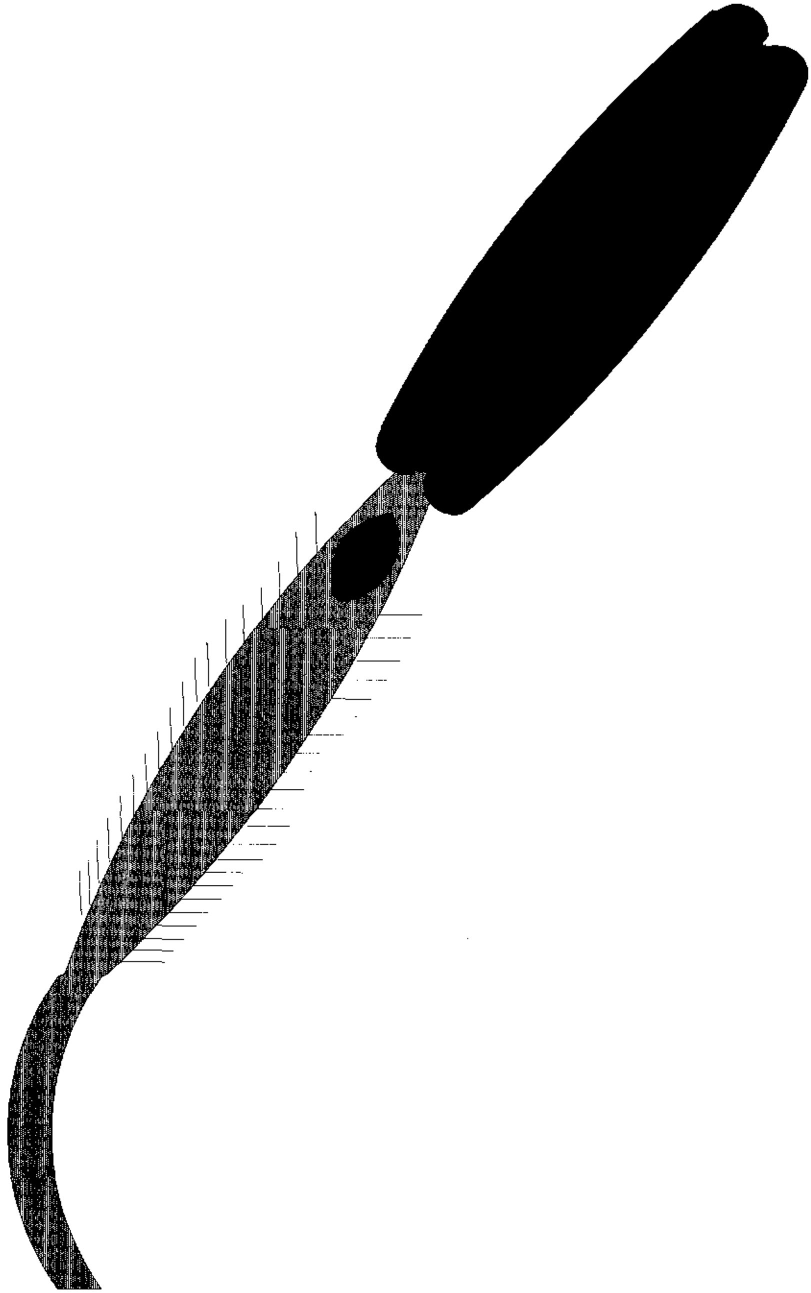


Figure 1.30. *Clematis orientalis* stamen.

Dark spotted area at the top of the filament marks the place where nectaria are localized.

Filaments filiform, or dilatate, glabrous, ciliate or pilose. Full-grown outer stamens sometimes have more elongated filaments than the filaments of inner stamens. Filament shape is sometimes a character in sectional classification, but in that case it is inconsistently applied.

Anthers have two thecae and a connective either as long as the anther, or elongated (section *Cheiropsis*), or with an appendix (section *Naravelia*). Although these connective characters are consistent in these two sections, they may also occur in other sections. In some sections, such as section *Viticella*, connectives are never present.

Are nectar leaves to be considered transformed stamina, thus being non-functional stamina or staminodia, at first sight in many *Clematis* spp. there are normal looking outer stamina, which are however sterile and hence staminodial. These staminodia function normally in every respect but for pollen production: nectaria are found in the upper part of the filament (figure 1.30.).

1.5.4.4. Pistils

Pistils are apocarpous, numerous and positioned in two whorls at the flower base. Due to the spiral-like structure of the flower, there is no fixed number of pistils per flower, as is the case in many other Ranunculaceae and also in Rosaceae (Bessey, 1898). In this respect quite large differences between *Clematis* spp. exist, the average number per flower ranging from 30 to 130. Gradual transitions between stamina and pistils sometimes occur, due to the whorl structure of the flower. Sterile organs occur then with a rudimentary ovary, a style/filament and a sterile or a reduced fertile anther at the top.

The stigma is glabrous, not markedly two-lobed, with a sticky surface, bent at the top. Apart from colour and size, there is hardly any structural variation in stigma morphology throughout the genus *Clematis*.

Styles are plumose, with branched or single hairs. Apart from colour and size, style morphology throughout the genus *Clematis* is quite uniform.

Ovaries are ellipsoid, rhomboid or deltoid, contain two integuments and 1-6(-8) ovules, of which only the lowest one is functional. The other ovules abort in an early stage or reduce, remaining non-functional.

1.5.5. *Fruit*

After fertilization, one-seeded achenes develop from the ovaries. There are, however, indications that fruits also develop after pollen tube growth into the style, due to adventive embryony or parthenocarpy (see 1.4.). Achenes are ellipsoid, rhomboid or deltoid, and sometimes strongly dorsiventrally ribbed. The fruit wall can be rather woody, leathery, smooth or intermediate in structure. A visually mature fruit contains relatively much endosperm, and a small premature embryo, that develops further during the long dormancy period (Schaeppi & Frank, 1962; Tamura & Mizumoto, 1972; cf. 1.4.).

A remarkable feature of several *Clematis* spp. is the strongly elongated, plumose style at the top of the achene. It is a conspicuous character of several *Clematis* sections, such as *Atragene* and *Meclatis*, which contributes considerably to the ornamental value of its plants in cultivation and in the wild.

1.6. **Summary description of *Clematis***

Woody climbers, subshrubs or perennials. If climbing, plants are doing so with winding petiolules.

Leaves opposite, rarely or occasionally alternate, simple or compound. When compound, leaves are one to many times regularly or irregularly ternately or pinnately subdivided.

Inflorescences basically one- to many-flowered cymes at the top of young stems or axillary on young or old growth, organized in raceme-like synflorescences.

Flowers with 4-8(-many) tepals in an undifferentiated perianth, numerous stamens and mostly many apocarpous pistils forming achenes sometimes with plumose, elongated styles.

A genus of about 150 species, dispersed throughout the world except for polar regions with its main distribution area in the northern temperate zone. The greatest diversity occurs in the Far East.

The majority of the large-flowered cultivars and a considerable amount of small-flowered ones are of hybrid origin and cannot be assigned to a particular species. Their classification will be dealt with in Chapter 4.

2. *CLEMATIS* SECTION *MECLATIS* (SPACH) BAILLON

2.1. Description of the section *Meclatis* (Spach) Baill.

Spach (1839) described *Meclatis* as a separate genus with two species:

- *Meclatis orientalis* (L.) Spach	(basionym: *Clematis orientalis* L.)
- *Meclatis sibirica* Spach	(synonym: *Clematis glauca* Willd. p.p.; *Clematis intricata* Bunge)

The characters to distinguish *Meclatis* from other *Clematis* spp. are according to Spach (1839):

> 'Sépales 4, pétaloïdes, pendant l'épanouissement étalés ou révolutés, divergents, en préfloraison imbriqués par les bords. Pétales nuls. Étamines paucisériées, conniventes; filets lancéolés (du moins les intérieurs), comprimés; anthères linéaires-oblongues, inappendiculées. Styles longs, filiformes, obtus. Nucules coriaces, subfusiformes, tétragones, un peu comprimées, légèrement marginées: bords tranchants. Gynophore subglobuleux.'

A further extensive description by Spach presents the following characters:

- 'Ramules florifères axillaires et terminaux, dichotomes (!), brachiés. feuillés aux bifurcations, nus inférieurement, 3-15 flores' (!);
- 'Feuilles pétiolées, glauques (!), molles, nonpersistantes';
- 'Fleurs légèrement odorantes (!), assez grandes, nutantes, disposées (..) en cyme subfastigiées' (!);
- 'Sépales jaunes (!), planes (!), 5-nervés (!); les 2 nervures marginales et la médiane saillantes, carénées; les 2 intermédiaires très fines), acuminés, cotonneux aux bords, plus long que les étamines';
- 'Filets violets (!), ciliés';
- 'Nucules petites, lisses, pubescentes de mêmes que le gynophore (!).'

The character states, indicated by exclamation marks above (present author), do not always hold or are absent:

- dichotomy does not occur, but is the result of a somehow artificially aborted terminal twig;
- solitary flowers also occur;
- glaucous leaves are present in many *Meclatis* specimens but not in all, whereas they also occur in other sections, such as *Viorna*;
- in some species have a remarkable, if not odd, fragrance, but this character varies in intensity;
- subfastigiate inflorescences were not observed by the present author;
- tepal colour is predominantly yellow, but variation occurs ranging from tinged or

spotted with violet to full violet as an exception (Spach terms tepals sepals);

- tepals may be flattened (plane) in some *Meclatis* specimens, but certainly not in all, whereas the presence of 5 nerves is a misinterpretation of the tepal venation;
- filaments (and tepals as well!) indeed often are tinged with violet or are even markedly violet, but many *Meclatis* specimens just have yellowish-green filaments;
- It is supposed that Spach meant by gynophore at least the androgynophore, as the transition zone between androphore and gynophore is often not markedly present.

These characters are not unequivocal: none is uniquely distinctive for *Meclatis*. Therefore, *Meclatis* cannot be maintained as a genus. Apart from the combination of some character states (bright yellow flowers, pinnatisect leaves and rather small, pubescent achenes), it possesses, however, a physiological trait which makes this group a systematic entity within the framework of *Clematis*: *Meclatis* spp. lack the strict and long seed dormancy, which is so characteristic for most *Clematis* spp. (Barton, 1967; Blair, 1959; Kinzel, 1913; Niethammer, 1928) and other representatives of the tribe Anemoneae. After sowing within three weeks the seeds germinate readily and seedlings are growing within one year into flowering plants. This lack of seed dormancy is clearly of interest for *Clematis* cultivation and breeding.

Clematis section *Meclatis* (Spach) Baillon (1867) - Histoire des plantes, vol.1: 52-62, 87.

Paris; type: *C. orientalis* L. (Lectotype Dillenius 2868, OXF-DILL).

Basionym:

Meclatis Spach (1839) - Histoire naturelle des végétaux, vol. 7 Les Clematidées: 257-284. Librairie encyclopédique de Roret, Paris; type: *Meclatis orientalis* (L.) Spach.

Homotypic synonyms:

Clematis series *Orientales* Prantl (1888) - Beiträge zur Morphologie und Systematik der Ranunculaceen. Botanische Jahrbücher **9**: 225-273;

Clematis section *Clematis* subsection *Orientales* (Prantl) Tamura (1967) - Morphology, ecology and phylogeny of the Ranunculaceae VI. Annual reports of the College of General Education Osaka University 1967: 13-35.

Description: Woody climbers, flowering in summer; (June)-July-September on the young growth of that season. Leaves very variable in shape and size, pinnately or partly or wholly bipinnate, in certain cases tripinnately subdivided. Inflorescence axillary and/or terminal ranging from solitary flowers to 3-many-flowered cymes; peduncle ranging from very short (almost absent) to predominantly present, thus giving the impression of very different inflorescential structures between species; pedicel curved at the apex. Flowers with 4, occasionally 5 tepals, yellow or greenish yellow, sometimes variously light purplish-brown inside or spotted or tinged with red-violet outside, lanate at the incurved margin. Stamens numerous; filaments dilatate, towards the base pilose, or ciliate; anthers without an elongated connective or other appendages. Pistils numerous; ovaries ellipsoid or rhomboid; styles long pubescent. Achenes rhomboid, variously ribbed at the margin, pubescent, dark brown with a more or less fibrous appearance; styles variously elongate, persistent, covered with long erect hairs.

2.2. Distribution and of the section *Meclatis* (Spach) Baill.

The natural distribution of the section is extensive; species are found in Turkey, Syria, Iraq, Iran, Afghanistan, Georgia, Armenia, Azerbaidzhan, Kazakhstan, Turkmenistan, Uzbekistan, Kirgiziya, Pakistan, the Himalayan region of India, Nepal, Bhutan, P.R. of China (Tibet, Xinjiang Uygur Ziziqu, Kansu, Shansi, Inner Mongolia, Sichuan, Yunnan), Mongolia, Russian Federation (regions adjacent to above mentioned countries), and North and South Korea.

Apart from their natural occurrence in the above regions, some species have escaped from cultivation. There is evidence from herbarium specimens that representatives of *Clematis* sect. *Meclatis* have been naturalised. In Canada (Alberta), *C. tibetana* subsp. *tangutica* has been escaped (Turner 2644 (S)), whereas in the neighbourhood of Georgetown (USA, Colorado), *C. intricata* must have been naturalised (Weber & Salamun 12937 (C, S)). Outside sect. *Meclatis*, there are more examples of naturalizing *Clematis* populations, such as *C. viticella* along the river Maas in Belgium and the Netherlands. As far as I know, this has never led to lasting large changes on the vegetation, but remains restricted to small isolated populations.

Based on distribution data of specimens cited for the taxa described in the following sections, tracks (to be understood as the graphic presentation of the circumscription of the total range of monophyletic taxa; Camp, 1947; Wiley, 1981) are presented in figure 2.1.

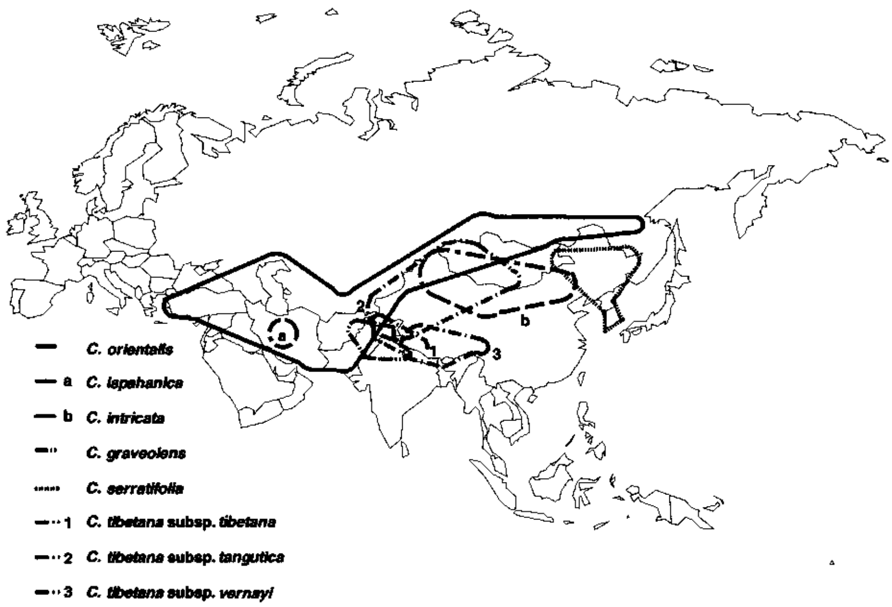
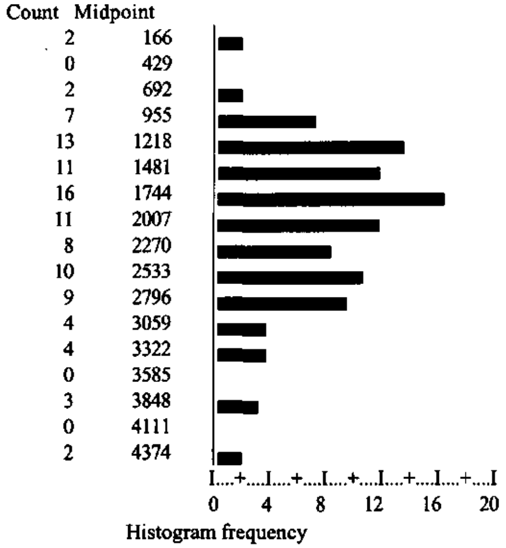
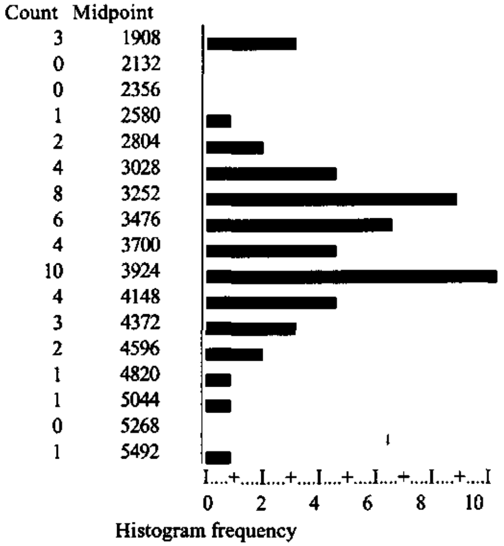


Figure 2.1. Tracks of taxa within *Clematis* sect. *Meclatis* (Spach) Baill.



Clematis orientalis L.
102 cases
Mean 2009.931 Std. Dev. 847.239



Clematis tibetana subsp. *vernayi* (C.E.C. Fischer) Grey-Wilson
50 cases
Mean 3639.800 Std. Dev. 737.429

Figure 2.2. Characteristic difference in range of altitudes between two taxa of *Clematis* sect. *Meclatis*.

There are mainly two types of habitats, to which taxa of the section *Meclatis* are adapted (figure 2.2):

- low-altitude, dry hills and lowlands, along streams and gorges on rocky slopes up to ±3.000 m above sea level;
- montane regions, along streams and gorges on rocky slopes, altitude ranging from ±2.500 m to ±5.000 m.

Speciation patterns coincide with borderlines between the above types of habitats. The mountain chains of Elburz (Iran), Hindu Kush, Chitral, Panjshir, Kashmir, Tibetan plateau, and Altai form effective geographical barriers between taxa of the section *Meclatis* (see also Ali, 1978; Endler, 1977; Good, 1964; Gould, 1984; Gould & Eldredge, 1977; Ledebour, 1830, 1841; Raven, 1979; Raven & Axelrod, 1974; Roche, 1974; Rosen, 1975, 1978; Schuster, 1976; Tarling, 1982). Where distribution areas may overlap, taxa are ecologically isolated principally by altitude. *C. orientalis* and *C. serratifolia* occur at lower altitudes; *C. graveolens* and *C. intricata* occur at lower altitudes, but inhabit montane regions as well (see further species descriptions); *C. tibetana* is dispersed in montane regions: its habitat ranges from 2.500-5.000 m above sea level.

One of the main problems of interpreting *Clematis* sect. *Meclatis* species is their response to particular habitats. If, for example, a species is adapted to montane regions, plants growing at higher altitudes show a dwarf, non-climbing habitus, whereas plants at lower ranges show vigorous growth trailing over other vegetation or rocky slopes. These different populations were often considered to be distinct species, but comparison in a single experimental garden, as was done at the AU Dept. of Plant Taxonomy's nursery, similarities are so great that conspecificity is obvious. This feature is not unique for this particular section of *Clematis*, but can be observed in other parts of the genus as well. The above phenomenon has misguided Grey-Wilson (1986, 1989) in his treatment of *Meclatis*. He described, besides *C. tangutica*, a separate species *C. pamiralaica*, with as only distinguishing character its non-climbing habit. According to Grey-Wilson, *C. pamiralaica* occurs only at higher altitudes. Plants from similar provenances in the Wageningen trial fields proved - unlike the single population grown at Kew - to climb as other populations.

Phenotypic plasticity is very difficult to interpret in terms of the delimitation between species and infraspecific taxa, since there is adaptive and non-adaptive components are involved (Morisset & Boudin, 1984), one cannot avoid studying it. Therefore, ecological effects on the plants have to be carefully examined, before concluding on species delimitation. Ranunculean species appear specially prone to environmentally induced variation; see the plant habit of e.g. *Aconitum*, *Anemone*, *Aquilegia*, *Delphinium*, and *Ranunculus*. In all these genera, classification tended to ignore such ecological responses, resulting in an excess of described species.

2.3. Morphological analysis of the section *Meclatis* (Spach) Baill.

Since there is a lot of confusion on the delimitation of species within the section *Meclatis*, a numerical analysis of the section has been undertaken, based on morphological characters in order to determine the discontinuities between species.

2.3.1. *Materials and methods*

For the morphological analysis of the section *Meclatis*, 206 herbarium specimens were selected. They were *a priori* assigned to species names (see table 2.1. and Appendix 1 available on disk).

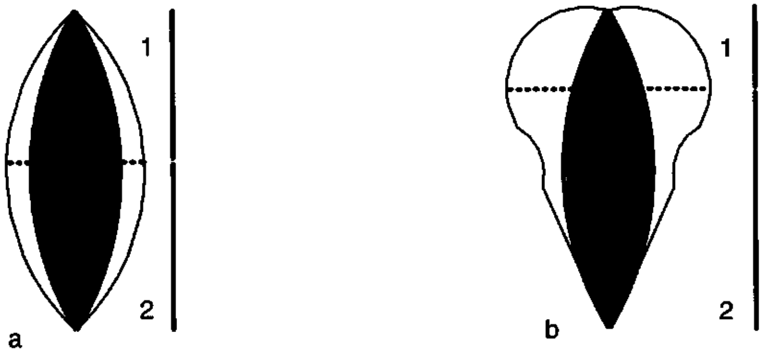
Table 2.1. A priori assignment of *Clematis* sect. *Meclatis* species used for morphological analysis to herbarium specimens used in the morphological analysis (for specimen details, see Appendix 1 available on disk).

- Nos. 1- 5, 126-127	*C. hilariae* Kovalevsk.
- Nos. 6- 11, 132-134	*C. serratifolia* Rehder
- Nos. 12- 24	*C. akebioides* Veitch
- Nos. 25- 51, 128-131	*C. glauca* Willd.
- Nos. 52- 66	*C. tangutica* (Maxim.) Korsh.
- Nos. 67- 81	*C. tibetana* Kuntze
- Nos. 82- 99	*C. graveolens* Lindl.
- Nos. 100-120	*C. vernayi* C.E.C.Fisch.
- Nos. 121-125	*C. vernayi/tangutica*
- Nos. 135-148	*C. ispahanica* Boiss.
- Nos. 149-206	*C. orientalis* L.

The list of herbarium specimens used is provided in Appendix 1 (available on disk). All specimens had been collected at natural sites, thus reflecting their natural phenotype. Following a standardised format both qualitative and quantitative characters were scored. Qualitative characters are presented in table 2.2.; quantitative characters in table 2.3. together with their frequency statistics (minimum and maximum value, median, mean standard deviation, variance, kurtosis and skewness of the curve). The ratio 1/2, as measure to characterise the position at which the greatest width is reached, is explained for tepals in figure 2.3. The ratio is also used for leaflets and achenes.

To analyse the data set, the software packages SPSS-PC4 and GENSTAT5 were used. In analysis procedures, both qualitative and quantitative characters were processed to create a similarity matrix. The contribution of a variate to the similarity is calculated as Euclidean distances between quantitative characters, as Jaccard's coefficient for binomial qualitative characters and as Manhattan distances for polynomial qualitative characters. The similarity matrix has been used to perform principal coordinate analysis and hierarchical clustering (average linkage). With the quantitative characters only (excluding the fruit characters as too many values are missing) principal component analysis and consequent hierarchical clustering (average linkage based on the principal component scores) have been performed. Only quantitative characters were used as the analysis is based on the correlation matrix of characters. Correlations between qualitative and quantitative characters are meaningless. Whether or not qualitative characters show general correlation has been analysed by χ^2-test and calculated significance scores (P).

After having established OTU's on morphological similarity, the groups scores for the qualitative characters were starting point for phylogenetic analysis using Hennig86, release 1.5. The restriction to the qualitative characters was based on the observation that most of the diagnostic characters were present in the qualitative data set. The OTU's were analysed by implicit enumeration, followed by 'bb' and successive weighting according to Farris (1988).



Ratio 1 / 2:

$$\frac{\text{Part of greatest length from apex until intersection with greatest width}}{\text{Part of greatest length from base until intersection with greatest width}}$$

epal forms used from fig. 1.28, but also applicable to other plant shapes

Figure 2.3. Ratio 1/2 as a measure to characterise the position of the greatest width.

Table 2.2. Qualitative characters used for the morphometric data matrix - *Vegetative parts*.

Character	Character state	Code
1 shape of young wood	round/angular	1
	costate	2
2 indumentum of young wood	glabrous	0
	pillose	1
3 shape of old wood	round/angular	1
	costate	2
4 stem habit	not climbing	0
	climbing	1
5 leaf blade structure	simple	0
	pinnate	1
	pinnate and bipinnate	2
	bipinnate	3
	ternate	4
	biternate	5
	triternate	6
6 petiole	glabrous	0
	pillose	1
7 leaflet shape	elliptic	1
	ovate	2
	ovate/lanceolate	3
	lanceolate	4
	lanceolate/linear	5
	linear	6
8 leaflet incision	entire	0
	± serrate	1
	± serrate/dentate	2
	± serrate/dentate/lobed	3
	± dentate/lobed	4
	± serrate/lobed	5
	serrate	6
	serrate/dentate	7
	serrate/dentate/lobed	8
	dentate/lobed	9
	serrate/lobed	10
	irregularly lobed	11
9 leaflet apex	acute	1
	acuminate	2
	mucronate	3
10 leaflet base	cordate	1
	cuneate	2
	angustate	3
11 indumentum of upper side of leaflets	glabrous	0
12 indumentum of ower surface of leaflets	glabrous	0
	at veins	1
	overall	2
13 indumentum of petiolule	glabrous	0
	at base	1
	overall	2
14 petiolule	not twining	0
	twining	1

Table 2.2. Qualitative characters used for the morphometric data matrix - *flower and fruit*

Character	**Character state**	**Code**
15 **flower position** (1)	terminal	1
	terminal and axillary	2
	axillary	3
16 **flowers per infl.**	many	1
	one	2
17 **flower stalk**	straight	1
	nodding at the top	2
	regularly bent	3
18 **bracts**	absent	0
	present	1
19 **bract shape**	simple/entire	1
	simple/lobed	2
	composite	3
20 **flower position (2)**	pending	1
	upright	2
21 **flower shape**	open/flat	1
	trumpet-shaped	2
	campanulate	3
	tubulate	4
22 **flowering**	abundant in a short time	1
	profuse (longer period)	2
	few flowers	3
23 **tepals**	free	0
	± overlapping, imbricate	1
	margins touching, valvate	2
24 **tepal curvature**	not recurved	0
	recurved	1
25 **tepal shape**	elliptic	1
	ovate	2
	ovate/lanceolate	3
	lanceolate	4
	lanceolate/lineariform	5
	lineariform	6
26 **tepal texture**	herbaceous	0
	fleshy	1
27 **tepal margin**	flat	1
	exduplicate	2
	induplicate	3
28 **tepal apex**	blunt	1
	acute	2
	acuminate	3
	mucronate	4
29 **tepal base**	cuneate	1
	angustate	2
30 **indumentum of tepals abaxial**	glabrous	0
	pilose	1
31 **indumentum of tepals adaxial**	glabrous	0
	pilose	1
32 **indumentum of tepal margin**	glabrous	0
	lanate	1
33 **gradual transition from tep. to stamens**	absent	0
	present	1
34 **indumentum of filaments**	absent	0
	at base	1
	overall	2
35 **filaments**	not dilatate	0
	dilatate	1
36 **indumentum of ovary**	absent	0
	present	1
37 **indumentum of style**	absent	0
	present	1
38 **shape of achene**	rhomboid	1
	ovate	2
	obovate	3
39 **achene lustre**	not shiny	0
	shiny	1
40 **achene surface**	not ribbed	0
	ribbed	1
41 **pericarp**	woody	1
	fibrous	2

Table 2.3. Quantitative characters used for the morphometric data matrix. (measures in mm; maximum number of observed specimens 206; list of observed specimens in Appendix 1 available on disk).

Character		Category	Minimu	Maximum	Median	Mean	S. dev.	Var.	Kurtosis	Skewness	N	Remarks
Diameter of young twigs	1	measure	1	5	2	2.5	0.7	0.5	0.2	0.5	206	
Number of leaflets per leaf	2	number	3	35	12	13.1	6.5	42.6	0.2	0.9	193	
Petiole length	3	measure	6	106	47	48.8	16.8	282.7	0.2	0.4	198	
Petiole diameter	4	measure	0.5	2.5	1	1.2	0.4	0.1	0.2	0.8	198	
Leaflet length	5	measure	10	75	32	34.7	12.5	156.2	-0.2	0.6	198	
Leaflet width	6	measure	2	49	15	17.1	10.1	101.0	0.9	1.1	198	
Leaflet ratio 1/2	7	ratio	0.9	14	2	2.7	2.0	4.0	11.3	3.0	198	see figure 2.3
Petiolule length	8	measure	2	45	12.5	14.8	7.4	55.0	0.9	1.0	198	
Petiolule diameter	9	measure	0.5	2	1	1	0.3	0.1	0.9	0.3	198	
Number of flowers per infl.	10	number	1	27	3	4.9	3.9	15.2	5.8	2.0	197	
Peduncle length	11	measure	0	97	21.5	28.2	21.3	453.7	0.1	0.9	190	0: inflorescence sessile
Pedicel length	12	measure	13	320	45.5	52.9	32.8	1072.6	24.2	3.6	190	
Number of bracteoles per br.	13	number	0	30	1	1.8	2.4	5.7	104.3	9.0	191	0: bract simple, but reduced
Bract stalk diameter	14	measure	0	36	6	8.5	7.3	52.8	3.5	1.8	188	0: bract sessile
Number of tepals per flower	15	number	4	5	4	4.0	0.1	0.0	59.9	7.8	190	
Tepal length	16	measure	9	35	17	17.7	5.3	28.3	0.0	0.6	189	
Tepal width	17	measure	2	21	7	7.2	3.1	9.9	1.2	0.8	188	one specimen incomplete tepals
Tepal ratio 1/2	18	ratio	0.3	5	1.2	1.4	0.7	0.5	7.1	2.3	189	see figure 2.3
Number of stamina	19	number	20	70	30	34.7	9.5	90.8	1.8	1.1	183	
Filament length	20	measure	2	10	5	5.6	1.6	2.5	0.5	0.7	186	
Anther length	21	measure	1	5	2.5	2.6	0.7	0.5	0.3	0.7	186	
Number of pistils	22	number	30	150	100	81.0	25.7	659.5	-1.0	-0.6	183	
Ovary length	23	measure	1	5	1	1.0	0.3	0.1	145.8	11.7	184	
Style length	24	measure	3	11	6	6.3	1.5	2.3	0.0	0.4	184	
Stigma length	25	measure	1	3	1	1.3	0.5	0.2	-0.2	1.2	184	
Achene length	26	measure	2	6	3	2.9	0.8	0.6	2.4	1.0	97	excluded from factor analysis
Achene width	27	measure	1	3	2	1.7	0.5	0.2	0.2	0.7	97	excluded from factor analysis
Achene ratio 1/2	28	ratio	0.2	2.5	1	1.1	0.4	0.1	4.0	1.4	96	see figure 2.3; excluded from factor analysis
Elongate style length	29	measure	14	86	30	32.4	12.5	155.1	4.7	1.6	97	excluded from factor analysis

2.3.2. *Results*

As the list of scored characters, presented in tables 2.2. and 2.3. is the general list used for all *Clematis* observations, some characters did not show any variation within sect. *Meclatis*. These were omitted from further analysis: indumentum of tepal margin (always lanate), indumentum of ovary (always present), indumentum of style and achenes shiny / dull (they are all dull). The same holds for number of tepals per flower: within section *Meclatis* this number is 4, only occasionally 5. The χ^2-test on general correlation between qualitative characters showed that most characters are generally correlated except for the shape of the old wood and the bract character; the latter character was omitted as the absence of bracts in herbarium specimens was in some cases artificial.

2.3.2.1. Factor analysis

Factor analysis was carried out with the quantitative characters in table 2.3. apart from the fruit characters. Factor loadings, and scores are presented in figure 2.4; the factor scores also in table 2.4.

Table 2.4. Character scores per factor by factor analysis. Character numbers, see table 2.3

Factor▸ ▾Character	Factor 1	Factor 2	Factor 3
1	-0.132	0.054	0.061
2	-0.004	-0.023	0.840
3	-0.205	0.758	0.011
4	0.257	0.375	0.069
5	-0.049	0.618	-0.445
6	0.027	0.523	-0.366
7	-0.010	-0.081	-0.035
8	0.037	0.852	-0.310
9	0.260	0.356	0.188
10	-0.514	0.099	-0.381
11	-0.363	-0.058	-0.690
12	0.111	-0.116	0.317
13	0.113	0.134	0.198
14	0.055	-0.120	-0.051
15	0.815	0.000	0.029
16	0.448	0.312	0.191
17	0.119	0.022	-0.068
18	0.107	-0.112	0.674
19	0.783	-0.073	-0.064
20	-0.104	0.083	-0.050
21	0.580	-0.015	0.462
22	0.119	-0.173	-0.064
23	0.638	0.038	-0.009
24	0.072	0.223	0.108
25	0.669	-0.061	0.046

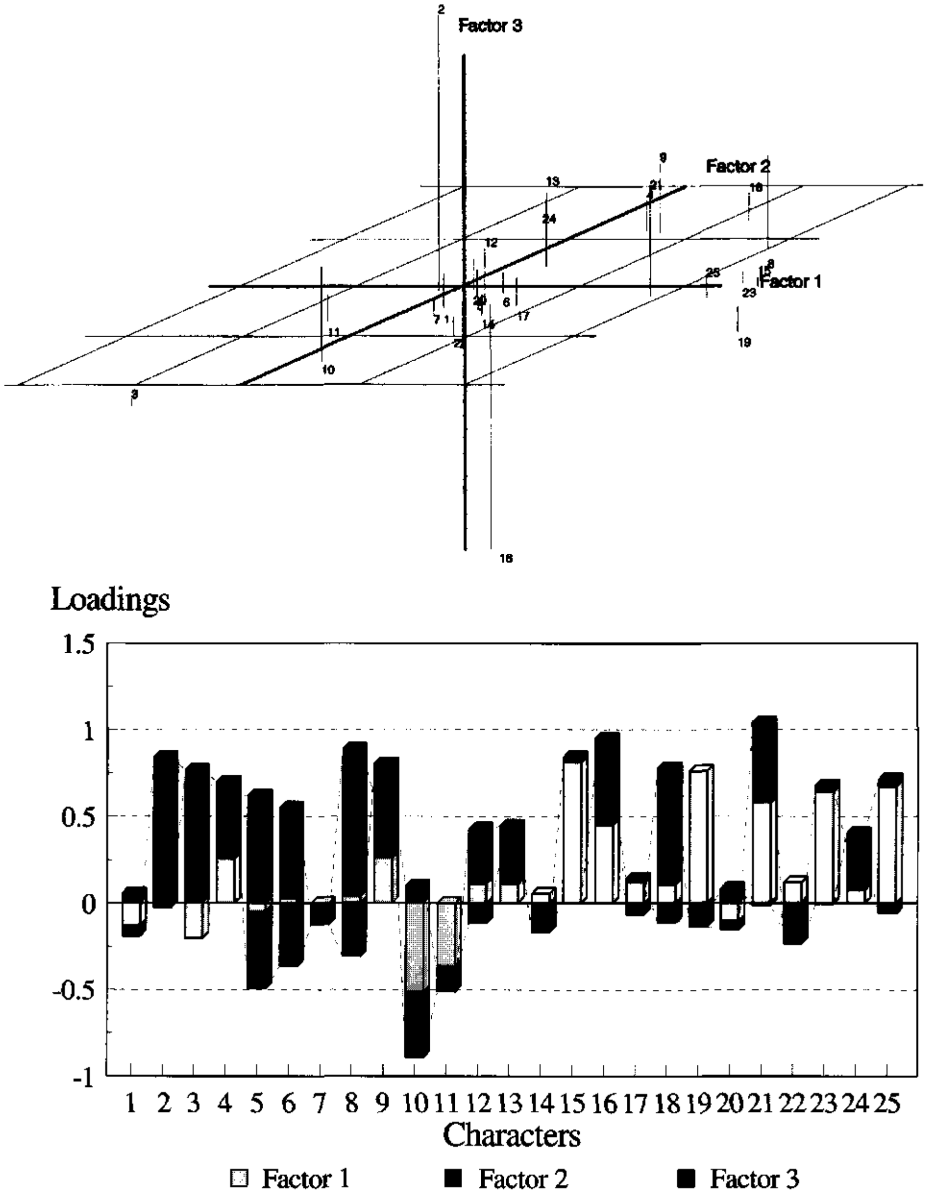


Figure 2.4. Factor diagram and loadings for the first three factors (loadings per character per factor next to each other and cumulative)in separate with the quantitative characters 1-25 of table 2.3.

