# A GLOBAL RIEASSESSMIENT 

# OF THIE GENERIC RRELATIONSHHIPS 

$\mathbb{N} \mathbb{T} \mathbb{T H E}$<br>BIELLIFLOWER IFAMIILY

## (CAMIPANULACEAE)

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1997

A thesis presemted im frolfilment of the requirememts for the degree (1)

Doctor of Phillosoplhy
The Umiversity of Edimburgh

1997

## IDECLARATION

II hereby declare that this thesis was composed by myself, amd that the work lnereim to be my own, umless otherwise stated.

Winliam $\mathbb{M}$. $\mathbb{M}$. Edddie
Edimburgh , 1997

ate 1. The Canary Bellflower, Canarina canariensis.
is palaeoendemic species is confined to the Canary Islands where it survives in the remnant laurel forests a relict of the largely-extinct Tertiary Floras which were once widespread of North Africa and western rasia. The genus Canarina, with three species, now has a disjunct distribution between Macaronesia and e mountains of tropical East Africa. It is highly probable that the ancestral taxa of the Campanulaceae re similar to this genus.

This study was undertaken to determine the phylogenetic relationships of the genera of the Campanulaceae and to discover the major factors determining the evolution of the family, particularly the origins of the higher taxa. It was also an attempt to utilise evolutionary data in order to produce a general purpose phylogenetic system of classification while simultaneously avoiding unnecessary nomenclatural changes or disturbances to patterns of overall similarity. An extensive introduction to the family is provided, dealing with morphology, ecology and geographical distribution as well as a detailed account of the historical classifications of the Campanulaceae and its global relationships. Some particular difficulties associated with patterns of variation encountered in the family Campanulaceae are outlined. Philosophical issues such as the historical treatment of the genus, generic concepts, homology and methodologies are extensively discussed. A pluralistic or eclectic approach was taken for the taxonomic analyses which involved the construction of five principal data sets (higher taxa, flowers and fruits, pollen, seeds, and molecular characters). Cytological and biogeographical data were also taken into consideration. Methodologies were varied, involving both phenetic and cladistic approaches and the problems of handling multiple data sets were discussed. A new phylogenetic classification of the higher taxa to the subtribal level of the Campanulaceae is presented and some guidelines for the recognition of genera are suggested. A general outline of the phylogenetic evolution of the family is given and the major factors which have influenced this evolution are discussed. Conservation measures and the areas for priority research are briefly outlined and an extensive list of literature citations is provided.
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Biological systematics since the publication of Darwin's "On the Origin of Species" (1859) has not been a gradual unfolding account of the history of the world's biota. Instead, it has been punctuated by several episodes when certain viewpoints or paradigms of science have held sway (Kuhn, 1970). During such episodes the viewpoint in vogue is usually considered revolutionary, and outmoded ways of thinking are swept aside as everyone rushes to jump on the bandwagon. Although it is often said that Darwin did not effect any major changes in the way systematics was actually carried out, he did at least provide a framework (a theory of evolution) and identify a process (natural selection) for the patterns (descent with modification) of nature to be understood. However, Darwin did not truly understand the mechanisms of heredity. Nowhere in the "Origin" does Darwin actually discuss the origin of species. He treats the species as just a stage (or slice in time) in a continuum of variation from the individual to the higher taxa such as genera and families, thus minimising any discontinuity between organisms. The rediscovery of Mendel's work at the turn of the 20th century could be said to have been the first upset in the systematics community since publication of the "Origin". The early geneticists such as De Vries believed that spontaneous large mutations were responsible for major phenotypic changes within evolutionary lineages in contrast to the selectionist, gradualistic views of Darwin.

Restoration of a Darwinian view in the early 20th Century was the result of the efforts of Ronald Fisher, J.B.S. Haldane and Sewall Wright who recognised the distinction between the genetic processes within individuals and those within populations and were thus able to reconcile genetics with natural selection. It was Dobzhansky (1937) who recognised that populations are parts of larger systems such as species, and the importance of geographic and reproductive isolation in evolutionary transformation. In effect he gave the phenomenon of discontinuity, relatively overlooked by Darwin, the prominence it deserved. The ornithologist Ernst Mayr, working largely with birds, particularly the rich avifaunas of New Guinea and the Pacific region, refined ideas of geographic speciation and developed the biological species concept (Mayr, 1942). Together with Dobzhansky (1937) and Huxley (1942), he heralded what has been considered as the greatest revolution in biological
systematics in the 20th century, the so-called "New Systematics". Generally speaking, the consensus view from then until the early 1970's was that there was nothing inconsistent with natural selection in the evolution of major groups of organisms and that major evolutionary changes to the phenotype could be explained by processes occurring at the population level. There were of course dissenters during the century following Darwin, such as Goldschmidt (1940) and Schindewolf (1950), but generally speaking such viewpoints were ignored.

There have been several "New Systematics" since the 1940s and indeed systematics is currently undergoing another major revolution due mainly to the impact over the last 20 years of spectacular advances in molecular techniques and the widespread popularity (in some quarters at least) of cladistic analysis, although it could be said to have begun earlier with the introduction of numerical techniques, technological advances in chemotaxonomy and in electronmicroscopy. These developments have been paralleled by, and also precipitated, debate on fundamental conceptual issues such as evolutionary theory, pattern and process, and whether systematics is an historical science or a functional science. It has also occurred at a period when systematists and evolutionists have been debating the patterns of variation found in fossil and extant organisms, the biological species concept (BSC), and the tempo and mode of evolution. In particular, the debates centred around issues such as stasis in the evolution of new forms, the units of evolution, and adaptation have been both voluminous and intense. Landmark papers such as Eldredge and Gould’s "Punctuated equilibria: an alternative to phyletic gradualism" (1972), Gould and Eldredge's "Punctuated equilibria: the tempo and mode of evolution reconsidered" ${ }^{(1977)}$ and Gould and Lewontin's "Spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme" (1979) have reverberations which can still be felt among the systematics community. We still lack a consensus view of what species actually are (or even if they exist) and how they and higher taxa such as genera and families should be treated from taxonomic and phylogenetic viewpoints. There is still no clear consensus as to the nature of discontinuity and the origins of the higher taxa. Some biologists believe that natural selection, operating at the level of the population and extrapolated through time, is sufficient to explain major phenotypic change. Others (mostly palaeontologists) believe that there is a macroevolutionary dynamic although most accept that natural selection is still
acting at the population/species level. In addition, the phenomenon of extinction and its effects on ecosystems is little understood and is likely to be found to play a major role in speciation events and biodiversity. Relict theory (Wright, 1941) may provide substantial weight for the construction of a model which explains the origins of the higher taxa.

Studies of evolution in major lineages of organisms have a practical relevance little appreciated until now, which is unfortunate because this has probably contributed to the decline of taxonomy during the latter half of the twentieth century. The new advances in molecular techniques and phylogeny will provide substantially additional data, particularly in the recognition of populations and their structures and genetic relationships. Such data can be used to answer questions about population dynamics, epidemiology, development, biodiversity and conservation (Harvey, et al., 1996). Above all, this data will be necessary if we are to avert the ecological disasters through bad planning, mismanagement and greed which are now facing us increasingly as we enter the 21 st century. Unfortunately as these new techniques become more universally adopted we are in danger of losing traditional systematic methods, especially the comparative approaches to morphology and plant development.

It is to address the problems posed in the recognition and handling of major discontinuities in phyletic lineages, as well as an attempt to understand the processes involved, that this study has been undertaken. Above all, it is an attempt to discover how phylogenetic and evolutionary studies can best be reconciled with the somewhat pragmatic aims of taxonomy and classification. The developing science of information technology will provide the basis for the utilization of much of the burgeoning data on the world's biota (mostly molecular) which is now appearing. Systematists have always had to be "Jacks of all trades" but this is more true now than ever before. Yet, in this age of specialisation, when techniques may take years to learn, this is rapidly becoming an impossible task. There is the added danger that there will be a real preoccupation with techniques at the expense of the main aims such as the understanding of species and population decline or the loss of biodiversity. No single individual holds a monopoly of knowledge and the number of multi-authored scientific papers now appearing makes it certain that cooperation between individuals is more
necessary than ever. It is to be hoped that this trend will evolve to a new adaptive plane for the next century...an integrated approach and a new paradigm for evolutionary systematics in the spirit of Mayr (1988) and Hall (1991).

The Campanulaceae Juss. * (= Campanulaceae s.l.) first attracted my attention in the early 1980s due to the worldwide association of tropical lobelias with bird pollinators which I was (and remain) interested in. As an undergraduate at the University of Aberdeen I studied the water lobelia (Lobelia dortmanna L.) and was intrigued by the patterns of variation in an aquatic plant which possessed both outcrossing aerial flowers and cleistogamous aquatic ones. This interest in variation at and below the species level was the main reason for a longterm study of speciation in the genus Campanula L. in the Aegean region (Eddie \& Ingrouille, in prep.), whereas my University of Reading studies of the endemic chrysangeas of the genus Musschia Dum. from the island of Madeira (Eddie, 1984) led me to consider the origins of the higher taxa, particularly island forms, and provided an opportunity to lay the foundations for the present study. As a vehicle for the study of evolution the Campanulaceae is an example par excellence particularly due to its association with oceanic islands. From a more emotional point of view my preoccupation with the Campanulaceae really began in 1980 in Greece when I first saw Campanula celsii A.DC. on the limestone rocks of Lycabettos Hill overlooking the city of Athens.

The family, although easily delimited from other plant families, has long been considered a difficult one to classify. Numerous genera have been described, many of which show no unique characters while variation at and below the species level finds numerous expressions. Ontogenetic contingency (Diggle,1994) is the phenomenon whereby an individual plant's developmental programme and groundplan can explain and constrain its capacity to respond phenotypically to environmental variation throughout its life (Watson, Geber \& Jones, 1995). Plants persistently attain size-correlated variations in their form and process due to the functional obligations imposed. This may be expressed through phenotypic plasticity, which, in the Campanulaceae, is rampant and has led to the recognition of numerous very dubious taxa and has burdened the nomenclature with synonyms. Organic proportion often reflects the consequences of natural selection operating on the relation between form and
function. The Baldwin Effect (Simpson, 1953), which is the phenomenon whereby phenotypically plastic traits in certain components of populations within a species are selected for and become genetically fixed, may have had profound importance in the radiation of species in many lineages of the family. In addition, the formation of polyploid complexes is a common feature of many species and genera in the family and the evolution of some genera through allopolyploidy seems certain. Therefore, at various levels in the taxonomic hierarchy, some taxa may possibly be polyphyletic in origin, eg. Hanabusaya Nakai or some of the polyploids within the harebell alliance (Campanula: subsect. Heterophylla). These ideas, at present, are purely speculative and need to be investigated further. Generally speaking however, the relationship between pollinators and floral mechanisms seems particularly important in the family (as well as among the Lobeliaceae) and pollinator-mediated selection is probably the greatest single factor in the evolution of the family.

A broad concept of the family Campanulaceae has been adopted in the works of Wagenitz (1964), Thorne (1976), Cronquist ( $1981 ; 1987$; 1988) and Brummitt (1992) which can all be traced back to the arrangements of Schönland (1889-1900). These authors include the lobelias (Lobelioideae Engl.), as well as genera such as Pentaphragma Wall. ex G. Don, Sphenoclea Gaertn. and Cyphia Bergius and its allies, in the Campanulaceae s.l. In such a broad taxonomic arrangement, the bellflowers are usually placed in the subfamily Campanuloideae Schönl., Cyphia and allies in Cyphioideae Reichb., and so on. Pentaphragma and Sphenoclea are treated by different authors as either monotypic families, subfamilies of the Campanulaceae s.l., or even as tribes of the Campanuloideae (= Campanulaceae s.str.). In this study a more restricted view of the family Campanulaceae is taken and the family name refers only to the bellflowers. This was the position adopted by De Candolle (1830), Fedorov (1957;1972), Kovanda (1978), Dahlgren (1980, 1983), Takhtajan (1987) and Lammers (1992a). In the text they are also sometimes referred to as belonging to the Campanulaceae s.str. (sensu stricto). The lobelias are therefore also given full family rank (Lobeliaceae). Further details are given in the Introduction.