2.3.2.2. Principal coordinate analysis

Starting from an OTU by OTU matrix of distances, principal coordinate analysis has been carried out to reveal distances between specimens with the aid of a set of orthogonal variates (principal coordinates). The first five principal coordinates explain 48.9% of the variation, see table 2.5.

Table 2.5. Characteristics of the first 5 principal coordinates.

P.C.	Latent root	Expl. variation	Main contribution of characters
1	7.2059	15.01%	indumentum characters of vegetative parts flower stalk/flower position tepal morphology
2	6.6469	13.85%	apex of leaflet/leaflet width shape of flowers/blooming/number of flowers per inflorescence tepals recurved/indumentum of tepals downside/tepal length number of pistils
3	3.5402	7.37%	tepal ratio 1 / 2 filament dilatate
4	3.2275	6.72%	petiolule length achene length
5	2.8584	5.95%	base of leaflet number of bracteoles per bract/ bract stalk length style length

The scores of specimens along the first 5 principal coordinates result in 10 plots, of which the four with principal coordinate 1 along the x-axis are displayed in figure 2.5. From this displays, it can be concluded that:

- Along the first principal coordinate specimens 136 - 148 are separate from the other specimens;
- Along the second principal coordinate specimens are gradually spread over the plot;
- Along the third principal coordinate specimens 82 - 99 and 177 are more or less separate from the rest of specimens in a scattered group;
- Along the fourth principal coordinate specimens 61, 116 and 140 are isolated from the rest;
- Along the fifth principal coordinate no clear groups but individual outliers are separated.

Specimens separated along the first principal coordinate must have a.o. distinct characteristics with respect to the indumentum of vegetative parts, flower stalk and flower position, which are, however, all characters that show high phenotypic plasticity. Along this axis separated specimens 136 - 148 have been previously labelled *Clematis ispahanica* Boiss. Principal coordinate 2 show much contribution of flower and flowering characteristics. They are relatively scattered over the relevant plots, hence explaining why these characters have not contributed much to the classification of *Clematis* sect. *Meclatis*. Principal coordinate 3 has one of its contributions by tepal ratio 1/2 (figure 2.3), which affects the flower morphology in its general appearance. As there are no groups of specimens distinguished by this coordinate, special flower morphology does not contribute to the distinction between groups. The third principal axis has further received its main contribution from filament dilatation. Along this axis specimens 82 - 99 appear to be separated in a scattered group. These specimens have been previously labelled *Clematis graveolens* Lindl. The fourth and fifth principal coordinate do not provide any clear separations between observed specimens. Most groups in the plots are highly overlapping.

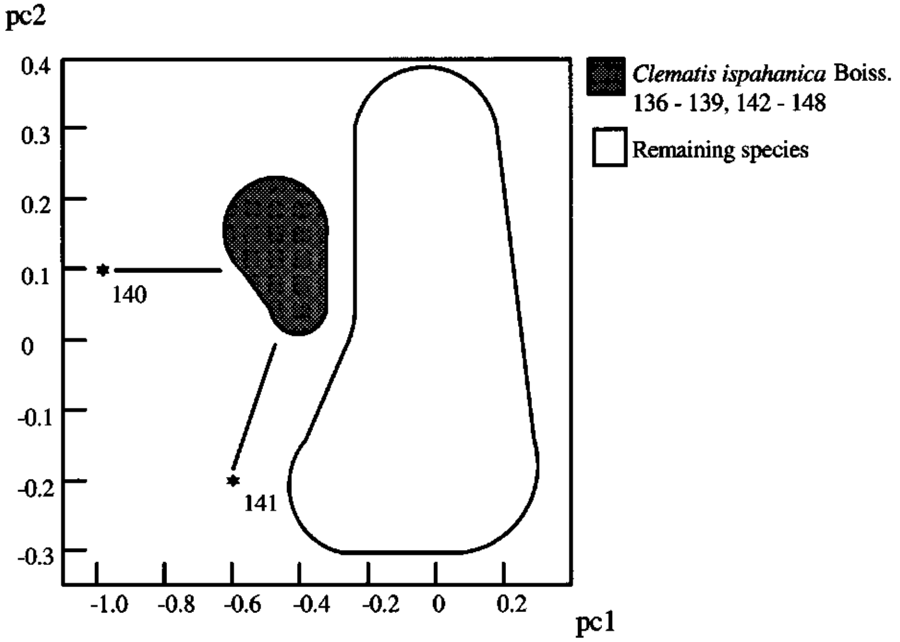
2.3.2.3. Cluster analysis

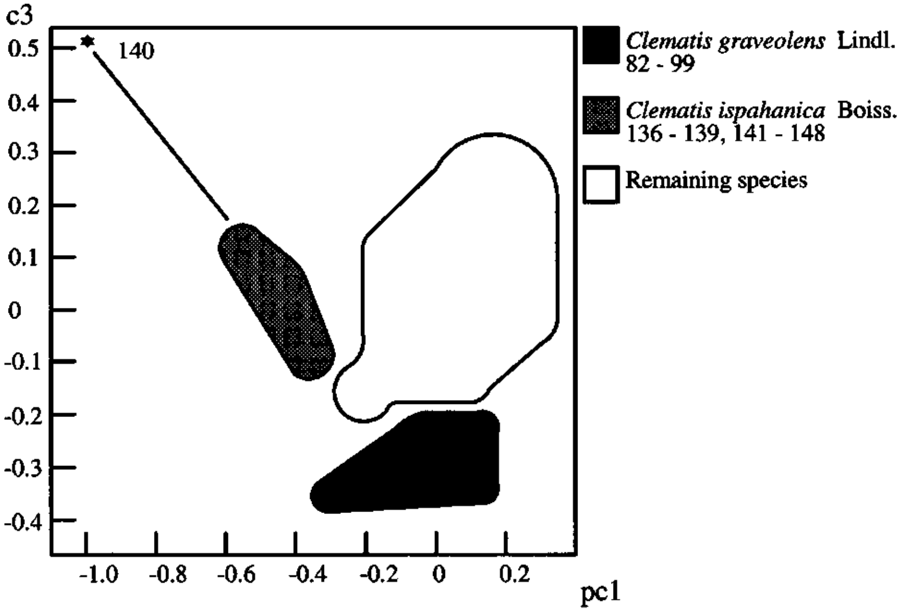
In search of subdivisions of the 206 specimens three further approaches have been applied. Firstly, as it is mathematically the most pure agglomerative device, the single linkage approach has been applied to the data to produce a nonrooted, minimum spanning tree (Gower & Ross, 1969). The minimum spanning tree is actually not a tree but a network connecting all individuals by a set of straight lines joining pairs of points, whose lengths are equal to the dissimilarities between individuals, and whose sum is minimal (Chatfield & Collins, 1980). The minimum spanning tree is helpful in revealing groups between individuals, whereas other clustering devices tend to impose a phylogenetic structure on the individual concerned rather than revealing their mutual relationship. The structure of the minimum spanning tree for the 206 *Meclatis* specimens is presented in figure 2.6. This figure confirms the conclusions from the principal coordinate analysis that *C. graveolens* and *C. ispahanica* appear to be separate groups. Furthermore, *C. orientalis* results as a rather cohesive group, and rest groups appear combining parts of the *a priori* groups *C. akebioides*, *C. glauca*, *C. hilariae*, *C. tangutica*, *C. tibetana* and *C. vernayi*. To visualise the data in a cluster dendrogram, the average linkage routine was applied to the data to stress between group differences. The dendrogram is presented in figure 2.7. This dendrogram is in agreement with the minimum spanning tree where, again, *C. ispahanica* and to a lesser extent *C. graveolens* are separated. *C. serratifolia* is partially separated, whereas *C. orientalis* is largely separated. The rest groups, consisting of the other *a priori* assigned species, appear scattered throughout the dendrogram. The overall similarity (± 60%) within the section explains the incomplete separation of groups by the average linkage clustering device.

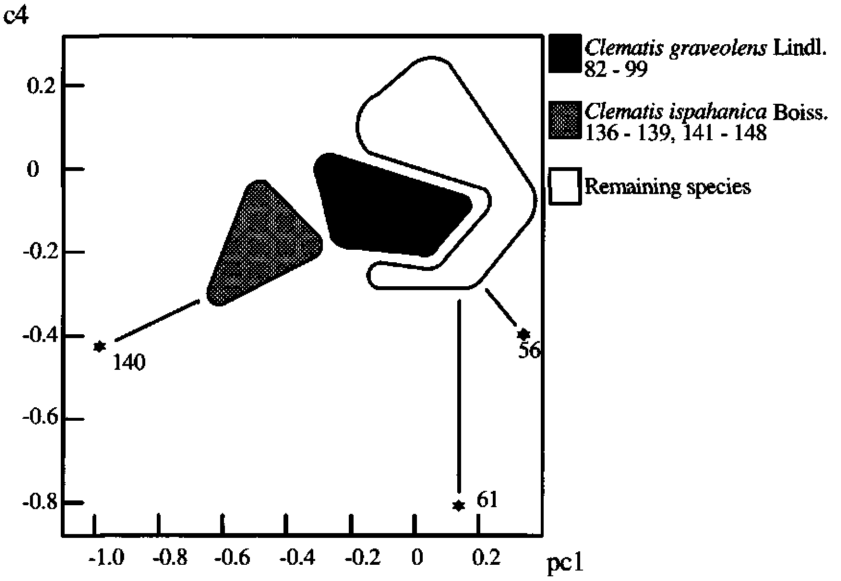
Based on the correlation matrix of quantitative characters without the fruit characteristics (these characters had too many missing values), principal components (a derived set of orthogonal variates) have been calculated. With the aid of this set of variates, again a cluster analysis (average linkage) has been carried out again, see figure 2.8. This analysis shows a further mixing up between groups due to the rather high overall similarity.

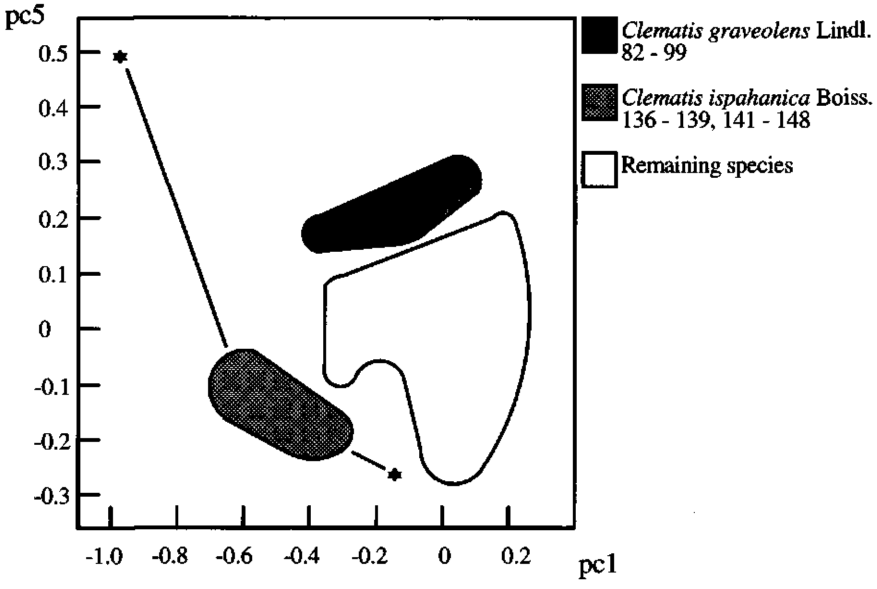
Figure 2.5. Principal coordinate scatter plots for 206 *Meclatis* specimens (Appendix 1 available on disk).

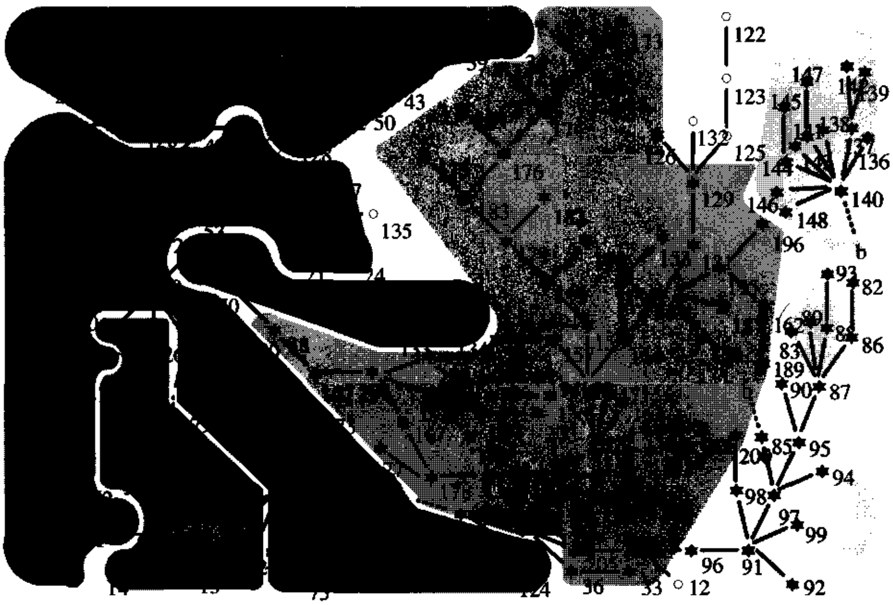
a	pc 1 vs. pc 2
b	pc 1 vs. pc 3
c	pc 1 vs. pc 4
d	pc 1 vs. pc 5


pc2
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-1.0
-0.8
-0.6
-0.4
-0.2
0
0.2
pc1
140
141
Clematis ispahanica Boiss. 136 - 139, 142 - 148
Remaining species


c3
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-1.0
-0.8
-0.6
-0.4
-0.2
0
0.2
pc1
140
Clematis graveolens Lindl. 82 - 99
Clematis ispahanica Boiss. 136 - 139, 141 - 148
Remaining species


c4
0.2
0
-0.2
-0.4
-0.6
-0.8
140
56
61
-1.0
-0.8
-0.6
-0.4
-0.2
0
0.2
pc1
Clematis graveolens Lindl.
82 - 99
Clematis ispahanica Boiss.
136 - 139, 141 - 148
Remaining species


pc5
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-1.0
-0.8
-0.6
-0.4
-0.2
0
0.2
pc1
Clematis graveolens Lindl.
82 - 99
Clematis ispahanica Boiss.
136 - 139, 141 - 148
Remaining species



Clematis graveolens Lindl.

■ *Clematis intricata* Bunge

▨ *Clematis ispahanica* Boiss.

▨ *Clematis orientalis* L.

■ *Clematis serratifolia* Rehder

■ *Clematis tibetana* Kuntze

✱ Specimens (numbers, see App. 1 on disk available)

○ Specimens with discutable systematic assignment

Figure 2.6. Minimum spanning tree of 206 *Meclatis* specimens; distances in the figure are presented as uniform (see for similarities Appendix 2 available on disk).

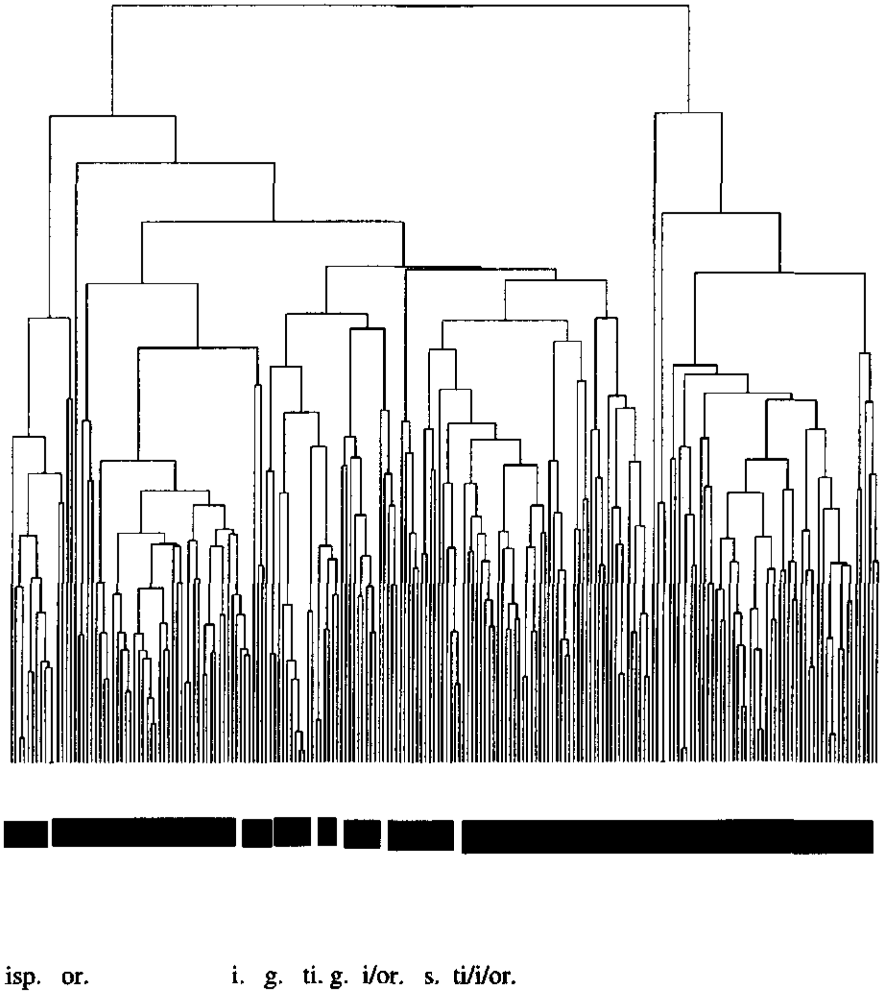


Figure 2.7. Cluster dendrogram of 206 *Clematis* sect. *Meclatis* specimens based on qualitative and quantitative characters and using the average linkage criterion.
isp.= *C. ispahanica*; or.= *C. orientalis*; i.= *C. intricata*; g.=*C. graveolens*; ti.=C. tibetana; i/or.= *C. intricata* with some *C. orientalis* specimens; s.=*C. serratifolia*; ti/i/or= *C. tibetana* with some specimens of *C. intricata* and *C. orientalis*.

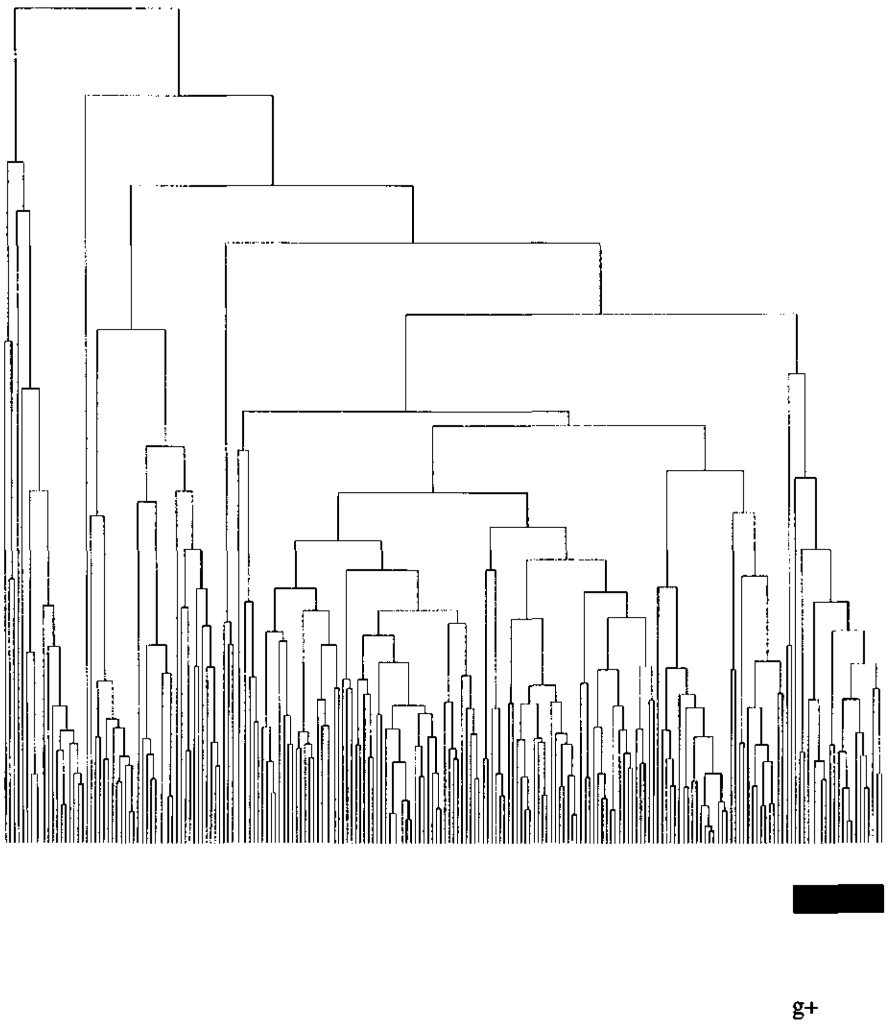


Figure 2.8. Cluster dendrogram (average linkage) using principal components as set of variates derived from the correlation matrix of quantitative characters the fruit characters excluded. g+=*C. graveolens*+ some *C. tibetana* specimens.

Table 2.6. Legend to figure 2.7.

Legend to figure 2.7															
O	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**
1	139	27	181	53	149	79	92	105	43	131	190	157	106	183	21
2	136	28	172	54	193	80	93	106	41	132	191	158	109	184	23
3	138	29	174	55	166	81	82	107	42	133	197	159	52	185	20
4	141	30	151	56	179	82	89	108	202	134	25	160	58	186	16
5	137	31	163	57	182	83	90	109	37	135	26	161	59	187	31
6	142	32	161	58	28	84	95	110	203	136	32	162	74	188	108
7	143	33	158	59	29	85	88	111	204	137	33	163	101	189	107
8	144	34	152	60	30	86	86	112	160	138	22	164	103	190	115
9	146	35	159	61	12	87	87	113	167	139	18	165	24	191	117
10	140	36	186	62	96	88	13	114	192	140	14	166	121	192	17
11	148	37	154	63	198	89	83	115	201	141	15	167	124	193	114
12	145	38	180	64	84	90	45	116	38	142	1	168	120	194	64
13	147	39	169	65	85	91	19	117	11	143	76	169	78	195	60
14	135	40	188	66	94	92	105	118	8	144	113	170	112	196	62
15	184	41	200	67	97	93	2	119	9	145	77	171	67	197	54
16	27	42	153	68	98	94	127	120	7	146	79	172	44	198	102
17	177	43	156	69	91	95	3	121	10	147	119	173	47	199	104
18	178	44	164	70	99	96	4	122	205	148	75	174	40	200	110
19	68	45	171	71	133	97	5	123	206	149	100	175	46	201	122
20	185	46	195	72	134	98	34	124	48	150	118	176	53	202	123
21	175	47	196	73	71	99	39	125	51	151	111	177	72	203	125
22	157	48	150	74	73	100	126	126	36	152	116	178	49	204	132
23	176	49	165	75	69	101	128	127	130	153	63	179	66	205	129
24	183	50	162	76	70	102	6	128	194	154	57	180	55	206	131
25	155	51	189	77	80	103	50	129	170	155	56	181	65		
26	173	52	187	78	81	104	35	130	199	156	61	182	168		

O = Order; S = Specimen

Table 2.6. Legend to figure 2.8.

Legend to figure 2.8															
O	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**	**O**	**S**
1	4	27	149	53	110	79	173	105	178	131	38	157	13	183	89
2	3	28	155	54	127	80	137	106	176	132	105	158	19	184	83
3	12	29	154	55	117	81	190	107	180	133	11	159	6	185	92
4	124	30	156	56	141	82	203	108	189	134	57	160	34	186	82
5	65	31	164	57	9	83	166	109	199	135	62	161	49	187	84
6	14	32	75	58	136	84	193	110	194	136	23	162	39	188	94
7	68	33	183	59	147	85	145	111	198	137	28	163	40	189	119
8	56	34	191	60	153	86	162	112	201	138	29	164	48	190	66
9	63	35	177	61	179	87	205	113	139	139	133	165	51	191	116
10	118	36	181	62	171	88	170	114	200	140	8	166	46	192	59
11	55	37	140	63	186	89	187	115	30	141	7	167	47	193	64
12	109	38	196	64	197	90	204	116	37	142	10	168	41	194	90
13	52	39	185	65	172	91	182	117	35	143	80	169	42	195	111
14	58	40	195	66	192	92	61	118	43	144	81	170	44	196	93
15	107	41	18	67	158	93	206	119	126	145	67	171	25	197	87
16	102	42	72	68	165	94	160	120	128	146	120	172	101	198	88
17	54	43	22	69	138	95	157	121	125	147	45	173	1	199	91
18	60	44	70	70	146	96	161	122	121	148	69	174	71	200	85
19	115	45	32	71	143	97	150	123	122	149	106	175	103	201	96
20	151	46	76	72	142	98	132	124	123	150	113	176	17	202	95
21	2	47	74	73	144	99	188	125	131	151	114	177	73	203	97
22	100	48	20	74	184	100	202	126	5	152	31	178	78	204	98
23	175	49	15	75	148	101	174	127	26	153	108	179	112	205	86
24	152	50	21	76	135	102	130	128	129	154	50	180	77	206	99
25	167	51	53	77	168	103	159	129	134	155	24	181	79		
26	169	52	27	78	36	104	163	130	104	156	16	182	33		

O = Order; S = Specimen

2.3.2.4. Phylogenetic analysis

From the morphometric analysis, it is clear that not all *a priori* groups are sufficiently distinguishable, but both *C. ispahanica* and *C. graveolens* appear to be separate groups. To a lesser extent, the same holds for *C. serratifolia* and *C. orientalis*. The rest group is invariably mutually intermixed and occasionally intermixed with the above species. This leaves us with rest groups of parts of *C. akebioides*, *C. glauca*, *C. hilariae*, *C. tangutica*, *C. tibetana* and *C. vernayi*, of which the relatedness to *C. orientalis* has been variedly stressed or neglected.

Phylogenetic analysis has been carried out to examine the relation between OTU's in view of polarity of character scores. *C. ispahanica* has been postulated as outgroup by its character states "perennial or subshrub" and "multi-flowered both axillary and terminal cymes, forming thyrsoid synflorescences". Implicit enumeration resulted in 10 equally parsimonious cladograms which were further reduced to one cladogram after succesive weighting according to Farris (1988). The data matrix is presented in table 2.7., the resulting cladogram in figure 2.9. and the corresponding ancestral nodes with their character states in table 2.7.

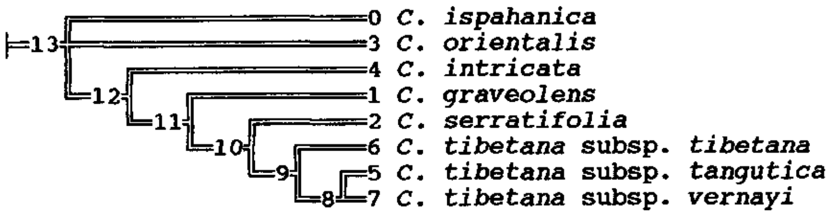


Figure 2.9. Cladogram of *Clematis* sect. *Meclatis*; the only one after successive weighting according to Farris (1988). For character states at ancestral nodes, see table 2.7.

Table 2.7. Data matrix of *Clematis* sect. *Meclatis*, as used for phylogenetic analysis, see figure 2.9.

Taxa ▾Character	0	1	2	3	4	5	6	7
1	1	2	2	2	2	2	2	2
2	0	1	0	1	1	1	1	1
4	0	1	1	1	1	1	1	1
5	1	3	5	1	3	3	3	1
6	0	1	0	1	1	1	1	1
7	5	3	3	3	4	3	5	2
8	4	4	5	4	4	3	2	4
9	2	1	1	2	1	1	1	1
10	3	1	3	2	3	3	3	3
12	0	0	0	1	0	0	0	1
13	0	1	0	1	0	1	1	1
14	0	1	1	1	1	1	1	1
15	2	3	3	2	3	3	3	3
16	1	1	1	1	1	2	1	2
17	1	2	2	2	2	2	2	2
19	1	3	1	1	2	3	1	3
20	2	1	1	1	1	1	11	1
21	1	1	1	1	1	3	3	3
22	1	3	2	1	2	3	2	2
23	0	2	2	2	2	2	2	2
24	0	0	0	1	0	0	0	0
25	5	1	2	4	3	3	2	1
26	0	0	0	0	0	0	0	1
27	3	1	3	3	3	3	3	3
29	2	1	1	1	1	1	1	1
30	1	1	1	1	0	0	1	1
31	0	0	0	1	0	0	0	0
34	0	2	2	2	2	2	2	2
35	1	0	1	1	1	1	1	1
38	1	1	1	1	1	2	1	1
40	1	1	0	1	1	0	0	0
41	1	1	2	2	2	2	2	2

Legend: Character numbers and state coding, see table 2.1. Character 3 has been left out the analysis because of too many missing values; characters 11, 18, 32, 33, 36, 37 and 39 are excluded for showing no variation.

Table 2.8. Character states at ancestral nodes of the cladogram of figure 2.9.

Ancestors ► **▼ Characters**	**8**	**9**	**10**	**11**	**12**	**13**
1	2	2	2	2	2	2
2	1	1	1	1	1	1
4	1	1	1	1	1	1
5	3	3	3	3	3	3
6	1	1	1	1	1	1
7	3	3	3	3	34	34
8	34	34	4	4	4	4
9	1	1	1	1	1	2
10	3	3	3	3	3	3
12	0	0	0	0	0	0
13	1	1	01	01	01	01
14	1	1	1	1	1	1
15	3	3	3	3	3	2
16	2	1	1	1	1	1
17	2	2	2	2	2	2
19	3	12	12	12	12	1
20	1	1	1	1	1	1
21	3	3	1	1	1	1
22	2	2	2	2	2	1
23	2	2	2	2	2	2
24	0	0	0	0	0	0
25	2	2	2	2	3	4
26	0	0	0	0	0	0
27	3	3	3	3	3	3
29	1	1	1	1	1	1
30	1	1	1	1	1	1
31	0	0	0	0	0	0
34	2	2	2	2	2	2
35	1	1	1	1	1	1
38	1	1	1	1	1	1
40	0	0	0	1	1	1
41	2	2	2	2	2	2

Legend: Character numbers and state coding, see table 2.1.; character weighting (char. - weight): 1 - 10; 2 - 0; 3 - 10; 4 - 3; 5 - 0; 6 - 0; 7 - 0; 8 - 10; 9 - 0; 10 - 10; 11 - 0; 12 - 0; 13 - 10; 14 - 10; 15 - 10; 16 - 10; 17 - 10; 18 - 1; 19 - 10; 20 - 10; 21 - 3; 22 - 10; 23 - 10; 24 - 4; 25 - 10; 26 - 10; 27 - 10; 28 - 10; 29 - 0; 30 - 10; 31 - 10; 32 - 10; 33 - 10; 34 - 10; 35 - 10; 36 - 10; 37 - 10; 38 - 10; 39 - 10; 40 - 0.

Character 3 has been left out the analysis because of too many missing values; characters 11, 18, 32, 33, 36, 37 and 39 are excluded for showing no variation.

2.3.2.5. Conclusions

The numerical analysis alone may support the view to lump the rest group together into one aggregate species. Inconsistent assignment to the 6 *a priori* groups is further evidence. The phylogenetic analysis, however, shows that the result would then be a polyphyletic group or the lumping of *C. graveolens* and *C. serratifolia* into the rest group. None of these options is acceptable, as both solutions will result in the original situation: one or two very variable species with implicit discontinuities.

If we also consider the geographic distribution patterns of specimens (see figure 2.1), the classification into six species is supported by the combination of the minimum spanning tree, the distribution data and the cladogram. Furthermore, the above combination supports the merger of *C. tangutica*, *C. tibetana* and *C. vernayi* as one species. As they have in common their preference to higher altitudes in montane regions and show at the same time their own geographic distribution, they are maintained at the subspecific rank following common practice as to subspecies (Meikle, 1957; Fuchs, 1958; cf. Hamilton & Reichards, 1992). The resulting classification for the section *Meclatis* is:

Clematis orientalis L.
Clematis graveolens Lindl.
Clematis intricata Bunge
Clematis ispahanica Boiss.
Clematis serratifolia Rehder
Clematis tibetana Kuntze
    subsp. *tibetana*
    subsp. *tangutica* (Maxim.) Brandenburg
    subsp. *vernayi* (C.E.C.Fisch.) Grey-Wilson

The *a priori* assumed species *C. akebioides* and *C. hilariae* were scattered throughout dendrograms and the minimum spanning tree. Their discriminating characters appeared to be highly variable, their description being based on a small set of specimens from only a few locations. They are therefore not maintained at any rank. *C. akebioides* is largely classified under *C. tibetana* subsp. *tibetana* and subsp. *tangutica*; *C. hilariae* under *C. intricata*. The nomenclatural consequences will be dealt with in section 2.4.

2.4. Species descriptions

2.4.1. Key to the species of *Clematis* sect. *Meclatis*

1a Plant habit shrubby or herbaceous .... ***C. ispahanica*** 2.4.5.

1b Plant habit woody climbers ***2***

2a Filaments ciliate .... ***C. graveolens*** 2.4.3.

2b Filaments dilatate ***3***

3a Leaves commonly biternate, leaflets regularly serrate/dentate .... ***C. serratifolia*** 2.4.6.

3b Leaflets variably in shape, not regularly incised ***4***

4a Inflorescences (1-)3-7 flowers, tepals later recurved ...... ***C. orientalis*** 2.4.2.

4b Inflorescences 1-3 flowers, tepals later spreading ***5***

5a Inflorescences usually with 3 open, flat flowers, tepals herbaceous .... ***C. intricata*** 2.4.4.

5b Inflorescences with 1-3 broadly to narrowly campanulate flowers ***6***

6a Inflorescences 3 flowers, narrowly campanulate, tepals not fleshy .... ***C. tibetana*** **subsp.** ***tibetana*** 2.4.7.

6b Inflorescences 1(-3) flowers, narrowly campanulate, tepals thin, fleshy .... ***C. tibetana*** **subsp.** ***tangutica*** 2.4.7.

6c Inflorescences 1(-3) flowers, broadly campanulate, tepals thick, fleshy .... ***C. tibetana*** **subsp.** ***vernayi*** 2.4.7.

2.4.2. *Clematis orientalis* L.[1]

2.4.2.1. Lectotypification of *Clematis orientalis* L.

The name *C. orientalis* dates back to the first edition of Linnaeus' *Species Plantarum* (Linnaeus, 1753: 543). The protologue consists of Linnaeus' diagnostic phrase-name, two earlier polynomials cited in synonymy and an indication of the type locality. The Linnaean diagnosis "*Clematis foliis compositis: foliolis incisis angulatis lobatis cuneiformibus*" is not taken from any of his earlier works.

In the Linnaean Herbarium (LINN), one specimen has been assigned by Linnaeus to *C. orientalis* (LINN 712.7). Both annotations on this sheet "orientalis" and - on the verso - "Clematis orientalis apii folio fl. reflexo T.C.", have been made by Linnaeus. When using specimens for descriptions in *Species Plantarum* ed. I, Linnaeus almost invariably indicated on the sheets the number under which he described the species. Such a reference is absent in the annotations on LINN 712.7. It was therefore almost certainly added to his herbarium after 1753. Consequently, it cannot be regarded as a syntype, nor as a putative choice of lectotype. In the Linnaean Herbarium at Stockholm, there is one specimen under the name *C. orientalis* (IDC fiche no. 224 5). On the verso of this sheet there is an annotation "Dahl a Linné P" in Dahl's handwriting. This specimen was apparently received by Anders Dahl from Linnaeus. However, the sheet is unannotated by Linnaeus and there is no evidence that he regarded it as belonging to this taxon or that he had studied it before publishing his *Species Plantarum* account. It, therefore, is not a syntype and must be excluded from consideration as a possible lectotype. Remarkably, two specimens of *C. orientalis* are present in the Hortus Siccus Cliffortianus (BM), although Linnaeus did not describe the species in *Hortus Cliffortianus* (1738). These specimens must either have been added to Clifford's Herbarium after Linnaeus studied it, or he may have overlooked these specimens when writing his *Hortus Cliffortianus* account. We have not been able to locate any other relevant specimens in any of the other

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[1] The paragraphs 2.4.2.1., 2.4.2.2. and 2.4.2.3. have been largely based on the earlier publication by Brandenburg et al. (1987).

general Linnaean herbaria (i.e. BM, H, MW, SBT, UPS). The first synonym cited in the protologue of *C. orientalis* is "*Clematis orientalis, apii folio, flore e viridi-flavescente posterius reflexo*", as a slightly altered phrase-name from the *Corollarium Institutionem* by Tournefort (1703): "*Clematitis Orientalis, Apii folio, flore e viridi flavescente, posterius reflexo*". In 1738, Linnaeus visited Paris. He may possibly have seen the four specimens of *C. orientalis* in Tournefort's Herbarium (P-TO). There is, however, no positive evidence that he thoroughly studied Tournefort's Herbarium (Stearn, 1957) and so we exclude these four specimens from consideration for lectotypification.

The second synonym cited under *C. orientalis* is "*Flammula scandens, apii folio glauco*" from the *Hortus Elthamensis* of Dillenius (1732). This unaltered quotation refers to a phrase-name, a description and an illustration. Linnaeus' own copy of this book, which he used in preparing *Species Plantarum*, is now at Jena (JE) having been sold by Smith (Schmidt, 1965). Two beautifully coloured copies, executed by Dillenius himself, are at Oxford (OXF) and at London (BM). Since there is no positive evidence that Linnaeus relied on specimens still in existence for his description of *C. orientalis*, the plate "*Flammula scandens, apii folio glauco*", Dill. Elth. 144, t. 119, f. 145 (1732) is hereby designated as the lectotype of *C. orientalis* (figure 2.10).

Figure 2.10. Dillenius Hortus Elthamensis 144, t. 119, f. 145 (1732). Lectotype of *C. orientalis* L.

Figure 2.11. Dillenian specimen 2868 (OXF). Typotype of *C. orientalis* L. (photograph by courtesy of OXF).

2.4.2.2. The Typotype of *Clematis orientalis* L.

If the choice of an illustration as lectotype is inevitable, it can sometimes be further supported by the existence of a typotype, i.e. a specimen on which the illustration has been based. Dillenius described in his *Hortus Elthamensis* plants which were grown in the garden of James Sherard at Eltham. At the same time, he collected specimens from this garden. This collection formed the nucleus of the Dillenian Herbarium (OXF) which was originally scattered throughout the Sherardian Herbarium, itself built up in the period 1680-1790. Druce separated both collections (Druce & Vines, 1907).

There are two specimens of *C. orientalis* in the Dillenian Herbarium (2868 and 2868_2), the first of which corresponds remarkably well with Dillenius' illustration, being mirror-images, apart from one of the basal nodes. We surmised that the anomalous node might be due to a twisting of the stem in the region of the node and we are very grateful to Dr. D. Mabberley (pers. comm. 1986) for kindly confirming that this is the case. Specimen 2868 shows the following annotations (figure 2.11):

> ‘119. 145. 144' (top right),
> ‘Clematis orientalis L." (bottom right) in the handwriting of G.C. Druce,
> ‘Europe' (bottom right, stamped),
> ‘Herb. Sherard' (bottom right) in the handwriting of John Sibthorp,
> ‘2868' (bottom right) in the handwriting of William Baxter.

A pinned label at the bottom left shows us the following:

> ‘2868' (red ink),
> ‘Clematide orient. Apii folio, fl. e viridi flavescente, posterius reflexo, Coroll. 20' (brown ink),
> ‘Flammula scandens. Apii foio glauco Hort. Elth.' with an initial ‘D' or `O' in the same handwriting (black ink).
> ‘fig 145 *orientalis*' (pencil).

The label shows us four different handwritings of which the one in pencil is recent. The number 2868 is again in William Baxter's handwriting. The Tournefort phrase-name in brown ink is neither by James nor William Sherard, nor by Dillenius. It is very similar to the handwriting on one of the four specimens of *C. orientalis* in the De Jussieu Herbarium (P-JU 10493). It is not by Antoine or Bernard de Jussieu, but resembles the handwriting of Sebastien Vaillant (1669-1722), who lived in Paris (Heine, pers. comm., 1986). We have not been able to identify the handwriting in black ink. Because of the striking resemblance between Vaillant's handwriting and the brown ink handwriting, connections between the Sherards and Parisian botanists should be considered. William Sherard (1658-1728) asked Dillenius in 1721 to come over from Germany and to work for him in Oxford arranging the Sherardian Herbarium and preparing an improved version of Bauhin's *Pinax* (which was never finished). After William's death, his brother James asked Dillenius to write a book on the plants in his garden, which was published in 1732 as *Hortus Elthamensis*. William Sherard was English consul at Smyrna (Izmir) from 1703 to 1717. He travelled extensively in Europe, and was on good terms with most contemporary botanists. His correspondence with them has been preserved in the library of the Royal Society in London. It clearly proves, that there was at that time quite an exchange of books and plants. Correspondence with Vaillant (MSS. Sh. 528-545) does not shed any light on the Tournefort phrase-name in - possibly - Vaillant's handwriting as it occurs on the label of sheet 2868.

According to Pasti (1950), Tournefort had promised Sherard specimens from the Levant for his *Pinax*. After learning that Sherard would go to Smyrna, Tournefort also promised to give him all new plants from the Paris Botanical Garden. However, Tournefort died, before he was able to fulfill his promises. Returning from Smyrna, Sherard stayed in Paris, where he hoped to receive the promised plants, but he was not allowed to take them with him to Oxford. He was again denied possession of those plants on another occasion in 1722. Sherard then spent six weeks to study Tournefort's Levant specimens. However the four specimens in P-TO do not show Sherard's handwriting and so we have not been able to show direct connection between the Vaillant label in Oxford and Vaillant's specimens in P. According to Clokie (1964), there are Tournefort specimens in the Sherardian Herbarium, so anyhow some exchange, and perhaps including specimens from Vaillant, occurred between Paris and Oxford. From correspondence between Sherard and De Jussieu (MSS. Sh. 276-292), we know that De Jussieu desired plants from England in exchange for Spanish plants and books on coins. It is, therefore, possible that Tournefort and Vaillant material, the latter forming the nucleus of Paris collections, could have been sent to Oxford.

After having been separated from the Sherardian specimens, the Dillenian sheets have been remounted (Druce & Vines, 1907). It is important to bear this in mind when studying these early specimens. The following four categories of specimens should be distinguished:

- specimens labelled by Dillenius and/or Humphrey Sibthorp, which form the basis for the illustrations in *Hortus Elthamensis*;
- rather shrivelled specimens, labelled by Dillenius (bearing phrase-names from the *Hortus Elthamensis* commonly with the annotation "duplicate");
- specimens from James Sherard's garden added after publication of the *Hortus Elthamensis* in 1732;
- specimens not originating from the garden of James Sherard at Eltham.

Considering the resemblance between illustration and specimen, sheet 2868 apparently has to belong to the first category despite of the absence of a Dillenian label. The occurrence of Vaillant's handwriting on sheet 2868 could be explained through interchange of labels after remounting.

The illustration in *Hortus Elthamensis* differs from sheet 2868 in that fruiting branchlets were depicted separately from the plant. These could conceivably have been depicted from sheet 2868_2, but there is no direct evidence for this as this sheet only shows recent handwriting. Because of the striking resemblance between the depicted plant and sheet 2868, an interchange of labels was assumed and the Dillenian specimen 2868 was consequently designated as the typotype of "*Flammula scandens, apii folio glauco*", Dill. Elth. 144, t. 119, f. 145 (figure 2.11; original reference: Brandenburg et al., 1987).

2.4.2.3. The type locality of *Clematis orientalis* L.

The ICBN (1988) does not state anything about type localities. Such detail is not required by the rules, but is quite interesting in its own right. In a narrow sense the type locality of *C. orientalis* should be James Sherard's garden at Eltham. In case of a cultigen this is very plausible. However, *C. orientalis* is a species occurring in the wild. It is, therefore, worthwhile tracing the natural provenance of the typotype material and it is meaningful to indicate this provenance as type locality.

From 1700 until 1702 Tournefort travelled in the Levant by order of the King of France. According to Becker (1957), he collected plants in the surroundings of Trebizonde (Trabzon), the surroundings of Erzurum, the sources of the Euphrates, Mount Olympus near Brousse (Bursa) and Mount Sypilus near Smyrna (Izmir). Supplementary to the *Institutiones*

Rei Herbariae (1700) he published in 1703 his *Corollarium* in which he mentioned: "*Clematitis Orientalis, Apii folio, flore e viridi flavescente, posterius reflexo*". This is the earliest record of *C. orientalis*, as far as now known. Tournefort described and sometimes depicted plants collected during his journey in his book *Relation d'un Voyage du Levant*, published posthumously in 1717. He neither described nor depicted *C. orientalis*, but stated that he sent some seeds unfortunately unnamed to friends in the Netherlands (Wijnands, 1983). Miller (1768) mentioned that most botanical gardens would have been provided with seeds from the Hortus in Paris. In view of Sherard's good connections with Tournefort and other botanists in Europe, it is likely that the *C. orientalis* plants in James Sherard's garden at Eltham stemmed directly or indirectly from plant material introduced by Tournefort. In P-TO there are four specimens assigned to *C. orientalis*, all of which well resemble the two specimens in the Dillenian Herbarium. One of these specimens (P-TO 2520), in the general part of Tournefort's Herbarium, is labelled: "*Clematis Armenia, Apii folio*". The remaining three are in the supplement under nr. 30 pag. 20, which refers to the thirtiest species on page 20 in the *Corollarium*. One of them shows no annotation. The first of the other two bears "*Clematitis oriental. Apii folio glauco flore fl. viridi petali reflexo Cor. Inst.*" (beneath in another handwriting "*C. orientalis* L."), and the second bears "*Clematis orientalis apii fol. fl. ex viridi flavescente posterius reflexo T.Cor*". The handwriting on the specimens in the supplement, apart from the note "*C. orientalis* L." is Tournefort's, as is that on P-TO 2520 (Dr. H. Heine pers. comm. 1986). The latter specimen however contains an indication where it was found: Armenia. In the absence of any other indications where Tournefort found *C. orientalis*, we consider 'Armenia' of that time in relation to Tournefort's route of travel i.e. the sources of the Euphrates and the surroundings of Erzurum as the type locality of *C. orientalis* (figure 2.12).

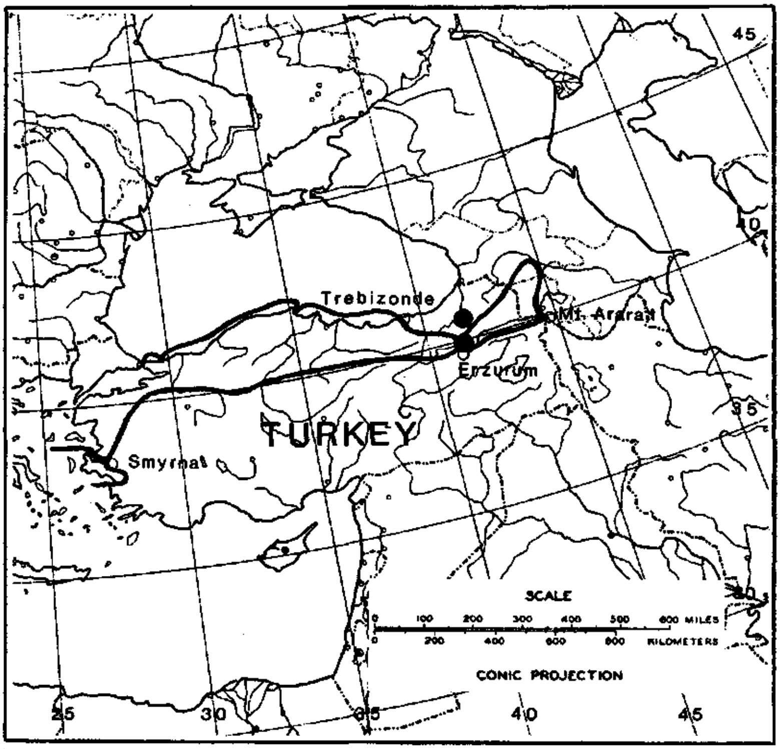


Figure 2.12. Map of type locality of *C. orientalis* L. Route taken by Tournefort.

2.4.2.4. Synonymy and description of *Clematis orientalis* L.

Cf. Meyer (1831); Müller (1857);

Synonymy:

Homotypic synonym:
Meclatis orientalis (L.) Spach
Heterotypic synonyms:

Clematis longecaudata Ledeb., in Flora rossica, vol. 1 (1842) Clematideae, 1-5 (Lectotype Claus, s.n., Desert Casp., 1834 B; isotype at LE).

Clematis albida Klotsch, in Die botanischen Ergebnisse der Reise seiner Königl. Hoheit des Prinzen Waldemar von Preussen auf Ceylon, den Himalaya und an den Grenzen von Tibet gesammelte Pflanzen (1862), 131 t.4 (holotype Hoffmeister s.n., B).

Clematis orientalis L. subsp. *orientalis* var. *flava* (Moench) O. Kuntze

Clematis flava Moench, in Methodus plantas horti botanici et agri marburgensis a staminum situ describendi (1794; type not seen).

Clematis orientalis L. subsp. *wightiana* (Wall.) O. Kuntze var. *longecaudata* (Ledeb.) O. Kuntze.

Clematis orientalis L. subsp. *orientalis* var. *normalis* and var. *albida* (Klotsch) O. Kuntze '*vulgaris*', '*angustifolia*' and '*fasciculata*'

Clematis orientalis L. var. *hindukushensis* Grey-Wilson, in Kew Bulletin **44** (1989): 33-60 (Type Grey-Wilson and Hewer 1224, Afghanistan, Djam (Ghowr); holotype K, isotype W).

Clematis orientalis L. var. *robusta* Grey-Wilson, in Kew Bulletin **44** (1989): 33-60 (Type Grey-Wilson and Hewer 1688, Afghanistan, between Urgun and Qazideh (Badakshan-Wakhan); holotype K, isotype W).

Clematis orientalis L. var. *baluchistanica* Grey-Wilson, in Kew Bulletin **44** (1989): 33-60 (Type Crookshank 373, Pakistan, Urang (Bahawalgawar); holotype and isotypes K).

Clematis orientalis L. var. *tenuifolia* (Royle) Grey-Wilson, in Kew Bulletin **44** (1989): 33-60.

Clematis tenuifolia Royle, in Illustrations of the Botany and other branches of the Natural History of the Himalayan Mountains and the Flora of Cashmere, vol. 1 (1839) Ranunculaceae, 43-51 (lectotype Royle s.n., LIV, see Lauener, 1978).

Clematis orientalis L. var. *latifolia* Hook.f. & Thomson (lectotype Royle s.n., LIV)

Clematis globosa Royle.

Clematis orientalis L. var. *globosa* (Royle) Mukerjee.

Clematis orientalis L. var. *daurica* (Pers.) O. Kuntze.

Clematis daurica Pers., in Synopsis plantarum seu enchiridium botanicum, vol. 1 1358 *Clematis*, 98-100. Paris (Holotype Patrin 10502, P-JU).

Clematis daurica Ledeb. nom. illeg.

Clematis glauca Willd., in Berlinische Baumzucht **65** (1796): 89-94, t.4, fig 1 (holotype Willdenow 10474, plant cultivated in the Botanical Garden Berlin, B-WILLD.)

Clematis orientalis L. var. *obtusifolia* sensu Trautv., non Hook.f. & Thomson.

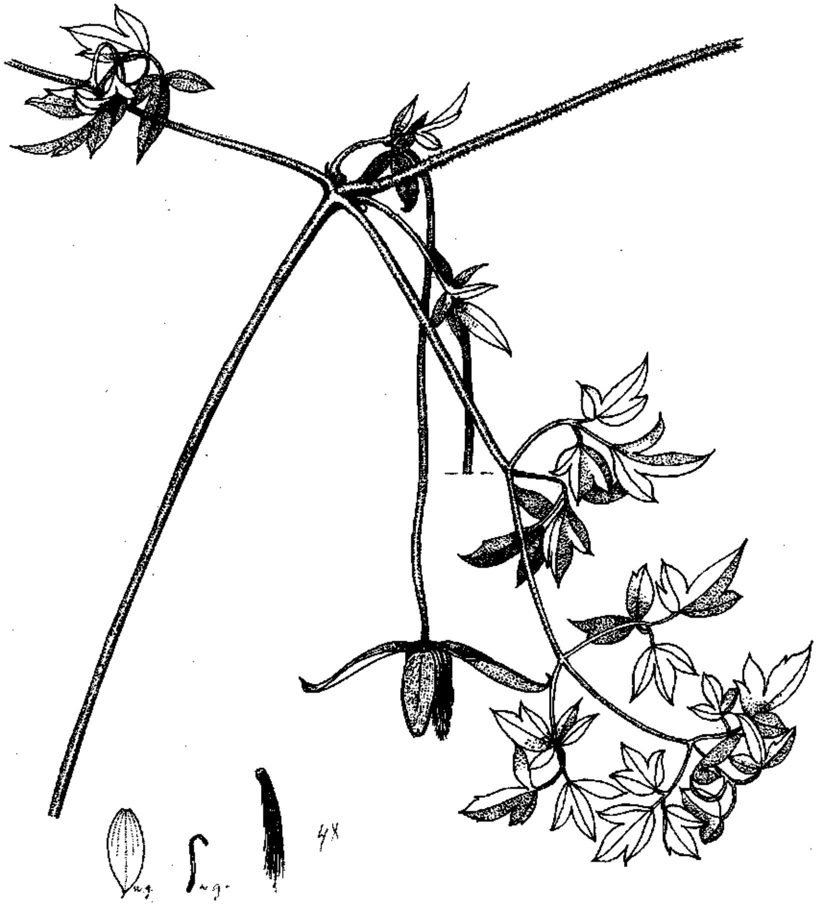
Clematis orientalis L. subsp. *orientalis* var. *daurica* (Pers.) O. Kuntze '*persoonii*'
Clematis orientalis Krylov, non L.
Clematis orientalis L. var. *obtusifolia* Hook.f. & Thomson f. *oblongifolia* Regel.

Illustration, see figure 2.13.

Description: Woody climber, up to 8m tall, flowering in summer; (June-)July-August(-September). Branchlets angular to costate, sparsely pilose. Leaves very variable in shape and size, imparipinnate with (3-)5-7(-9) leaflets; petioles 2-10 cm long; leaflets oblong, lanceolate, elliptic or ovate to broadly elliptic or broadly ovate, herbaceous, greyish green, glabrous or sparsely pilose, 3-65 x 5-50 mm, 1-10 x as long as wide, entire, lobed, cleft almost to the base in 1 main part and 1 or 2 smaller lateral parts, or composed of 3 leaflets of second order, the parts mostly with a few teeth, acute or acuminate at the apex, more or less abruptly narrowed and cuneate at the base; petiolules pilose, 5-30 mm long. Inflorescences terminal and axillary, being 3-many-flowered cymes only on branchlets, apical flowers of cymes sometimes aborted or absent; peduncle 5-80 mm long; pedicels pilose, 5-50 mm long, curved at the apex, but elongate and straight when fruiting. Flower buds often dark red, ovoid with acute apex; aestivation induplicate. Flowers actinomorphic, hemicyclic; tepals 4, yellow, pale or greenish yellow, sometimes light purplish brown inside or tinged with red-violet outside, oblong or elliptic, 11-15(-20) x 4-7.5 mm, 2-4 x as long as wide, acute at the apex with broadly cuneate bases touching each other, lanate at the incurved margin, less lanate within than at the margin, sparsely pilose to villose outside, spreading, recurved later. Stamens numerous, 20-40; filaments dilatate, yellow, mostly dark red-purple, towards the base pilose, up to 1.5 cm long; anthers yellow, up to 0.5 cm long. Pistils numerous, 5-11 mm long; ovaries ellipsoid or rhomboid, pubescent, ± 1 mm long; styles long-pubescent, 4-10 mm long; stigmas straight or slightly hooked, glabrous. Achenes rhomboid, slightly ribbed at the margin, pubescent, dark brown, 2-4 x 1-2 mm; elongate persistent styles, 25-55 mm long, covered with long erect hairs.

Clematis orientalis L.

a



b

c

Figure 2.13.
a. *C. orientalis* L. (drawing by Mariet de Geus; 1. Part of flowering branch, 0.7×; 2. flower, 1.3×; 3. tepal, 1.5×; 4. stamen, 4.7×; 5. pistil, 4.7×; 6. fruit head, 0.7×; 7. achene, 2×; 8. longitudinal section of achene, 5.3× (1, 3, K.P. and E. Buttler 20284 M; 2, 4, 5, K.P. and E. Buttler 20053 M; 6, 7, 8, K.M. Guichard T/127/60 BM).
b. *C. orientalis* L. (drawing by Mariet de Geus; pop. 78018; Bra 185, 186 WAG)
c. *C. glauca* Willd. (Willdenow, 1796), synonym of *C. orientalis* L.

Distribution: Russian Federation (Khabarovskiy Kray, Buryetskaya ASSR, Dagestan Autonomous Region), Kazakhstan, Turkmenistan, Uzbekistan, China (Xinjiang Uygur Ziziqu), India (Himachal Pradesh), India/Pakistan (Jammu and Kashmir), Armenia, Georgia, Azerbaidjian, Pakistan, Afghanistan, Iran, Turkey, N-Syria, Eastern Aegean Isles (see figure 2.14).

Specimens examined: USSR: *Khabarovskiy Kray*: Khrebet Ket-Kap, E. Serova & E. Ryschowa 23 (NY); *Buryetskaya ASSR*: Ilka, Schrenk s.n. (U); *Kazakhstan*: Alakol, Schrenk s.n. (K, M, U); Lepsa, Karelin & Kiriloff 1130 (G, K, M, NY); Ili, A. Regel s.n., 1876 (M); Zailitskiy Alatau, A.K. Skortsov s.n., 15-9-1963 (M); Khrebet Karatau, N.V. Pavlov 1148 (B); Khrebet Chatkalskiy, A.K. Skortsov, s.n., 3-10-1963 (M); Dzhambul, J. Raikova s.n., 1917 (C, G, K, MO, NY, S); *Uzbekistan*: Shimgan, Baranov & Raikova s.n., 23-8-1924 (B, G, K, MO, NY, S), Fedchenko s.n., 19-8-1897 (G), L.P. Velikanov s.n., 22-9-1962 (C); Chircik, M. Capus 2 and 3 (P); Syr-Dar'inskaya Oblast, A. Michelson 295 (S); Karankul, O.N. Korowina & N.M. Oernomorskaya s.n., 9-8-1976 (G, LD, M); *Tadzhikistan*: Kafirnagan, Newissky 4660 (M);Khrebet Gissarskiy, P.N. Ovczinnikov 2088 (NY), V. Vasak & A. Zlatnik s.n., 23-5-1974 (M), D.H. Wilken, R. Hebb & T. Crovello 29 (NY); *Turkmenistan*: Farab-Pristan, N. Androsov s.n., 2/23-9-1902 (C, G, K, M, MO, NY, S); Ashkabad, D. Litwinow 23 (G, M), E. Regel 812 (NY), P. Sintenis 848 (B, BM, G, K, L, MO), 1108 (G); Kazandhik, P. Sintenis 1287 (WAG); Krasnovodsk, D. Karelin s.n., 1834 (G); *Dagestanskaya ASSR*: Akhty, Th. Alexeenko s.n., 5/17-8-1898 (B, G); *Azerbaidzhan* : Kirovabad, Fedoseeff s.n., Aug. 1899 (B), R.F. Hohenacker s.n., 1834 (G), Aug./Sept. 1838 (G, L, M, P, WAG); *Georgia*: Tbilisi, K. Browicz s.n., 27-7-1968 (K); *Armenia*: Khrebet Gegamskiy, V.Vasak s.n., 12-7-1975 (M).

CHINA: *Xinjiang Uygur Zizhiqu*: Kumishi, Fedchenko s.n., 2-8-1897 (G); Kuerchu, A. Regel s.n., 25-8-1877 (K); Ertix He, G.N. Potanin s.n., 1876 (K); Yining, A. Regel s.n., 5-7-1877 (BR, K, M); Shuiding, A. Regel s.n., 8-7-1877 (K); Suoche, C. Persson 228 (S); Bositan, C. Persson 522 (S).

INDIA: *Himachal Pradesh*: Spiti, V. Jacquemont 644 (K); Nahan, V. Jacquemont 1107 (K); Simla, J.H. Lace 530 (OXF).

INDIA/PAKISTAN: *Jammu and Kashmir*: Shigar, W. Koelz 9655 (NY); Basha, R. Scott

Russell 1785 (BM); Hunza, F. Lobbichler 469 (M), O. Polunin 6414 (BM, G); Chalt, O. Polunin 6453 (BM, G), J.E. Winterbottom 932 (K); Gilgit, G.M. Giles All (G); Sher Qila, Dr. Giles 519 (K); Imit, F. Schmid 2015 (BM, G).

PAKISTAN: *Bahawalganar*: Urang, H. Crookshank 373 (K); *Chitral*: Chitral, A.A. Barrett 14873 (K); Killa Drosh, A.A. Barrett 14835 (K), Hamilton 17861 (K), S.M.Toppin 596 (K); *Kurram*: Darband, J.E.T. Aitchison 415 (K, P).

AFGHANISTAN: *Badakshan*: Wakhan Corridor, H. Roemer 274 (M); Urgun, C. Grey-Wilson & T.F. Hewer 1668 (K); *Kunar*: Bashgal river, D. Podlech 16638 (G, M); *Takhar*: Farkhar, P. Furse 8163 (K); *Paktia*: Orgun, O.H. Volk 71/754b (M); *Baghlan*: Ashraf river, H.F. Neubauer 4374 (B); *Bamian*: Shibar Pass, R. Gibbons 0747 (K, MO); Doabi-Mekh-i-Zarin, P. Furse 8280 (K), Griffith s.n. (CGE); Bamian, Carter 619 (K); Band -i-Amir, A. Dieterle 756 (G, M); Surkhoy, D. Podlech 18872 (M); *Ghowr*: Djam, C. Grey-Wilson & T.F. Hewer 1224 (K); *Faryab*: Sangilak, M. Capus s.n. (K); *Helmand*: Lashkari Bazar, G. Frumkin 54 (G).

IRAN: *Khorassan*: Dogharun, Herb. Bunge s.n., Aug. 1858 (G); Mirabad, Assadi & Masoumi 21266 (K); Kuh-e-Mish, K.H. Rechinger fil. 1424 (BM, K, S); Sharifabad, Herb. Bunge s.n., June/July 1858 (L); *Fars*: Sivan river, J. Bornmüller 1980 (K); *Mazandaran*: Elburz, Gauba 19 (B); Amol, P. Furse 9063 (K); Esfahan, Aucher-Eloy 4025 (B, P), 4029 (G), A.C. Trott 783 (K); *Lorestan*: Bisheh, M. Køie 735 (C); *Kermanshah*: Kermanshah, C. Haussknecht s.n., Sept. 1867 (BM).

TURKEY: *Kars*: Iğdir, P. Furse 9123 (K); *Hakkari*: Dize, P.H. Davis & O. Polunin 24022 (BM); *Artvin*: Artvin, W. Andronaki s.n., 11/24-7-1907 (K, LD), 18-7-1907 (LD), 20-7-1907 (G), July 1907 (WAG); *Erzurum*: Erzurum, H.H. Calvert & J. Zohrab 753 (CGE, OXF); Söylemez, Fraser Jenkins 2408 (BM); Tortum, Stainton & Henderson 6155 (K); *Gümüşane*: Gümüşane, E.K. Balls & W.B. Gourlay 1984 (BM, K), P. Sintenis 7117 (LD); *Erzincan*: Tanyeri, K.P. Buttler & R. von Bottmer 22655 (M); Erzincan, P. Sintenis 2998 (BR, G, K, P); *Elâziğ*: Elâziğ, K.P. & E. Buttler 20284 (M); *Tokat*: Tokat, P. Furse 9183 (K); *Samsun*: Bafra, P.H. Davis & O. Polunin 24960 (BM, K); *Amasya*: Amasya, Manissadjian 639 (B, K, LD), J. Bornmüller 1318 (BM, BR, K, LD, M, S); *Kayseri*: Ürgüp, W. Kottes s.n., 28-7-1933 (M); *Nevşehir*: Nar, G. Roper 86 (BM); Avcilar, K.P. & E. Buttler 20053

(M); *Kastamonu*: Kösen, P. Sintenis 4881 (B, LD, M); *Ankara*: Kalecik, K.M. Guichard T/127/60 (BM).

SYRIA: *Halab*: Barsa Dagh, C. Haussknecht s.n., 1865 (K).

GREECE: Kos, W. Barbey 602 (G).

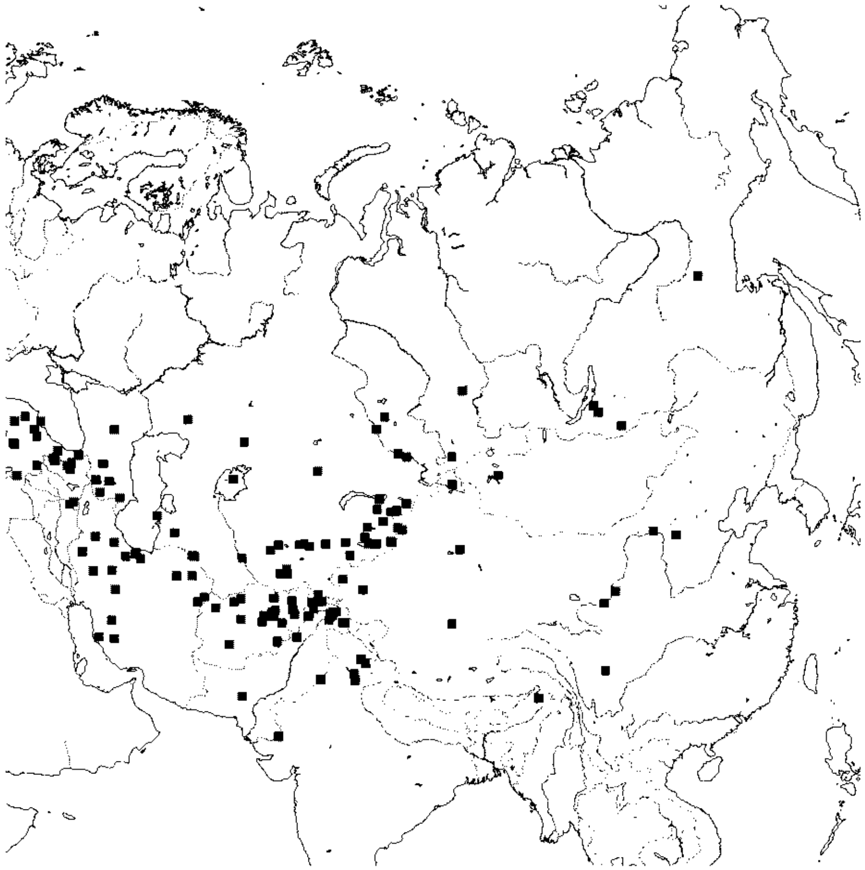


Figure 2.14. Distribution of *C. orientalis* L.

2.4.3. *Clematis graveolens* Lindley

Clematis graveolens Lindley, in Journal of the Horticultural Society (London) (1846): 307-308.

Holotype: Munro, s.n. Chinese Tartary (CGE-Lindley Herb.).

Synonymy:

Homotypic synonym:

Clematis orientalis L. subsp. *graveolens* (Lindl.) O. Kuntze in Monographie der Gattung *Clematis*. In: I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg (1885), 83-202. Berlin

Heterotypic synonyms:

Clematis orientalis L. subsp. *graveolens* (Lindl.) O. Kuntze var. *aitchisonii* O. Kuntze in Monographie der Gattung *Clematis*. In: I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg (1885), 83-202. Berlin (type Aitchison 614, 718, Pakistan, Darband (Kurram); holotype B, isotypes BM, FI-W, K, P).

Clematis orientalis L. subsp. *thunbergii* (Steud.) O. Kuntze var. *intricata* (Bunge) O. Kuntze p.p. in Monographie der Gattung *Clematis*. In: I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg (1885), 83-202. Berlin *pro parte*.

Clematis parvifolia Edgew. in Trans. Linn. Soc. **20** (1851): 25 (Type: Edgeworth 1051, India, Kundau and Beas Valleys; holotype K, isotype OXF).

Description: Woody climber, up to 4m tall, flowering in summer; [(June-)July-August(-September). Branchlets mostly costate, initially pilose, later glabrous. Leaves variously bipinnate, sometimes pinnate or tripinnate with (15-)25-30(-35) leaflets; the petioles pilose at the base, 1.3-6.5 cm long; the leaflets very variable in shape and size, ovate to lanceolate/leariform, herbaceous, green, glabrous or slightly pilose at the veins(12-)18-23(-50) × 6-20 mm, 1-8 × as long as wide, irregularly lobed or dentate, acute or acuminate at the apex, cordate or angustate at the base; the petiolules pilose, (4)-10-13(-30) mm. Inflorescences 1-3(-7)-flowered axillary cymes, if more than 3 flowers per inflorescence the secondary flowers not fully developed; peduncle 27-60(-100) mm long; pedicels pilose, 25-85 mm long. Flowers open, flat to broadly campanulate; tepals 4, bright yellow or lime yellow, ovate-obovate, 11-17(-20) mm × 6-10 mm, ± twice as long as wide, blunt to acuminate at the apex, cuneate to angustate bases touching each other, tomentose at margins, slightly pilose both inside and outside, spreading. Stamens numerous, (30-)40-60(-70); filaments ciliate, greenish yellow, sometimes tinged with violet, pilose, up to 1 cm long; anthers yellow, 2-3 mm long.

Pistils numerous, 80-100; ovaries rhomboid, pubescent, ± 1 mm long; styles long pubescent, 3-9 mm long; stigmas straight or slightly hooked, glabrous. Achenes rhomboid, markedly ribbed at the margin, slightly pilose or glabrous, dark brown, 2-4 × 1-3 mm; elongate, persistent styles, 20-35(-50) mm long covered with long erect hairs.

Illustration: See figure 2.15.

Distribution: Nepal, Jammu and Kashmir, India (Punjab), Pakistan (Peshawar and Rawalpindi), Afghanistan (Kandahar). See figure 2.16.