For this study traditional use of the terms phylogenetic and monophyly are maintained and the views given by Stuessy (1990) are upheld. The term "phylogenetic" implies three principal processes of evolution. Cladogenesis refers to branching events, anagenesis refers to progressive change over time within the same evolutionary lineage and stasigenesis refers to an evolutionary lineage which does not change or branch over time. Cladistics, in contradistinction to phylogenetics refers omly to cladogenesis. Monophyly refers to organisms which have a common evolutionary ancestor but may not necessarily include all the descendants of that ancestor. Monophyly, as defined by cladists, is usually totally inclusive and has to include all the descendants. Thus, there may occasionally be some degree of ambiguity in the text but it is hoped that the context will always be clear. Where it is not, the term holophyly is given in parenthesis (see Ashlock, 1971; 1984). Students of cladistics may find this regrettable but it has to be said that there are many in the biological community, including myself, who have been schooled in an entirely different tradition. Within a purely cladistic discussion and analysis, the term paraphyletic is particularly useful to recognise ancestral groups from which taxa have evolved by anagenesis, and therefore has been maintained for this study. For discussion of these issues see Bock, 1977 and Cronquist, 1987.

* Author names are given when first mentioned only. The abbreviations used follow Brummitt \& Powell (1992).

This study has extended over many years and it would be impossible to name all those individuals who have contributed. Since 1985 when my studies of the Campanulaceae commenced as a PhD programme at Birkbeck College, University of London, a large number of people have given freely of their time and expertise, firstly in London and then later in Papua New Guinea where I was temporarily resident from 1988-1992. Since 1993, when I resumed my studies at the Institute of Cell and Molecular Biology (ICMB), University of Edinburgh, I have had tremendous encouragement and support not only from my original colleagues but also from many new friends and individuals who may or may not have shared a common interest in the Campanulaceae and have contributed, even if only in small ways. It is a pleasure to acknowledge them here:

Jim Archibald (Sherborne, Dorset); Tina Ayers (University of Northern Arizona); Jean Casey (Garvald); Richard Bateman, Mary Bates, Nicola Brown, B. L. Burtt, Quentin Cronk, Ian C. Hedge, Olive Hilliard, Helen Hoy, Roger Hyam, David S. Ingram; Ross Kerby, Ronald J. D. McBeath, Michael Möller, Richard J. Pankhurst, Jill Prescott, Martin Pullan, Colin Will, Paddy and Jennifer Woods (Royal Botanic Garden, Edinburgh); Rod Page (University of Glasgow); Mark W. Chase, Michael F. Fay, David Frodin, J. L. S. Keesing (Royal Botanic Gardens, Kew); Richard Ennos, John Findlay, Zoë Gowler, Andrew Hudson, Cathie Hutchon, Ian Oliver, Philip M. Smith, Bill Adams, John Love, Nicola Prescott (ICMB, University of Edinburgh); Pinkie Setshogo (University of Botswana); E. Stamatiadou (Athens); Stephen Waldren (University of Dublin); Robyn Cowan, Martin Ingrouille, Gita Panchal (Birkbeck College, University of London); Stephen Jury (University of Reading); Alan Morton (Imperial College, University of Londion); Olivier Gascuel (University of Montpellier); Cédric Notredame (The European Bioinformatics Institute); Angela Ivison (ABC, Charing Cross Medical School); Per Hartvig, Kit Tan, Arne Strid (University of Copenhagen); Mats Thulin (University of Uppsala); Peter Hein (Botanisches Museum Berlin-Dahlem); Wolfram Lobin (University of Bonn); Daniel Crawford (Ohio State University); Tod Stuessy (Inst. f. Botanik, Univ Wien); Robert K.

Jansen, David M. Hillis (University of Texas, Austin); J. Felsenstein (University of Washington); Tom Lammers (Field Museum of Natural History, Chicago); Nancy Morin, Tatyana Shulkina (Missouri Botanic Garden, St.Louis); M. J. Dallwitz (CSIRO, Canberra); Sheila Collenette (Hampshire); M. Hirst (Houghull College, Durham); Peter Lewis (National Campanula Collection, Padlock Croft, Cambridgeshire); Peter Wyse-Jackson (Botanic Gardens Conservation International, London); Peter Linder (University of Cape Town); Marcia Ricci (CONAF, Viña del Mar, Chile); Adriana Hoffmann (Fundacion Claudio Gay, Chile); Raul Vincencio (Commonwealth Science Council, London); A. W. Owadally (Mauritius); D. Valck (Conservatoire et Jardin Botanique de Mascarin, Ile de la Réunion); Mark Wilkinson (University of Bristol).

The Regius Keepers of the Royal Botanic Garden, Edinburgh and the Directors of the Royal Botanic Gardens, Kew are warmly thanked for the facilities I have enjoyed in both herbaria and in the gardens in general for many years. The library staff of the Royal Botanic Garden, Edinburgh, the Darwin Library and the staff of the Biology Computer-Support Group, University of Edinburgh and the staff of the Goulandris Natural History Museum (Athens) are gratefully acknowledged for their help, patience and great forbearance with my numerous, and often difficult requests. The following institutions are gratefully acknowledged for help towards the funding of this research: The Central Research Fund of the University of London; The Keddy Fletcher-Warr Studentship of Birkbeck College, University of London; The Molecular Biology Fund of the Institute of Cell and Molecular Biology (Travel to the Jodrell Laboratory, 1994); The Edinburgh Botanic Garden (Sibbald) Trust (Travel to Greece, 1994); The James Rennie Bequest of the University of Edinburgh (Travel to Turkey, 1995).

Several individuals must be singled out for their overwhelming support during the course of my studies. Andrew Hudson and Ian Oliver kindly let me use numerous facilities in their lab at ICMB and led me through the minefield of molecular biology at an age when I should have known better. I have benefitted in so many unforeseen ways from their knowledge but I am sure I must have exhausted their patience on numerous occasions. The lab, however, is
still in good shape. John Findlay gave assistance and much-needed humour during my SEM investigations and was always available, particularly when computing problems arose. Philip Smith, my supervisor at ICMB, has continued to provide the foundations under the shifting sands of a self-financed four-year research programme. Alan Gillies was instrumental in making my work on the automated sequencer possible by obtaining funds at the eleventh hour. Bill Adams and Bob Astles provided the skills necessary for the maintenance of a large and demanding mixed collection of living plants and have been good friends during the last four years. Richard Pankhurst has been a continual friend and mentor during this study and I thank him for help on numerous aspects of plant systematics, for writing various modifications of his PANKEY computer programs for me and for collecting Petromarula on Crete.

For sheer generosity and good conversation over many years, and for companionship in Papua New Guinea (1989), Greece (1994) and Costa Rica (1996) I dedicate much of this work to Martin Ingrouille. Martin has also provided help in numerous other ways, particularly aspects of systematic analyses during the time when he was my supervisor at Birkbeck College and since. But for those who know me personally it will have already been realised that it is to Fiona Pirie that I owe practically everything, for without her, all this would have been meaningless, if not impossible.

## For Fioma

Mar rivaisa the m irisleacha<br>co-ionaumbre rimes ruaill<br><br>'nom ceàl-gàire buam.

Som hairle MIacgill-Eain, 1943
"Irisleachd" (DDàim do Eimhir agus $\mathbb{D}$ dain Eile)

## "And you give me the choice between a description that is sure but teaches me nothing and hypotheses that claime to teach me but that are not sure"

Albert Camus, 1955<br>"The Myyth of Sisyphus"

The family Campanulaceae, although of moderate importance for horticulture, has been somewhat neglected from a systematic point of view since the excellent monographic treatment by De Candolle (1830). However, there has been a tremendous volume of cytological and palynological work done on the family during the latter half of the twentieth century. Chromosome counts exist for the majority of the genera, most of which have also been surveyed palynologically. Although all is not chaos, much of the research has been on a regional basis and rather piecemeal with the result that we no longer have a consensus of what characters define the family nor the number of genera it contains. The polarisation of debate between the conservative and/or phenetically orientated systematists and the "radical", purportedly phylogenetically-orientated cladists, has hindered progress towards an acceptable resolution for the systematisation and classification of the Campanulaceae. The debate between advocates of the biological species concept (BSC) and the phylogenetic species concept (PSC) are as alive as ever. We lack common agreement about species and generic limits, major factors of evolution which may be operating upon the group, and even proper typification for many of the names employed. In short, we have very little basis for the establishment of a proper information system for the Campanulaceae which is one primary long-term goal of this study and which is to provide taxonomic "products" for the users of taxonomy in the sense of Abbott et al. (1985).

It is considered in this study that the Campanulaceae, although by no means unique in this respect, pose severe problems for the practising taxonomist because of the nature of variation at several levels within the family. Only if a change in approach to classification procedures is adopted will progress be made. Firstly, a multiple approach to handling data
sets is considered a prerequisite. This has been a unanimous conclusion of all workers on this family (Gadella, 1964, 1966; Thulin, 1975). Secondly, I believe that we can no longer accept a static or typological approach to the handling of discontinuity and that phenetic variation must be interpreted within a relational or evolutionary framework. It is for these reasons that the biological species concept, despite difficulties in its application to plants, remains profoundly important (Snow, 1997). Thirdly, the proper placement of phylogenetically related organisms within a pragmatic classificatory scheme can only be hindered by a strict adherence to the logical deterministic pursuit of monophyly as advocated by many cladists. The resolution of the apparently opposing conflicts within systematics lies in the evaluation of multiple approaches in a dialectical or dynamically reciprocal way. More specifically, it is to address the problems posed in the recognition and handling of major discontinuities in phyletic lineages of the Campanulaceae, as well as an attempt to understand the processes involved, that this study has been undertaken. Finally, and no less important, it is an attempt to discover how phylogenetic and evolutionary studies can best be reconciled with the somewhat pragmatic aims of taxonomy and classification.

# Q. AIMIS, IDATA SOURCES AND GENIRAT MIETIHOIDS 

"The thesis that the only reputable, scientific classification is that based on phylogenetic or evolutionary principles is one that cannot be accepted for the Angiosperms on either theoretical or practical grounds"
$\mathbb{P} . \mathbb{H} . \mathbb{D}$ avis \& $\mathbb{V} . \mathbb{H}$. Heywood, 1963
"Far from being a dead field ips which most of the important discoveries were made long ago, systematics is ips its infancy. If a truly evolutionary systematics is to flourish, it must take the concept of evolution as an axiome rather than a superficial interpretation. This will necessitate a reevaluation of systematic concepts and the methods used to determine systematic relationships as well as the taxonomies derived from them."

$$
\mathbb{K} . \mathbb{D e} \mathbb{Q} \text { ueiroz, } 1988
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## 4. 1 Aims

The followimg are the primeipall mims ofthis stody:

1. To obtain a phylogeneric reconstruction (system) of the bellflower family Campamulaceae, parricularly for the higher taxa above the subtribal level, which is potentioully discoverable through the methods of moderve systemautics. This should provide a stoutement (hypothesis) about presumed relauionships of the genera.
2. To produce a classification of the higher faxa at the subtribal levell and above based on such an system but guided by the essemital aval traditional view of morphological criteria, ie. classes will essentially be based on their attributes. Comparisons will be made with the classifications produced by earlier authors, particularly De Canalolle (1830) ausd Schüralamed (1889-1899).
3. To explore modern techniques and methodologies with which to evaluate and validute both the system and the claussification.
4. To examine variation at the generic level and to identify the evolutionary processes leading to the hierarchical structure to be found in the family.
5. To determive whether such processes are in accord with currever models such as the grodualistic Neo-Darwimian modell or the punctuated equilibria macro-evolutionary model, or botlo.