Specimens examined: NEPAL Chong near Tibrikot, Polunin, Sykes & Williams 3339 (BM, E, UPS); Dunaihi along Behri river, Shrestna 5266 (G);

INDIA Kundan and Bean Valleys, Sangla, Edgeworth 1051, (K, OXF); Chamba to Darmtawer, Falconer 6 (K, M); Sarahan (Punjab), Ram Baksh 4323 (K);

JAMMU and KASHMIR, Kishtwar, Clarke 31450B (BM); Garki, Rich 1314 (K);

AFGHANISTAN, Kurrum Mandah (Kandahar), Aitchison 614,718 (BM, FI-W, K);

PAKISTAN (Peshawar), Mansehra Hazara, Duthie 7423 (BM, K), Kalapani Hazara, Stewart 27748 (G), Swat Valley, Weatherhead 100 (BM); (Rawalpindi), Kulu, Larji, Parker 3363 (K), Murree, Stewart 4034 (K), Narani Dag, Drummond 4326 (BM), Kabis, Drummond 14474, (BM).

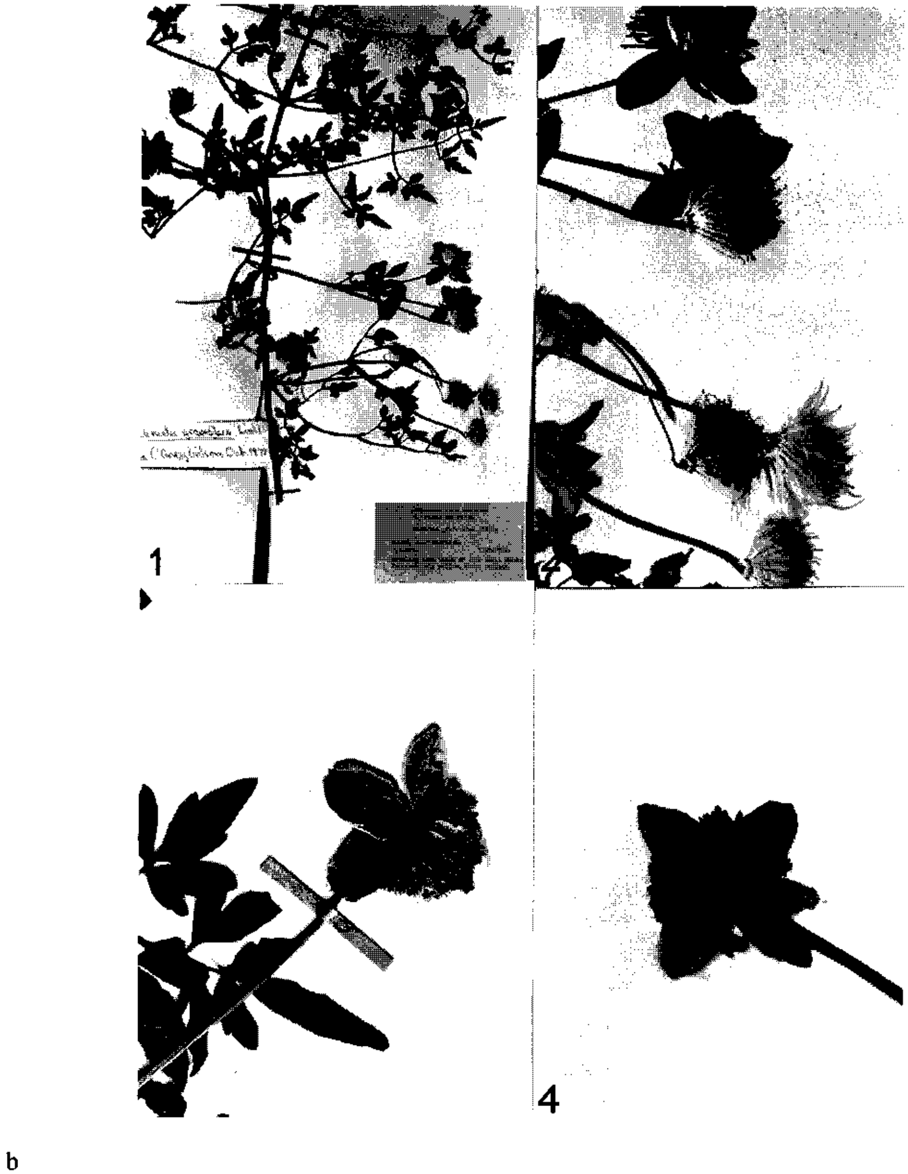


Figure 2.15. Illustrations of *C. graveolens*.

a. Illustration from Lindley (1846)

b. 1 Polunin, Sykes & Williams 3339 (E).

2 Detail of 1.

3 and 4 Flowers of specimen 5396 of the Forest Research Institute, Dehra Dun (E).

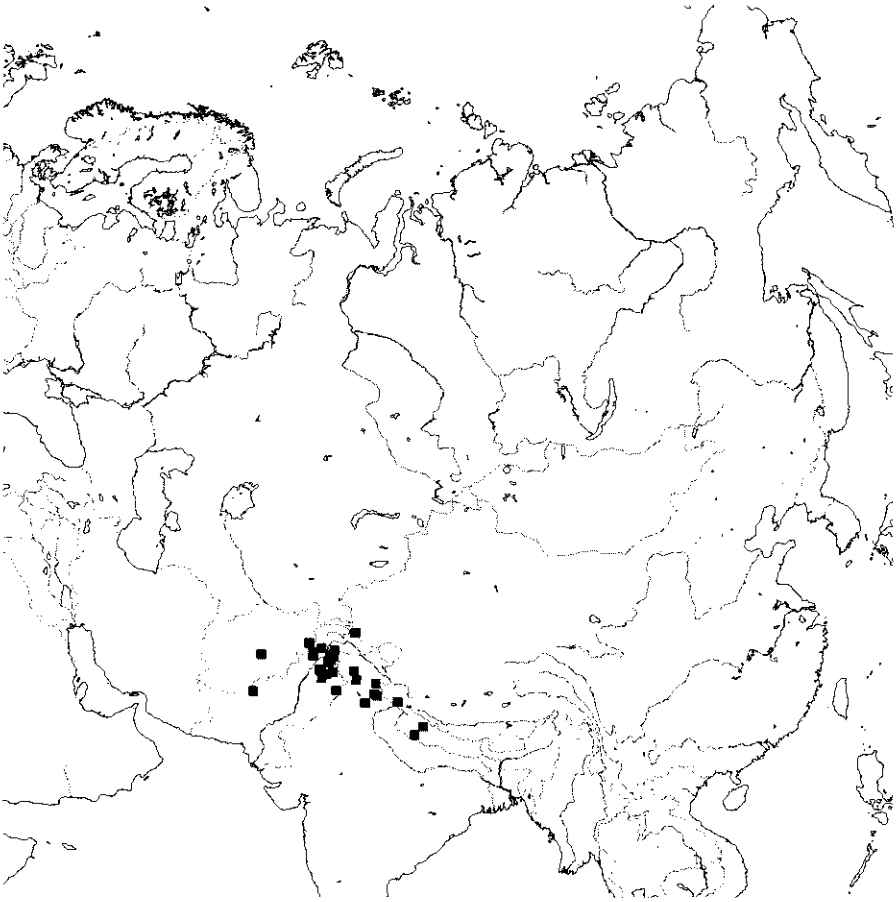


Figure 2.16. Distribution of *C. graveolens*.

2.4.4. *Clematis intricata* Bunge

Clematis intricata Bunge (1833) - Enumeration Plantarum China Borealis, Mém. Sav. Etr. Acad. SCi. St.-Pétersb. **2**: 75 (1833). Holotype: Bunge 1/3 (1831), China Borealis (LE), cf. Limpricht, 1922.

Synonymy:
Homotypic synonyms:
Clematis orientalis L. var. *intricata* (Bunge) Maxim.
Clematis orientalis L. subsp. *thunbergii* (Steud.) O. Kuntze var. *intricata* (Bunge) O. Kuntze p.p. in Monographie der Gattung *Clematis*. In: I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg (1885), 83-202, *pro parte*.
Heterotypic synonyms:
Meclatis sibirica Spach.
Clematis orientalis L. var. *glauca* Maxim.
Clematis glauca sensu Sargent, non Willd.; sensu Rehder; sensu Ling.
Clematis hilariae S. Kovalevskaya in Not. Syst. Herb. Inst. Bot. Acad. Sci. Uzbekistan **18** (1967): 34 (Type: Kovalevskaya, s.n., 17-9-1966, plant cultivated in the Uzbek Botanic Garden (Tashkent) from seeds collected in the Pamir valley; holotype LE, isotypes BM, E, G, K).
Clematis chrysantha var. *monantha* Tamura in Kitamura Add. Corr. Fl. Afghan. **92** (1966): 92 (Holotype Yosii 801, Afghanistan, Ishkashim, KYO [not seen]).
Clematis chrysantha var. *paucidentata* Tamura in Kitamura Add. Corr. Fl. Afghan. **92** (1966): 92 (Holotype Yosii 488, Afghanistan, Qazideh, KYO [not seen]).
Clematis sarezica Ikonn. in Novosti Sist. Vyssh. Rast. **14** (1977): 231 (Type: Ikonnikov 5830, Uzbekistan, Sary Tugai (Pamir); holotype LE, isotype K).

Illustration: Ling (1980) in Flora Reip. Pop. Sin. **28**: 142, f. 15; see also figure 2.17.

Description: Woody climbers, up to 4m tall, sometimes with a compact, bushy habitus due to environmental conditions. Branchlets angular to costate, the young twigs pilose, later almost glabrous. Leaves variously composite, pinnate, bipinnate, sometimes biternate with (5-)7-15(-21) leaflets; the petioles 12-57 mm long; the leaflets ranging from ovate/lanceolate to narrowly lanceolate, green or greyish green, 16-56 × 2-47 mm, 1-10 × as long as wide, entire, or irregularly serrate, dentate or lobed with a few incisions at the base of the leaflet, sometimes cleft almost to the base in 1 main part and 1 or 2 smaller lateral parts, or composed of three leaflets of second order, the parts sometimes with a few teeth, acute, acuminate or mucronate at the apex, more or less abruptly narrowed or cuneate at the base; the petiolules glabrous or sparsely pilose, 5-38 mm long. Inflorescences mostly axillary but sometimes terminal 1-3-flowered cymes - occasionally more than 3 flowers per cyme in vigorous growing specimens -; peduncle (3-)8-23(-52) mm long; pedicels glabrous or sparsely pilose, 20-67 mm long, straight or nodding at the top . Flowers ± pending, open, flat or broadly campanulate, profusive flowering; tepals 4(-5), bright yellow sometimes veined or with a flush of violet, herbaceous, ovate to lanceolate, (12-)14-22(-24) × 4-10 mm, ± twice as long as wide, acuminate or mucronate at the apex with broadly cuneate bases touching each other, lanate at the incurved margin, pilose inside, glabrous outside, spreading.

Distribution: China (Hopei, Shansi), Russian F. (Gorn Altai), Kirgiziya, Uzbekistan, Tadzhikistan (see figure 2.18).

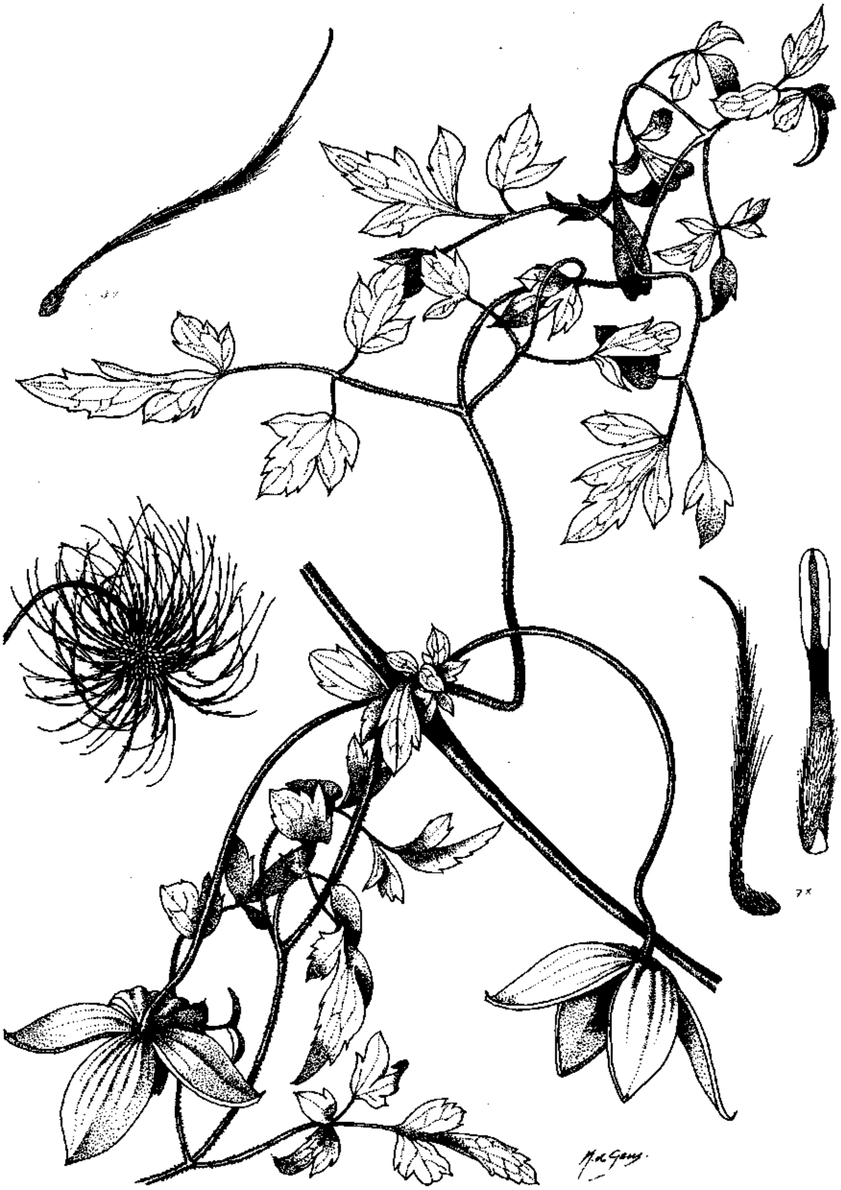
Specimens examined: CHINA Hopei, Hsiao-Li-Chen, Liu 12684 (NY, S); Hsiao-wu-tai-shan/Che-tao-kou, Smith 294 (BM, LD, S, UPS); Peking, David 2904 (P); Pei'ping, Bushell, s.n., 7-1869, (K), Carles, s.n., 1882, (BM); CHINA Shansi, Taiyman, Licent 2163 (BM); Limpricht 680, Taiyuang fu/ T'ai-yian-chen (S); Pingyang, Serre A673 (UPS); Yang Ch'en, Serre, A764 (G); Chiao-ch'eng, Smith 7214 (BM, LD, S, UPS);

RUSSIAN F., Gorn Altaisk, Elias, Weber, Tomb & Krasnaborov 4411 (NY);

KIRGIZIYA, Issyk-kul Ozero, Brocherel 13 (G);

TADZHIKISTAN, Tianshan, Appleton 674 (K);

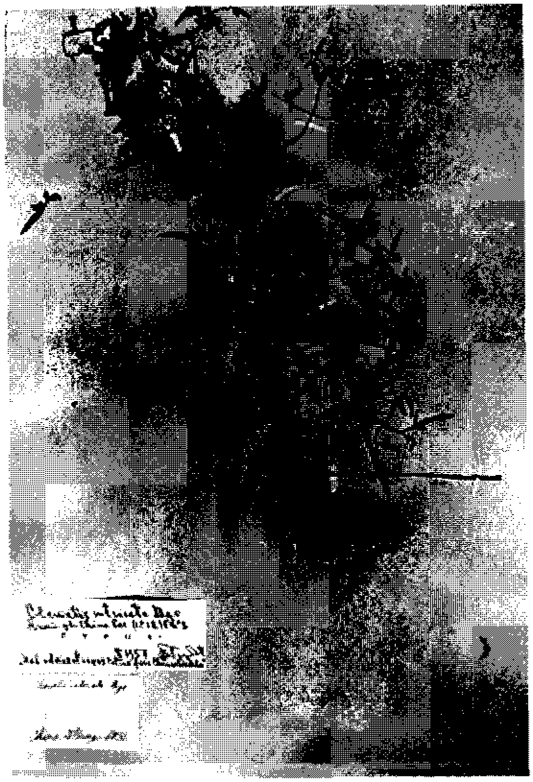
UZBEKISTAN, Sary Tugai, Ikonnikov 5830 (K)



a

Acute tip at apex of tepal

b



c

Figure 2.17. Illustrations of *C. intricata* Bunge

a. Drawing by Mariet de Geus

b. Photograph of flower (Bra58 WAG)

c. Photograph of holotype (LE)

Figure 2.18. Distribution of *C. intricata* Bunge.

2.4.5. *Clematis ispahanica* Boissier

Clematis ispahanica, in Boissier, Diagnoses orientalum novarum (1845), **1** (6):3-4; Ranunculaceae, Flora Orientalis (1867), **1**: 1-98.

Lectotype (designated here): Aucher Eloy 4026, Iran, Isfahan (Ispahan) (G), isotypes FI-W, G, K, LE, P. Paratypes: Kotschy 3266 (B, G, K, M), Kotschy 374,638 (FI-W)

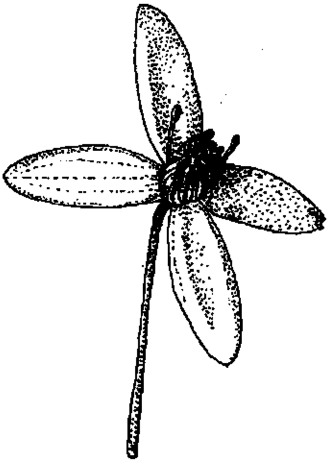
Synonymy:
Heterotypic synonym:
Clematis pseudoorientalis O. Kuntze, in Monographie der Gattung *Clematis*. In: I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg (1885), 83-202. Berlin (Syntype Aucher-Eloy 4025, 4026, P; since Aucher Eloy 4026 is already chosen as lectotype of *C. ispahanica*, *C. pseudoorientalis* is a nomen illegitimum).

Illustration: see figure 2.19.

Description: Slender erect perennial or subshrub, up to 2m tall, summer flowering, July-August. Twigs not twining, round/angular, sometimes to costate, initially slightly pilose, later glabrous. Leaves pinnate, sometimes bipinnate or biternate, with 7-9(-27) leaflets; the petioles variable in length, 23-85 mm; the leaflets lineariform to narrowly lanceolate, herbaceous, pale green or greyish green, glabrous, variable in size, 28-67 × 4-21 mm, 3-10 × as long as wide, entire, or partly serrate, dentate, lobed at the base, or irregularly lobed, acute or acuminate at the apex, angustate at the base; the petiolules pilose at the base, erect or slightly twining, 5-21 mm long. Inflorescences, terminal and axillary cymes with 7-17 flowers per cyme, the cymes being part of a large, loose thyrsoid synflorescence at the top of the young twigs; peduncle 7-62 mm long; pedicels glabrous, 22-70 mm long, ± straight, or at the top somewhat nodding, but when fruiting elongate and straight. Flower buds pale green, ovoid, acute or acuminate at the apex. Flowers open, flat, ± upright, abundant flowering in a rather short period; tepals 4, creamy white to pale yellow, lanceolate to lineariform, 9-25 × 2-8 mm, 3-4 × as long as wide, blunt or acute at the apex, angustate at bases, hardly not touching each other, lanate at the incurved margin, shightly pilose to glabrous inside, glabrous outside, spreading, sometimes recurving later. Stamens relatively few, 20-30; filaments dilatate, greenish white, sometimes tinged with violet, or dark violet, glabrous, up to 1 cm long; anthers greenish white, pale yellow or violet, 2-3 mm long. Pistils numerous, ± 40, ranging from 30-80; ovaries ellipsoid, pilose, 1 mm long; styles long-pubescent, 4-6 mm long; stigmas straight or slightly hooked. Achenes rhomboid, slightly ribbed at the margin, glabrous, 2-3 × 2 mm; elongate persistent styles, 16-33 mm long, pubescent.

Distribution: IRAN (Esfahan), see figure 2.20.

Specimens examined: IRAN (Isfahan), Bornmueller 18 (B), 1981 (G), Foroughi 958 (K), 7937 (K), 7949 (K), 7950 (K), Furse 3158 (K), 9062 (K), Hewer 1492 (G, K), Kotschy 3266 (B, G, K, M), Kotschy 374,638 (FI-W), Pravitz 225 (S), Rechinger 56185 (B, M).



a

b

Figure 2.19. Illustrations of *C. ispahanica* Boiss.

a Flower of *C. ispahanica* (drawing by Mariet de Geus)

b 1/2 Isotypes of *C. ispahanica* (Aucher-Eloy 4026 FI-W, LE)
3 Kotschy 641,3266 (FI-W)
4 Kotschy 374,638 (FI-W)

Figure 2.20. Distribution of *C. ispahanica*.

2.4.6. *Clematis serratifolia* Rehder

Clematis serratifolia Rehder in Mitteilungen der Deutschen Dendrologische Gesellschaft **19**: 248 (1910), and in Fedde, Repert. Spec. Nov. Reg. Veg. **13**: 362 (1914); Holotype: J.G. Jack, s.n., 1905, Korea Ping Yang (A), isotype (LE, MO).

Synonymy:

Heterotypic synonyms:

Clematis orientalis L. var. *serrata* Maximowicz in Bull. Acad. Sci. St. Petersb. **9**: 211 (1879) p.p. (holotype Goldenstädt 255 (10-8-1872; LE)
- *Clematis intricata* Bunge var. *serrata* (Maximowicz) Komarov in Act. Hort. Petrop. **22**: 289 (1904) p.p.
- *Clematis serrata* (Maximowicz) Komarov in Alis. Key, Pl. Far East Reg. USSR **1**: 549 (1931) p.p.

Clematis orientalis L. var. *wilfordi* Maximowicz in Bull. Acad. Sci. St. Petersb. **9**: 211 (1879) p.p. (type Wilson 1150, Plastun (Russian F./Manchuria); holotype LE, isotypes G, K, M, P).
- *Clematis wilfordi* (Maximowicz) Komarov in Alis. Key, Pl. Far. East Reg. USSR **1** t. 168. (1931) p.p.

Illustration: figure 2.21.

Description: Woody climber, up to 5m tall, producing vigorous stolons, flowering in summer (July-)August-September. Branchlets costate, sparsely pilose or glabrous. Leaves biternate, sometimes the first order division pinnate, not ternate, with ± 9 leaflets; the petioles 35-65 mm long; the leaflets oblong-lanceolate to ovate-lanceolate, herbaceous, dark green, glabrous, 28-70 x 12-30 mm, 2-4 as long as wide, regularly serrate, sometimes with a pair of basal lobes, acute or acuminate at the apex, angustate or cordate at the base; the petiolules glabrous or with a few scattered hairs, strongly twining, 11-35 mm long. Inflorescence axillary, (1-)3(-5)-flowered cymes, sometimes the lateral flowers of cymes aborted; peduncle 3-20 mm long; pedicels sparsely pilose, 25-70 mm long, curved at the apex, but when fruiting elongate and straight. Flower buds often reddish, or green yellow, ovoid with an acuminate apex. Flowers ± nodding, ± open, flat, profuse flowering; tepals 4, pale yellow tinged or veined with violet, ovate-lanceolate sometimes narrowly lanceolate, 16-25 x 6-8 mm, 2-4 x as long as wide, acuminate at the apex, with broadly cuneate bases touching each other, lanate at the incurved margin, glabrous outside, sparsely pilose inside, spreading, not recurving later. Stamens numerous, 20-35; filaments dilatate, greenish yellow, tinged with violet or dark violet, pilose; anthers greenish yellow, tinged with violet or violet, up to 3 mm long; incidental occurrence of staminodia as transitional form between tepals and stamens. Pistils numerous, 80-100; ovaries ellipsoid or rhomboid, pubescent, ± 1 mm long; stigma slightly hooked, glabrous. Achenes rhomboid to (ob)ovate, not markedly ribbed at the margin, pubescent, brown with fibrous performance, 2-3 × 1-2 mm; elongate persistent styles up to 4 cm long, covered with long erect hairs.

Remarks: The name *Clematis koreana* Komarov is frequently used in cultivation for plants belonging to *C. serratifolia*. It differs from *C. serratifolia* in having mostly ternate leaves with broadly ovate leaflets with cordate bases and solitary yellow to violet flowers. It is doubtful whether this species itself is in cultivation. *C. koreana* is, like *C. serratifolia* endemic to Korea and Manchuria.

Distribution: Endemic to Korea and Manchuria (see figure 2.22)

Specimens examined: Jack 18-9-1905 (A, MO); Komarov 710 (P); Parejas H968 (G); Skortsov, 13-9-1967 (C, FI, LD, M, MO); Trotter 33 (K); Uchiyama, 12-8-1902 (LD); Wilford 1150 (G, K, LE, M, P, S); Wilson 8927 (BM, MO); Wilson 10711 (BM, MO).

Figure 2.21. Illustrations of *C. serratifolia* Rehder

a. Holotype, J.G. Jack, s.n., 1905, Korea Ping Yang (A)

b. Illustration from Riekstina (1990).

c. Photograph from Riekstina (1990).

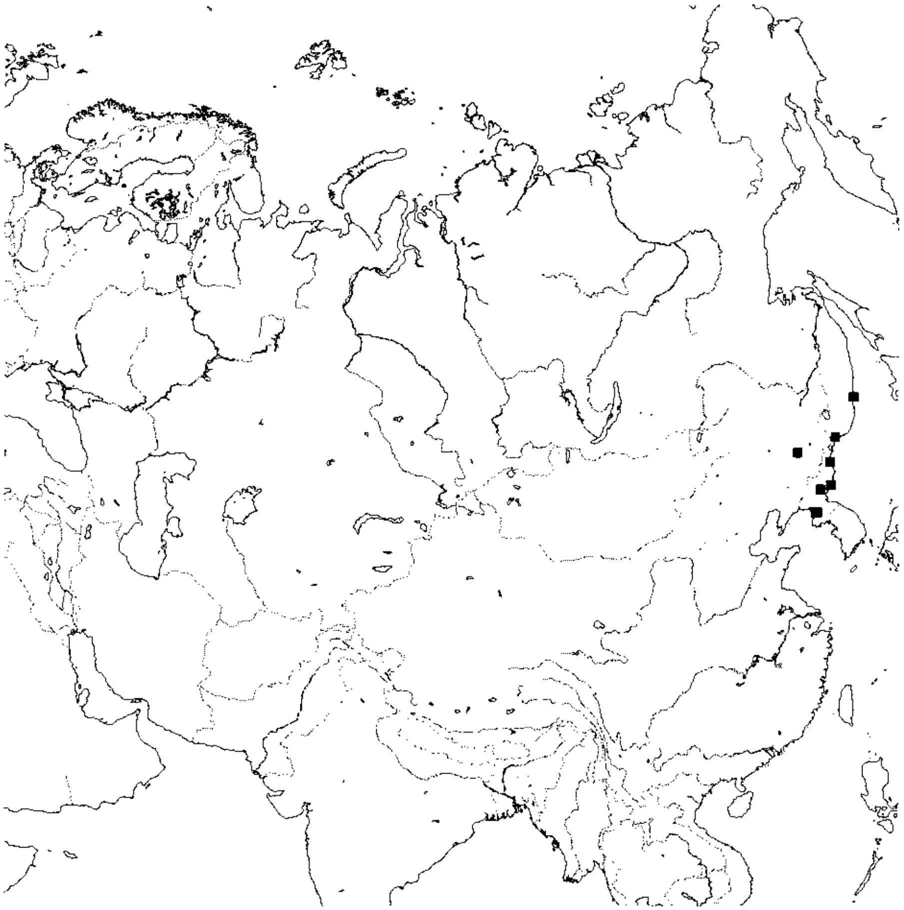


Figure 2.22. Distribution of *C. serratifolia*.

2.4.7. *Clematis tibetana* O. Kuntze

Clematis tibetana O. Kuntze, in Monographie der Gattung *Clematis*. In: I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg, 83-202.
Holotype: Strachey & Winterbottom 3, India, Milam Kumaon (Uttar Pradesh), K; isotypes: BM, BR, P). Cf. Hara (1978).

Description: Woody climber, up to 5m tall, flowering in summer; (June-)July-September. Branchlets costate, pilose. Leaves commonly pinnate or partly or wholly bipinnate with 7-21 leaflets; the petioles 14-72 mm long; the leaflets variable in shape and size, ranging from ovate, lanceolate to linear, herbaceous, glaucous or green, ± glabrous, sometimes pilose downside at veins, 15-75 × (3-)8-22(-44) mm, 1.5-10 × as long as wide, leaflet incision very variable but most often irregularly serrate, dentate, sometimes with 1 or 2 basal lobes, acute at the apex, cordate, cuneate and most often angustate at the base; the petiolules pilose, (2-)5-29(-45) mm long. Inflorescences axillary or terminal cymes with commonly 1 or 3 flowers - in case of a solitary flower the lateral flowers of the cyme are aborted; peduncle 0-65 mm long, thus leading to rather different looking inflorescences at first sight; pedicels pilose, nodding at the top, 25-120(-320) mm long. Flower buds greenish yellow, yellow sometimes with a flush of violet or spotted with violet, occasionally violet, ovoid. Flowers variably shaped, ranging from almost open, flat, broadly campanulate to narrowly campanulate; tepals 4(-5), basal colour bright yellow or golden yellow, either or not tinged with or spotted with violet, rarily completely dark violet, ovate to lanceolate, 16-35 × 4-21 mm, 1.5-4 × as long as wide, acute, acuminate or mucronate at the apex with cuneate bases touching each other, lanate at margins, glabrous or pilose inside, mostly glabrous or less commonly slightly pilose outside, in any case spreading later. Stamens numerous, 30-60; filaments dilatate, variously coloured from greenish yellow to dark violet, pilose, 2-10 mm long; anthers, greenish yellow, up to 5 mm long. Pistils numerous, ± 100; ovaries ellipsoid or rhomboid, pubescent, ± 1 mm long; styles pubescent, 4-11 mm long; stigma slightly hooked, glabrous. Achenes rhomboid, rarily (ob)ovate, not markedly ribbed, woody or fibrous appearance, 2-6 × 1-2 mm; elongate persistent styles up to 4 cm long (in cultivation up to 7 cm long!), covered with long erect hairs.

2.4.7.1. *Clematis tibetana* Kuntze subsp. *tibetana*

Synonymy:

Heterotypic synonymy:

Clematis akebioides (Maxim.) Veitch in New hardy plants in Western China, 9. p.p. (China Kansu, holotype Potanin s.n., 22-7-1885 LE, isotype K).

Clematis ladakhiana Grey-Wilson in *Clematis orientalis* (Ranunculaceae) and its allies. Kew Bulletin **44**: 33-60 (holotype: Thomson s.n. Kashmir, Nubra, K)

Clematis orientalis L. var. *acutifolia* Hook.f. and Thomson in Flora Indica, vol. 1. (1855) Clematideae, 3-12 Syntype: Thomson, s.n. Ladakh, K).

Clematis orientalis L. subsp. *orientalis* var. *daurica* (Pers.) O. Kuntze subvar. *thomsonii* O. Kuntze in Monographie der Gattung *Clematis*. In I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg (1885), 83-202 (Type: Thomson, s.n.; holotype B, isotype K).

Clematis orientalis L. subsp. *orientalis* var. *daurica* (Pers.) O. Kuntze subvar. *dyeri* Clarke ex O. Kuntze in Monographie der Gattung *Clematis*. In I. Urban et al. (eds.) - Verhandlungen des Botanischen Vereins der Provinz Brandenburg (1885), 83-202 (Holotype: Clarke 30329B, Kashmir, Askole, K).

Illustration: see figure 2.23.

Description: Woody climber, up to 4m tall, flowering in summer; (June-)July-September. Branchlets costate, pilose. Leaves pinnate to bipinnate with 9-21 leaflets; the petioles 33-72 mm long; the leaflets lanceolate to lineariform, herbaceous, glaucous, ± glabrous, 30-75 × 3-34 mm, 2-10 × as long as wide, acute at the apex, angustate at the base; the petiolules pilose at the base, 10-45 mm long. Inflorescence (1-)3(-7)-flowered axillary or sometimes terminal cymes; peduncle 5-55 mm long; pedicels pilose, 40-90 mm long curved at the apex. Flower buds greenish yellow to yellow or greenish violet to violet, ovoid, acuminate. Flowers campanulate; tepals 4, yellow, spotted or tinged with violet to dark violet, ovate to broadly lanceolate, 16-27 × 4-21 mm, 1.5-4 × as long as wide, acute, acuminate or mucronate at the apex with cuneate bases touching each other, lanate at margins, pilose inside, glabrous outside, spreading later. Remaining characters, see species description.

Remarks: Its more or less glaucous foliage and its tepals with violet spots make this subspecies different and easily recognizable from *C. tibetana* subsp. *tangutica*.

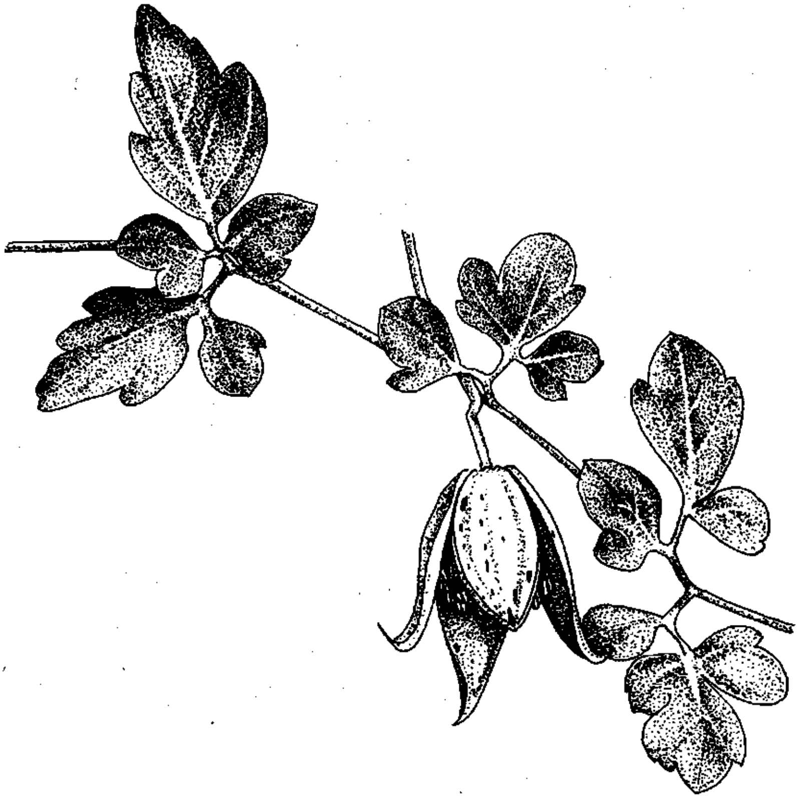
Distribution: China (Tibet), India (Uttar Pradesh), Jammu and Kashmir, Pakistan (Baltistan). See figure 2.26.

Specimens examined: CHINA Tibet, La-ma-ts'o Shank'ou, Meebold 3366 (G);

INDIA (Uttar Pradesh), Milaon Kumaon, Strachey & Winterbottom 3 (BM, BR, K, P);

JAMMU and KASHMIR, Askole, Clarke 30329A (K), Chenure, Koelz 2537 (K, L, NY), Hushe Saltara junction, Ludlow 369 (BM), Panamik, Ludlow 540, 542 (BM), Shushah, Ludlow 835 (BM), Leh, Ludlow & Sheriff 8476 (BM, UPS), Stok Nullah, Ludlow & Sheriff 8552 (UPS), Nubra valley, Meinertzhagen s.n., July, (BM), Schomberg 27, (BM), Dras/Kargil road, Stainton 7981 (K);

PAKISTAN (Baltistan), Sopor, Koelz 9593 (NY).



a

b

Figure 2.23. Illustrations of *C. tibetana* Kuntze subsp. *tibetana*
a. Drawing by Anja van der Neut (Bra285 WAG)
b. Aquarelle by Mariet de Geus (Bra255 WAG)

2.4.7.2. *Clematis tibetana* subsp. *tangutica* (Maximowicz) Brandenburg comb. nov.