### 4.2 Am ©verview of $\mathbb{D}$ ata Sources amd Gemeral Methodalogy

The accuracy of phylogenetic reconstruction is dependent not only on the quality of the raw data but also on the methods of analyses of that data and the experience of the systematist. All systematic analyses are ultimately character dependent, even if one is basing a system on branching pattern. Few botanical systematists would advocate the use of a single character to distinguish one taxon from another but basing a classification or a phylogenetic reconstruction on more than one character frequently leads to difficulties. A broad range of characters is appealing however, because it avoids consistent bias among characters that might yield erroneous results. The relationship between number of characters and probability of estimating the correct phylogeny corresponds intuitively with ideas of how phylogenetic methods should work and justifies combining partitions when the method is consistent (ie. it converges to the correct phylogenetic tree when more data, including other partition data, are added to the analysis) (Huelsenbeck, et al, 1996). For this study five data sets for the Campanulaceae were constructed. Each of these data sets requires different methods of analyses, eg. phenetic or cladistic, details of which are given separately in the relevant section. Some of the names applied to taxa are purely names of convenience and have no taxonomic validity, eg. "Himalcodon" for Codonopsis, Subgenus.Obconicapsula, "Fernandeziana" or "Fernandeziocodon" for the group of Wahlenbergia species from the Juan Fernandez Islands, "Helenacodon" for the group of Wahlenbergia species from St. Helena, and "Isophylla" for the group of species of Campanula in the C. garganica complex.

From the total diversity of species within the Campanulaceae a number of key taxa or exemplars (ie. taxa which are commonly accepted as being representative of known genera or sections within genera because they show morphological discontinuity) were chosen as the starting point for analysis in this study and as "terminals" in the phenetic and cladistic
analyses. This initial selection process is largely a synthetic one based on empirical procedures which depend greatly on the skills and intuitive evaluation of the systematist. The taxa which were selected included a small number of largely monotypic genera which have been split off from the two large genera, Campanula and Wahlenbergia. Also included were species which represented either subgenera or sections, principally again within Campanula or Wahlenbergia. Species were also selected to represent a range of diversity shown by each genus, eg. species from Codonopsis included prostrate, upright and climbing species. All these key taxa, regardless of rank, were treated as OTUs for analysis and provide the crucial first approximation of systematic relationships. The use of the term "OTU" should be taken in its broadest sense for it is a convenient term to include key taxa which are not necessarily equivalent. It is not used here in a narrowly phenetic sense. Initial examination of herbarium specimens of the majority of genera has shown that the recognition of certain character states in the Campanulaceae is difficult or impossible using preserved material. This is particularly the case for floral and fruit characters and to a lesser extent for vegetative characters. Characters obtained from herbarium specimens were verified in living material whenever possible and certainly for the majority of morphological characters used. From the outset, every attempt has been made to examine living material either cultivated in botanic gardens (primarily the Royal Botanic Gardens, Kew and the Royal Botanic Garden, Edinburgh) or in the wild. In some cases, fresh material was fixed in FAA for further examination in the laboratory. Many taxa have been cultivated in the glasshouses of the Institute of Cell and Molecular Biology (University of Edinburgh) in order to study ontogeny and character development more closely, and as a source for fresh DNA samples. Approximately $75 \%$ of the genera were studied as living material, the exceptions being some of the South African, North American and Central Asian endemics. Voucher specimens exist for the majority of the species sampled (see Appendices). Gaps in data sets have been filled largely by recourse to herbarium or pickled material, combined with a very judicious assessment of published descriptions. All DNAs used in the molecular analyses were obtained from fresh material cultivated in Edinburgh or, in a few instances, from relatively fresh material which had recently been collected and dried in silica gel.
Seeds were obtained from numerous sources worldwide, either from personal contacts or through botanic garden seed lists, or from herbarium material. Identification of seeds was
confirmed either by the existing voucher specimen or by subsequent cultivation. In the latter case, voucher specimens were then obtained for possible future corroboration. The data set for seed characters was obtained by an extensive survey of available genera using scanning electron microscopy (SEM) and augmented by the data already published by Shetler and Morin (1982) for North American taxa and by Haridasan and Mukherjee (1988) for Indian taxa.

Pollen data were obtained principally from published sources, especially the very detailed palynological studies of Dunbar (1973-1984); Dunbar and Wallentinus (1976) and Morin (1987) and Nowicke et al. (1992). Cytological data were obtained from diverse published sources worldwide, but mainly from the studies of Gadella (1962-1974), Gadella \& Kliphuis (1963; 1972); Contandriopoulos (1964-1984) and Contandriopoulous et al. (1972-1984). Biogeographic data have been gleaned from distributional data published in regional floral works or monographs.

Table 1. Outline summary of the methods, analyses and procedures which form the basis of this study.

| TIIESES | METHODOLOCY |  |  |
| :---: | :---: | :---: | :---: |
| Hypothesis | SYNTHETIC |  |  |
|  | Eclectic | OTU selection | Empirical |
| ת ${ }^{\text {® }}$ | $\Omega$ |  |  |
| Antithesis | ANALYTIC |  |  |
|  | Phenetic | Ordination Clustering $\hat{\pi}$ | Algorithmic Algorithmic |
|  | Recinrocal Comparison |  |  |
|  | Cladistic | 3 <br> Parsimony | Algorithmic |
| $\Omega$ | ¢ ${ }^{\text {a }}$ |  |  |
| Synthesis | SYNTHETIC |  |  |
|  | Phylogenetic | Historical Reconstruction | Empirical (Intuitive) |

> "Our argument, however, is not that one must always partition data sets. Rather the point is that, when faced with biologically defensible divisions, the nature of these partitions should be taken into accoumt in the choice of analytical methods"

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\text { A. de Queiroz, N. J. Donoghue and J. Kim, } 1995 .
$$

Miyamoto and Fitch (1995) have argued most convincingly that distinct classes of evidence (characters) exist, eg. gene trees versus species trees, although Kluge and Wolf (1993) believed erroneously that such subdivisions have no discoverable boundaries and therefore there is no justification for analysing separate data sets. If it is accepted that different classes of characters do exist, it may be questionable whether phylogenetic methods have greater stability when these different classes of characters are sampled. Incongruence may be due to the different classes of characters involved or to the sampling methods. If different classes of characters represent different adaptations, then phenetic methods should yield different topologies. Phenetic classifications of the same taxonomic group but based on different classes of characters may be less similar to each other than those based on randomly chosen subsets of characters. In contrast, cladistic methods should be more similar since there is only one true cladistic topology. In reality, such methods may only produce a theoretically greater degree of congruency since they are exceedingly sensitive to sampling procedures.

The degree of correlation of the characters within a data set has to be carefully considered. Where there is conflict between characters of a single data set the tree topology will usually be weakly supported. In phylogenetic studies it can be observed that most frequently the distribution of characters between taxa under consideration is such that some characters reappear in taxa unexpectedly. Characters evolve at different rates and are rarely coincident in their distribution (the "Non-Congruence Principle" of Crowson, 1970). It is unreasonable to expect the topology of trees generated by different data-sets to be completely congruent. Generally speaking different data sets, when subjected to reliable methods of phylogenetic analysis, are expected to converge on the true phylogeny (the probability of estimating the correct tree should converge to 1.0 ). We can then expect a reasonable degree of congruency which should give us a measure of confidence in the putative phylogeny and that isolated or well-marked groups are indicated (Crowson, 1970). The best method of analysis in a given
instance may depend on the relative importance given to resolving power versus avoidance of error. Combined analysis avoids loss of information whereas separate analysis takes into account heterogeneity of data sets. The advantage of using a combined approach is that by directly utilizing the testimony of all the characters a closer approach to the true phylogeny may be possible. Combining data sets can enhance the detection of real groups, avoids loss of information and can give greater global parsimony. It maximises the "informativeness" and "explanatory power" of the character data used (Huelsenbeck, et al., 1996). Brower (1996) agreed and added that combining data sets in simultaneous analysis also incorporates the fewest ad hoc assumptions (i.e.of homoplasy) on a character by character basis. A combined tree may be more resolved than a consensus tree because information that resolves certain relationships may only be present in some of the data sets. Also, where there is conflict among characters and therefore weak phylogenetic signal masked by "noise" (homoplasy), increasing the number of characters may allow the signal (synapomorphies) to assert itself. However, combining "bad" data with "good" data may give a less accurate estimate of the phylogeny because combined analysis may also obscure significant patterns of congruence or conflict among characters. Furthermore, enhancing the detection of phylogenetic signal may result in a restructuring such that the combined tree contains groups not found in any of the trees generated from separate analyses of the different data sets. In this case the resolution of the character conflict embodied in the combined tree may represent a better estimate of the phylogeny than would even a fully resolved consensus tree. Once it has been established that the different data sets give strongly supported conflicting trees, it is clear that the conflict is not among individual characters but among data sets. Where conflict is among characters, not data sets, a combined approach should be used.

Bull et al. (1993) presented a general argument against combining and in favour of separate analysis in some circumstances, based on the view that estimates of phylogeny assume an evolutionary model. Each data set may be governed by different evolutionary models. Consensus methods give equal weight to each data set, thus reducing the potential for data sets with relatively large numbers of characters to swamp data sets with fewer characters (Kluge, 1983) and are thought to give a conservative estimate of phylogeny (Hillis, 1987). Consensus trees are simple statements about areas of agreement among trees, they are not
putative phylogenies. When different data sets yield significantly different phylogenetic estimates (ie. too great to be attributed to sampling error) the characters in question must have evolved at different rates, through different processes and/or have different histories. Partitioning data provides insight into the evolutionary processes and seems a safer course because it allows us to test whether particular characters violate our assumptions about these processes. Testing for incongruence of topologies estimated from different processes will help improve the robustness of phylogenetic methods. Separate analyses may be seen as a means of exploring possible disagreements among data sets. If independent data sets are combined this would violate fundamental assumptions of parsimony analysis. This is not the case with consensus because here one is not invoking a global parsimony. Areas of agreement are likely to represent real groups. Characters within data sets are more likely to be non-independent than between data sets and therefore conflict among trees from different data sets can be seen as a means of assessing heterogeneity (de Queiroz, 1993). Miyamoto and Fitch (1995) contended that, if there are biological reasons for believing that there is heterogeneity among data sets, then they should not be combined, regardless of the level of disagreement among the phylogenetic estimates. These latter authors place great emphasis on corroboration of phylogenetic hypotheses by independent data. There may not be any need to proceed towards consensus but if the goal is to achieve an estimate of true phylogeny, then one has to address such arguments rather than merely explore the conflicts. However, a consensus tree can be less parsimonious and often less resolved than the trees from a combined analysis. In addition, two data sets might not be in conflict, yet consensus methods might still yield an unresolved tree (Hillis, 1987). It therefore may not represent the best summary of the character information. Loss of information may be the most general argument against consensus. The nature of the differences among the data sets and the support these data sets provide for conflicting trees determine whether a consensus approach, a combined approach, or both are warranted (de Queiroz, 1993). The idea that different data sets may be independent (in relation to the estimation of phylogeny) is central to the justification for a consensus approach. Characters within data sets may be more likely to be non-independent estimators of phylogeny than characters in different data sets and thus may be more likely to support the same wrong hypothesis (Doyle, 1992).

### 5.11 Plillosoplhical Approaclies Adopted im this Stundy

"Philosophic arguments on the basic nature of biological classification need to be tempered by pragmatic corsiderations before too much time is spent."

BB. LI Burft, 1964

## S.1.1 Same Cardimal Poimts

In view of the continuing controversy in the systematics community over philosophy and methodology (although somewhat diminished) it seems desirable in a study of this nature to clearly state at the outset the philosophical views which have guided the author.