Basionym: *Clematis orientalis* L. var. *tangutica* Maxim. Type: Przewalski 105, China Kansu, Terra Tangutorum; holotype LE, isotypes E, K, P; syntypes Przewalski 171, China Kansu, Terra Tangutorum, LE; Przewalski 185, Tibet, Zai'dam, K, LE, P).

Synonymy:

Homotypic synonyms:

Clematis tangutica (Maxim.) Korsh. in Fragmenta florae Turkestaniae: 1. *Clematis tangutica*; 2. *Clematis orientalis* var. *roschanica*. Bulletin de l'Académie Impériale des Sciences de St.-Pétersbourg V^{e} ser., vol. **9** (1898): 399-400.

Clematis tangutica (Maxim.) Korsh. subsp. *tangutica*.

Heterotypic synonyms:

Clematis akebioides (Maxim.) Veitch in New hardy plants in Western China, 9. p.p. (China Kansu Holotype Potanin s.n., 22-7-1885 LE, isotype K).

Clematis eriopoda Koehne, in *Clematis*. Deutsche Dendrologie (1893), 152-160; 567.

Clematis chrysantha Ulbr. in Fedde Repert. Beih. **12** (1922): 374 (Lectotype Limpricht 2086, China Kansu, Tsokadu B; paratype Limpricht 2146, B).

Clematis alpina sensu Kapoor, non Mill.

Clematis tangutica (Maxim.) Korsh. var. *obtusiuscula* Rehder & Wilson in: C.S. Sargent (ed.) - Plantae Wilsonianae an enumeration of the woody plants collected in Western China for the Arnold Arboretum of Harvard University during the years 1907, 1908 and 1910, vol. 1 *Clematis* (1913), 319-343 (Wilson 2487, China Sichuan, Ta-p'aoshan; holotype BM, isotypes E, K).

Clematis tangutica (Maxim.) Korsh. subsp. *obtusiuscula* (Rehder & Wilson) Grey-Wilson.

Clematis tangutica (Maxim.) Korsh. subsp. *mongolica* Grey-Wilson in *Clematis orientalis* (Ranunculaceae) and its allies. Kew Bulletin **44**: 33-60 (holotype: Jeffrey 1436, Mongolia, Tula River N.E. Ulan Bator).

Clematis pamiralaica Grey-Wilson in *Clematis orientalis* (Ranunculaceae) and its allies. Kew Bulletin **44**: 33-60 (Type: Tolmatcheva 4367, Tadzhikistan, Pamir, Murghab; holotype K, isotypes BM, C, E, G, LD, LE, MO, S).

Clematis orientalis var. *akebioides* Maxim. In Acta Horti Petrop. 11: 6 (1890).

Clematis glauca var. *akebioides* (Maxim.) Rehder and Wilson in Sargent Plantae Wilsonianae 1: 342 (1913).

Illustration: Botanical Magazine t. 7710 (1900); Revue Horticole 1902, p. 528. see also figure 2.24.

Description: Woody climber, up to 5m tall, sometimes with a compact, bushy performance due to environmental conditions (altitude, drought). Branchlets costate, pilose. Leaves pinnate or partly or wholly bipinnate with 7-15(-20) leaflets; the petioles 18-70 mm long; the leaflets ovate to lanceolate, irregularly serrate-dentate or slightly lobed (1-2 lobes at the base), herbaceous, green, glabrous above, pilose at veins below, 15-56 x 6-19 mm, 2-5 x as long as wide, acute at the apex, cordate, cuneate or angustate at the base; the petiolules pilose at the base, 5-20 mm long. Inflorescence mostly solitary at the apex, cordate, cuneate or angustate at the base; the petiolules pilose at the base, 5-20 mm long. Inflorescence mostly solitary axillary and terminal flowers - occasionally 2-3 flowers together in a cyme -; peduncle 0-25 mm long; pedicels pilose, at the top nodding, 7-32 cm long, profuse flowering. Flower buds greenish yellow changing over into bright yellow when maturing, ovoid, acuminate. Flowers narrowly campanulate; tepals 4, bright yellow, herbaceous, ovate-lanceolate, 18-35 × 8-12 mm, 2-3 × as long as wide, strongly ribbed, acute or acuminate at the apex with broadly cuneate bases touching each other, tomentose at margins, glabrous inside, glabrous or with a few scattered hairs outside, spreading later. Achenes ovate, pilose with persistent plumose styles up to 7 cm long in cultivation.

For the remaining characters see species description.

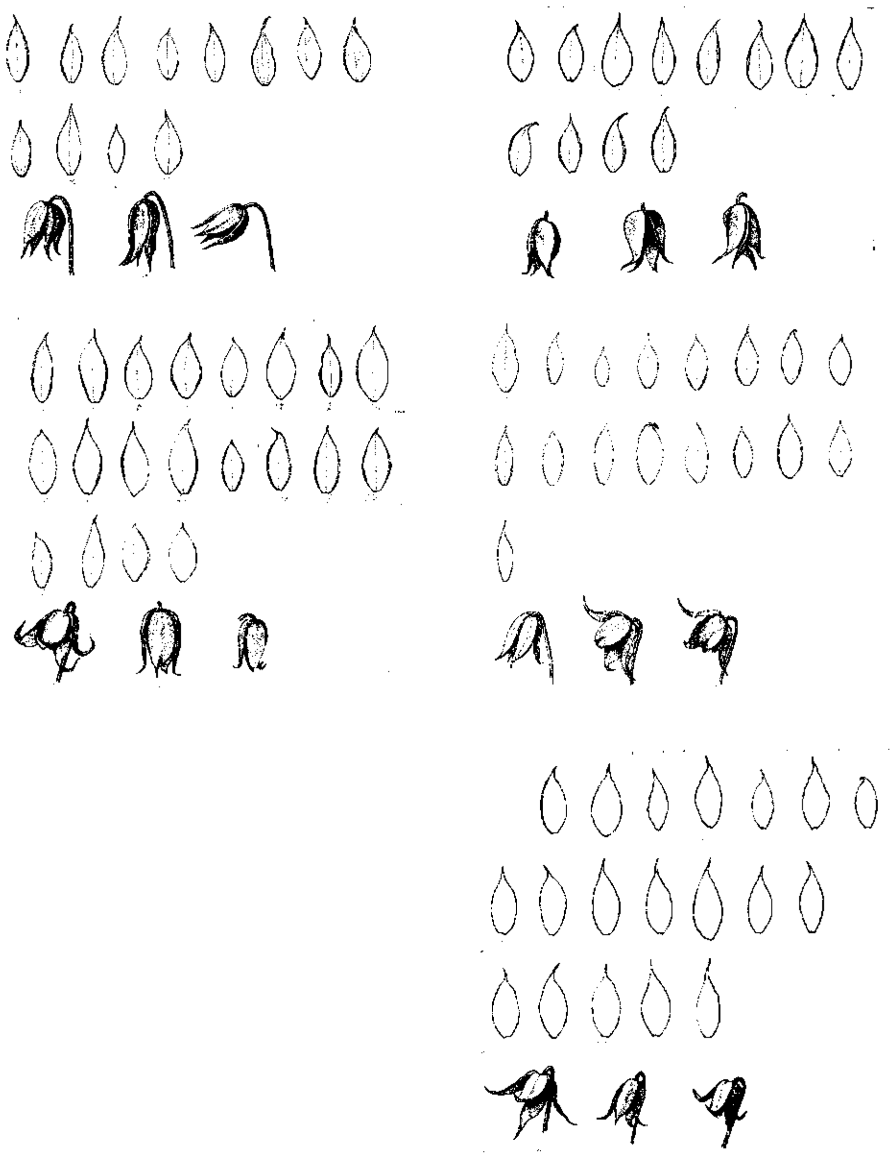
Distribution: Mongolia, China (Shansi, Kansu, Xinjiang Uygur Ziziqu, Tsinghai, Sichuan, Yunnan), Kazakhstan, Tadzhikistan, Jammu and Kashmir (see figure 2.26.).

Specimens examined: MONGOLIA, Tula River N.E. Ulan Bator, Jeffrey 1436 (K); CHINA Shansi, Lu Yak Shan, Smith 8122, (LD, S, UPS); Kansu, Przewalski 105 (K, LE, P), Przewalski 171 (LE), Zaidam, Przewalski 185 (K, LE, P); Xinjiang Uygur Ziziqu, Chaka, Tsinghai, Deasy 45 (BM, C), Deasy 77, Jolan Khola valley (BM), Aksu, Merzbacher 89 (B), Imyltsh valley, Raicheng, Merzbacher 1236 (B, M), Jarkand / Serek-kol, Norstedt 4 (S, U); Yunnan, Mekojg Sakvin, Forrest 13381 (K); Sichuan, Song'pan, Smith 2913 (LD, UPS); Tsinghai, Kokonor, Rock 13277 (C, UPS);

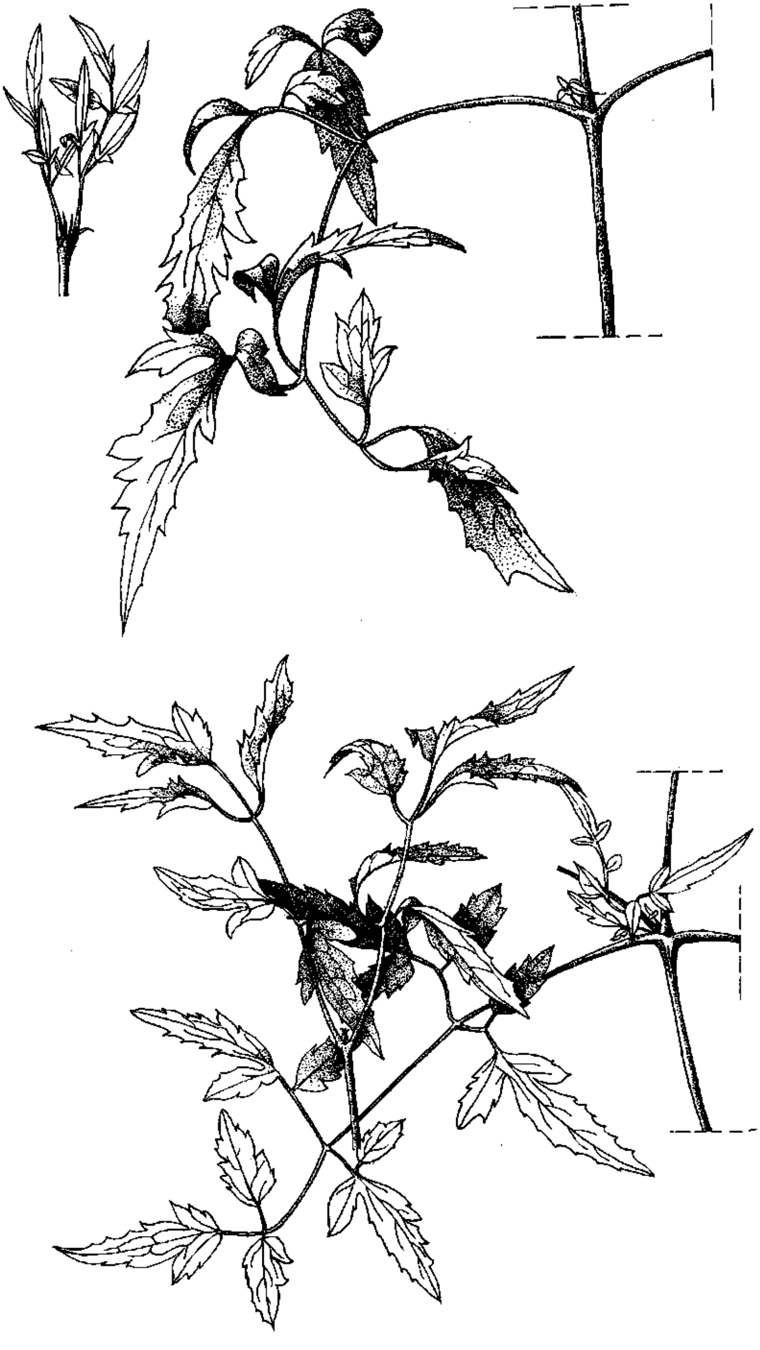
KAZAKHSTAN, Dzungarskiy Alatau, Mynas, Merzbacher 1022 (M);

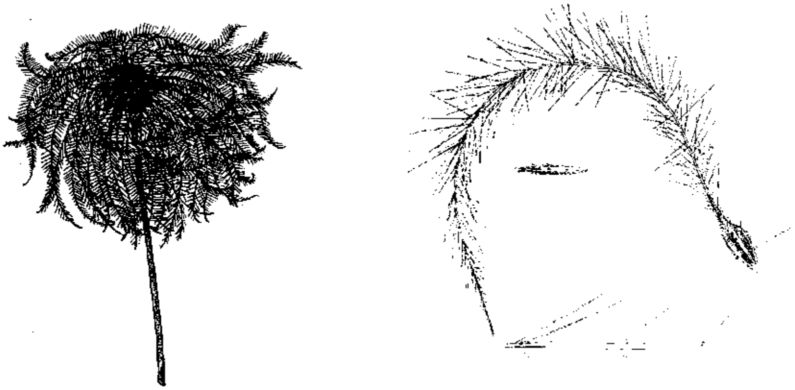
TADZHIKISTAN, Woshikini ozero, Rantsjoem, Konnov 3076 (TAD);

JAMMU and KASHMIR, between Da and Hanla, Rupshu, Koelz 2288b (K, NY).

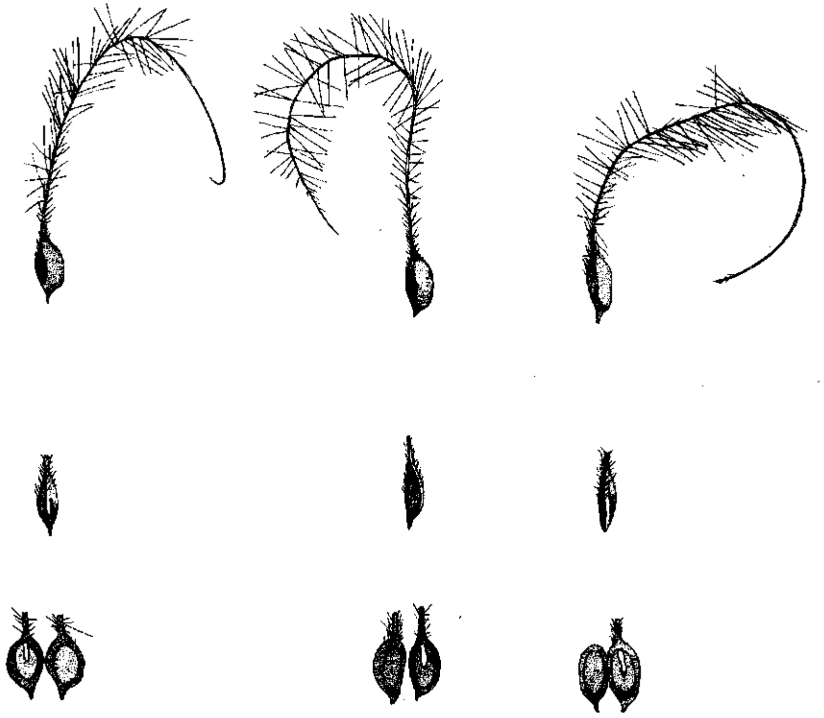


a

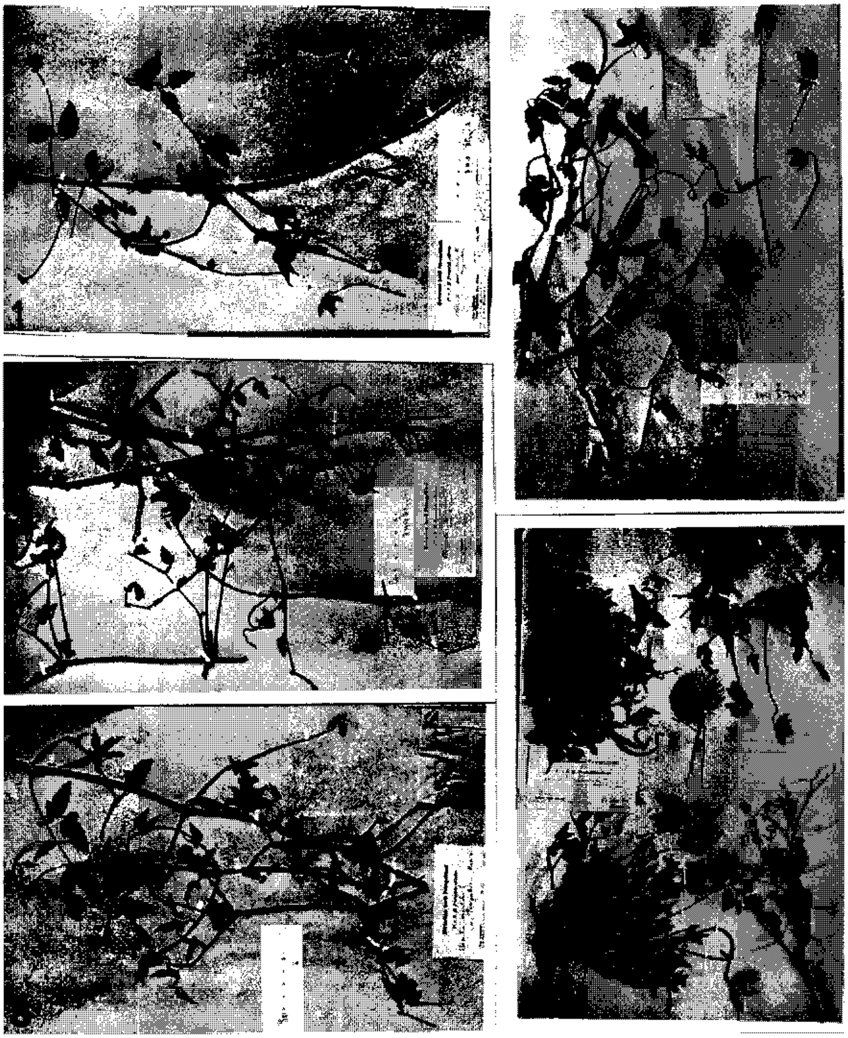

b



c



d



e

Figure 2.24. Illustrations of *C. tibetana* subsp. *tangutica* (Maxim.) Brandenburg

a. Variation in flower size and shape of tepals (Populations 76045, 76054,77017, 77020 and 77022)

b. Leaf morphology (population 76045)

c. Fruiting head and achene of plant 75-4

d. Achenes: shape, dorsal view and longitudinal section (plant 77017-4)

e. 1 holotype of C. tibetana subsp. tangutica (Przewalski 105 LE); 2/3 isotype (Przewalski 105 LE); 4 paratype (Przewalski 171 LE); 5 paratype (Przewalski 185 LE).

2.4.7.3. *Clematis tibetana* subsp. *vernayi* (C.E.C.Fisch.) Grey-Wilson in *Clematis orientalis* (Ranunculaceae) and its allies. Kew Bulletin **44**: 33-60

Basionym: *Clematis vernayi* C.E.C. Fischer, in Bull. Misc. Inform. Kew 1937 (1937): 95 (Holotype: Cutting & Vernay 57, China Xizang, Gyantse, K).
Synonymy:
Homotypic synonym:
Clematis tibetana O. Kuntze subsp. *vernayi* (C.E.C.Fisch.) Grey-Wilson var. *vernayi*.
Heterotypic synonyms:
Clematis chrysantha Ulbr. var. *brevipes* Tamura in Acta Pytotax. Geobot. **23** (1968): 30 (Holotype Namikawa 124, Nepal, Pijehl, KYO [not seen]).
Clematis tibetana sensu Hara & Williams in An enumeration of the flowering plants of Nepal II (1979): 16.
Clematis orientalis auct. non L. in Bull. Dept. Med. Pl. Nep. **7** (1979): 33.
Clematis tenuifolia sensu Ling, non Royle in Flore Rei Popularis Sinicae **28** (1980): 140, f. 41.
Clematis tibetana O. Kuntze subsp. *vernayi* (C.E.C.Fisch.) Grey-Wilson var. *laciniifolia* Grey-Wilson in *Clematis orientalis* (Ranunculaceae) and its allies. Kew Bulletin **44**: 33-60 (Holotype: Stainton, Sykes & Williams 2130, Nepal, Kali Gandaki, BM).
Clematis tibetana O. Kuntze subsp. *vernayi* (C.E.C.Fisch.) Grey-Wilson var. *dentata* Grey-Wilson in *Clematis orientalis* (Ranunculaceae) and its allies. Kew Bulletin **44**: 33-60 (Type Rock 14124, China Xizang, Radja River Gorge; holotype K, isotypes C, E, P, S).
Clematis tangutica (Maxim.) Korsh. var. *pubescens* M.C. Chang et P.P. Ling.

Illustration: Botanical Magazine t.4495 (1850); see also figure 2.25.

Description: Woody climber, up to 4m tall, flowering in summer; (June-)July-September. Branchlets angular to costate, pilose. Leaves pinnate or bipinnate with 7-21 leaflets; the petioles 14-64 mm long; the leaflets ovate to narrowly lanceolate, herbaceous, green, ± glabrous upside, pilose at veins downside, 18-50 × 6-44 mm, 1-8 × as long as wide, incidentally entire, but commonly irregularly serrate, dentate or lobed, cleft almost to the base in 1 main part and 1 or 2 smaller lateral parts, or composed of 3 leaflets of second order, the parts sometimes with a few teeth, acute, acuminate or mucronate at the apex, cordate, cuneate or angustate at the base; the petiolules pilose, 2-26 mm long. Inflorescence mostly solitary axillary and terminal flowers - occasionally 2-3 flowers together in a cyme; peduncle 0-65 mm long; pedicels pilose, 25-120 mm long. Flower buds greenish yellow, later turning to bright yellow, broad ovoid, acuminate or blunt. Flowers broadly campanulate to almost open, flat; tepals 4, bright or golden yellow, sometimes with a flush of violet (sometimes the colour changes to a bright orange yellow when flowers wilt), fleshy, sometimes very thick, broad ovate to lanceolate, 17-30 × 7-16 mm, 2-3 × as long as wide, acute at the apex with broadly cuneate bases touching each other, lanate at margin, pilose inside, glabrous outside, spreading. Stamens sometimes with dark violet filaments. Achenes with showy long plumose styles up to 6 cm in cultivation. For the remaining characters, see species description.

Remarks: Differing from *C. tibetana* subsp. *tangutica* by its fleshy spreading tepals in open, flat to broadly campanulate flowers.

This form was very long in cultivation under the misapplied name *C. orientalis*.

Distribution: China (Sichuan, Tibet), Nepal, Bhutan (see figure 2.26.).

Specimens examined: CHINA Sichuan, Tung-Ch'en San-k'ou, Smith 3663 (LD, S, UPS), Drachogi, Smith 4478 (UPS), Batang-Paan, Soulie 3016bis, (P), Sungp'an, Wilson 3131 (BM, K), 3131a (BM), 3132a (K), Ta-p'as-chan, Wilson 2487 (E, K); Kansu, Tsinghai, Farrer & Purdom 522 (E, M), Xhungyashan Shu'ka, Trippner 196 (M); Xinjiang Uygur Ziziqu, Su-kai-t'i, Ludlow 607 (BM); Tibet, near Gyantse, Cutting & Vernay 38, 57 (K), Ludlow 75 (BM), Karlung, Humphreys 5016 (BM), Tongkyuk, Kingdon Ward 6081 (BM), Lhasa, Ludlow & Sheriff 8678 (BM), Tsogo: Pasum Tso, Ludlow, Sheriff & Elliott 13928 (BM), Tsangpo valley, Simbiteng, Ludlow, Sheriff & Taylor 4472 (BM), Tsangpo valley, Timpa, Ludlow, Sheriff & Taylor 5151 (BM, E), Chu Kyabden, Ludlow, Sheriff & Taylor 6199 (G, UPS), Tongolo, Soulie 921 (P), Tzeku, Soulie 923 (P), Samada, Spencer Chapman 911 (K);

NEPAL, Tukule, Grey-Wilson & Phillips 366 (K), Namdo, Grey-Wilson & Phillips 693 (K), Marsiandi valley, Lowndes L1078 (BM, UPS), Barbung Khola, Kakkotgaa, Polunin, Sykes & Williams 1086 (BM), Dunaihi Behri river, Polunin, Sykes & Williams 2314 (BM, UPS), Kali Gandaki, Yara, Stainton, Sykes & Williams 2130 (BM), Muktinath, Stainton, Sykes & Williams 5645 (BM).

Figure 2.25. Illustration of *C. tibetana* subsp. *vernayi* (C.E.C.Fisch.) Grey-Wilson (drawing Anja van der Neut).

Figure 2.26. Distribution of the subspecies of *C. tibetana*.

● *Clematis tibetana* subsp. *tibetana*

□ *Clematis tibetana* subsp. *tangutica*

■ *Clematis tibetana* subsp. *vernayi*

2.5. Cytology

2.5.1. *Material and methods*

Four different methods to make squash preparations of root tips to study somatic metaphase chromosome morphology, have been used to characterise *Clematis* sect. *Meclatis* chromosomes. The procedures are described and the rationale of their use is given.

Method for Feulgen staining of mitotic *Clematis* chromosomes (Darlington & La Cour, 1967):

- Germinate;
- Pre-treat the roots with 0.002M 8-hydroxyquinoline for 4 hours at room temperature;
- Eventually, keep the roots in 1:3 acetic ethanol;
- Macerate 8 minutes in 1N HCl of 58°C;
- Stain with Feulgen for 4 hours;
- Rinse the root tips in running tap water;
- Squash them in 45% acetic acid;
- Make preparation permanent with Euparal, or dehydrate in three steps, rinse in xylol and mount in Canada Balsem.

Because of the specific biochemical reaction between stain nucleotides, the Feulgen staining method is very suitable to describe the metaphase karyotype. Chromosomes were measured in metaphase plates in preparations according to the above schedule.

Method for adsorptive staining of mitotic *Clematis* chromosomes:

- Germinate;
- Pre-treat the roottips with 0.002M 8-hydroxyquinoline for 4 hours at room temperature;
- Eventually, keep the roots in 1:3 acetic ethanol;
- Macerate 8 minutes in 1N HCl of 58°C;
- Staining procedure at room temperature (20°C) 5 - 20 minutes (1) and (2); 30 minutes (3).
  - (1) 1% carmin in
    45% acetic acid, or
    45% propionic acid;
  - (2) 1% orcein in
    45% acetic acid, or
    45% propionic acid;

(3) haematoxylin (Henderson & Lu, 1968);

- Squash in 45% acetic acid;
- Make preparation permanent with Euparal, or dehydrate in three steps, rinse with xylol and mount in Canada Balsem.

Sometimes, preparations were made permanent according to the quickfreeze method after Conger and Fairchild (1953).

The acetocarmin staining was used for the purpose of chromosome counting. If the staining was weak, subsequent preparations of the same series were stained with carmin in propionic acid.

The orcein staining was also used for counting purposes. Details of the chromosome morphology were, however, more clearly expressed than with carmin staining.

Haematoxylin is an unusual stain for chromosome studies. It proved to be an appropriate method for staining small chromosomes (1-2μ) in cytological work in *Begonia* and *Kalanchoe*. Applying this staining procedure to *Clematis* chromosomes appeared to be useful as quick method to screen metaphases for details such as satellites.

Method for Giemsa C-banding of mitotic *Clematis* chromosomes. The used method is slightly modified from Greilhuber (1973) and Schwarzacher et al. (1980):

- Germinate;
- Pre-treat the roots with 0.002M 8-hydroxyquinoline for 4 hours at room temperature (20°C);
- Eventually, keep the roots in 1:3 acetic ethanol;
- Keep the roots in aquadest for 20 minutes on the day of squashing;
- Transfer roots into 1N HCl for 5 minutes at room temperature (20°C);
- Macerate the roots in an enzyme solution containing 1% cellulase and 0.5% pectinase in 0.01M citrate buffer (pH 4.0) at 38%C for 25-30 minutes;
- Soften the roots in 45% acetic acid for 25-30 minutes at room temperature (20°C);
- Squah the root meristems in a drop of 45% acetic acid;
- Remove the coverslip after freeze drying in liquid nitrogen and air dry the slides for two days;
- Immerse the slides in 45% acetic acid at 60°C for 25-30 minutes;
- Denature the preparations in 6% BaOH solution for 6-7 minutes at room temperature (20°C) and wash them in runing tap water for 1 hour;
- Incubate the slides in 45% acetic acid at 60°C for 20 minutes;
- Rinse the slides in 0.04M phosphate buffer (pH 6.8) and stain with 4% Giemsa solution (in 0.04M phosphate buffer at pH6.8) for 10-15 minutes;

- Rinse the slides again in phosphate buffer and air dry;
- Mount the slides in Euparal.

Clematis C-banding patterns were studied in preparations, made according to the above schedule. In this preparations, the chromosomes were measured and the relative position of bands towards the centromere were drawn with the aid of a camera lucida.

A standard karyogram, based on measurements with the microscope micrometer is presented below together with the means of data. The centromere position is expressed in the short arm /long arm ratio, as was done by Kalkman (1984) and de Putter and van de Vooren (1988), but see also Denver Study Group (1960), Levan et al. (1964).

Microscopes used were various variants of the Zeiss Standard line; measurements were partly carried out at a magnitude of 1250×, using a 100× (plan)apochromatic objective Phase contrast (PH3). Photographs were made with Zeiss MC63 Photomicroscope equipment.

2.5.2. *Results and discussion*

The basic chromosome number in *Clematis* is $x = 8$, the majority of species being diploid: $2n = 2x = 16$. The overall chromosome morphology in a *Clematis* genome is not subject to large variation and to characterise as follows (nomenclature after the Denver Study Group, 1960; see also figure 2.27. and 2.28.):

- three large ($\pm 8\mu$) metacentric chromosomes;
- three relatively short (± 6-6.5μ) submetacentric chromosomes;
- two relatively short ($\pm 5.5\mu$) telocentric chromosomes.

One or two telocentric chromosomes may bear satellites (secondary constrictions on the short arm. No relation between *Clematis* classification and the occurrence of satellites can be indicated.

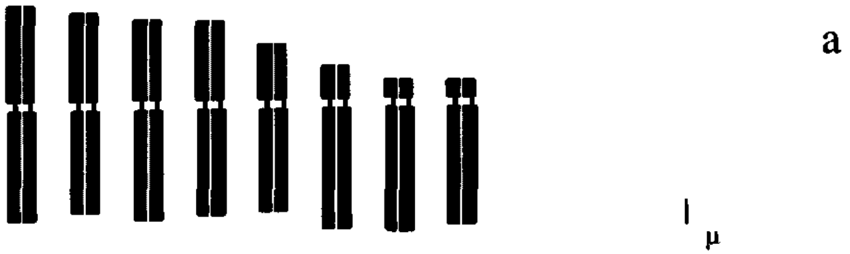
Polyploidy occurs only occasionally in the genus. $2n = 4x = 32$ has been reported as present in several species, but it is never a characteristic trait, occurring consistently, for any *Clematis* species. In the Wageningen collection, tetraploids have been detected in populations of *C. tibetana* subsp. *tangutica* and subsp. *vernayi.*

Focusing on *Clematis orientalis* and its allies, no consistent difference between *C. orientalis* and *C. tibetana* subsp. has been observed in the overall chromosome morphology. In table 2.9., the results of measurements on somatic metaphase chromosomes are presented. In general, the chromosome morphology between these species is similar, which can be seen from the idiograms of both species in figure 2.28. The satellites that occasionally occur are not drawn, as they are inconsistent in appearance. The idiograms of *C. orientalis* and *C. tibetana* subsp. *vernayi* were drawn from metaphase plates stained according to the Giemsa procedure; heterochromatic bands were only drawn, if they were present in all plates. The idiogram of *C. tibetana* subsp. *tangutica* were drawn from metaphase plates stained according to the Feulgen procedure. Measurements between both methods can be compared as both preparation and staining procedures are based on a similar reaction to DNA (Sharma & Sharma, 1972). The adsorptive staining procedure was used for chromosome countings of populations to make sure that no polyploid variation could influence the results of the interspecific hybridization programme. These results are not further detailed as the majority of populations is regularly diploid. Only in *C. tibetana* subsp. *tangutica* tetraploid plants and even some triploid plants were detected in certain populations. Photographs of representative metaphase plates are presented in figure 2.27. The populations used are vouchered by herbarium specimens as mentioned in the legend of this figure.

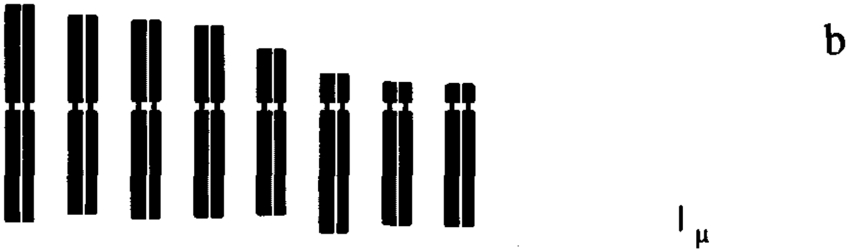
Table 2.9. Mean and standard deviation per chromosome of some *Meclatis* species.

Chromosomes ▸ **▾ Species**		**1**		**2**		**3**		**4**		**5**		**6**		**7**		**8**	
		M	**SD**	**M**	**SD**	**M**	**SD**	**M**	**SD**	**M**	**SD**	**M**	**SD**	**M**	**SD**	**M**	**SD**
C. tibetana* subsp. *tangutica	**TL**	8.62	2.10	7.90	1.76	7.92	0.90	7.74	2.30	6.82	1.70	5.82	1.06	5.43	1.12	5.66	1.25
	SA	4.09	0.97	3.54	0.79	3.47	0.42	3.26	0.96	2.36	0.68	1.18	0.59	0.78	0.23	0.61	0.19
	LA	4.53	1.15	4.36	1.00	4.44	0.50	4.48	1.36	4.46	1.32	4.64	1.12	4.65	0.96	5.06	1.10
	S/L	0.91	0.06	0.82	0.07	0.78	0.04	0.73	0.06	0.56	0.16	0.28	0.19	0.17	0.04	0.12	0.02
C. tibetana* subsp. *vernayi	**TL**	8.55	2.05	7.92	1.75	7.91	0.85	7.65	1.75	6.42	1.74	6.13	1.15	5.45	1.13	5.42	1.11
	SA	4.11	0.94	3.51	0.77	3.48	0.44	3.20	0.94	2.14	0.69	1.09	0.61	0.71	0.28	0.55	0.15
	LA	4.44	1.09	4.41	0.98	4.43	0.52	4.45	1.29	4.28	1.28	5.04	1.15	4.74	0.95	4.87	1.02
	S/L	0.93	0.05	0.80	0.06	0.79	0.04	0.72	0.07	0.50	0.14	0.22	0.18	0.15	0.08	0.11	0.03
C. orientalis	**TL**	8.59	2.15	8.05	1.85	7.98	0.92	7.85	2.31	6.89	1.76	6.40	1.20	5.65	1.18	5.55	1.19
	SA	4.02	0.95	3.59	0.85	3.45	0.47	3.35	0.95	2.41	0.75	1.32	0.64	0.58	0.27	0.59	0.16
	LA	4.57	1.18	4.46	0.97	4.53	0.58	4.49	1.33	4.47	1.35	5.09	1.19	5.07	0.91	4.97	1.09
	S/L	0.88	0.04	0.80	0.05	0.76	0.05	0.75	0.06	0.54	0.15	0.26	0.17	0.11	0.05	0.12	0.03

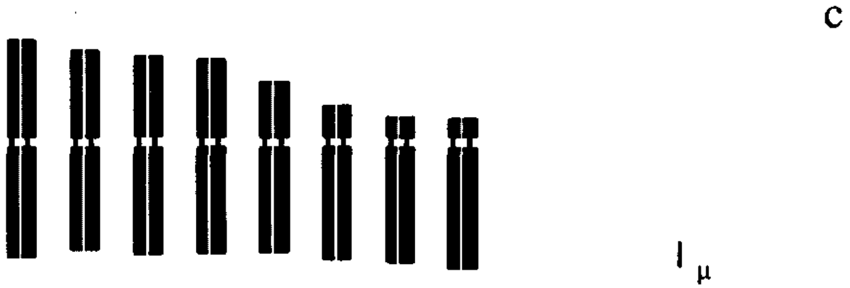
Figure 2.27. Somatic metaphase plates stained with Giemsa of *C. orientalis* L. (82374-9; specimen van der Neut (WAG); photographs Jos van de Vooren).