1. Evaluation lhas occurred and is occurring at different rates within the Componulaceare affecting characters in a moultitude of different ways, both indeppendently amd in correlation.
2. The evolution of the Campomallaceae originated as a single event in the history of angiosperm evolution amal there is only mene umique phylogeny for the Componataceae lineage as a whole. If science is defined as the "pursuit of truth" then the pursuit of theat true phylogeny places such studies firmaly withim its realme even if we cam only ever realise the mearest apppoximortion to the truse phylogeny.
3. Evaluation within the Compomulaceae has produced patterns of discontionuity which theoretically should reflect the phylogeny or genealogy of the fomily (descent with modification) but there is considerable evidence to suggest that the distribution of charracter states resultus from hybridisation and possibly other causes such as introgression, lack of expression, evolutionary stasis amad extinction. The resultamt patterns of descert may thus allso be tokngenetic (reticulate), not clearly hierarchical and
consequently more difficult to iveterpret．Such aliscontinuity may be the result of cousoul processes acting at different levels．

4．The ultimate mechamism of evolutionary change within the Campanulaceas is natural selection actimg upon genetic variation within popultarions amed within the constraivets of morphogenesis（the so－called＂epigenstic traps＂）as determined by the 厄istory and the gemetic mokeup of the fomily．Mechamistic explamations connot be evaluorted ive the absence of an explicit plaplogeneric fromeworl．

5．The true phylogeny of the Compomulluceue is potentially discoveralole principally therough the combinarion of a variety of methods atthough it is considered undikely that it will ever be known completely．Ir is considered unalikely to be discovered through purely pleneric methods or purely clowistic methods allone．$A$ more adequate understanading of the 隹istory of the fomoily can only be achieved through a plumality of opproaches uatilising molecullar and cytolagical，as well as morpholagical amd biogeographtic dara－ traditionally what may be described as the＂evolutionary approache＂（Mayr，1969）．The arealyses of characters mast also embrace character corcelnaions in order to approach the totulity of rellations between or with in the organismas．

6．A purative phylogeny is an hypothesis based largely on a phylogenetic or evolurionary inaterpretarion of the availlable daudu．It may not be divectly suituble as a classification but is the most important bosis for one，especially if it is based on data obtained by an eclectic approach．Theis must include clodistic anoulyses anal evoluationary scenarios，and implicit in these is an arpriori assessment of the evolutionary status of characters（palarisation）as well as ave empatley with the arganism。 Such intuitive processes buill on experience are，if used with care，importont components of phylogenetic anoulysis and should not be dismissed lightly．

7．Claudograms are patterns（tree topologies），classifications or hypotheses based on a Wierarchy of shared derived characters（synapomorphies）and aim to establish patterns of genealogy．However they resull from mumberical processes and one cannot assume that
they necessarily reflect genealogy. No implicir models of relationships are incorporated in cladistic aralyses. To establish genealogical relarions additional data are usually required. Cladogrames are usually not suituble in themselves as taxanomic classificarions. The patterns of discontinuity may reflect the patterns of ancestor-descendane relationships as predicted by the synapomomphic douta but do mot mecessarily ivodicate generic closeness. Mamy phenotypes are nor expressed or the patrerns are confounded by the distribution of plesiomorphies, homoplasy and missing data. Therefore clodograms should not have primacy over other results. One should be sceprical of attempais to elucidure phylogenetic relarionships througle cladistic anoulyses undill an extensive dara-base is available for reference.
8. Discontimuity of form ultimately may be the most legitimate basis for recogneition of traxonomic groups but a character-based system can probably be bettered if combined with a history-based one such as ancestor-descendana relationships (patierres of symapomorphic alistribution) which olso prove to be lowgely in accord with patterns discovered by other methodologies. The is is particularly truse for faxa below the generic level. In addition, a pheylagenetic systeme requires criteria for grouping and raveking. Als a greiding principle, the grouping criterion is monophyly (in the traditional sense, not the cloudistic sense) tempered by evalbuation of cladistic abod non-cladistic dota sets. It is recognised that absolute monophylesis is rarely revealed and some taxa may be polyphyletic avod unresolvable. Furthermore, the tempo of evolution may have to be taken into account thws resulting inn the recognition of paraphyletic taxa. The ranking criteria may be causal processes or, more pragmatically, they may be synapomorphic grades.
9. A raxonomic biological classification is a compromise which usually does not completely reflect relationships nor reveal the complexities of relationships among its members. It need not reflect evoluation at all. Nevertheless, such a classification is often considered to function as a biological theory with all the explanatory, predictive and heuristic properties of a theory (Mayr, 1969) and so the construction of classificarion should not be a whimsical process. Classifications are made up of classes. A class is a construct, the membership of which is determined by the closs definition or class concept.

Classes are spatio-temporally buboursded and any entity that firs the defivition of a particular class belomgs to that class regardless of its historical origin in time and space (which is why phylogeneric analysis leas primacy for a classification which purports to have hesuristic evolusionary valuse). Therefore:
10. A phylogenetic classification (im the troditional sense) is a special kined of taxomomic classification the structure of which is defined by process as well as pattern. It weay be legitimately compared to other clossificarions such as phenetic ones the structure of which is defined by attributes of the classes and where relationsthips are based on overall or aggregare resemblance alone, or cladistic classifications where relationaships are based on a hierarchical patiern of characters. When phenetic classifications are also considered to be simultaneously phylogenetic, then the genealogical patiern is presumed to be generated by oll kinds of chavacters (both synapomonpleies and symplesiomorphies).

### 5.1.2 IDiscussion

"We denote this primary wisdom (spontaneity or instinct) as intuition, whilst all later teachings are called tuitions. In that deep force, the last fact behind which analysis cannot go, all things find their common origin"

> Ralph Waldo Emerson, $184 \mathbb{1}$
> "Self Reliance"

The restoration of evolution is critical to biological classification. Without it, the whole edifice of biology collapses. Despite the legitimacy of other kinds of classifications, none can unify all the disparate subdivisions of the biological sciences in the way that the evolutionary classification can. Therefore, for the general purposes of biology, we must give primacy to classifications which reflect as accurately as possible the facts of evolution although a workable taxonomic classification cannot provide a perfect reflection of evolution, no matter how abundant the evidence on which it is based. "Taxonomy can provide only a somewhat muddy reflection of evolution, but a reflection all the same" (Cronquist, 1988). "No system of nomenclature and mo hierarchy of systematic categories is able to represent adequately the complicated set of inter-relationships and divergences found in nature" (Mayr, 1942). Classification should be guided by phylogeny but must also be based on practical considerations such as morphology. Molecular taxa and those based extensively on TM or SEM characters,
cytology or biochemistry are not practical for the identification of taxa but for delimiting them. The problem is that phylogenetic patterns which are discovered have to be converted into a classification and they are not always immediately compatible. It is this conversion process from the results of phylogenetic analysis ("pure taxonomy") to taxonomic expediency ("applied taxonomy") which causes the greatest concern and strife among systematists. A classification is generally regarded as the primary product of systematic effort (Minelli, 1993) but it may not be the sole or even the best way of representing the outcome of systematic work (Griffiths, 1974, 1976). A distinction can be drawn between a classification which is the arrangement of entities into classes, and systematization, the ordering of entities into systems whose structure is the result of some natural process such as common descent and heterobathmy (Takhtajan, 1991). The view adopted in this study is that the latter approach should have primacy and that the classification should reflect this as accurately as possible (see also: Hennig, 1975; de Queiroz, 1988; de Queiroz and Donoghue, 1988; and Minelli, 1991). The classification is a by-product of the systematic process and it may only give limited access to the ultimate basis for comparative knowledge of the family which is the phylogeny. Without a knowledge of the genealogical history of the organisms, any comparative data will be suspect. Modern classifications should not only fulfil these criteria but should also be the gateway to information systems which will provide comparative data for genetic, conservation, pathological and pharmaceutical studies among others, which critically depend on the phylogenetic status of the organism being known. Neither lumping together organisms on the basis of resemblances nor the idea that the totality of relationships is expressed by genealogy is satisfactory.

For the last two centuries, taxonomic classification based on morphology has served us well, mostly as a means of diagnosis or as a framework for floral compilation, and continues to do so. It was the uniqueness of the phenotype based on (usually) a suite of shared arbitrary characters which served to delimit the higher taxa (Davis \& Heywood, 1963; Crowson, 1970; Sneath \& Sokal, 1973). Unfortunately the choice of characters used to delimit higher taxa were often limited and the characters themselves often highly adapted, reflecting a grade of organisation in the respective plant. The characters may also have evolved in parallel within sub-lineages of the family and represent homoplasy. Such characters are poor
at providing genealogical signal although they may be useful for providing a means of identifying a plant or placing a plant in an artificial classification. They may be most useful in a phylogenetic system which takes account of grades. Phenetic classifications, by concentrating on the phenotype (the product of descent and evolution), are attempts to achieve the same ends as phylogenetic ones since it is implicit that similarities at the phenotypic level reflect similarities at the genotypic level. The logic of using this approach alone is somewhat flawed because it is built on the false premises that resemblance is a measure of relatedness. To some extent, this is also a weakness in cladistic interpretations which equate the cladogram with genealogical relations. The homology of phenotypes does not imply the similarity of genotypes (de Beer, 1951). Certainly there is a large measure of congruence between phenetic and genetic similarity although it is usually not of a simple nature, and it may be recalled that the seminal studies of phenotypes by Darwin and others in the 19 th century provided the basis for our understanding of evolutionary hierarchy. This, however, is only a starting point. "New" genes can be utilised to control previously unrelated developmental processes, the so-called "genetic piracy" of Roth (1988; Van Valen, 1982). In addition, many taxa represent polyphyletic grades of organisation, not monophyletic clades. There is an increasing body of evidence to show that many organisms share primitive characters (symplesiomorphies) which could influence a classification. When a group based on overall similarity corresponds to a group based on synapomorphies, it is due to the fact that the noise of irrelevant characters does not substantially influence the performance of the true group characters which are also used in the analysis. Since it is not possible to determine which characters create noise, it is impossible to critically evaluate the groups which cluster.

In the construction of a phylogenetic classification we have to adopt a strategy which, in addition to other aspects such as phenotype, takes into account the history of descent of organisms, or, in other words, their branching (cladistic) patterns. It should be a historybased system as well as a character-based one. This requires very specialised treatment of the characters to be used. The monophyly of terminal taxa will consequently be determined by the hierarchical pattern of ancestor-descendant relationships (clade) in additition to the groude which is subjected to evolutionary interpretation. The cladistic relationships of
organisms are more likely to be discovered by an analysis using shared derived characters (synapomorphies) although it has to be borne in mind that not all characters (including synapomorphies) may be expressed in certain lineages. Therefore a selection of only synapomorphies in an (cladistic) analysis may give more misleading results than a selection of all characters (symplesiomorphies and synapomorphies) in a phenetic analysis. Although methodologies which utilise only plesiomorphies or a combination of character types cannot produce truly genealogical systems, aggregate similarity (and difference) will produce an improved classification compared to one based on only a few characters. Cladistic methods can generate patterns (topologies) or classifications of branching but are not, in themselves, necessarily phylogenetic. The patterns achieved by a cladistic approach which utilises evolutionary hypotheses of character polarity can be legitimately called a phylogenetic classification (in most cases only narrowly so) but these require either additional data sets or careful interpretation. In the majority of cladistic studies a number of equally likely cladograms are obtained and a resolution involving procedures such as parsimony or maximum likelihood is necessary. Heywood (1964) called such patterns "evolutionary interpretations" but by calling cladograms "interpretations" in contradistinction to a classification he logically implied that they must presuppose a classification. This is mere hair-splitting rhetoric in support of the supposed primacy of phenetic classification. In practice every process is theory-laden and most systematists start with a selection of OTUs which form terminals in a structureless classification. It may be granted that such first approximations can be called classifications but they are hardly suitable for most applications which require organisms to be organised in structured systems of hierarchies or nested groups in which there is usually some theoretical content of their evolutionary history.

It is accepted that evolutionary or phylogenetic classifications are mostly unsuitable for general use but they are the bases upon which we can build the taxonomic classifications utilized by botanists and the general public. A phylogenetic pattern may, in addition, be derived from a plurality of cladograms, phenograms, scenarios, etc. It may contain directionality, ie. a time dimension, and possibly ancestral taxa as well. It is best suited to diagrammatic expression as a phylogram (or as a "Dahlgrengram" showing the distribution
of character states). Often phenetic classifications are more expedient, eg. for identification purposes, as in bacteriology, or for applied interests such as horticulture or pharmacy. However it is firmly believed that a greater number of more meaningful generalizations can be obtained from a classification based on phylogeny, for in reality a phylogenetic system encompasses the data to be found in a purely phenetic system in addition to other data such as biogeography, etc. Phylogenetic systems are, in practice, justifiable by the plausibility of their conclusions, not their information content nor their repeatability whereas taxonomic classifications usually are judged by their "workability".

To achieve a taxonomic classification based on phylogeny it is necessary first to provide a logical framework (the phylogeny) and consistent criteria (grouping and ranking) for the higher taxa, particularly at the generic level and above, but also, in the case of the large genera such as Campanula and Wahlenbergia, at the level of sections and subsections. These approaches should reduce the problems of non-equivalence in taxa (see next section). In a perfect world unique genealogy that corresponds in a one to one relationship with grade of organisation would be the necessary and sufficient condition for recognising a historical group, the supraspecific taxon. This would be the monophyletic group in the purest sense. In practice however, we have to balance between a monophyletic (holophyletic) group sensu Hennig which is a group of species that includes an ancestral species (known or hypothesised) and all of its descendants (see Farris, 1974) and the monophyletic group in its traditional or evolutionary sense of Mayr which takes account of evolutionary grade and recognises paraphyletic taxa.

Several of the smaller genera of the Campanulaceae are certainly monophyletic, but the largest genera, Campanula and Wahlenbergia and probably also Asyneuma, are very heterogeneous and most probably are paraphyletic. The concept of monophyly is, of course, only a grouping criterion. It does not imply that any group so recognised must be treated in any particular way. It only specifies the supposed genealogy under which such groups can be recognised (if this is desirable) and/or the degree to which they have diverged. The ranking criterion applied in a particular case must support recognition at a particular level.

Monophyletic groups can exist at all levels of inclusiveness so ranking criteria are needed to delimit them.

A prerequisite to a phylogenetic analysis of the Campanulaceae is a thorough familiarity with most of the living genera. Despite some general claims over the last few decades that systematics should be objective and repeatable, there is no substitute for field experience and a thorough personal knowledge of the group under consideration especially by actually cultivating the plants themselves. Fulfilling this criterion necessarily brings some element of subjectivity (as well as increasing logistic difficulties) but it is considered that the methodologies adopted in this study go some way to negate the effects of personal bias. Many of the assumptions that systematists hold about the relationships and evolution of plants are based on untestable hypotheses but are necessary in order to assemble a cladistic matrix of polarised characters based on outgroup comparisons, homology, ontogeny, etc. Personal familiarity with the subject material is, in most cases, the only means by which we can evaluate these hypotheses. Morin (1983) has listed several philosophical criteria which she adhered to in her study of Githopsis. These are considered to be sound viewpoints and have largely been adopted in this study, together with similar viewpoints of Hutchinson (1959), Takhtajan (1991), D-Y. Hong \& L-M. Ma (1991) and others.

## 5. 2 Historicall amd Comeeptual Treatmemt of the Gemus

"Above the level of the species of species group II suspect that our classifications in most groups are not much different from what they would have been if no account had been taken of evolutionary theory "
V. H. Heywood, 1964

Edgar Anderson (1940) concluded, from the result of a questionaire to numerous working biologists and taxonomists, that "there is no basic uniformity in taxonomic groups. Taxonomy is only a glorified guess and an attempt to construct a cross-section of lines of descent ine a form intelligible to the human mind. It always contains two variable quantities - the plasticity of animate nature and the differing points of view of the people who work at it. It is not a matter of mechanically applying a universal set of categories to given groups of facts. Each group which one tackles presents a fresh and origiral problem; for each, one has to work out anew the method by which he may achieve that transforming of confusion into order which is the great satisfaction of pure taxonomy". The following discussion is an attempt to explore this idea further.

Certainly there is no taxonomic framework which can be applied equally throughout the living world. Taxa of unrelated groups show little or no equivalency and frequently, at the group level, single characters which show consistency within that group (the "ingroup") are used to delimit it instead of an assessment of overall correlations of equally weighted characters (Burtt, 1964). The genera of the Campanulaceae present the familiar problem of there being no obvious generic equivalence within the family. The delimitation of species and genera represent the two greatest headaches for taxonomists and often there is a strong practical bias in the methods used. Differences may depend on philosophy, perception, or more pragmatic factors such as methods employed and character valuation. In addition there may be imperfect knowledge of many groups.

Several trends in the establishment of taxonomic frameworks are apparent, both historically and within human societies. H. H. Bartlet (1940) has given an excellent account of the relationships between species/generic concepts and language and presented an historical narrative outlining such concepts in folk taxonomies and among mediaeval botanists of Europe until the time of Tournefort. Much of this is largely superfluous to the present discussion except insofar as it emphasises the psychology of perception in the recognition of genera. He believed that genera were set up by analysis and by synthesis and that the
grouping of distinguishable but similar kinds into genera has always been a linguistic necessity if there were to be both flexibility and precision in the nomenclature of plants. The flexible but undefined categories of genus and species sufficed for most purposes of folk science and this is still largely true today. The inclusiveness or size of genera, now as in the past, is less a matter of science than of linguistic preference and convenience. Folk nomenclature may provide good indications not only for practical but for scientific generic grouping.

Scientific nomenclature, prior to the influence of Darwin was constrained by the Doctrine of Special Creation as well as by the concept of Aristotelian naturalness. According to Bartlett (1940), Tournefort was the first to place the concept of the genus on a sound footing. He had a well-defined underlying philosophy which enabled him to judge what constituted a genus (expounded in Isagoge in $\mathbb{R e m} \mathbb{H}$ erbariame which forms the introduction to his Instituationes $\mathbb{R e i}$ Herbariae). He showed that plants generally have roots, stems, leaves, flowers, fruits and seeds, of which at least five may generally be considered in the establishment of a genus). These were the five most important organs to consider but close correspondence in all five was not required for establishment of a genus. If correspondence only occurred in one, then it was difficult to arrive at a "good genus". Flower form alone as a criterion was no better. Correspondence in two or three organs was considered necessary, but special combinations such as flowers and fruits (but not roots + flowers or roots + fruits, etc.) made the best criteria. However he said that any "rule of thumb" may be too rigidly applied, and so made exceptions to maintain distinct natural genera. Therefore Tournefort recognised two orders of distinctness for genera. The first order applied to genera recognised by conformity of organs whereas the second order applied to those recognised by distinctive or unique features or other organs. He stated, "the concept of the small genus comprehends more that is commor to all the species, so that the names of the latter may be brief and sonorous. Better to propose new genera with audacity thave to force species into places where they do not fit". If new generic names would be conducive to understanding the nature and affinities of plants, he had no scruples about establishing them, but not thoughtlessly or without good reason.

Linnaeus and his immediate successors' view of the genus was a broad one (W. WrightSmith, 1947). Linnaeus generally accepted the genera established by Tournefort (1700) and Plumier (1703) and gave all genera single names. In Funedomereta $\mathbb{B r a t a n i c a}$ (1736) he laid down the fundamental principle that the genus and species are entities of nature. Linnaeus's famous dictum states, " The genus makes the characters, the characters do not make the genus" although his advice was to recognise species first and synthesise these into genera. In practice he tended to emphasise characters of the fruit (Larson, 1971). Many large genera were erected during the period of "Special Creation", and were based on a traditionally rigid concept of specific and generic delimitation. Close morphological similarity was interpreted by Linnaeus as signifying real generic relationship. No true genus was other than a natural genus. Linnaeus believed in the relationship of species and genera by descent although the process called for an original divine creation followed by subsequent hybridization by miraculous intervention through various combinations and stages until all the genera and species were produced. He stated that the morphological combinations, if botanists were perceptive enough to interpret them, would indicate the true genera. His approach to generic circumscription was outlined in detail in the Phillosophial $\mathbb{B o t a n i c a}$ (1751) and it consisted of searching for three characters (Svenson, 1945) :

1. the natural character giving the complete description of all its features and upon which the classification system should be based.
2. the factitious character being a selection of features suitable for discrimination among genera in an artificial system of classification or even in a key.
3. the character essentialis which equated to the features allowing for easiest description.

The changes that have come about since Linnaeus have been to define genera as groups of species that do not seem to violate the conceptions of natural affinity by descent that were developed by Darwin, but modern botanists still adopt a rather Linnean approach to genera and seek criteria mostly from morphology. Large genera as well as small ones may be "entities of nature" and naturally an attempt is made to find the characters which will best
express this entity. This view has predominated in botany until the present day. Although taxonomists' views on the delimitation of genera are often influenced by geography, most have concerned themselves with the search for suitable characters which would delimit genera rather than philosophical or conceptual issues. A review of the subsequent (post Darwinian) historical and current treatment of the higher taxa has shown that the genus is largely thought not to exist as a real entity, that it is a concept or construct of the human mind; it is a collective category, the membership of which is based on purely subjective criteria of the taxonomist. Yet from the criteria used to delimit genera, it would appear that they may still be inadvertently treated as if they were entities. Anderson's (1940) survey concluded that genera were considered to be, on average, more natural units than species, and that generic differences could be compounded from specific differences. This was especially the case of those who had done monographic work. It may well be that the more natural unity of the genera accorded to them by participants in Anderson's survey was due to the greater discontinuity between genera as opposed to the species they delimit.

The search for characters with which to delimit taxa has been like a search for the holy grail. With technological advances in electronmicroscopy and cytology, attention has been turned to microcharacters, particularly chromosomes, pollen and seeds. There has been an increasing use of microcharacters to prune away the large genera. However, it has since been realised that microcharacters are no better or worse than traditional macrocharacters. Genera cannot be identified by such microscopic characters but as Löve (1963) has pointed out, their value is not in the identification of, but in the delimitation of natural boundaries for genera. Unless correlated with gross morphological (and/or distributional) characteristics, chromosomes are of limited value in the determination of generic boundaries (Jones, 1985). Dissimilarity in some or all of the principal chromosomal characters (number, size, morphology) may be a reasonably safe indicator for evolutionary divergence at the generic level, but the opposite is not implicitly true and cannot be interpreted as an indication of close relationship. Chromosomal features are basic to an understanding of relationships, but they are more useful at the infrageneric than the generic level.

Comparative studies of SEM-level characters in the Asteraceae have shown that they are taxonomically useful but that they are neither more nor less useful as a means of generic delimitation than are macro- or micromorphological ones. The utility of any character at any taxonomic level depends on the consistency with which states of the character occur within and between taxa, and the correlation of that character with other features. It may be that studies of adaptive significance of ultrastructural characters will be more fruitful for evolutionary systematics than those of gross morphological ones, in part because the relationship between anatomy and biochemistry is clear at this level and because their interaction with elements of the physical environment can be measured (Bolick, 1978, 1981, 1983; Barthlott, 1981, 1984). True homologies should be more easily discerned when the adaptive role of characters is known (Stuessy, 1979), and phylogenies based on those characters should therefore be more predictive. The extent of intra and inter-taxon variability or consistency must be determined before confidence is placed on classification based upon them (ultrastructural characters). There is the added danger of the typological trap with microcharacters whose variability is unknown. Therefore, as Lane (1985) suggests, one must do a proper survey of such characters to assess their variability.

Chemical data present certain problems, but they also have some unique advantages for systematic purposes. When a compound has been identified it represents an unambiguous character state. Furthermore, it is often possible within one chemical class to relate constituents to one another in terms of their biosynthesis. Despite the fact that reversals and convergence in pathways do occur (Mabry \& Bohlmann, 1977), good hypotheses for the biogenesis of natural products do exist. These make interrelationships of character states more directly interpretable than those for other kinds of taxonomic data. The more unusual or derived a structure, the greater its classificatory value.

Breeding data can also be used with some sucess but is not always easy to obtain. If a group of species can be crossed successfully among themselves (ie. F1 hybrids can be examined for fertility) then artificial hybridisation provides a good method for the delineation of genera especially when used in context with data from other approaches. In many groups crossing data may be more useful at the genus level than at the species level. (Powell, 1985).

It can enhance the distinction of closely related genera. High fertility in interspecific hybrids is not so valuable, whereas sterility in intergeneric hybrids indicates crossing data which is more meaningful at the generic level. The ability to cross also indicates relative close relationship. Successful experimental crosses are to be expected, especially where allopatric, outcrossing, perennial taxa, or K-selected species are involved (Stebbins, 1950; Grant, 1971; Raven, 1976, 1980) as opposed to annuals or r-selected species which often have strong internal reproductive barriers. Intergeneric hybrids are expected to be highly sterile. This often amounts to a "biological genus" concept in the spirit of experimental categories (Clausen 1962). The biological species concept however is not undermined because even the highly fertile interspecific crosses are likely to be ultimately sterile in later generations. Natural "intergeneric" hybridisation, where at least partial fertility of the hybrids can be established, should be strongly considered as evidence that the taxa involved are congeneric. Crossing data are as equivocal as any other data when it comes to evaluating genera. Crossability and interfertility of species are distinct and unrelated phenomena. The ease with which two species can be artificially hybridized may not be related to the subsequent fertility of the hybrid (Ornduff, 1969). Kruckeberg (1962) advises that successful artificial hybridization between two species of related genera is not sufficient in itself to cause the joining of those species into a single genus but crossability does indicate that the genera are related.