Idiogram of *Clematis orientalis* L.



diogram of *Clematis tibetana* subsp. *vernayi* (C.E.C. Fischer) Grey-Wilson



diogram of *Clematis tibetana* subsp. *tangutica* (Maxim.) Brandenburg

Figure 2.28. Idiograms constructed after somatic metaphase plates, stained with Giemsa (a, b) and Feulgen (c).

a *C. orientalis* L. (BRA 185,186 WAG)
b *C. tibetana* subsp. *vernayi* (C.E.C.Fisch.) Grey-Wilson (BRA 67, 73 WAG)
c *C. tibetana* subsp. *tangutica* (Maxim.) Brandenburg (BRA 66, 119 WAG)

2.5.3. *General discussion*

The cytotaxonomic study of Langlet (1932) has contributed considerably to the understanding of the Ranunculaceae. Numbers of chromosomes per genome showed correlations with relationships towards the overall shape of chromosomes. Moreover, both aspects could be related to the higher classification of the Ranunculaceae based on morphological characters. Within Ranunculaceae, the most frequently occurring basic number of chromosomes per genome is x = 8, which is the number of a.o. most *Anemone* spp. and *Clematis*; besides that x = 7 is also commonly present (e.g. *Aquilegia* and *Hepatica*). Gregory (1940) and Okada and Tamura (1979) compared the classification of Ranunculaceae based on morphological characters by Prantl with another one taking into account chromosome form and number, and showed a certain degree of agreement between both approaches. Rothfels et al. (1966) studied chromosome size and DNA content of *Anemone* and related genera and found a positive correlation.

Clematis spp. are normally diploid (2n=2x=16) and only occasionally tetraploid (Meurman & Thermann, 1939; Gregory, 1940; Kurita, 1956, 1957, 1958a, 1958b, 1960, 1962, 1964; Fedorov, 1969). Gregory (1940) reported *C. mandshurica* Rupr. and *C. paniculata* Thunb. being tetraploid, but countings at Wageningen (unpubl.) indicate that these are populational deviations at the utmost. Meurman and Thermann (1939) already showed that within *Clematis* there is not much variation as to chromosome form and size, a conclusion which has been confirmed repeatedly. The occurrence of satellites on the short arm on one or both telocentric chromosomes has appeared to be an inconsistency throughout *Clematis* spp. and never a consistent, characteristic element on any genome. To localise heterochromatic zones in chromosomes with Giemsa staining has proven to be a useful tool in characterizing genomes that otherwise look very similar, as can be learned from cytotaxonomic studies with *Allium* (Kalkman, 1984; de Putter & van de Vooren, 1988) and *Lactuca* (Koopman et al, 1993). Comparing the idiograms of *C. orientalis* and *C. tibetana* subsp. *vernayi* leads to the conclusion that Giemsa bands occur in *C. orientalis* at the terminal zones of the chromosomes and that *C. orientalis* shares most of these bands with *C. tibetana* subsp. *vernayi*. However, the latter shows double bands in the long arms of chromosome 3, 4 and 8. As in both species, plants are analyzed of a single population it is not possible to conclude that there are interspecific differences. Further analyses have to reveal whether this polymorphism within the section *Meclatis* occurs at the populational level, as it does in other studies, e.g. *Scilla* (Greilhuber, 1973), or that it concerns interspecific differences. Within the section *Meclatis*, once the occurrence of B chromosomes has been reported (Shambulingappa, 1965), but although in the present investigation we have counted chromosomes for all populations used in the interspecific hybridization diallele, B chromosomes have never been observed within the section *Meclatis* nor in other *Clematis* spp.

2.6. Pollen morphology

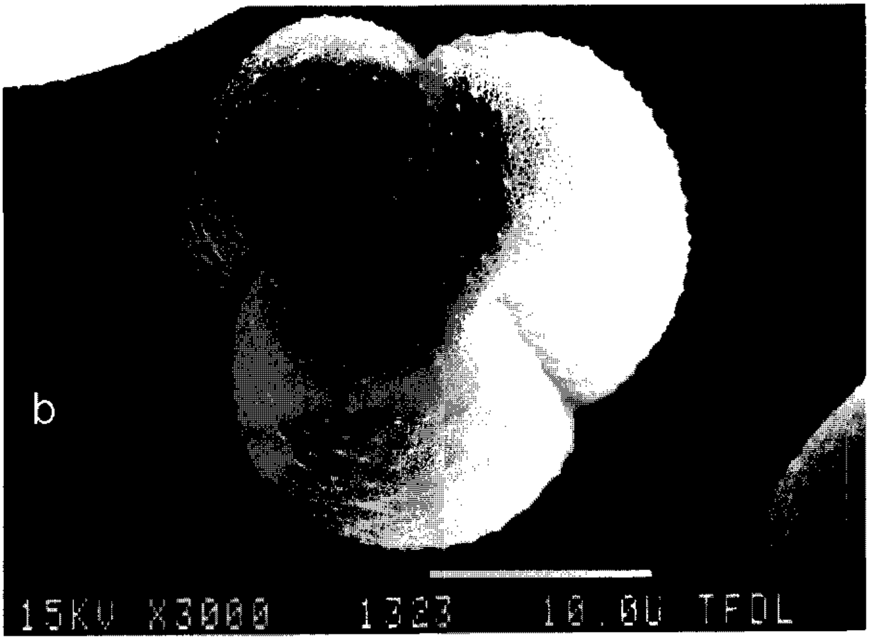
Within the framework of this *Clematis* study, there was considerable interest in either fresh or stored pollen (see 1.3.2.), and additional observations of the pollen morphology were made with the aid of Scanning Electron Microscopy. Moreover, pollen morphology has proven to be useful for plant systematic studies (Blackmore, 1984; Tobe, 1974).

Pollen slides were made at TFDL-DLO (Gold plating; andincluding or excluding pretreatment by rinsing with chloroform to remove the extexine layer). Observations were made with a JEOL S.E.M.

Kumazawa (1936) and Wodehouse (1936) studied already the pollen morphology of Ranunculaceae. From their studies, it is obvious that the basic type of pollen in Ranunculaceae is the tricolpate ellipsoidal type with deep colpes and no distinct germ pores (Erdtman, 1952). Pollen of *Clematis* sect. *Meclatis* meet this basic type of pollen. Note the scabrate surface of pollen at the polar sides and in the equatorial view between the colpes. Within section *Meclatis*, pollen has been observed of *C. ispahanica*, *C. tibetana* subsp. *tangutica*, and subsp. *vernayi*, *C. orientalis* and *C. serratifolia*. Photographs of pollen in both polar and equatorial position of *C. tibetana* subsp. *vernayi* are presented in figures 2.29a and b.

Kumazawa (1936) noted apart from the above basic type other pollen types in Ranunculaceae with no clear colpes but being polyporate. Within the Anemoneae, he depicted this phenomenon for *Anemone coronaria* L. and for *C. texensis* Buckl., *C. viorna* L., *C. stans* Sieb. et Zucc., and *C. patens* Morr. et Decne., whereas he depicted the basic type for *C. apiifolia* DC. and *C. fusca* Turcz. var. *mandshurica* Takeda. Our S.E.M.-observations confirm Kuwazaga's drawings as to *C. patens* (figure 2.29c). As no light microscopical observations were made and no measurements were carried out on *Clematis* pollen morphology, it is not possible to make more detailed characterisations of pollen per species. It is, however, obvious that the difference between both types is so large, that further pollen morphological study is expected to be significant for *Clematis* systematics.


a
15KV X3000 1222 10.0U TFDL


b
15KV X3000 1323 10.0U TFDL

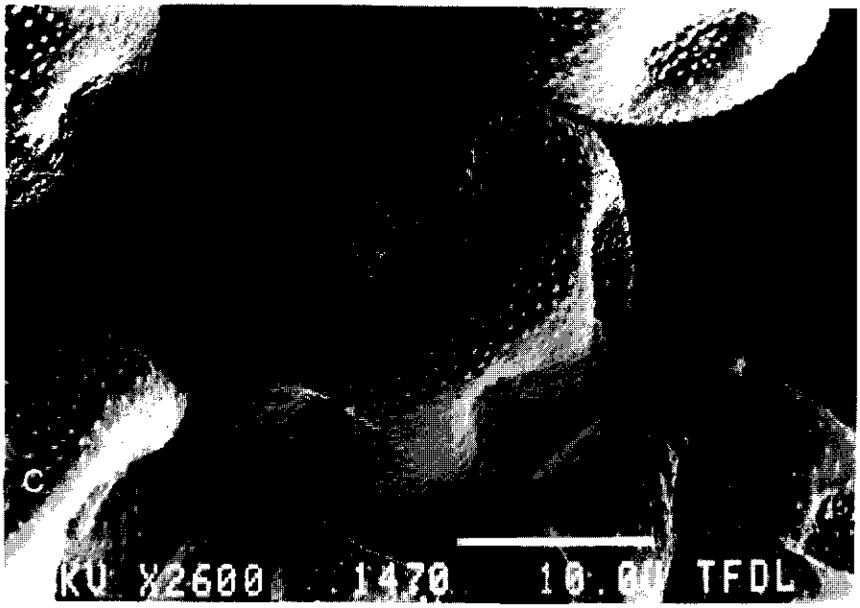


Figure 2.29. S.E.M.-photographs of *Clematis* pollen.
Approximate magnitude at photographs: 4200×
a. *C. tibetana* subsp. vernayi - equatorial view;
b. *C. tibetana* subsp. vernayi - polar view;
c. *C. patens*.

2.7. **Isozyme polymorphism in *Meclatis***

Since morphological characters are more or less affected by environmental conditions (Crawford, 1985), and karyotypic analysis does not show much variation, electrophoretic analysis of total proteins was carried out in order to get some insight in variation patterns within *Clematis* sect. *Meclatis*. This experiment was carried out in 1984. Since then, the developments in electrophoretic research have greatly progressed. The experiment is only reported here because of the results showing starting points to further electrophoretic research within *Clematis*.

2.7.1. *Material and methods*

Plant material is used of *C. orientalis* (1 vouchered by BRA185 and 186; 2 vouchered by Brandenburg BRA 166), *C. serratifolia* (3 vouchered by herbarium specimen Brandenburg BRA170), *C.* 'Bravo' (4 vouchered by herbarium specimens Van der Neut 35, 36 and 37) and *C. tibetana* subsp. *vernayi* (5 vouchered by herbarium specimen Brandenburg 188). The two *C. orientalis* individuals were seedlings from different populations.

Young fresh leaves were yielded, ground and frozen with liquid nitrogen. 0.5g dowex buffer (4g dowex in 5ml phosphate buffer [2.68g $Na_2HPO_4.7H_2O$ and 3.1g $KH_2.PO_4$ in 100ml demi water]) was added to 1g leaf sample to bind phenoles. The samples were left for 45 minutes at 4°C. The leaf samples were squeezed. 12.5µl 0.25M tris-borate buffer (pH=7.9) was added to 50µl leaf extract and centrifuged (15000tpm) for 20 minutes. The samples were then dialysed for 16 hrs to remove undesired salty compounds. At this stage, the extracts can either be used immediately for further analysis or stored in a refrigerator.

The PAGE gels were of 12.5 ml 0.25M tris-borate buffer (pH=7.9), 50 ml stock solution (75g acrylamide and 2g methylene-bis-acrylamide in 500 ml demi water), 37.5ml demi water, 1ml sodium sulfite solution (43mg sodium sulfite in 1ml demi water), 1ml ammonium persulfate solution (30mg ammonium persulfate in ml demi water) and 0.03 ml TEMED. After 30 minutes of polymerisation the gel was ready for use.

The electrode buffer is a trisborate buffer (pH=7.9).

Vertical running was carried out at 10 °C after prerunning during 45 minutes. Before soaking the wicks with leaf extract (30µl), 25µl DMSO stain was added to 100 µl leaf extract. Running time is approximately 2hrs. and ends when the voltage of 500V had been reached.

Gels were stained with Coomassie blue or esterase overnight under continuing turning.

2.7.2. *Results and discussion*

From at least three runs slots of the same individual were compared. Due to the character of an aspecific protein stain, there were lots of hardly distinct (overlapping) bands. The bands conspicuous in all replications were screened and are presented in figure 2.30c. This figure shows some differences within and between species in these bands. Both provenances of *C. orientalis* show polymorphism in bands and do not have such pronounced bands as in with *C. serratifolia*. *C. tibetana* subsp. *vernayi* as well as *C.* 'Bravo' (which as cultivar has been selected from hybridization with *C. tibetana*) share at least one pronounced band with *C. orientalis*.

Comparison with other incidental runs make clear that further analysis with isozyme specific stains may contribute in determining genetic distances between species of *Clematis* sect. *Meclatis*.

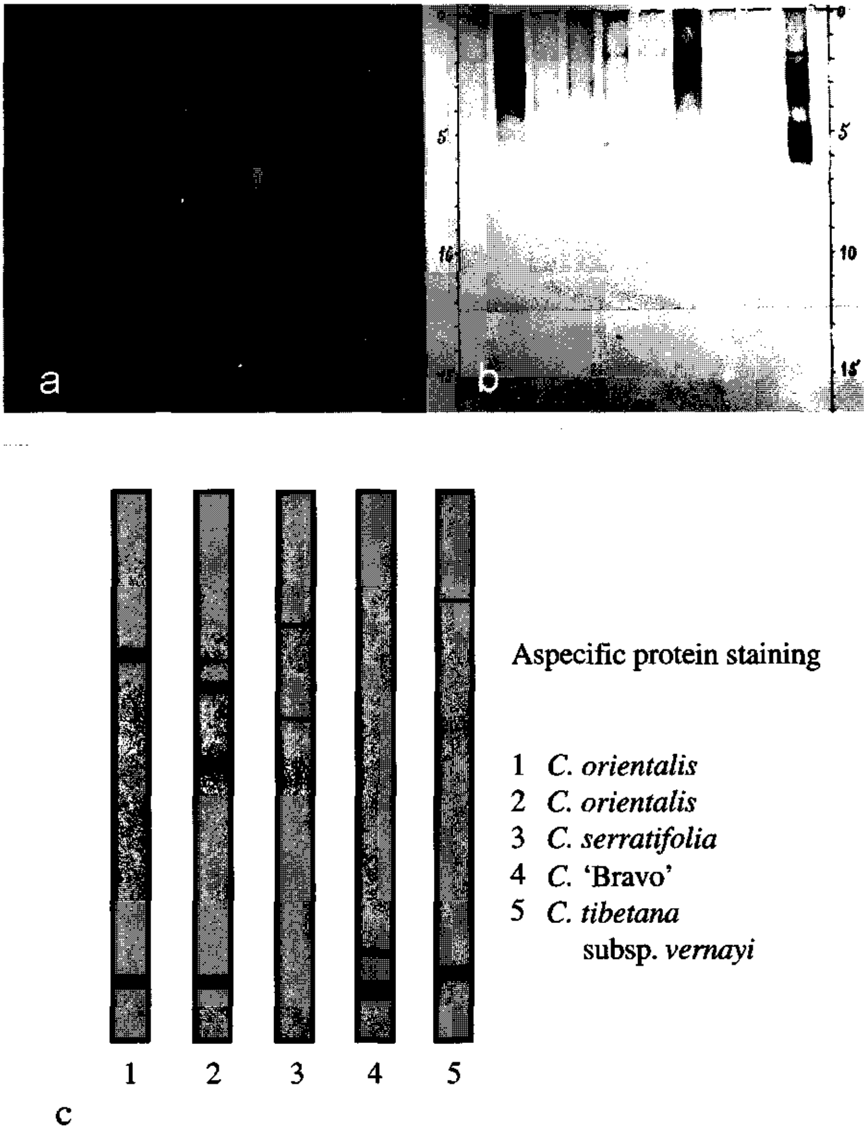


Figure 2.30. a. Isozyme polymorphism aspecific protein staining of *Clematis* sect. *Meclatis*. b. Isozyme polymorphism esterase protein staining of *Clematis* sect. *Meclatis*. c. Schematic presentation of pronounced protein bands by PAGE of 5 specimens of *Clematis* sect. *Meclatis*.

3. CLASSIFICATION OF CULTIVATED PLANTS[1]

3.1. History of classification schemes concerning cultivated plants

At the dawn of taxonomic consciousness, cultivated plants rather than wild plants were subject of classification. In those days economically and culturally important plants - useful or poisonous and cultivated plants - were almost the only species treated, as is obvious from herbals since Theophrastos' time.

With the publication of Linnaeus' Species Plantarum, 1st May 1753, attitudes towards classification of cultivated plants became clearer through the consequent introduction of binomial nomenclature (Jarvis, 1986; Wijnands, 1986a). Some cultivated plants were regarded as species separate from their wild or weedy relatives and putative ancestors, e.g. *Ribes uva-crispa* vs. *Ribes grossularia*, whereas others were regarded as unnamed or named varieties within species, e.g. *Brassica oleracea* (Oost et al., 1989), *Daucus carota* (Wijnheijmer et al., 1988) and *Dianthus caryophyllus* (de Langen et al., 1984). sometimes combinations of these approaches are used, e.g., *Brassica rapa* vs. *Brassica campestris* (Oost et al., 1987) and *Lactuca sativa* vs. *Lactuca serriola* (de Vries & Jarvis, 1987). In other cases Linnaeus hesitated which of both approaches should be chosen, e.g. *Beta vulgaris* inclusive of the *Beta maritima*, vs. *Beta maritima* as separate species (Letschert, 1993; Linnaeus, 1753, 1762).

From Linnaeus until the second half of the 19th century, there was a decreasing interest in the taxonomy of cultivated plants (Heiser, 1986). Botanists became aware of the huge variation in the Plant Kingdom. They mainly described and named plants from all parts of the world, focusing their attention on the hitherto unknown plants rather than to the well-known cultivated plants of those days. Cultivated plants were classified at various infraspecific ranks. These ranks were largely determined by tradition and not by number

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[1] This chapter has been largely based on the earlier publication by Brandenburg & Schneider (1988; 3.1. and 3.2.), and the publication by Hetterscheid & Brandenburg (1995a; 3.3. and 3.4.).

and mode of distinguishing characters. Vegetable and silvicultural crop plants were usually classified as subspecies or varieties, whilst ornamentals, including woody ornamentals, with the same kind of distinguishing characteristics were termed varieties or forms! The only rationale behind it may well be that vegetables and silvicultural crops are predominantly reproduced generatively, whereas most ornamentals are propagated vegetatively. There was a remarkable connection between attitudes towards classification and various sectors of plant cultivation.

In the 19th century, especially after Alphonse de Candolle's Origine des Plantes Cultivées (1883), cultivated plants attracted much attention again. In 1866, Alefeld published his Landwirtschaftliche Flora, in which he introduced the term 'variety group', which became later the systematic category **convariety**. With the convariety a special rank was created between subspecies and variety to designate crops, or, sometimes, crop groups. The convariety soon became a commonly used systematic category, applied for several cultivated plants (Grebensçikov, 1949, 1950; Mansfeld, 1950).

As reviewed by Stearn (1986), the first edition of the International Code of Nomenclature for Cultivated Plants (ICNCP) was published by Stearn in 1953 after decades of discussion about the desirability to make a distinction between cultivated and botanical varieties. The convariety was adopted in the 1953, 1958, and 1961 editions of the ICNCP as a means of cultivar classification. This attitude was almost parallel with statements about classification of cultivated plants (Mansfeld, 1953, 1954; Helm, 1954, 1963; Danert, 1962). Further developments in creating special categories for cultivated plants were made in an attempt to solve complex classification problems like those in *Brassica*. Jirasek (1966), among others, created an extensive hierarchy of special categories, summarized below:

specoid (spd.)	species
subspecioid (subspd.)	subspecies
cultiplex (cpl.)	
subcultiplex (subcpl.)	
convarietas (convar.)	
subconvarietas (subconvar.)	
provarietas (provar.)	
subprovarietas (subprovar.)	

conculta (conc.)
  subconculta (subconc.)
    cultivar (cv.)
      subcultivar (subcv.)

In later work, Jirasek deleted the subcultivar, as it is in contradiction with the statement in ICNCP (Brickell et al., 1980), Art. 10 second paragraph:
'The cultivar is the lowest category under which names are recognized in this Code.'

Jeffrey (1968) tried to reduce the number of categories and to develop a synthesis of differing opinions:

species		
subspecioid	or	subspecies
convarietas		
		(subconvarietas)
provarietas		
		(subprovarietas)
cultivar		

In the 1969 edition of the ICNCP (Gilmour et al., 1969), a new approach to cultivar classification was adopted by replacing statements about the convariety with the concept of **cultivar-group**. From that time onwards it was possible to subdivide large assortments of crop plants into cultivar-groups, defined by characters of agricultural importance. By discarding the traditional botanical classification of the convariety, and replacing it with the cultivar-group concept, it is possible to create flexible classifications which can be easily replaced after being superseded by further developments in plant breeding. These so-called **open classifications**, starting from the cultivar have proven to be practical and useful for gene bank documentation (Brandenburg et al., 1982; Brandenburg, 1983) and for registers, statutory and nonstatutory, of cultivated plants (Brandenburg & Schneider, 1985; Duyvendak et al., 1981).

The problem left is the linkage between botanical classification and cultivar classification in developing one unequivocal classification system for cultivated plants. At several occasions it was proposed to do so at the subspecies level (Harlan & de Wet, 1971; de Wet, 1981; Pickersgill, 1986) with the apparent drawback that subspecies would be an ambiguous term to be used for different entities (Brandenburg, 1983, 1984a), distinguishing both geographically and morphologically distinct populations and wild, weedy and cultivated populations. Proposals to link botanical and cultivar classification at forma level have similar drawbacks (Brickell, 1973; Wijnands, 1986b).

3.2. Principles of open classification outlined

Strictly fitting cultivars into the hierarchy of botanical classification would lead to suggestive, pseudoexact non-information, which has already given systematics a bad name. The suggestion that most cultivars can be assigned to a species can be belied by just following the developments in plant breeding, especially in wide hybridization programmes and in the field of incorporating desired new traits by molecular biological methods.

The introduction of a special nomenclature for hybrid cultivated plants is the denial of these developments, since for botanical classification there is hardly any need for special provisions in nomenclature and classification. The International Code of Botanical Nomenclature (ICBN; Greuter et al., 1994) admitted in that respect that the prefix notho- to all ranks is not obligatory.

Whether ornamentals, vegetables, fruit crops, agricultural or silvicultural crops, many cultivars are of (complex) hybrid origin. With the advanced techniques of plant breeding, such as the application of molecular biology, somatic hybridization and various methods to prevent dying of young embryos produced by hybridization of distantly related plants (Feldmann, 1983), cultivar classification cannot be linked with botanical classification at any *a priori* rank. Although this linkage will often happen at the specific level or at the generic level, it is certainly not always the case. Apart from already mentioned shortcomings of the ICNCP, it is difficult - if not impossible - to classify unequivocally all different kinds of hybrids, as both ICBN and ICNCP contain a set of rules providing definitions of terms and guidelines for hybrid nomenclature (Brandenburg, 1984a, 1986a, 1986b).

Although the ICNCP thus far is meant to be additional and, consequently, subordinate, to the ICBN, the Hybrid Appendix (Appendix 1 of the ICBN) is unsuitable for general usage with respect to hybrids raised in cultivation. This is due to the following statements:

- 'A hybrid between named taxa may be indicated by placing the multiplication sign between the names of taxa' (Art. H.2).
- 'When all the parent taxa can be postulated or are known, a nothotaxon is circumscribed so as to include all individuals (as far as they can be recognized) derived from the crossing of the stated set of parent taxa (i.e. not only the F_1 but subsequent filial generations and also backcrosses and combinations of these). There can thus be only one correct name corresponding to a particular hybrid formula; this is the earliest legitimate name (see Art. 6.3) in the appropriate rank (Art. H.5), and other names to which the same hybrid formula applies are synonyms of it' (Art. H.4.1).

The first statement is not meant to indicate hybrid cultivars which have to be synthesized each generation by crossing of parent lines and implies that a hybrid cultivar may bear a **nothotaxon** designation. It is not obligatory to combine the nothotaxon name with a cultivar epithet. The result is that plant populations which meet requirements of the cultivar definition may be often covered by a nothotaxon name, thus being hidden cultivars. *C.* × jackmanii Th. Moore has been described as interspecific hybrid between *C. viticella* 'Hendersonii' and *C. lanuginosa* Lindl. et Paxt., the latter now being regarded a cultivar (Brandenburg & van de Vooren, 1986; 1988a). From the original publication (Moore, 1864) it is clear that the author had a particular clone in mind. This clone has also been described in Moore & Jackman (1872) under the name *C.* ×*jackmanii*. Since other clones of the same interspecific cross received cultivar epithets in modern language, it is logical to consider *C.* ×*jackmanii* a cultivar: *C.* 'Jackmanii'.

The second statement does not agree with agricultural and horticultural practice for plant denominations. Since it is possible to breed different crops from reciprocal crosses (i.e. ×*Brassicoraphanus* vs. ×*Raphanobrassica*; Oost, 1984), it was confusing that they should bear the same name! Repeated backcrosses are used to transfer desired characters to cultivated plants. If rye characters are introduced into wheat, and if the rye influence remains recognizable after backcrossing, the resulting hybrid cultivars have to be assigned ×*Triticosecale*. They are usually regarded in common practice to be wheat cultivars. Registration authorities are left in confusion, as under Art. H.4.1 a distinction between wheat and triticale cannot be made (Baum, 1971a, 1971b; UPOV, 1984; Gupta & Baum, 1986), as the dogmatic approach does not provide us with the possibility to name different crop forms. When dealing with intergeneric cultivated hybrids, it is worthwhile considering to define cultivar-groups. For the reciprocal intergeneric hybrids, the oldest available intergeneric name can well be combined with cultivar-group epithets making clear the various types of cultivated plants concerned. The backcross situation may well be solved to define cultivar-groups in the recurrent parent species. Triticale can be regarded, doing so, as a cultivar-group in *Triticum aestivum* L.

The ICNCP (Brickell et al., 1980) also contains rules concerning the naming of hybrid cultivated plants, mainly based on the most recent version of the Hybrid Appendix at the date of the ICNCP publication, but with adding the possibility of using the term grex. The ICNCP (Brickell et al., 1980) states in Art. 18 (marks in bold by the present author):

> 'A collective epithet may also be a word or a phrase of not more than three words in a modern language. For the purpose of this article, an arbitrary sequence of letters, an abbreviation, or a numeral is counted as a word. All derivatives from the combination of the same two or more parental species have the same collective epithet in a modern language **except where established custom or special circumstances demand otherwise, as for example, in orchids.**'

The grouping of seedlings, belonging to one progeny, in **greges** (sing. **grex**) under collective names is entirely different from cultivar-grouping. Recommendation 18A reads, 'A phrase used as a collective epithet may contain a word such as Hybrid, Hybrids, Cross, Crosses, grex (abbreviated g., Latin for swarm or flock), etc., indicating the collective nature of the unit'. This implies that a grex is basically a population of individuals of the same parentage. There is no need to describe cultivars within a grex, but, of course, it is possible. So, a grex can be an independent entity, part of which does not necessarily meet the requirements of the cultivar definition.

Looking at classification and registration of cultivated orchids according to the ICNCP and the special Handbook on orchid nomenclature and registration, one must come to the conclusion that with the purpose to create clarity and an unequivocal, stable nomenclature the result is confusing, leaving the user with named seedling populations that are sometimes only segregating populations, but may also concur with the definition of the cultivar. The conclusion is that forthcoming editions of the ICNCP should neither contain statements concerning grex nor references to the Hybrid Appendix, except for the pragmatic one to the nothogenus to warrant in all cases the connection between botanical and cultivar nomenclature. In the forthcoming edition of the ICNCP, articles concerning grex will therefore be deleted with the one reference to the fact that it is possible to make an informal classification by greges.

The term cultivar-group is defined in the ICNCP (Brickell et al., 1980), Art. 26:

> 'When a species, interspecific hybrid or intergeneric hybrid includes many cultivars, an assemblage of similar cultivars may be designated as a group. This category is intermediate between species and cultivar. It is not an essential part of the full cultivar name. If used between the species name or collective name and the cultivar name, the name of the group is placed between parentheses (round brackets).'

This definition contains some contradictory elements:

- "Interspecific or intergeneric hybrids may also include assemblages of similar cultivars," so cultivar-groups, making it impossible to rank cultivar-groups exclusively intermediate between species and cultivar!
- the word "essential" has been misplaced in Art. 26, because of what is stated in art. 27, second sentence, the cultivar-group name is not a part of the cultivar name at all, let alone an essential part. Although it is not an essential part of the full cultivar name, there is an indication where to place a cultivar-group designation in a full cultivar name, but there is nowhere else in the Code a guidance how to form cultivar-group names, except implicitly in the examples given for Art. 26.

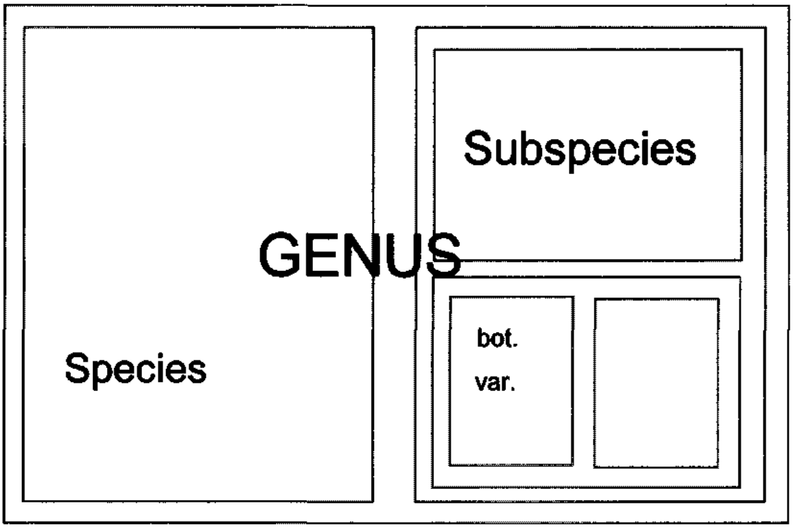
Therefore, it would be desirable to include rules providing a statement how to establish a cultivar-group, based on one or more standards so that everybody, no matter where in the world, can most likely determine on general appearance whether a cultivar can be assigned to a certain cultivar-group under local circumstances. This is especially important for obligate cross-fertilized crop plants like many vegetables and fruit crops. Moreover, a statement should be made as to whether a cultivar-group is of local significance or is meant to be valid worldwide.

A note added to Art. 26 states:

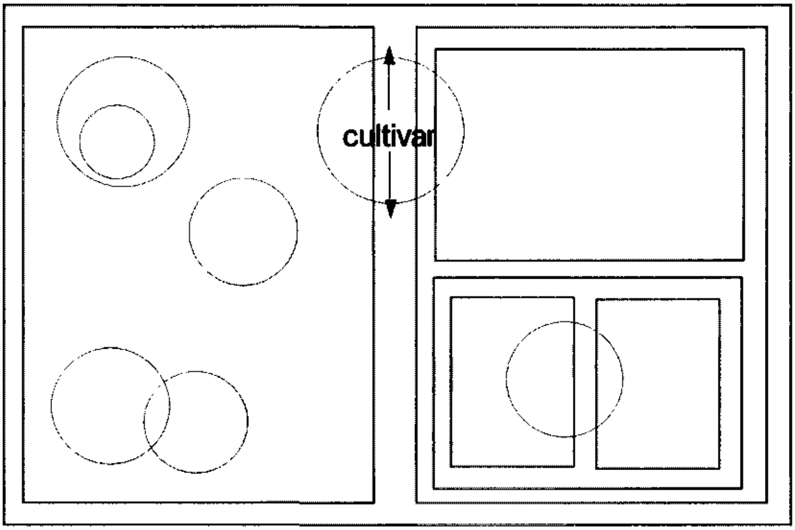
> 'In complex crops, for example, in apples and some cereals, a hierarchy of categories has been applied, the use of which is not governed by this Code.'

This note is confusing, since the concept of cultivar-grouping does not agree with a concept of hierarchical relationships among cultivar-groups. A hierarchy unnecessarily hampers the connection with botanical classification and, consequently, nomenclature as governed by the ICBN. On the contrary, this note should explicitly state that cultivar classification in cultivar-groups replaces more hierarchical cultivar classifications, even in complex crop plants. The current concept is simple and it is therefore feasible and conceivable to judge when and if a cultivar-group classification should be replaced by a more up to date one. It thus describes current variation in large assortments which undergo rapid change by plant breeders' efforts.

The most recent edition of the ICNCP (Trehane et al., 1995) contains statements on the nomenclatural consequences of merging or splitting cultivar-groups to adapt the classification to shifting cultivar assortments (Art. 4.6). In both cases old cultivar-group names should be replaced to avoid that the same name reflects various circumscriptions. Although at first sight this will not serve a stable nomenclature, it does just that by its simple connection to one circumscription, as opposed to the former convarietal classifications, which strictly fitted the botanical hierarchy. Circumscription implies that distinguishing characters are presented with the included character states, whereas description omits ranges of variation. Circumscription thus provides a representative text concerning the identity of the particular unit concerned. Description only provides a diagnostic text, which is not necessarily representative in all its aspects. This difference necessitates a separate basic concept in classification of cultivated plants and forms the main difference between cultivar-group classification and former convarietal classification because of its consequences (see figure 3.1; sections 3.3. and 3.4.).



a



b

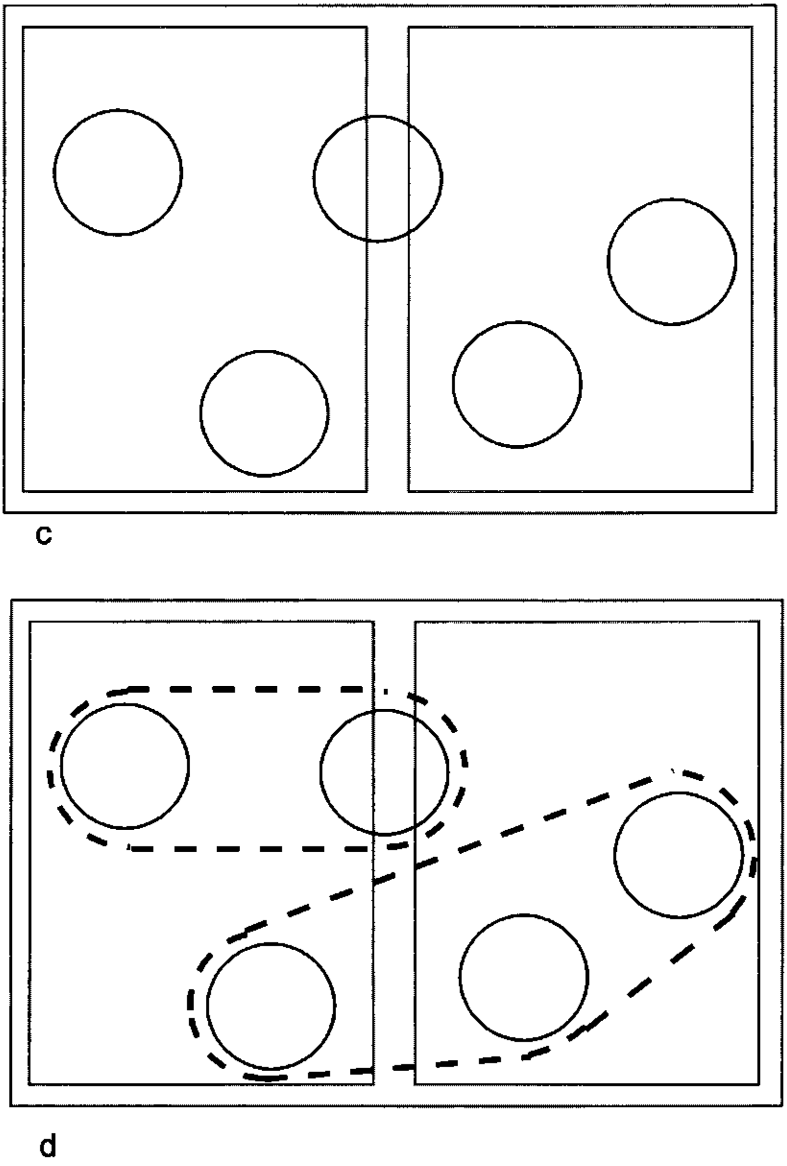


Figure 3.1.

a - Botanical (closed) classification, a hierarchical system of mutual exclusive taxa (genus, species, subspecies, botanical variety).

b - Open classification of circumscribed cultivars (they may partially or wholly overlap), laid over the botanical classification of 3.1a.

c - Another open classification of circumscribed cultivars (genus, species, cultivar).

d - Open classification of cultivars of 1c, but partially classified in two cultivar-groups (dotted lines).