Many authors have overlooked the lack of equivalency in plant genera and attempted to establish rules for their recognition despite the fact that such an a priori approach is philosophically unsound. Wright-Smith believed that Mayr (1942), by advocating an average of about 5 species per genus verged on invoking a mechanical approach, and thus regarding the genus as merely a subjective unit without true representation in nature, and but a taxonomic idea. For Mayr, the question was not whether the genus as such has reality but whether or not the borders of the genera are real. He concluded that boundaries between genera are not as distinct as between species (Wright-Smith disagreed and attributed this to the extreme splitting in ornithology and the high level of expertise among its adherents). Mayr states, "The genus if it is to remain useful, has to retain its character as a collective category". Convenience, despite its appeal, seems to be a particularly invalid criterion for the
delimitation of genera. Others have tried to invoke nomenclatural rules for the recognition of genera. Greenman (1940), for example, stated that the type concept should influence the generic concept. The species of a genus must conform in all essential morphological characters to those of the type species of the genus under consideration. The generic concept thus centres around a type specimen whereas formerly the generic and the specific concept centred around the complex which represents the genus in its general area of distribution, and more particularly the dominant form. Regardless of this view, the use of the nomenclatural system imposes a conservatism on systematics. As long as the binomial system of nomenclature is used, conservative botanists will be reluctant to recast generic concepts or limits except upon the most convincing evidence (E. E. Sherff, 1940).

Legendre \& Vaillancourt (1969) attempted to place the concept of the genus on mathematical grounds, but the result was largely a cladistic definition based on holophyly and adaptive zones (Legendre, 1971). Studies utilising phenetic characters or data matrices for the delimitation of genera include Bohm et al. (1978); James (1953); Prance et al.(1969) and Baum (1978), but perhaps the greatest advocate of operationalism was McVaugh (1945b). Rogers McVaugh studied the Campanulaceae and it is no surprise that many of his ideas stems from this group. "MicVaugh's Principle" as Cronquist (1988) calls it was formulated in 1945 specifically to address the question of relationships between two campanulaceous genera, Triodanis and Specularia (= Legousia) and is basically an operating principle for the delimitation of satellite genera. It is worth quoting in full :
> "Any segregate genus should be sharply delimited; that is, any species which is intermediate in one or more respects toward a more inclusive genus should be relegated to the latter. The retention of the anomalous species in the more inclusive genus will change its limits, if at all, but very slightly, and only in this way can the segregate genus be precisely defined"

This was rephrased by Gillis (1971) and Grashoff (1975) as follows:

1. Special consideration should be given to qualitatitive morphological characters.
2. The recognition of segregate genera based on minor or single characters should only be allowed in particular instances to preserve usage.
3. The biological unity of a genus is more important than the gap between it ard close relatives.
4. Changes made in generic limits should be done only after a full study of variation within the complete range of the group.
5. Decisions ond whether to establish segregate genera should be based on the relationship of the segregate to its core genus. (Robinsop \& King, 1985, believe that the idea of "core genera" is untenable even in its name) and not on relationships of the core group to other established segregates.
6. Segregate genera should be sharply delimited (any iptermediate species should be included in the larger gevius).
7. The strength of the argument to recognise segregate genera varies proportionally to the number of differertiating characters.
8. The decision to recogrise a generic segregate is strengthened if the group has a distinctive geographical range.

This may seem a reasonable operating procedure but it is still leaves us with the problem of deciding how "anomalous" is anomalous. There are some isolated genera the status of which seems beyond question. Anomalous genera often have phylogenetic significance vastly out of proportion to their bulk in the taxonomic sense. The more genera are studied, the more they defy neat clear relationships to neighbouring genera. Both taxonomists and anatomists probably tend to become impressed by the distinctiveness of a genus as they study it more closely and discover more differences than had originally been known. Most systematic workers have stressed the necessity of intensive study of a particular group before any taxonomic changes are made. With respect to Senecio, Stebbins (1953) recognised that individual characters were significant only when they happened to be useful and noted that reliance on characters presumed to be fundamental in previous taxonomies had led to the recognition of unnatural assemblages. It was possible to recognise natural assemblages only after the species were satisfactorily well-known. There are also several philosophical objections to a strict adherence to operationalism.
W. H. Camp (1940) hinted at an approach to the problem of generic delimitation from the processes involved in the evolution of the higher taxa rather than the characters they possess. He stated that "the genus is less a taxonomic catch-all and increasingly a unit expressive of close phyletic relationship". In attempts to rationalize a static system of immutability with the known facts (ie. mutability), he believed that the use of the sub-genus will not satisfy the desire to express phyletic segregation. There has to be rationalization between taxonomic categories and phyletic units. The nomenclatural system should express the rank and degree of relationship between organisms. He further stated that the difficulty of arriving at useful generic concepts is frequently compounded by a misapprehension as to the nature of evolution of taxa, a naive assumption that for each supraspecific taxon there was at some time in the past a single species that had the essential characters of the group and became ancestor to all other members. This was also confirmed in Anderson's survey (1940) which supported the notion that "individual differences which are gradually built up into varietal, and these progressively into differences of specific and generic rank is so logical that it has, conciously or unconciously, been accepted by many taxonomists as absolute dogma". There is some evidence of dissent however as shown by Cronquist (1985) who believed that this was not the only way for supraspecific taxa to originate. He believed that members of a taxonomic group could evolve in parallel to a new "adaptive plane" and collectively become a new group ( $=$ genus). A genus could have several species as its ancestor. Therefore a determined pursuit of absolute monophylesis is destructive rather than helpful to the taxonomic system. Some have claimed that the genus is a unit of evolution. For example, according to De Queiroz (1985), an "assemblage", usually of two of more species (but can be one), can be a supraspecific taxon, which is a spatiotemporally bounded entity. It can therefore be considered as an individual with cohesion and continuity.and thus a participant in natural processes (ie. units of evolution and history). Wiley (1981) however concluded that natural supraspecific taxa are neither individuals (in a philosophical sense) nor classes. Rather they are historical groups derived from individuals. He believed that it is the objective of phylogenetic systematics to discover which taxa have an objective basis in evolutionary history and either name them or make their presence immediately apparent. Supraspecific taxa differ from species and other "individuals" in several respects. Cohesion in a species is maintained by reproductive ties, evolutionary stasis and responses to evolutionary processes.

There is no active cohesion in a supraspecific taxon because its units have the potential to evolve independently. Natural supraspecific taxa only have historical continuity and are therefore not units of evolution, whereas species have both historical and ongoing continuity and are units of evolution. Supraspecific taxa are units of history. The following implications derive from Wiley's view:

1. There is no ovgoing process which gives a pratural higher taxon cohesion nor is there a process by which
such taxa arise which care be divorced fropr speciotion.
2. Therefore, supraspecific taxa must be historical units that have resulted from speciation.
3. Genealogical lineage splitting and other speciation processes are both necessary and sufficient conditions for the origin of natural supraspecific taxa. Those taxa that do not accurately display these necessary and sufficient corditions cannot be matural taxa.
4. A matural supraspecific taxon cannot overlap another at the same level of universality, ie. one taxon contains species which are closer to those in another. The definitions of two supraspecific taxa cannot overlap. Any single character may only be used once to define a group but not any entities (subgroups or lesser supraspecific taxa) withirs it.
5. Although species as ipdividuals have no adequate definition except that of their insertion in history, historical groups must be justified by evidence, ie. by characters (synapomorphies) that demonstrate their status as natural groups.

Few authors other than the above-mentioned have attempted to speculate on the origin of genera or on possible macroevolutionary processes which may be unique to higher taxa. Funk (1985) has approached the problem from a philosophically different angle although apparently in contradiction to the views of Cronquist regarding monophylesis. She stated that cladistic classifications seek to recognize monophyletic ( = holophyletic) groups while changing the existing nomenclature as little as possible. When applied to the discussion of generic concepts this approach means that new descriptions and combinations are justifiable only when they are necessary for the delimitation of natural groups of species (monophyletic
groups, sensu Hennig). "If we strive to make our species represent the units of evolution then all higher ranking categories are really just monophyletic groups of species no matter what we choose to call them". She further stated: "the various levels at which the "groups of species" are recognised is not of major concern to cladists". It is the quality of these groups that Funk was concerned about. She believed that to discuss generic concepts, we should begin with a properly constructed cladogram in which species are the terminal taxa and that cladograms are converted into genera by accepting that the cladogram represents the classification. Her guidelines for turning it into a hierarchy are as follows:

1. Whale maximsizing information, strive to minimize novelty. The only justification for describing new genera is to develop a system of classification that contains monophyletic groups when this was not previously the case. A taxon is not circumscribed from an existing genus undess:
2. It is more closely related to species in a different genus.
3. The group of species on the cladogram is a_paraphyletic assemblage that can never be defined because it contains orily the "leftover species" that are not "different enough" to have inspired previous treatment at the generic level.

Treatments that rely on ease of recognition to delimit genera can lead to two major problems, core genera and artificial genera. Although disruption in the nomenclature is minimized, information is not necessarily maximized by the use of core genera over smaller holophyletic groups (Turner, 1981). The segregates must be defined by synapomorphies and the parent group must not be left paraphyletic. Classifications giving consistent information cannot be achieved by whim. Funk believed that the cladistic approach provided wellreasoned guidelines for evaluating and comparing classifications, and can aid in making decisions about the retention of existing genera or descriptions of new ones. All groups must be defined by a unique set of characters. If classifications are to be employed in the study of relationships, biogeography, coevolution, speciation, or many othẹ interesting subjects, we must strive to identify and recognise monophyletic groups (that reflect the pattern of evolution). "Whether such a well-defined cladistic methodology will solve the problems of generic delimitation and recognition is debatable, but the extent to which botanists resist the changes in classification is often the extent to which they do not really know the phylogeny of their particular subject".

Some botanists believe large genera to be conceptually useless. Many old genera (ie. Campanula) have received their present taxonomic identity by piecemeal accretion. Senecio L., a genus of 3000 species is held together by a suite of characters which are not present in all species (T. M. Barkley, 1985). Robinson and King (1985) believed that a broad generic concept misrepresents evolutionary diversity and may also project false impressions of its true age and complexity. The increase in recognised genera is of course paralleled by the increase in recognised species and it is only to be expected that this would change our views of the limits of some genera. Too many genera may obscure rather than elucidate relationships. The creation of microgenera would obscure relationships among groups of species unless an elaborate hierarchical system was inserted between the generic and tribal levels. The primary purpose of taxonomic hierarchies above the specific level is to reflect relationships among groups of species. Any system which is based on single characters is bound to obscure those relationships. For a taxonomic character to be reliable, its presence must be correlated with that of other taxonomically useful characters. (Sundberg 1985).

A particular genus may be so unique in its suite of characters or "gestalt" that it imposes restraint on further division. In such cases generic delimitation is notoriously difficult, because a great many of the recognizable groups are connected by palpable intermediates. In order to have conceptually useful genera, we must accept the fact that many of them are inherently ill-defined and unresponsive to efforts at precision. A large genus may be diverse but may be undivisible due to imperceptible gradations within it, whereas several small genera may lack internal diversity but show greater discontinuity between closely related genera. The large genus may have subdivisions but the unity is not affected. If subgenera are raised in rank to genera we have a dilution of criteria. Divergence has been emphasised although the gaps have been narrowed. An accepted unity has been lost. It may well be that a genus can be divided but that is not a reason for its division. A large genus may not be easier to handle by calling its sections "genera". Perhaps it would be useful to have large genera with infrageneric ordering so that meaningful internal substructuring might be presented. (Philipson, 1987).
"Hope springs eternal among taxonomists who study complex groups"
T.M.Barkley, 1985

### ๘.1 Descriptiom; Geographical Distribuntiom; Ecology

### 6.1.1 Descripriom

The bellflowers (including bluebells, canterbury-bells, harebells, ladybells, starbells, swampbells, rampions, throatworts, sheeps-bits, venus's looking-glass and chrysangeas, etc.) comprise the family Campanulaceae s.s. Most of them are generally easily recognisable as such and are fairly well-delimited from other plant families by unique combinations of characters, particulary the pollen-transfer mechanism, invaginating presenter hairs and actinomorphic corollas. The lobelias (family Lobeliaceae), which are equally distinctive, have an almost cosmopolitan distribution, resupinate flowers, zygomorphic corollas, fused staminal columns and a less sophisticated pollen transfer mechanism. They also possess a complex armoury of alkaloids which are absent in the bellflowers. Both groups are thus relatively homogeneous and distinct from each other due to pronounced gaps in their overall spectrum of variation. There is no doubt that they are closely related but the usefulness of retaining them in a broader concept of the Campanulaceae is doubtful. Family descriptions then become so generalised that no clear picture of each group emerges and are usually quite inadequate to do justice to the diversity and complexities of form to be found in the two evolutionary lineages. The following somewhat enlarged introductory account of the bellflowers is an attempt to redress this shortcoming.

The Campanulaceae $s . s$. is a medium-sized cosmopolitan family comprising mostly annual, biennial or perennial herbs while about 13 genera are suffrutescent or suffruticose small shrubs. Only about $10 \%$ of the family are annuals. Pachycauls such as Musschia wollastoni Lowe are rare but there are numerous species of caespitose montane herbs and a few species such as Campanula thyrsoides L. resemble dwarf versions of the African giant lobelias
(Lobelia L.: Lobeliaceae) or the Hawaiian silverswords (Argyroxiphium DC.: Asteraceae). The association of rosetted pachycauls or " pachyflors" with alpine regions can be explained by the fact that such plants experience small fluctuations in daylength (at least in tropicalpine regions) and high irradiance levels. Photosynthesis exceeds respiration so much that they can double in dry weight in less than one month. There are a few tropical or subtropical weak climbers and twiners. Some members of the family are monocarpic and some are evergreen but the majority fruit over several seasons and either lose their leaves in an unfavourable season or die back to ground level (cryptophytes and hemicryptophytes). Some species such as Wahlenbergia campanuloides (Delile) Vatke (Fig.1) are ephemeral in areas of shifting sands in Africa and Arabia. Lateral branching may be sympodial or monopodial (Schulkina, 1980c). The leaves are of the dilleniid type of Hickey \& Wolfe (1975) and in most species are alternate with a $2 / 5$ phyllotaxy, but occasionally they are opposite or whorled (Ostrowskia Regel and some species of Adenophora Fisch. ). In some genera such as Roella L. the leaves are ericoid or densely amplexicaul, while in Edraianthus (A.DC.) A.DC. they are


Fig. I. Woulenbergia comopanauloides (IDelile) Vatke, am eplhemerall species fromn areas of shiftimg samds im Arrabia amd Africa. Note the slemaler taproot. (Natural size, from Collemette 8591)
slender and grasslike. Some species such as Azorina vidalii (Wats.) Feer and Section Platysperma Damboldt of Campanula have thick fleshy leaves. Mostly the leaves are simple
and exstipulate, entire, serrulate to serrate, or lobed. In a few genera such as Campanula Sect. Platysperma, Codonopsis Wall. and Platycodon A.DC. the leaves and buds possess a fine glaucescent farina. Many species are rather hispid while an even greater number have a leaf indumentum to varying degrees. Trichomes are simple and unicellular with perhaps only a moderate diversity of form. Bracts are small and bracteoles are frequently absent. Stomata are anomocytic. All species so far investigated possess articulating laticifers and a whitish latex, the chemistry of which has not been thoroughly investigated. Stem anatomy is occasionally anomalous. Some lineages have an elongated storage tap root while in others the storage organs are root tubers or corms which may be fusiform to various degrees. Chasmophytes have a woody storage caudex which is quite variable in size and form depending on the fissuring of the rocks upon which they grow. Ephemerals such as Wahlenbergia campanuloides have a long tap root, an essential adaptation for life in desert sands. More advanced forms have rhizomes as storage organs. Perennating organs are frequently stoloniferous or rarely soboliferous. The root system is usually fine and ramifying, particularly in chasmophytic species. Nodes are unilacunar or seldom 3-5 lacunar. Vessel segments have simple or seldom scalariform perforations. Two types of seedlings apparently exist in the family (Schulkina, 1980c): 1. those with a well-developed hypocotyl and epicotyl, and elongated internodes. The mature plants of this type have multinodal elongated shoots; 2. those with a shortened epicotyl and basal internodes which form a leaf rosette. The mature plants of this type display a diversity of rosette types (Schulkina, 1980c). There is a great diversity of seedling form within the Campanulaceae. For example, Ostrowskia only produces cotyledons during its first year. The correlation of seedling morphology with taxonomic status may be a rewarding avenue for further systematic research but at present it is by no means resolved.

Morphological variation within the Campanulaceae is complex and has led to much taxonomic confusion. At the individual level there is direct ontogenetic variation during the life-cycle due to the genotype but also ontogenetic contingency which is expressed in the form of phenotypic plasticity. Thus, on a seasonal basis one can observe considerable variation in leaf size and development, indumentum and floral parts within even-aged populations. Phenotypic plasticity is even more pronounced between populations which
differ in age, elevation, aspect, shading and soil conditions, etc. This confusion is also exacerbated by the presence of polyploid complexes in many species, particularly within the harebells of the Subsection Heterophylla (Nyman emend.Witasek) Fedorov and the genus Adenophora Fisch. Hybridisation and introgression appear to play a lesser role in complicating the patterns of variation but intergeneric-hybridisation in particular may have led to the evolution of some monotypic taxa such as Hanabusaya Nakai. Apomixis is unrecorded in the family.

In most species of the Campanulaceae the flowers are protandrous but this may be incomplete or absent altogether in some species of annuals such as Githopsis tenella Morin (Morin, 1983). Precocious development in Campanulaceae flowers may therefore lead to the establishment of autogamy. For discussion of pollen presentation see Carolin (1960b) and Shetler (1979b). The flowers are mostly conspicuous, 4-whorled, hermaphrodite (rarely unisexual) and actinomorphic (3-4)-5-(6-10)-merous. The number of floral parts is phenotypically quite plastic and this appears correlated with growing conditions. It is no surprise that in some taxa such as Phyteuma tetramerum Schur, Canarina L. and Michauxia L'Herit. such departures appear to have become genetically fixed. The calyx, except in Cyananthus Wall. and partly in Codonopsis and Craterocapsa Hilliard \& Burtt, forms a hypanthial tube, the walls of which are connate to the ovary walls. This tube may extend above the ovary and be adnate to the corolla, forming a hypanthial cup but usually the calyx lobes and the corolla develop at a level approximating to the top end of the ovary. It is only Cyananthus which has a strictly superior ovary. In all other taxa the ovary is surrounded to various degrees by the adnate hypanthium although the top end may bulge upwards before or after fertilisation giving the impression of a semi-superior ovary. The calyx usually has 3-8 lobes, most of which are free and divided to the base, alternate with the corolla lobes, and are persistent. Frequently the calyx lobes are accrescent in fruit and in some species may aid dispersal (eg. Campanula: Subgenus Megalocalyx Damboldt). Unlike the lobelias, there is no resupination and the odd dorsal lobe (mid) arises from the dorsal portion of the floral primordium. Calyx appendages are frequently present and variable in size and ornamentation. In Middle-eastern taxa such as Michauxia, Sicyocodon, Zeugandra and in Campanula (Sections Rupestres and Quinqueloculares) the appendages are so large that they
envelop the ovary in a pseudo-capsule. This development appears to give extra protection to the ovary from herbivorous insects and dessicating heat. In South Africa a parallel but less elaborate development occurs in a few species of Wahlenbergia which have protrusions or gussets between the calyx lobes. The corolla is often large and showy, gamopetalous and more or less divided into 5 (rarely 3-4 or 6-10) lobes which alternate with the calyx lobes. The lobes are usually short or about half the length of the corolla or sometimes longer, but rarely so divided as to appear free. They are connate to varying degrees forming a tube which is so short as to be almost unrecognisable in some taxa such as Wahlenbergia Schrad. ex Roth. The corolla is persistent in all but a few genera and even then is only weakly caducous. Rarely are two whorls of corolla lobes abnormally present (eg. Michauxia tchihatchewii Fisch. \& C.A.Mey.). The corolla is most commonly tubular-campanulate, infundibular, cylindrical or stellate-rotate but there are some bizarre exceptions (eg. Campanula zoysii Wulf. and Merciera A.DC.). Aestivation is strictly valvate although with some species displaying a twisting which is reminiscent of a contorted arrangement. Lobes are rarely free at anthesis, but compactly united apically before finally separating. In some genera (eg. Phyteuma L.) this separation is delayed until the flower matures while in Physoplexis (Endl.) Schur, the corolla lobes are permanently adherent. Corolla colour is mostly conspicuous blue in various hues from azure and sky blue to violet and indigo, or pink or white but rarely yellow or reddish. Frequently the base of the corolla and/or the nectar dome are contrasting whitish or crimson-violet colour forming a conspicuous "eyespot" or there are distinct coloured bands in the mid-corolla region. In other taxa the lobes have conspicuous veins (eg. Platycodon, Codonopsis) or honeyguides (Legousia Dur.) or tesselated with irregular markings (Codonopsis). Campanula Sect. Tulipella Fed. has the corolla marked by crimson spots and blotches while Roella rhodantha Adamson of South Africa has a red corolla with blue spots on the lobes.

In many taxa of seasonal climates the mature overground parts consist predominantly of inflorescences and it is often difficult to distinguish the zones of vegetative branching from the floral regions. In some taxa however, the vegetative stem has contracted to form a basal rosette and the inflorescence then is clearly demarcated eg. Wahlenbergia androsacea A.DC. The inflorescence of the Campanulaceae is usually determinate (Roeper, 1826) and
described as monotelic (Troll, 1964/1969; Carolin, 1967), ie. the flowering shoot ends in a terminal flower. In contrast, most of the Lobeliaceae are polytelic. The underlying uniform developmental pattern is essentially cymoid in character but confusing due to the order of maturation of flowers on the main axis and on the branches. Solitary flowers appear to predate the evolution of floral aggregations although numerous taxa have solitary flowers which are secondarily derived. Most commonly the inflorescence in the family is compound with several orders of branching. Such a structure is properly termed a synflorescence and the repetitive branching structures are partial inflorescences. The inflorescence is often bracteolate, branching pattern is usually simple (Weberling, 1989) but, depending on the species, may develop as either short dichasia, spikes, panicles, umbels, corymbs or thyrses, or may rarely be reduced to solitary flowers, particularly in arctic or alpine habitats where apical dominance is pronounced, eg. Wahlenbergia saxicola A.DC. of New Zealand or $W$. pusilla A. Rich. of East Africa. Inflorescences are rather plastic and the number of flowers produced is often dependent on the stature of the plant which itself may be a function of age, vigour, or morphotype. The reproductive zone most commonly has subtending leaves which are bracteose rather than foliose but there are occasional exceptions. Flowers may be terminal or axillary and may be sessile or pedicellate. When it is condensed to form a capitulum as in Jasione L. or Phyteuma, or a glomerule as in Campanula Sect. Involucratae (Fomin) Charadze and Edraianthus, the bracts form a subtending involucre. Many genera show a trend towards aggregation of flowers in glomerules (eg. Campanula glomerata L., C. tymphaea Hausskn., Edraianthus spp., Microcodon glomeratum A.DC.) or umbels (Physoplexis) and thyrses (Trachelium L. spp., Diosphaera Buser s.s., Campanula Sect. Tracheliopsis (Buser) Damboldt). Other genera have achieved the same effect by being multi-stemmed and cushion-like (eg. Diosphaera asperuloides (Boiss. \& Orph.) Buser, and Asyneuma Grisebach \& Schenk spp.). The stamens are most commonly free, alternate with corolla lobes and are usually of the same number. They are attached at the extreme base of corolla close to the nectar disk, or sometimes a little higher in some South African genera and are then epipetalous. The anthers are always coherent forming a tube around the style in early stages of anthesis but usually separate by the time the corolla has opened. They may remain coherent for a little longer as in Campanula flaccidula Vatke and in Campanula: Sect. Symphyandriformes (Fomin) Charadze, permanently at maturity along their full length
as in Symphyandra A.DC. and Hanabusaya, at the middle only as in Cyananthus, or at the base only as in Jasione. The basifixed anthers are two-celled, tetrasporangiate and dehisce longitudinally inwards (introrse). The thecae are parallel. There is a complex pollen presentation mechanism which is unique to the Campanulaceae. Before anthesis pollen is transferred from the introrse anthers which are synchronous in their development to specialised collecting hairs or papillae on the outer surface of the stigmas and/or upper style (presenter region). Pollen may then be seen adhering in regular lines on the presenter region. They are not "swept up" in a brush-like movement as is sometimes stated in the literature. Some genera such as Jasione, Trachelium, Phyteuma and Physoplexis have very short presenter regions which have the pollen-collecting hairs pointing forward and forming a cup or "pseudo-indusium" which gathers the pollen in a less regular manner. In the latter two genera the elongating style could be said to have a piston-like mechanism since it carries the pollen through the connivent tips of the corolla lobes. In this respect they almost approach the situation to be found in the Lobeliaceae. After pollen transfer, the anthers and upper filaments usually then wither and play no further part in pollination. Several hours to days after anthesis, the pollen hairs may either wither or invaginate to release the pollen. This action may be correlated in some way with the visitations of insects. The stigmatic lobes then reflex to reveal the receptive inner surface as the flower enters the female phase. The filaments are membranous and free but often dilated at the base and ciliate, and partially (rarely completely) fused at their bases to form a nectar dome ("saftdecken") surrounding the base of the style. The nectar, in the majority of species in the family, is concealed.