The cultivar-group concept has already proven its usefulness, as can be learned from several examples: *Lactuca sativa* (Rodenburg, 1960), *Dahlia* (Anon., 1969), *Lilium* (Leslie, 1982), *Brassica rapa* (Oost & Toxopeus, 1986), *Clematis* (Brandenburg & van de Vooren, 1982, 1986, 1988a), *Narcissus* (Donald, 1986), *Dracaena* (Bos et al., 1992), *Aster* (Hetterscheid & van den Berg, 1996), *Philadelphus* (Hoffman, 1996) and *Beta vulgaris* (Lange et al., 1999). From these examples, it is clear that cultivar-group classification should agree with common practice. Since it must be useful for breeders, growers, registrars, merchants and all other conceivable users (not to forget the "public"), it should rely on clear characters, directly connected with growth conditions and/or consumer's usage. Biosystematic relationship (degree of relationship and descendance), therefore, is not a sound base for cultivar-group classification. It may agree in some cases, but it usually will lead to confusion as can be exemplified with *Rosa*. Although breeders like to refer to descendance, Polyantha roses and Floribunda roses cannot be distinguished in an experimental field. In common practice, these groups have no significance at all. A better procedure would be to define *Rosa* groups on characteristics such as flower size and flower colour, occasionally combined with other economically important traits (Buck, 1967). Another reason not to use biosystematic evidence is that documentation about old, sometimes extinct, cultivars is often very poor and statements about their descendance are not rarily either false, putative or just lacking. Requiring biosystematic criteria would preclude cultivar-group classification in many assortments. This would be the case in many ornamentals, as in *Clematis* (Brandenburg & van de Vooren, 1986). Furthermore, cultivar-groups would then suggest biosystematic relationships between involved cultivars, which can be rarily proven. Cultivar-group classification based on biosystematic criteria seems a service to plant breeders. This will often not be the case, since breeders would then be looking for new breeding material under supposedly allied cultivars which may be in fact genetically distant (Baum, 1981).

Various registration authorities, both statutory and nonstatutory, have already included cultivar classifications in their registers, despite the absence of any article or recommendation in ICNCP.

If cultivar-groups are meant to be applied worldwide, for reasons of stability, it is recommended to use the oldest or, in doubtful cases, the current names, as is done with the cultivar classification of *Clematis* (Brandenburg and van de Vooren, 1986). Sometimes common crop names, if not confusing and if not in conflict with Art. 27, can be used (Brandenburg, 1984b; Schneider, 1984). It is even possible to have translations for them through the Multilingual Glossary of Common Crop Names (Koster and Schneider, 1982).

In case of cultivar-groups of local significance, growth conditions or easy identification characteristics are often indicated in the names. As performance in other environmental conditions can be quite different, the context of the classification should be stated clearly.

In conclusion, cultivar-groups are useful in cultivar classification and serve to standardize common practice without implying biosystematic relationships within the groups.

3.3. The taxon concept and cultivated plants

In order to understand the reasoning behind the introduction of a new basic term for the taxonomy of cultivated plants, it is worthwhile considering the backgrounds of the term taxon, as it is used in both botanical and zoological taxonomy. In 1926, Meyer-Abich introduced the term taxon as a philosophical concept opposed to "phylon". Its application was never followed. In June 1948, a conference was convened in Utrecht (the Netherlands) to discuss and prepare proposals to amend the ICBN at the Stockholm Botanical Congress to be held in 1950. Lam (Proceedings, Chron. Bot. 12) proposed to '..indicate a taxonomic group of any rank with the term taxon...' (p.12). The exact wording of the proposal to be submitted was, '....; taxonomic groups of any rank will, in the Rules, generally be referred to as taxa (singular: taxon);...'.

This proposal was accepted and incorporated in the 1952 ICBN but the word "rank" had been changed into "category", which was changed back in subsequent codes. The wording of this proposal was later given the status of a separate article (art.1), which has not been changed since.

The introduction of the word "taxon" in the botanical society was thus definitely tied to ranking. Taxa are assigned to categories, which are part of an axiomatic hierarchical ranking system (the taxonomic hierarchy).

Zoologists have adopted the word taxon as used by botanists. Simpson (1961) devotes an extensive discussion on the subject:

- 'A taxon is a group of real organisms recognized as a formal unit at any level of a hierarchic classification';
- 'A taxonomic category or simply a category is a class the members of which are all the taxa placed at a given level in a hierarchic classification. The rank of a category is either its absolute position in a given hierarchic sequence of categories or its position relative to other categories. The rank of a taxon is that of the category of which it is a member.'

Taxa, thus tied to the taxonomic hierarchy, show important mutual relations, viz. exclusion and inclusion. Taxa of one rank in one classification always exclude each other. Taxa in one classification at one rank are all included in one or more taxa at the next-higher rank. This leads to the total exclusion of overlap between taxa in one classification (see figure 3.1a). Overlap between taxa with the same name but figuring in different classifications, is usual.

Since taxa are the main subjects in evolutionary discussions, the taxon concept should be restricted to represent groups of organisms that are based on the evolutionary assumptions (their ontology). And so this leaves no room for groups of cultivated plants to be treated as proper taxa, as this would create non-evolutionary "noise".

It is thus apparent that the taxon concept nowadays has two notions:

- a classificatory device tied to the taxonomic hierarchy;
- an evolutionary connotation, which is best expressed by the widely-held view, that, if taxa have to have any relevancy, they should be monophyletic.

Consequently, aside from a general classification - reflecting the results of evolutionary discussions - in the sense of McKelvey (1982), special classifications may serve other purposes. Simpson (1961) states:

- 'We must thus accept the possibility and in fact the need not only of many classifications but also of many kinds of classifications, that is, of classifications based on different sorts of relationships and serving different purposes.'
- 'Teleological classifications define sets (again, not taxa) according to their usefulness or lack of it, usually with respect to man. Such sets might be, for example: domesticated animals,[.......]. They do not have much general scientific interest, and again in modern usage they require the prior classification of organisms on some other system.'

This definition of teleological classifications is directly applicable to the philosophy behind classifying cultivated plants. Schwanitz (1967) defines cultivated plants as follows:

> 'Die Kulturpflanzen sind das Ergebnis von Evolutionsvorgängen, die sich in vorgeschichtlicher und in geschichtlicher Zeit bis in unsere Tage hinein, teils unter dem unmittelbaren, teils unter dem mittelbaren einfluß des Menschen vollzogen haben und heute noch vollziehen.'

Schwanitz' definition shows ambiguities. On the one hand, classification of cultivated plants starts from evolutionary processes; on the other hand it includes human influence, albeit in part indirect. It stresses the very beginning of the domestication process, whereas the nowadays general process of domestication (formulating the demands of a new plant, breeding and reproducing it) is underemphasized. A more modern definition of a cultivated plant is according to Hetterscheid & Brandenburg (1995a), adapted from Trehane (pers. comm.):

> 'A cultivated plant is one, whose origin or selection is due to the activities of mankind. Such plants may arise either by deliberate or chance (garden!) hybridization or by further selection from existing cultivated stock or they may be selected from a wild population and maintained as an entity by continuous cultivation.'

The relevant point here is emphasized by **deliberate** and **by man**. Plants are cultivated **by man, deliberately** to improve his standard of living, either by improving his diet (agriculture/horticulture), surrounding himself with ornamental plants (horticulture), or improving / maintaining his environment on a larger scale (silviculture/forestry). In order to do so, man has to manipulate plants. From the moment a plant is taken from nature (selected) by man and propagated or maintained under his own controlled circumstances, it is no longer exclusively subject to the forces of evolution. From irrespectively any survey of plant breeding research and results, it can be concluded that design, production and reproduction of new cultivars are labour-intensive human activities.

Since the cultivar is the basal unit of cultivated plant classification, its nature is all-important to the question whether it can be a taxon or not. The many and often complicated ways in which cultivars are produced and reproduced (ICNCP, Brickell et al.,1980 art. 11; Trehane et al., 1995; art. 2.7-2.17), illustrates their status as products of, often large-scale, commercial industry.

For instance, present-day technological developments lead to the introduction of "synthetic" cultivars in which genetic information of widely different taxa (or cultivars derived from them) is brought to expression. These cultivars will defy any attempt of ranking in the taxonomic hierarchy (see Grosser & Gmitter, 1990, for an example of synthetic cultivars in *Citrus*). Grosser and Gmitter's paper shows the radically different nature of "processes" (and order in which they are allowed to operate), leading to cultivars, compared to processes in nature leading to e.g. species.

Another important, non-taxon, character of cultivars is homogeneity and its retention during reproduction. This typically industrial demand serves to gain and keep confidence of consumers and growers. One must be able to safely buy a large stock of e.g. immature plants (or plant-parts) of a cultivar that meets certain demands and that, after a while, indeed shows the relevant characters instead of an array of unwanted variation. Taxa on the other hand, are conceptualized to show variation as a result of evolution and, consequently, are described by taxonomists allowing and including this variation. Contrary to this, present-day newly developed cultivars that show much variation are usually regarded as inferior, a totally different (teleological) approach. On the other hand, primitive cultivars or landraces show this unwanted variation, but have the useful plasticity as their purpose, and still do harbour genes that can be selected.

Cultivars cannot go extinct as e.g species do in nature. Material of a cultivar may disappear from the face of the earth for a certain time but the same cultivar may be reconstituted at any time, if parental material is being conserved. This is especially clear in hybrid cultivars that are being created again every season by making a particular cross between maintained inbred lines. New techniques make it possible to prepare a 'recipe' for obtaining (synthesizing) a certain cultivar. Furthermore, it is stated in the ICNCP (Brickell et al., 1980 art. 10, note 1: Trehane et al., 1995 art. 2.18, art. 3.1), that cultivars are being recognized irrespective of their way of origin. When plants have been produced that exactly match the description of an existing cultivar (or one of which no material is extant at the time), they are regarded to be that cultivar! The cultivar therefore is philosophically a class concept. The "class" (the cultivar) is being circumscribed and all plants meeting the circumscription are grouped in the class. The class may be empty for a while when no plant exists that fits the circumscription, but such plants may "appear" at any time and refill the class (the cultivar comes into existence again). This is typically the "behaviour" of a class-like entity. Logically any grouping of cultivars is a class as well, whereas taxa are singularities in nature (they come into existence and disappear but never reappear) and are regarded individuals.

Cultivars thus result from a mixture of natural and man-enforced processes, the influence of both process-groups being very different from cultivar to cultivar. These days, the development, maintaintenance and multiplication of new cultivars has, in many countries, developed into a genuine, large-scale industry. Many new techniques have been developed and the application of hybridization, somatic fusion, mutation-breeding, genetic engineering, etc. enhances the awareness that the final result - the cultivar - is a typical "industrial product" and much less a member of Mother Nature. This increased shift in ontology has not been recognized by most taxonomists/systematists. A classification of such man-influenced and/or man-made entities, cannot be termed "natural".

In view of the above-stated, a classification of cultivars can only be a special-purpose classification, this purpose being man's choice of any set of characters, relevant for the cultivation and use of certain cultivars. Such classifications are teleological, and define classes and not taxa! In conclusion systematic categories of cultivated plants need to be recognized as a new systematic concept, different from the taxon concept.

3.4 The culton concept

The present-day use of the taxon concept obviously does not properly cover the essence and identity of cultivated plants. The conceptual shift in looking upon cultivars as industrial products being manufactured instead of evolving, calls for a new concept with a teleological inclination. It is proposed by Hetterscheid & Brandenburg (1995b) to introduce the term "culton (plural: culta)" into the systematics (including classification and nomenclature) of cultivated plants:

> **A culton is a group of cultivated plants, based on one or more user-criteria. A culton must have a name according to the rules of the International Code of Nomenclature for Cultivated Plants.**

The culton as a classification-category is essentially different from botanical categories as referred to in ICBN. Culta principally defy extensive hierarchical ranking as seen in proper taxa and are not necessarily complementary to each other in a classification (see below). A culton and a taxon may be entirely or partly or temporarily co-extensive. In order to avoid any further conceptual and practical confusion between taxa and culta, a number of nomenclatural devices relevant to the naming of culta must be reformulated or omitted in both ICNCP and ICBN. Invoking the culton concept and its nomenclatural ramifications justly stresses the only relevant essence of cultivated plants, that is improving man's standard of living.

The term "culton" is not entirely new. During discussions at past horticultural congresses (Hamburg, 1982; Davis, 1986), the idea that groups of cultivated plants do not behave as proper taxa, was recognized. At the Davis congress, F. Schneider (Netherlands) and C. Brickell (U.K.), jointly proposed to introduce the term "culton", with a similar inclination as used here, viz. parallel to "taxon". The discussion stopped there and the introduction of the new concept was not pursued any further. After many years of obscurity, the term was suddenly introduced in the "glossary of plant taxonomy" in part 1 of the New Royal Horticultural Society Dictionary of Gardening (1992). Its definition there does not nearly describe its original intention accurately. The Dictionary states:

> 'a taxonomic unit describing distinct plants originating in or maintained in cultivation. This term has been proposed to reflect the fact that not all such entities can be considered or treated as cultivars. It stands in somewhat artificial contrast to taxon, which it was hoped would come to mean a unit of naming for wild plants regulated by the Botanical Code.'

For reasons stated above, a culton encompasses (*not* describes) **groups of plants** and *not* just plants. The second sentence speaks only of cultivars, whereas culton is not restricted to that category. Although it is stated what the word taxon was hoped to come to mean, it is apparent from its present day usage that this is exactly what its meaning is today, namely a unit of naming wild plants and so legitimising the introduction of the culton concept.

The criterion of usefulness is basic to classifications of culta. The characters upon which such classifications may be based are entirely dependent on man's subjective choice.

Therefore, culton classifications and taxonomic classifications are very distinct. For instance: to a group of people, it may be relevant to a group of people to divide a number of cultivars into a number of cultivar-groups based on flower-colour. For another group of users it may be more important to group the same set of cultivars on the basis of pest-resistance. The result is two different classifications for the same set of cultivars. They can only be judged on their usefulness and they may be rejected for lack of it but both may also be retained. In such a case, one cultivar may be found in two different cultivar-groups without anyone bothering.

Contrary to this, when a given number of taxa is classified in more than one way, a taxonomist will inevitably choose one classification that he thinks best reflects evolutionary relations among the taxa. The mere fact that taxonomy works with the axiom that life is monophyletic and as such supports only one true phylogeny, leads to the statement that of two or more alternative classifications of the same set of taxa, at most **one** may be the "true" one! Choice therefore is inevitable and inherent to the system, contrary to the above stated for culton classifications.

The extensive hierarchical nature of taxonomic classifications, forces the taxonomist to define (often morphologically) every taxon above the species level to which a certain species is assigned. Starting from the cultivar (basal category), such a mechanical hierarchy (see e.g. Jirasek, 1966) would lead to a number of subordinate cultivar-groups (or new categories), which have to be defined at every "level". The required large number of characters to define these groups, would be forced upon the classification, which would be in serious conflict with man's free choice for one or a few "useful" (teleological) characters to propose a satisfactory "one-level" classification. Another drawback would be a general inflation of ranks and categories, whereas we feel that the single category of cultivar-group, could encompass all classificatory needs presently known above the cultivar "level" (Hetterscheid & Brandenburg, 1995a, 1995b; Hetterscheid et al., 1996).

Complementarity is another aspect absent from culton classification. When a large number of cultivars of a crop is in need of cultivar-group classification, the choice for useful characters will define the number of relevant cultivar-groups, but these may not necessarily cover all cultivars. Inevitably a number may remain that do not have any of the characters defining the cultivar-groups (see Bos et al., 1992 for an example in *Dracaena fragrans* Ker Gawl.). In this situation there is no need for a mechanism that would automatically assign the remaining cultivars to a cultivar-group. This group would have to be defined by the non-existence of characters, which is contrary to the positive choice of characters to define cultivar-groups. It is also contrary to classification philosophy in general.

Classifications in which entities at one level do not necessarily fill that level entirely to produce the next-higher level entity, are designated **open classifications** as opposed to **closed classifications**, like taxonomic ones (Brandenburg et al., 1982; Brandenburg, 1986a). Classifications of cultivated plants are, by their nature, open classifications by virtue of the absence of obligatory hierarchy and complementarity.

4. CLASSIFICATION OF CULTIVATED *CLEMATIS*

4.1. *Clematis* as a garden flower - the first modern treatment of cultivated *Clematis*

In 1872, Moore & Jackman published their book on cultivated *Clematis*, entitled '*Clematis* as a garden flower'. Already after publication it became the very handbook on the subject and remained so at least until the nineteen-thirties. Having produced a standard for *Clematis*, Moore and Jackman also realised that both growers, amateur and professional, need quite different classifications than botanists do. The subtitle of their second chapter contains the meaningful statement: 'Classification unimportant for Garden purposes - Cultural Classification preferable'. Two more citations:

- 'The sectional groups, then, which we suggest, are intended to be strictly cultural and seasonal, and are to be so regarded - in fact, as being framed entirely for the guidance and convenience of the cultivator, and not as having any special relation to the botanical affinities of the various plants';
- 'This mode of classification will be found to bring together all those species and varieties which are similar in habit and character, and will, moreover, assist us in arranging, in some intelligible order, the instructions we shall have to offer regarding the cultivation of the different types of *Clematis*.'

The seeds of the current definition for the cultivar group are already present in the above quotations. The "sectional groups" by Moore and Jackman consist of species, hybrids and cultivars. By lack of a separate term distinguishing botanical varieties and cultivated varieties, it was logical not to bother too much about it, although their nomenclature of (cultivated) varieties is almost always in modern language, as it is by other producers of cultivars at that time, and as it was in other ornamentals, such as *Rosa* cultivars.

The Moore & Jackman system of "sectional groups", referred to as e.g. Patens type, appeared to be very stable as far as large-flowered *Clematis* cultivars are concerned. The cultivar group classification of large-flowered *Clematis*, as it is presented in the next section is largely based on the "sectional groups" of 1872. For the small-flowered *Clematis* groupings are less stable. Moore and Jackman (1872) defined the Graveolens type around the species *C. campaniflora*, *C. fusca*, *C. grahami*, *C. grata*, *C. graveolens*, *C.*

orientalis, *C. viorna*, *C. virginiana* and *C. vitalba*. This is a rather peculiar combination of species, showing great differences in growth performance, pruning requirements and vegetative propagation, as well as ornamental value. In current cultivar groups, only cultivars figure. Therefore, this and other "sectional groups" in small-flowered *Clematis* have never caught on as cultivar groups.

4.2. Cultivar classification of large-flowered *Clematis*

The distinction made between small-flowered and large-flowered *Clematis* has been and is rather arbitrary, and is based on traditional usage and current practice and not strictly on flower size. Large-flowered *Clematis* cultivars are considered to belong to *C. florida* Thunb. ex Murray, *C. lanuginosa* Lindl. and Paxt., *C. patens* Morr. and Decne., *C. viticella* L., and *C. texensis* Buckl., or are interspecific hybrids between two or more of these species with various degrees of introgression from one or more of the other species. Small-flowered Clematis cultivars are considered to belong to the remaining species. This distinction was already formulated by Spingarn (1935) and has been applied since then.

To classify large-flowered *Clematis* cultivars, it is important to know the characteristics of the parental species (Brandenburg, 1981, 1984c, 1985, 1989a, 1989b; Brandenburg & Van de Vooren, 1982, 1984, 1986, 1988a, 1988b). As far as relevant for cultivation, these characteristics has been used for the circumscription of the cultivar groups. The cultivar groups are of mondial significance and, except for the Texensis group, stable for more than one century. A survey of these cultivar groups is presented in table 4.1. More details will be presented in the forthcoming checklist of the large-flowered *Clematis* cultivars of the International *Clematis* Register (Brandenburg & Van de Vooren, in prep.). Jouin (1907) and Spingarn (1935) already produced authorative surveys of Clematis assortments after Moore and Jackman (1872).

Table 4.1. Cultivar groups of large-flowered *Clematis*.

Florida group	Plants flowering on the old or ripened wood, mostly with semi-double or double flowers; flowering time spring-summer; woody climbers.
Jackmanii group	Plants profusely flowering on the young growth during a long period; flowering time summer-autumn; woody climbers. The group is originally based on *C.* 'Jackmanii' (*C.* × *jackmanii* Th. Moore)
Lanuginosa group	Plants flowering on short side axes on the young growth; very large flowers spread over the whole plant; flowering time summer-autumn; woody climbers.
Patens group	Plants predominantly flowering on the old or ripened wood; mostly with single flowers having pointed tepals; flowering time spring-summer; woody climbers.
Texensis group	Plants profusely flowering on the young wood during a long period; ± bell-shaped flowers; flowering time summer; subshrubs.
Viticella group	Plants profusely flowering during a rather short period; flowering time summer-autumn; woody climbers.

4.3. **Introduction into cultivation of *Clematis* sect. *Meclatis***

As early as in 1700, *Clematis orientalis* was introduced into cultivation by Tournefort (for details, see 2.4.2). It is remarkable how fast the species has spread over European botanic gardens and private gardens of wealthy banquers and merchants, as can be seen from their correspondence (Van der Neut, 1983). At the same time, Dillenius described the species in Hortus Elthamensis (1732), it had become a well-known species in the Netherlands; in Leiden and Amsterdam. Although the species was grown all over Europe, no cultivars were selected from it. From the beginning of the 19th century onwards, plants were introduced from other areas than the original provenance (Turkey).

Willdenow (1796) described the species *C. glauca* in 'Berlinische Baumzucht, oder Beschreibung der in den Gärten um Berlin, im Freien ausdauernden Bäume und Sträucher, für Gartenliefhaber und Freunde der Botanik'. The described plant was already grown in the Berlin Botanic Garden since 1752 under the name *C. orientalis.* A new seed lot, received by Willdenow a few years before 1796, induced him to compare his plants with the Dillenian plate. Based on leaflet morphology and the indumentum of the tepals, he decided to describe both accessions as a new species: *C. glauca.* His extensive description in German and the beautiful accompanying plate are the first of many statements in horticultural literature how to distinguish *C. glauca* from *C. orientalis*, thus resulting in diverse attitudes concerning the variability of both species. The original herbarium specimens of *C. glauca* prove to belong to *C. orientalis. C. glauca* is therefore a heterotypic synonym of *C. orientalis.* In horticultural literature, the name has obtained a separate meaning. This has complicated *Clematis* sect. *Meclatis* nomenclature a great deal. Apart from *glauca* being an infraspecific epitheton in various combinations, there was still a part of the variation that might be considered a separate species and which anyhow performed quite differently from *C. orientalis.* These plants originate from Siberia, Mongolia and the Northern plains of China. It was Bunge, who recognized this in 1833 and he described a separate species *C. intricata* (cf. Bunge, 1854). The species itself had been distributed over many botanic gardens, although it was usually labelled *C. glauca. C. glauca* referred also to populations of *C. orientalis.* So, the range of variation in *C. intricata* had never been clear.

In the middle of the 19th century, there were various botanic travellers collecting specimens in Central Asia, and the far east of Russia, Mongolia and China. They did this either on behalf of their mission by Government (Bunge, Przewalski, Potanin for Russia; Clarke, Edgeworth, Griffith, Strachey and Winterbottom for England) or as missionaries (David from France) (cf. Bretschneider, 1898). Their collections gave a new impulse in *Clematis* growing. Many large-flowered *Clematis* resulted from these activiities, and the interest in small-flowered species was definitely aroused. Systematists described the various forms of *Meclatis* either as separate species or as infraspecific combinations. The plants were introduced into cultivation as seedling populations and did not receive further attention as to selection.

Complicating aspects of the introduction into cultivation were the discrepant interpretations by botanists and horticulturists. *C. graveolens* as described by Lindley in 1846, was known by its heavy but unpleasant scent. The plant depicted and described by Hooker under the name *C. graveolens* in Botanical Magazine t. 4495 was all but *C. graveolens* Lindley. After Hooker's publication, the name was ambiguous in its meaning in horticulture. The later published *C. vernayi* C.E.C.Fisch. - here reduced to *C. tibetana* subsp. *vernayi* - fits the plate by Hooker perfectly. The same holds for the introduction of *C. tangutica* (Maxim.) Korsh. into cultivation. The publication by André (1902; Morel actually wrote the paper!) contributes much to recognize its value for the *Clematis* assortment. Horticulturists after him, however, gave a restricted interpretation of the material involved, ending up with two views about *C. tangutica*: s.s. sensu André (according to horticultural literature) and the original view, s.l., by Maximowicz (1889), with his description of *C. orientalis* var. *tangutica*.

In the 20th century, *C. tangutica* was distributed over the world and became soon very popular among *Clematis* enthusiasts. When in the late thirties *C. vernayi* also became available, the interest for yellow-flowered *Clematis* increased again: in the Netherlands, there were breeding and selection programmes at Boskoop and initially also at Wageningen, of which some cultivars are described in the next section. The very reason behind it was and - may be still is - the wish for a yellow, large-flowered *Clematis* cultivar, which would set off another trend in *Clematis* cultivation.

In the beginning of the 20th century, *C. serratifolia* was recognized as a distinct species by Rehder (1910). Material was distributed from the Arnold Arboretum. Especially plants with the combination of the pale yellow tepals and markedly dark violet stained filaments made many horticulturists believe that this was the very distinction of the species, whereas it is only part of its variation. Its delimitation with *C. intricata* was a further subject to discussion, but nowadays it is well agreed that its relatively late flowering in the summer, its typical pale yellow flower colour and its biternate leaves with regularly serrate leaflets are the distinguishing characters of the species. Nevertheless, the plants with the dark violet filaments are very showy and it is hoped that they will gain in popularity.

Flower variants with violet spots, just a flush of violet or even dark violet colours have always confused taxonomists as to *Clematis* sect. *Meclatis*, because horticulturists were often impelled to give these variants separate names. Rehder (1920) described such plants under the name *C. glauca* var. *akebioides* f. *phaeantha* Rehd., which is synonymous to *C. intricata* var. *purpurea* described by Y.Z. Zhao (1979). The occurrence of violet colouration of tepals is variable and therefore in my opinion it is not worthwhile maintaining names, based on this phenomenon, at any rank. I agree with Grey-Wilson (1989) that if any of these plants are still in cultivation, worthwhile genotypes should be given cultivar names. Under the present International Code of Nomenclature for Cultivated Plants (1995) 'Phaeantha' as epithet is allowed, but my preference is a fancy name in modern language to avoid any confusion concerning the identity of the cultivar indicated.

At the beginning of the 20th century, there were still authors (Finet & Gagnepain, 1903; Krasheninnikov, 1937) who like Kuntze (1885) reduced all species to one species: *C. orientalis*. Surveying the horticultural literature (Bailey, 1917, 1976; Bean, 1970; Boom, 1980; Rehder, 1974; Fisk, 1975; Johnson, 1998; Krüssmann, 1976; Lamarck, 1786; Lavallée, 1884;) on *Clematis* sect. *Meclatis*, it is remarkable how vague the descriptions of the assigned species are, and how everyone just repeats errors in previous literature. This is especially striking where it concerns the maintenance of a broad description of *C. orientalis*, and at the same time maintains an pseudo-exact narrow difference with *C. glauca* (the indumentum of the tepals is a very variable character).

4.4. Cultivars of *Clematis* sect. *Meclatis*

A selection of yellow-flowering *Clematis* cultivars is surveyed here. Recently the assortment has been extended. A concern about this assortment especially and to *Clematis* in general is that any new introduction varies little beyond the already existing. There is really a need for cultivars with improved ornamental value, more resistance against pests and diseases and better growth performance.

4.4.1. *Clematis* 'Aureolin'.

Winner: Experimental Station for Arboriculture, Boskoop.

Introduction into cultivation: 1979.

Description: Grootendorst (1979) in Dendroflora **15/16**: 62.

Selected from various interspecific crosses within *Clematis* sect. *Meclatis* with as recurrent parent *C. tibetana* subsp. *tangutica.*

Woody climber with the habitus, foliage and inflorescence similar to *C. tibetana* subsp. *tangutica*, profuse flowering in the summer, (June-)July-September. Flowers nodding, broadly campanulate with tepals 4, lanceolate, bright yellow (HCC3, aureolin), ± 40 × 20mm. Achenes with showy long plumose styles.

Remark: Material of this cultivar was considered meritorious by the Trial Committee of the "Koninklijke Vereniging voor Boskoopse Culturen" in 1979.

Conserved standard (designated here): Brandenburg 201 (WAG).

Illustration: See fig. 4.1.

Figure 4.1. *Clematis* 'Aureolin'.

4.4.2. *Clematis* 'Bill McKenzie'.

Winner: unknown.

Introduction into cultivation: 1969 by Mrs. Finnis (UK).

Description: Plant similar to *C. tibetana* subsp. tangutica, but more vigorously growing and large yellow, campanulate, nodding flowers, up to 2cm long.

Remark: Material of this plant received an R.H.S. Award of Merit in 1976.

Conserved standard: Wilders 390 (WAG).

Illustration: see fig. 4.2.

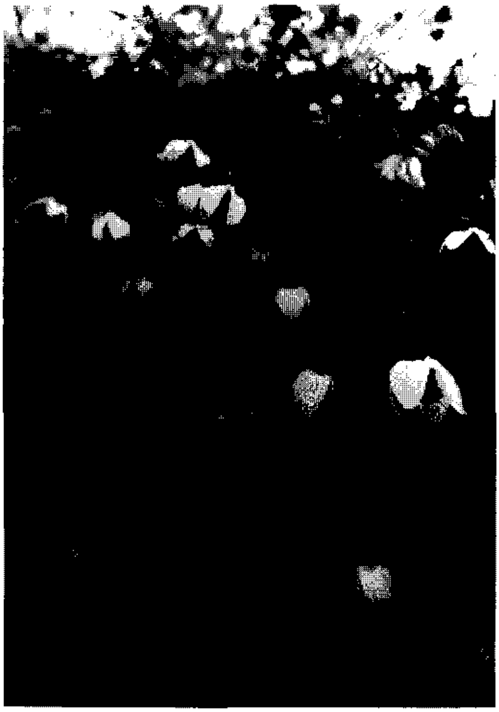


Figure 4.2. *Clematis* 'Bill McKenzie' (photograph by A. van der Neut).

4.4.3. *Clematis* 'Bravo'.

Winner: Agricultural University, dept. Plant Taxonomy (former dept. Taxonomy of Cultivated Plants and Weeds; Brandenburg/Van de Vooren).

Introduction into cultivation: 1981.

Description:

Woody climber with the habit, foliage and inflorescence similar to *C. tibetana* subsp. *vernayi*, up to 3.5 m tall (the relative compactness of the plants may be due to the great mass of large flowers produced; at the time of flowering vegetative growth ceases), profuse flowering in the summer, (June-)July-September. Flowers nodding, broadly campanulate with tepals 4, broadly lanceolate, bright yellow going over in golden yellow, ± 45 x 25 mm. Achenes with showy long plumose styles up to 7 cm long.

Conserved standard (designated here): Van der Neut 35, 36, 37 (WAG), including alcohol collection (Van der Neut 35).

Illustration: see frontispiece, fig.4.3 and fig.4.4.

Figure 4.3. *Clematis* 'Bravo' (Photograph by R.A.H. Legro).

Figure 4.4. *Clematis* 'Bravo' (drawing by Mariet de Geus).

4.4.4. *Clematis* 'Burford'.

Winner: Treasures of Tenbury, England.

Introduction into cultivation: 1975

Description:

Plant similar to *C. tibetana* subsp. *tangutica*, except for its almost globular shaped flowers. The tepals are bright yellow and relatively fleshy.

Remark: Plants of this cultivar were originally introduced into cultivation under the name 'Burford Variety'; such names are illegitimate under the International Code of Nomenclature, 1980, Art. 31c:

> 'On or after 1 January 1959, new cultivar names in the following form are invalidly published: (c) Names including the word variety (or var.) or the word form. However, when var. denotes variegated, the name is not rejected but the word is written in full.'

Invalidly published names are at the same time illegitimate. For reasons of stability, the name is hereby replaced by a legitimate equivalent.

Conserved standard (designated here): Brandenburg 202 (WAG), Van de Laar 5335 (Experimental Station for Arboriculture, Boskoop).

4.4.5. *Clematis* 'Corry'.

Winner: Zwijnenburg, Boskoop.

Introduction into cultivation: 1975.

Description:

Selected from the cross *C. tibetana* subsp. *tangutica* × *C.* 'Orange Peel'. Woody climber up to 3.5m tall. Free flowering in the summer (June-)July-September. Leaves similar to *C. tibetana* subsp. *vernayi*. Flowers broadly campanulate golden yellow, ± nodding. Tepals 4, rather fleshy.

Remark: Material of this cultivar was considered meritorious by the Trial Committee of the "Koninklijke Vereniging voor Boskoopse Culturen" in 1975.

Conserved standard (designated here): Van de Laar 4994 (Experimental Station for Arboriculture, Boskoop).

Illustration: see fig. 4.5.

Figure 4.5. *Clematis* 'Corry' (photograph by A. van der Neut).

4.4.6. *Clematis* 'Drake's Form'.

Winner: unknown.

Introduction into cultivation: unknown.

Description: R.H.S. Dictionary of Gardening (1993).

Plant similar to *C. tibetana* subsp. *tangutica*, but more vigorously growing. Flowers bright yellow, large; tepals ± 40 × 20mm, narrowly campanulate. Achenes with showy plumose styles. Further details thus far unknown.

4.4.7. *Clematis* 'Golden Harvest'

Under this name, a selection is cultivated in the Netherlands, rather similar to *C. serratifolia*. The plant has pale yellow flowers with dark violet stamens.

4.4.8. *Clematis* 'Helios'.

Winner: Experimental Station for Arboriculture, Boskoop.

Introduction into cultivation: 1988.

Description: Van de Laar (1988) in Dendroflora **25**: 72.

Woody climber up to 1.75m tall, ceases growing when it comes into flower. Flowering time May-October. Leaves similar to *C. tibetana* subsp. *tangutica*. Profuse flowering. Flowers mostly solitary, sometimes 3-flowered axillary cymes, nodding, open, flat, tepals 4, bright yellow (RHS 14B), lanceolate, 35-45 × 15-20mm, 2-2.5 × as long as wide, acute at the apex, which is slightly recurved when full flowering. Achenes with long plumose showy styles.

Remark: The Trial Committee of the "Koninklijke Vereniging voor Boskoopse Culturen" issued a positive judgement on material of this cultivar in 1988.

Conserved standard (designated here): Preferably a specimen from the Van de Laar collection, still to be designated.

4.4.9. *Clematis* 'Lambton's Park'.

Winner: unknown.

Introduced into cultivation: unknown.

Description: R.H.S. Dictionary of Gardening (1993).

Plant similar to *C. tibetana* subsp. *tangutica*. Flowers nodding, large, up to 2cm long, bright yellow. Further details thus far unknown.

4.4.10 *Clematis* 'Orange Peel'.

Ludlow, Sherriff and Elliot have made extensive collection trips throughout Tibet and Nepal. 19 October 1947 they came across a fruiting specimen of *C. tibetana* subsp. *vernayi* at Kongbo near Kyimdong-Dzong: Chin-Tung (Tibet, 29'N 93'25"E, alt. 3600m). They recorded: 'Branch of seed taken'. The seeds of this specimen were introduced into cultivation in England under the name *C.* 'Orange Peel'. It is therefore a generatively reproduced cultivar, with as distinguishing characters the broadly campanulate flowers with thick fleshy tepals, that turn from golden yellow to deep orange during flowering. Foliage is very variable in shape and size. This has caused some confusion whether or not one has the "correct" 'Orange Peel' or not. From the specimens available for this study, I have therefore designated a composite conserved standard to warrant the identity of this "collective" cultivar.

Conserved standard (designated here): Caldwell s.n., 7-10-1967, Exeter (BM); Van de Laar 2451, 2452 (Experimental Station for Arboriculture, Boskoop); Brandenburg 282.

Illustration: See fig. 4.6.

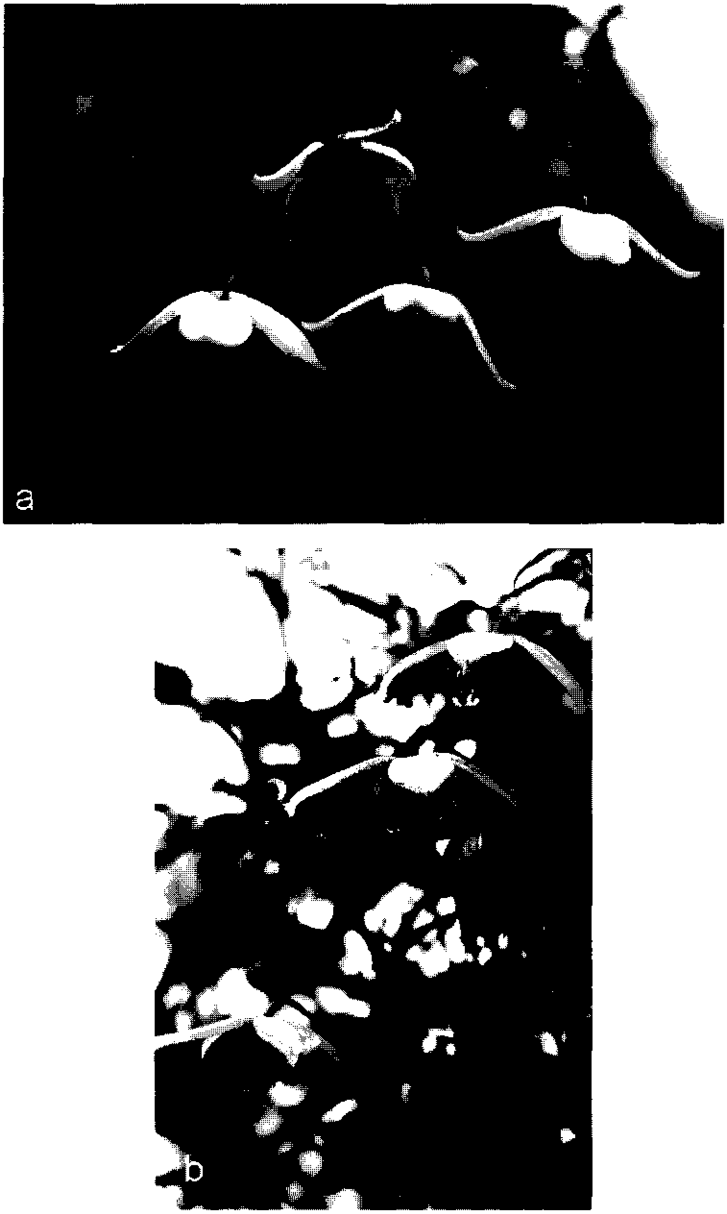


Figure 4.6. *Clematis* 'Orange Peel' (photographs R.A.H. Legro).

4.4.11 *Clematis* 'Wallsal'.

Winner: Guernsey Clematis Nursery Ltd.

Introduced into cultivation: 1986.

Description: Plant similar to *C. tibetana* subsp. *tangutica*, flowers bright yellow. Leaves trifoliolate to pinnate. Achenes with long plumose styles, up to 7cm long.

Conserved standard (designated here): Wilders 391 (WAG).

4.5. **Conclusions**

Surveying *Clematis* sect. *Meclatis* in cultivation, it is remarkable that most if not all cultivars are similar to a subspecies of *C. tibetana*. The introduction of these plants at the end of the 19th and the middle of the 20th century has received the attention by breeders, but so far they have only made combinations within the section. True *C. orientalis* and *C. serratifolia*, have not hitherto been used very much in these hybridization programmes, whereas especially *C. serratifolia* has interesting characters such as propagation by producing lots of rooted stolons.

The assortment of *Clematis* sect. *Meclatis* cultivars is too small to necessitate classification into cultivar groups. As soon as *C. orientalis*, *C. intricata* and *C. serratifolia* play a more prominent role in *Clematis* breeding, it is worthwhile considering to circumscribe a cultivar group around cultivars similar to *C. tibetana* and one around *C. orientalis*, *C. intricata* and *C. serratifolia* because of their different reaction to growth conditions, pruning requirements and propagation, and their predicted difference in ornamental value.

5 GENERAL DISCUSSION

The structure of this investigation permits the discussion of three biological topics relating the fields of plant systematic research, plant breeding research and evolutionary biological research. It is worthwhile considering these relationships in times in which plant systematics as a discipline has been questioned as a separate discipline to be maintained. It is at the same time important to advocate the significance of plant systematics in a realistic scenario and not in an uncritical approach to use systematic conclusions to predict relationships between taxa, their importance for plant breeding or, mutually, to predict from crossability data in an absolute way the relations between taxa (Barber, 1970). Both have been frequently done.

It will be shown in the next paragraphs that systematics are indispensable for modern biological research. A model will be presented how plant systematic research can be involved in all kinds of botanical research facing diverse types of scientific questions.

5.1. *Clematis* species with regard to various species concepts

Many Ranunculean genera are characterized by showing morphologically almost continuous variation patterns by which it is difficult to define species. This phenomenon is common by plant families which are abundant in dynamic or disturbed habitats, such as Asteraceae and Poaceae. Ranunculaceae are a relatively old family of Dicotyledonous plants. Although the Ranunculaceae are less abundant in above mentioned habitats - and less successful than Asteraceae and Poaceae if we count numbers of species - they show unique combinations of old and derived characters, as can be demonstrated by traits of flower morphology throughout the family: hemicyclic flowers and at the same time various forms of zygomorphy.

A confusing situation in *Clematis* systematics has always been the mixture of species concepts as used in monographs and consequently in garden textbooks. Whatever concept used, it is important to be used consistently throughout a monograph. Kuntze's system (1885) has not been followed, instead it was criticised very much by his contemporaries, but he was about the first to raise the issue of using a species concept and then following this consistently. When species of a genus become popular garden plants and many cultivars have been raised, it is extremely important to make a strict distinction between the genus' botanical classification and the desire by man to classify the garden plants by their usage, ornamental value or horticultural characteristics. At the moment, a monographic treatment of a genus mixes up both, so the botanical species are distinguished by characters that are relevant to horticulture and gardening, and that have little to do with modern plant systematics (Rehder, 1920, 1974). At the same time, a cultivar classification will suffer from the opposite, if it is partly based on characters relevant to describing natural populations and to phylogenies (Baum, 1981; De Wet, 1981; Pickersgill, 1986). In systematics it means that elements are used from all species concepts and combinations between them, although the application of the Linnaean and natural species concepts are most abundant.

The Linnaean species concept is based on his sexual classification system. The genera are classified by numbers of parts and other characters of flowers (figure 5.1), and for species Linnaeus used vegetative characters: in case of flowering plants his first characters to be used are those of leaf morphology. He tended to use as few as possible characters which inevitably leads to an artificial classification. He stated that species are created by God, but he also accepted manmade varieties originated within species. Was his statement on the creation of species initially very firm, later he accepted some species as being derived. Especially in *Clematis*, there are indications for this. Linnaeus basically adopted his species concept from Ray and after him there were only a few colleagues who adopted similar species concepts. Without Linnaeus this artificial species concept would not have been very influential: it is just that Species Plantarum is such a landmark in systematic history, compiling over 40% of the world economically important (flowering) plant species. Through agricultural botany, his species concept continued to be influential up to now as he simply included agronomic characters to distinguish e.g. *Brassica rapa* from *Brassica campestris*, *Ribes grossularia* from *Ribes uva-crispa*, *Triticum aestivum* from *Triticum hibernum* etc.

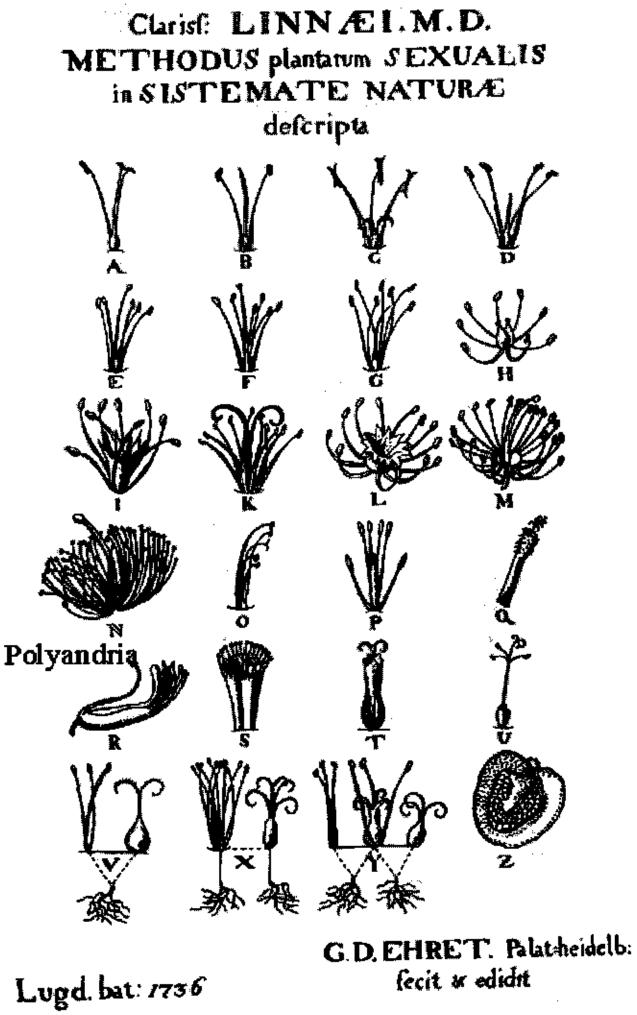


Fig. 5.1. Linnaeus' classification system. Polyandria near the letter N indicating the class to which *Clematis* belongs (Polyandria Polygynia, shown here is Polyandria Monogynia).

Adanson (1763) introduced a natural species concept, which was above all made popular by later systematists. The principal difference with the Linnaean species concept was that it took into account not only a few but all observed morphological characters and consequently was interpreting variation in terms of overall (dis)similarity. In more elaborate treatises of economic plants it was especially this species concept that was implicitly applied. The recently published monograph of *Clematis* by Magnus Johnson (1998) suffers from such a combined treatment, and has therefore restricted value despite the overwhelming amount of collated data.

Dobzhanski (1935) introduced the biological species concept thus integrating genetic and systematic knowledge. Basically, the biological species concept states the species as an entity within which individuals can mate and therefore generatively reproduce. Consequently a lot of experimental hybridization work was carried out to characterize species relationships. Much interspecific hybridization work had already been built in plant breeding schemes in order to broaden the (narrow) base of many crop plant species. The biological species concept became very popular among plant breeders as they saw it as a scientific base behind their hybridization work. With respect to *Clematis* - and other ornamentals - interspecific hybridization had already begun in the early 19th century (Moore & Jackman, 1872) and it continues until now. These hybridizations produced food for thought on classification of especially cultivated plants, and were the factual beginning of the definition of the cultivar group and the basic concept behind it: culton. Remarkably the species concept remained untouched for long, thus leaving botanical systematics with a complete range of interpretations of what a species should be, despite all instability that it causes to nomenclature (Brandenburg, 1991; Brandenburg & Schneider, 1983, 1985).

5.2. Crossability data and their value for plant breeding research

Whereas plant systematics aims at ordening the Plant Kingdom, classifying organisms by all characters at our disposal, plant breeding by making use of plant systematic evidence causes entropy in the systematic framework: as soon as species relationships has been revealed by plant systematic research, plant breeding disturbes the integrity of the specific entities concerned. Understanding the relationship between both disciplines will help in determining the value of systematic data for plant breeding.

Before the era of molecular breeding, the limits of plant breeding were determined by possibilities to make crosses between individual plants either belonging to one species (intraspecific hybridization) or to different species (interspecific hybridization). At the end of the 19th century and the first three decades of the 20th century, many European and American horticulturists were confronted by a lot of new introductions of ornamental plants. In their extensive collections they occasionally found chance hybrid seedlings, and later they deliberately made crossings themselves either to confirm the putative parentage of chance seedlings or just to create new cultivars. The spread of genetic knowledge in the early 20th century induced many interspecific hybridization experiments in genera such as *Anthirrhinum*, *Galeopsis* and *Nicotiana* to study biosystematic, genetic and even ecological questions. In all these studies, it was assumed that interspecific crossability is directly correlated to the degree of relationship between species. Consequently, the term species was biased by the view that all individuals that could be mutually crossed should belong to the same (biological) species. In the second half of the 20th century, after Camp and Gilly (1943) and Camp (1951) had introduced experimental research in plant systematics and called this part of the discipline biosystematy or biosystematics, more and more evidence was found that the biological species concept was an oversimplification of reality and therefore not applicable. With the *Aquilegia* study, Grant (1952, 1971) delivered one of the classical examples in this respect. He demonstrated that sympatric *Aquilegia* species were perfectly isolated in nature at certain localities (no hybrids found), whereas at the same time these species brought together in one experimental garden gave unlimitedly rise to interspecific hybrids by manual crossing. Although these species are genetically closely related, they are also isolated by their specialization to different pollinators (hawkmoths, bumblebees and even birds). By rigorously applying Dobzhansky's biological species concept, however, the concerned *Aquilegia* species had to be considered to be one species, as would be valid for the species of *Clematis* sect. *Meclatis* too (this thesis). By considering their coevolution with pollinators and the consequent adaptations - trends in variation - the recognition of several species in *Aquilegia* by Grant (1952, 1971) and in *Meclatis* (this thesis) has been justified. Anderson (1949) surveyed a lot of other studies pointing in this direction. By taking into account adaptive trends in plant variation the evolutionary species concept was defined. Grant (1971) distinguished several speciation mechanisms:

1. Primary speciation
    a. Geographical speciation (*Gilia* species)
    b. Quantum speciation (especially in birds)
    c. Quantum speciation with chromosomal repatterning (*Clarkia* species)
    d. Sympatric speciation (postulated on theoretical grounds)
2. Hybrid speciation with sexual reproduction
    a. Hybrid speciation with external barriers as pollinators (*Carex*, *Delphinium* and *Ophrys* species)
    b. Recombinational speciation (e.g. *Crepis* and *Nicotiana* species)
    c. Amphiploidy (e.g. *Brassica* and *Nicotiana* species)
3. Hybrid speciation with asexual or subsexual reproduction
    a. Apomictic speciation (e.g. *Festuca* and *Poa* species)
    b. Permanent or numerical hybridity (e.g. *Oenothera biennis* and the *Rosa canina* complex by special meiotic mechanisms)
4. Wallace effect (*Lycopersicon*, *Solanum* species by incongruity)

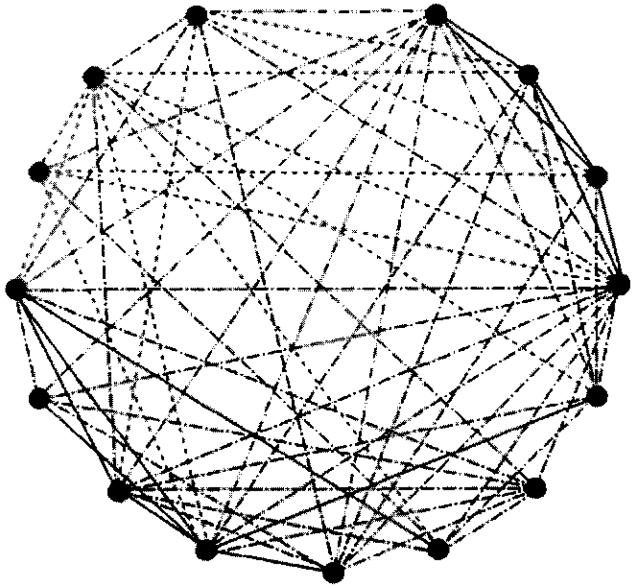


Figure 5.2 Hybridization polygon (generalized figure of figure 1.21).

The nature of speciation mechanisms has been revealed by the combination of the analysis of natural distribution patterns, cytological investigations and experimental hybridization polygons such as the generalized one from fig. 5.2. In these schemes the results of interspecific hybridization experiments are schematically depicted characterizing the crossing behaviour between species under artificial conditions (cf. Cain & Harrison, 1958; Carson, 1985; Coyne, 1974; Davis, 1978; Davis & Heywood, 1965; Dobzhansky, 1935; Ehrlich, 1961; Funk, 1985; Hutchinson, 1923; Huxley, 1940, 1958).

The evolutionary species concept has the advantage over the biological species concept that it takes into account the aspects of reproduction biology, distribution mechanisms and adaptive trends, but it does not deal with trends such as divergent and convergent developments, the systematic development of characters and geographical regularities in ditribution patterns. By taking this into account, the phylogenetic species concept was introduced, based on cladistic analysis methods rather than phenetic methods. The analysis of chapter 2 clearly reveals the power of the cladistic approach as opposed to purely phenetic approaches. Especially where similarity is rather large as is the case in *Clematis* sect. *Meclati*s, but also in other *Clematis* sections, it has been clearly shown again that phenetic approaches give insight in the overall structure of the variation without revealing the direction of the development in variation trends, whereas the cladistic analysis provides a higher resolution by taking into account the direction of variation trends. Moreover, by studying these trends plant systematics has become for the first time a real science with hypotheses that can be either proven or rejected. One problem with the phylogenetic species concept is its focus on monophyletic genealogies, thus not dealing with evidence from interspecific hybridization that has also been described from natural complexes. Kornet (1993) tried to combine both into one theorem in order to be able to analyze reticulate complexes, in which interspecific hybridization was one of the driving forces. I assume that it will be only possible to realize her analysis by adding more data sets, containing molecualr data. Molecular biology makes it possible to deliver an objective set of data in which the relatedness of genomes - and therefore of populations or even species - can be characterized. Combining this with morphological trends, that stand for certain adaptations to the habitat, and hybridization data, that stand for the nature of isolation between populations or even species by sexual means, we may develop a species concept that will be universally applicable and that is reflecting both its current biological meaning and its phylogenetic derivation. The application of such a species concept has also the advantage that hypotheses can be clearly formulated, tested and consequently either accepted or rejected in a biologically meaningful way (cf. Estabrook, 1972; Farris, 1971, 1974, 1980, 1985; Fink, 1982; Ghiselin, 1981, 1984, 1987, 1988; Gilmour, 1961; Hull, 1976; Humphries & Funk, 1984; Meglitsch, 1954; Rieppel, 1991) despite of the adverse opinion of some authors (e.g. Cronquist, 1987).

Application of a phylogenetic species concept in the modern sense (cf. Kornet, 1993) provides a magnificent starting point to establish a firm base for infraspecific botanical - thus closed - classification. Many things have been said about infraspecific taxa and their application (Baum, 1981; Burtt, 1970; DuRietz, 1930; Fuchs, 1957; Hamilton & Reichards, 1992; Meikle, 1958; Pickersgill, 1986; Stace, 1986, 1989; De Wet, 1981; Wijnands, 1986a, 1986b) ranging from rather artificial systems as pragmatic combinations of current uses of infraspecific categories to more fundamental considerations, but none of them taking into account the species concept to start from. Not doing so, implies that it is not possible to define infraspecific categories, thus providing an objective way to apply them.

5.3. Evolution and domestication of *Clematis*

5.3.1. *Evolutionary aspects of* Clematis *within the Ranunculaceae*

As a Ranunculean genus, *Clematis* has many complex features, and yet it is considered primitive within the family. Its flower morphology is basic, being hemicyclic, actinomorphous. However, the leaves are decussate and the stems woody. The woody stems have the anatomy of perennial plants (Smith, 1928), and the phyllotaxis is not a critical discriminating character (Tepfer, 1960) as we see several gradual transitions through an alternate leaf position (e.g. in *Clematis alternata*) within *Clematis* and the occurrence of alternate phyllotaxis in other Ranunculean genera as well. Looking at cytological characters, the basic number of chromosomes in *Clematis* is x = 8, the number that occurs most frequently in Ranunculaceae thoughout the genera that are considered most primitive (Gregory, 1940). In general, I agree that *Clematis* has to be regarded as primitive among Ranunculean genera, sharing many characters with another primitive genus, *Anemone*.

From the data presented in this thesis, it cannot concluded with certainty where *Clematis* originated on earth. For two hypotheses there is some support:

- For a Laurasean origin the support is to be found in palaeobotanical evidence and the fact that almost every variation trend present in *Clematis* is represented in especially the Chinese area (Croizat, 1962, 1964; Croizat et al., 1974; Krassilov, 1983; Nelson & Platnick, 1981);
- For a Gondwanean origin the presence of the variation trend from *Anemone* through *Clematopsis* to *Clematis* is very supportive (Brummitt, 1976; Hutchinson, 1920; Raynal 1978; Tobe 1980c).

In my opinion, it is only possible to make a better discrimination between both hypotheses by a molecular biological approach, especially by looking at conserved regions in chloroplast and mitochondrial DNA (cf. Hoot et al., 1994). To my knowledge, such a study is lacking for *Clematis* and related genera. Molecular genetics make it possible to test the above kind of hypotheses, to test the cladistic analysis of the genus as been carried out for this thesis and to shed a better light on the subdivision between Monocotyledons and Dicotyledons, which is essential for a better understanding of similarities and dissimilarities between both groups, thus contributing towards a better and sustainable exploitation of their variation, and to test the phylogenetical assumptions by Tamura and coworkers (1958, 1962, 1963, 1964, 1965, 1967, 1968a, 1968b, 1970, 1987; Tamura & Vogel, 1993).

5.3.2. *Domestication of* Clematis

Domestication of *Clematis* dates back in Europe towards the late Middle Ages. The European wild species, especially *Clematis recta*, were often planted in medicinal gardens. Although there are no exact data to find there are some indications that in China domestication of *Clematis* dates back at least to the 8th century BC. (Usher, 1974). It is therefore likely that the first *Clematis* species that were introduced from China and Japan were already cultivated plants if not cultivars. Robert Fortune pointed out that he found an interesting *Clematis* in a garden along his route to Nanking. Later it was named *Clematis lanuginosa* (Brettschneider, 1898). Remarkably, this species was never found in the Chinese wild flora (Ling, 1980), thus giving evidence that it was indeed a cultivar: *Clematis* 'Lanuginosa'. The assumed period of domestication that may date back to the western early Middle Ages (!), suggests that the concerned species complex may be regarded as a compilospecies (Harlan & De Wet, 1963). The long period of domestication for cultivated plants in China suggests similar migration patterns, e.g. the silk route, as described for other cultivated plants by Sauer (1957, 1967a, 1967b, 1988).

Domestication of *Clematis* has always been focused on flower colour, size and other morphological characters such as double flowers, anthers being variously transfered into a kind of petaloid organs or to just another whorl of tepals. This focus was so strong that it has led to physiological problems in large-flowered *Clematis* cultivars. Cultivars, such as 'Prins Hendrik', once popular as a cutflower in the Netherlands, could only be grown grafted on *Clematis vitalba*. Many of todays' large-flowered cultivars seriously suffer from the *Clematis* wilt disease. This is not a real disease, but a physiological problem: by lack of water the stems get aerated and as a consequence of the combination of air in an aqueous environment (the stem), fungi, such as *Ascochyta clematidina* or the common *Botrytis cinerea* form colonies in xylem vessels thus blocking the water supply of the plant. *Clematis* wilt occurs most prominently when the plants are about to burst into flower. The flower buds are big and require a lot of water to expand. When plants then are growing in a sandy soil under sunny conditions and watering is not adequate, they will just collapse. *Clematis* has a rather superficial rooting system. Consequently, the one-sided focus on profuse flowering with large flowers without selection towards a stronger rooting system causes these problems. Although the small-flowered *Clematis* cultivars do not generally suffer from the *Clematis* wilt disease - as their flowering is in balance with the capacity of the root system -, their ability to compete under garden conditions is usually rather weak and should be improved by breeding and selection. The same holds true for resistance against pests and diseases.

5.4. **Cultivar documentation**

There are more cultivars of flowering plants in the world than wild species. Taking into account all the obsolete cultivars the difference will be even more. Despite this fact, the system of cultivar documentation is not yet very advanced. Different topics of concern range from aspects of cultonomy, identification and characterization towards cultivation and usage characteristics.

5.4.1. *Cultonomy, identification and characterization*

If we recognize that cultivated plants result from domestication rather than from spontaneous evolutionary processes, it is important to accept that for classification and nomenclatural purposes (Chapter 3). By doing so, it is possible to establish a open, flexible classification of cultivars, adaptable towards new breeding developments without sticking to an everlasting nomenclature for the entities between cultivar and botanical taxa. The culton concept clearly leaves space for such flexibility thus creating cultivar group classifications that can easily be updated or altered. The culton concept also leaves room for re-use of cultivar epithets under certain conditions. Merely the fact that more cultivars are obsolete block the provisions for good names. Re-use mechanisms have to be developed for the International Code of Nomenclature for Cultivated Plants. By not putting re-use mechanisms in place, the development will inevitably go towards the replacement of cultivar epithets by trade names or even trade marks, a development that is already rather popular in ornamentals.

Another aspect is that of Intellectual Property Rights. In order to stimulate plant breeding, there should be a reasonable mechanism to get the breeder paid for his efforts. Such a mechanism has been laid down in the Plant Breeders' Rights legislation under the international UPOV Convention as revised in 1993. The problem with this legislation is that it is only implemented in a restricted number of countries while in some other countries PBR legislation is only used de facto. In order to ensure control over their products, breeding companies, especially as for horticultural crop plants, have often chosen to label their cultivars with trade marks and only have a cultivar epithet for registration purposes. In this way, the significance of the cultivar name is reduced in communication. People do not realize, however, that the only one to one relationship between cultivar and name is that of the cultivar name including the cultivar epithet. A trade mark may change between cultivars, thus giving the consumer no warrant whatsoever about the true identity of plant material just bought. It is one of the biggest challenges in systematics of cultivated plants to address this point properly and to solve it. The fact that International Registration Authorities just deny this fact is a most worrying attitude, that can place cultonomy - and with it taxonomy - in a backyard position. Strengthening the relationships between statutory and nonstatutory registration authorities is a priority. The attitude by nonstatutory registration authorities, as frequently demonstrated by e.g. the Royal Horticultural Society, as one of the principal nonstatutory registration authorities, just to prescribe statutory registration authorities how to act in matter of disagreement, ignoring the fact that statutory registration authorities have to fulfill legislative requirements, is far from constructive. In this era of information technology it must be possible to create mechanisms to overcome this kind of problems and to work on practical solutions in the spirit of what has been achieved by PlantScope (Aalsmeer) in the Netherlands.

5.4.2. Clematis *cultivars and their validation of cultivation and usage characteristics*

Validation of cultivation and usage (vcu) characteristics has been largely carried out by nonstatutory organisations, such as the Koninklijke Vereniging voor Boskoopse Culture in the Netherlands or the Royal Horticultural Society in the UK. Although it is of great value that there are such vcu trials anyhow, the methodology being applied in these nonstatutory trials - or sometimes only on site judgements - is merely watching the ornamental value and the performance of the cultivars at one site without replications and often a single time. Consequently, one can hardly base serious recommendations for practical horticulture and gardening on them. There are however good reasons to set up a good scheme of vcu trials for the main arboricultural crop plants:

- to improve the information about the most popular assortments;
- to restrict the assortments to the best performing cultivars;
- to formulate good breeding objectives and to establish good breeding research to meet these objectives.

The country that first organizes such vcu trials is the one that will secure its export position!

6 SUMMARY

The general classification of the genus *Clematis* (Ranunculaceae) was subject of study in chapter 1. Based on species character scores, the infrageneric classification was analyzed by applying Hennig86 as phylogenetical analysis package. As result of this analysis *Clematis* was subdivided into 18 sections, one of them subdivided in 3 subsections.

The world distribution of *Clematis* was also studied with Hennig86. It was not possible to postulate the area of origin of the genus *Clematis* with the available data set.

A interspecific cross polygon was made and analyzed by seed set and pollen tube growth. Its systematic significance with regard to *Clematis* and in general was discussed. Dependent on the adopted species concept, these crosses are crucial or just academic. The adoption of the phylogenetic species concept made that this choice for *Clematis* is academic. Nevertheless, it is useful information for plant breeders.

A general description of the genus *Clematis* was presented with some background information on certain characters, such as overall habitus, nectar leaves and the position of nectaries.

Chapter 2 was devoted to *Clematis* sect. *Meclatis*. This particular section consists of the yellow-flowering *Clematis* spp., that are gaining popularity in gardening. Many efforts were directed to reveal the species delimitation. It appeared that the phenetic methodology is of restricted value in such a complex of quite similar species. Using a combination of methods, the phylogenetic analysis by Hennig86 finally revealed the species delimitation: *Clematis orientalis*, *C. graveolens*, *C. intricata*, *C. ispahanica*, and *C. tibetana*. *C. tibetana* was subdivided into three subspecies: subsp. *tibetana*, subsp. *tangutica* and subsp. *vernayi*. Well-known 'horticultural species' such as *C. tangutica* and *C. vernayi* were reduced in rank and others such as *C. glauca* and *C. akebioides* were reduced to synonymy. A summary of chromosome, pollen and isozyme data was presented.

Chapter 3 was focusing on more fundamental aspects of systematics of cultivated plants. It has been shown that the cultivar group is of crucial importance in classifying cultivars, that the classification principle for cultivated plants is open instead of closed and consequently that the basal term in systematics of cultivated plants for an entity cannot be taxon, but should be a new term culton (plur. culta; cultonomy for culta vs. taxonomy for taxa).

Clematis is one of the first genera for which a cultivar group classification was presented in a systematic way, as was outlined in chapter 4. A short survey was given of the introduction into cultivation of yellow-flowering *Clematis* spp., and a major part of the yellow-flowering *Clematis* cultivar assortment has been described. So far no cultivar groups are needed for these cultivars.

SAMENVATTING

De algemene classificatie van het genus *Clematis* (Ranunculaceae) was onderwerp van studie in hoofdstuk 1. Met gebruikmaking van kenmerkscores per soort werd de infragenerische classificatie geanalyseerd met behulp van Hennig86 als fylogenetisch analyse pakket. Het resultaat van deze analyse was dat *Clematis* werd ingedeeld in 18 secties, waarvan een werd onderverdeeld in 3 subsecties.

De wereldwijde verspreiding van *Clematis* werd eveneens bestudeerd met behulp van Hennig86. Met de gebruikte set van gegevens was het niet mogelijk om het gebied te postuleren waar *Clematis* moet zijn ontstaan.

Een interspecifieke kruisingspolygoon werd gemaakt en geanalyseerd aan de hand van zaadzetting en pollenbuisdoorgroei. Het systematisch belang hiervan met betrekking tot *Clematis* en in het algemeen werd besproken. Afhankelijk van het soortsconcept waarmee wordt gewerkt zijn dit soort kruisingen wezenlijk dan wel academische informatie. Uitgaande van het fylogenetisch soortsconcept zijn de kruisingen academische aanvullende informatie. Niettemin blijft het bruikbare informatie voor plantenveredelaars.

Een algemene beschrijving van het genus *Clematis* werd gecompleteerd met enige achtergrondinformatie over bepaalde kenmerken, zoals de habitus, de honingbladeren en de positie van nectariën.

Hoofdstuk 2 is gewijd aan *Clematis* sect. *Meclatis*. Deze sectie bestaat uit geelbloeiende *Clematis* soorten, die toenemen in populariteit in tuinen. Veel inspanning is verricht om tot de soortafbakening te komen. Het bleek dat fenetische methodes niet toerekend zijn in een dergelijk soortscomplex waarin de soorten een hoge mate van overeenkomst kennen. Met gebruikmaking van een combinatie van analysemethodes, leidde de fylogenetische analyse met Hennig86 tot een goede soortsafbakening: *Clematis orientalis*, *C. graveolens*, *C. intricata*, *C. ispahanica* en *C. tibetana*. *C. tibetana* werd onderverdeeld in drie ondersoorten: subsp. *tibetana*, subsp. *tangutica* en subsp. *vernayi*. Bekende soorten uit de tuinbouw zoals *C. tangutica* en *C. vernayi* werden in rang verlaagd en andere zoals *C. glauca* en *C. akebioides* werden tot synoniemen gereduceerd.

Daarnaast werd een samenvatting van gegevens over chromosomen (x=8), pollenkorrels en isozymen.

Hoofdstuk 3 is gericht op meer fundamentele aspecten van de systematiek van cultuurplanten. Er wordt aangetoond dat de cultivargroep van wezenlijk belang is bij de classificatie van cultivars, dat het basisbegrip voor een eenheid in de cultuurplantensystematiek niet taxon kan zijn, maar een nieuw begrip, culton (meervoud culta; cultonomie voor culta vs. taxonomie voor taxa) moet worden ingevoerd.

Clematis is een van de eerste genera waarvoor op een systematische wijze een cultivar-groep classificatie werd gemaakt. Dit wordt duidelijk gemaakt in hoofdstuk 4. De introductie van de geelbloeiende *Clematis* soorten in de cultuur werd beknopt samengevat en eveneens van een groot gedeelte van het sortiment geelbloeiende *Clematis* cultivars is beschreven. Momenteel is het nog niet noodzakelijk om voor deze cultivars cultivar-groepen te creëren.

7 CURRICULUM VITAE WILLEM A. BRANDENBURG

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Education:

Primary School (Groningen)	1965
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Taxonomy of Cultivated Plants	
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Career:

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Taxonomy of cultivated plants and weeds, and	
Plant Taxonomy	
RIVRO, head of methodology research	1987 - 1990
CRZ, CPRO, head of dept. Cultivar Strategy	1990 - 1994
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Plant Research International, senior scientist	2000 -
Economic Botany	

Membership Committees:

International Commission for the Nomenclature of Cultivated Plants (IUBS)
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International Nomenclature Committee (ISTA)
International Nomenclature Committee (IOPI)
Commission on Genetic Modification (COGEM)

Freetime:

Music by Mahler and Bruckner, walking and cycling.
Board member of a large Dutch funeral society; stimulating among others the organization of activities on mourning.

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9 INDEX TO *CLEMATIS* SPECIES IN CHAPTERS 1-5.

Page numbers in bold=description; italics=illustration; names between brackets are reduced to synonyms.