Pollen grains may be porate, colpate or colporate and variously ornamented. The porate grains are almost invariably spinuliferous but the colpate and colporate grains have the ornamentation reduced to verrucae. Both binucleate and trinucleate grains have been recorded for the Campanulaceae s.l. (Brewbaker, 1967). Pollen grains are occasionally blue, crimson or purple-coloured and this is often correlated with a coloured presenter region and/or style. They are often rather sticky and clumped and in one genus (Namacodon Thulin) they are dispersed in tetrads instead of monads which is the norm. A nectary disc is usually present and may be an inflated ring, continuous or interrupted lobes or a cylinder. When no nectar dome is present this is often conspicuously coloured or patterned although
in this respect some species of Adenophora with their orange-yellow cylindrical nectary protected by a dome are an exception. Otherwise it is greenish or colourless. Nectar is colourless with one bizarre exception, Nesocodon which has bright scarlet nectar which drips like blood from the mouth of the corolla !

The style is solitary, filiform or thickened, usually straight but occasionally curved and sometimes strongly exserted. The stigmatic lobes number $2-5$, rarely are multifid, and are filiform to club-shaped or capitate, spreading initially from tip, or sometimes from the middle or base. The ovary is inferior, semi-inferior or rarely superior (Cyananthus). Epigyny in the Campanulaceae has an appendicular origin (Carolin 1959, 1960b, 1978). The ovary is syncarpous and usually 2-(3)-5-locular (6-locular in Canarina; rarely 8-10-locular in Michauxia and Ostrowskia by interlocular septa), but sometimes unilocular by failure or disintegration of the septa (Merciera, Craterocapsa). Each locule is usually multi-ovulate but sometimes the number of ovules is reduced to 1 (Merciera) or 2 (Siphocodon Turcz.). Placentation is axile, rarely apical (Siphocodon), basal (Merciera) or sub-parietal (Triodanis). Ovules are characteristically anatropous and tenuicellar, with a massive single integument and an integumentary tapetum that is often incomplete at the micropylar end. Capsules may be erect or nodding, and usually crowned by the persistent sepals and the marcescent corolla. Dehiscence is lateral and poricidal, rarely by transverse fissures or irregular rupture of capsule wall, or loculicidally by apical valves, or splitting irregularly at apex. Rarely is the capsule indehiscent. In some genera (Campanumoea Blume and Canarina) a berry is the norm. The majority have dry dehiscent capsules with numerous seeds. Some annuals of the desert and semi-desert regions of the Mediterranean and the Middle-East such as Roucela Dum. sp. or Campanula sidoniensis Boiss. have capsules which are tardily dehiscent or indehiscent but there is also a trend towards indehiscence in several independent lineages of Campanula which may be correlated with islands or high mountain habitats. Examples are C. sartorii Boiss. \& Heldr., C. incurva Aucher ex A. DC., C. morettiana Reichenb., C. scoparia (Boiss. \& Hausskn.) Damboldt, C. munzurensis Davis and C. ptarmicifolia Lam.

In many respects, fruit formation and capsule dehiscence have very similar parallels in the Lobeliaceae. For example, in the Hawaiian endemic genus Trematolobelia A. Zahlbr. ex Rock the capsule disintegrates to release the seed. In the Andean genus Lysipomia Kunth the capsule dehisces by an operculum whereas in the American genus Downingia Torrey the capsule opens by lateral slits. Other lobelioids have baccate fruits or valvate capsules.

With the exception of Campanula robinsiae Small, Triodanis perfoliata (L.) Nieuwl. and Gunnilaea Thulin spp., the seeds of Campanulaceae lack superficial processes. Seeds are usually numerous, rarely few, and are small. They are fairly smooth, shiny, occasionally with a well-developed reticulate pattern to the testa, sometimes winged and/or with conspicuous hilum. The seeds have abundant protein in a fleshy albumen and the dicotyledonous embryo is erect and straight. The endosperm is copious and oily (sometimes starchy) and development cellular, with or without terminal haustoria. The radicle is near the hilum.

The most common chromosome number in the Campanulaceae is $\mathrm{n}=17$ and this appears to have evolved independently several times in relatively unrelated lineages, eg. in Campanula, Nesocodon and in Canarina. 42\% of the published chromosome counts have this number (Lammers, 1992a). The base number in the family has been suggested to be $x=8$ (Böcher, 1964; Contandriopoulos, 1984) but Raven (1975) suggested that $x=7$ is the ancestral number. However there are some persuasive arguments to suggest that the ancestral base number may be as high as $\mathrm{x}=14$ (Stace $\&$ James, 1996). An ancestral base number of $\mathrm{x}=7$ is supported by counts for Cyananthus (Kumar \& Chauhan, 1975; Hong \& Ma, 1991). This genus is usually considered the most basal taxon in the family (Hutchinson, 1969; Carolin, 1978; Takhtajan, 1980; Dunbar, 1984; Hong \& Ma, 1991) although it does possess several autapomorphic characters. In almost all large genera in the family, particularly Campanula, Adenophora and Wahlenbergia there are polyploid series.

Protein intranuclear inclusions with a fibrillar structure (F-type) are unique to the Campanulaceae (Thaler \& Gailhoffer-Dengg, 1972; Bigazzi, 1986) and have been found in Campanula, Edraianthus, Jasione, Phyteuma and Trachelium. They are absent from
examined species of Asyneuma, Canarina, Legousia, Petromarula Vent. ex Hedwig, Platycodon and Wahlenbergia. They appear to be absent from the Lobeliaceae. Campanulaceae generally have S-type sieve-element plastids which lack proteinaceous inclusions (Behnke, 1981; Behnke \& Barthlott, 1983).

The Campanulaceae commonly store carbohydrate as inulin, an oligosaccharide consisting of straight chain polymers of 1-40 fructose residues linked alpha (1-2) to a terminal sucrose molecule. A diversity of species are recorded as producing 14-carbon polyacetylenes (highly unsaturated hydrocarbons produced from oleic acid)( Lammers, 1992a). Alkaloids are virtually absent in the Campanulaceae (Willaman \& Schubert, 1961; Hegnauer, 1973). Caffeic acid (a phenolic compound) occurs in Campanulaceae as an ester with quinic acid, most notably chlorogenic acid. These are absent from the Lobeliaceae where it is replaced by chelidonic acid (Hegnauer, 1966; Molgaard, 1985). Only rarely are the Campanulaceae cyanogenic (triglochinin) (Tjon Sie Fat, 1978) or saponiferous (Cronquist, 1981). For primary and secondary metabolites, see Gershenzon \& Mabry, 1983; Harborne \& Turner, 1984.

### 6.1.2 Ecalogy

"It is precisely closely allied forms with very similar ecological habits and much genetic homology in
common, which are liable in different parts of the earth to slip into related habitats, arnd converge because
in thems they compe under parallel selection pressure. But standard taxonomic practice would regard their
comvergent characters as equally ancestral with those that were genuinely continuous ins time".
A.J. Cain, 1982

The majority of species are fairly tolerant of a variety of soil types and, although adequate drainage and stable mature soils seem to be a prerequisite for most of them, there are conspicuous exceptions. A large percentage of species, especially endemic taxa of the Eurasian mountains, are confined to areas of limestone. Rather fewer taxa are found in areas of serpentine or oligotrophic soils, or on unstable soils such as those found in river beds, sand dunes, scree slopes or disturbed/marginal habitats while Brachycodon would appear to grow mainly in solonetzic soils (Fedorov, 1957). Most of the tropical species grow in humus-rich soils in wet mountain forests.

Many species are confined to high mountains, some at extremely high elevations where climatic conditions are severe. The majority of montane species inhabit crevices and have the adaptations typical of chasmophytes, ie. long storage caudices, basal rosettes, short-lived perennial or biennial habits and often a monocarpic fruiting mode. Few have adapted to sheer vertical cliff-faces in the way that the genus Diosphaera has. Some species prefer extremely sunny conditions, eg. Musschia aurea Dum., Azorina vidalii (H.C. Watson) Feer, Petromarula pinnata, Campanula merxmuelleri Phitos, C. saxatilis L., etc. Although not very succulent, many of these helophytic species of coastal habitats approach the adaptations of halophytes to some degree, eg. tough shiny leathery leaves, fibrous suffruticose stems, etc., but their levels of salt-tolerance are unknown. It is not known if any member of the Campanulaceae is a $\mathbb{C A M}$ (Crassulacean Acid Metabolism) plant but genera such as Azorina and Musschia might be worth investigating. The leaves of Azorina tend to form dense subglobular clusters which resemble those of the recently-described Lobelia vivaldii Lammers \& Proctor from hot sunny cliffs on the island of Mona between Puerto Rico and Hispaniola. Many other species of sunny habitats have varying degrees of indumentum or glaucescence, presumably as a protection from solar radiation. The majority of the southern

African species, and many of those from oceanic islands are small woody shrubs and are ericoid in form. Some, such as Mericiera, Prismatocarpus and the "Lightfootia" lineages of Wahlenbergia, from the fynbos vegetation of Cape Province are adapted to withstand periodic fires in their environment. Temperate species are often found in open mesophytic woodland or subalpine meadows, while many grow along the banks of streams, but few can tolerate very shady woodland. The majority are upright and herbaceous but some are prostrate or decumbent. There are a few climbers (Campanumoea, Canarina, Codonopsis), but none has any special adaptations for climbing apart from a loose twining habit. None of the genera are truly epiphytic but the climbing genera may occasionally be so, or occur on rocks. Wahlenbergia linifolia is facultatively epiphytic on tree ferns (Cyathea sp.) on St. Helena where it maintains a very precarious existence. Many of the Campanulaceae are caespitose plants of mountain crevices but true rosette species do occur. A few species such as Wahlenbergia pusilla Hochst. ex A. Rich., Craterocapsa tarsodes Hilliard \& Burtt, Campanula tridentata Schreb., C. biebersteiniana Roem. \& Schult., and C. petrophila Rupr. form "carpets", but only a few species of Diosphaera, Asyneuma and Campanula pulvinaris Hausskn. \& Bornm. in Eurasia, or Wahlenbergia pulvillus-gigantis Hilliard \& Burtt of the Natal Drakensbergs can strictly be termed pulvinate. Musschia wollastoni from Madeira is the largest known campanuloid. It is a tall pachycaul plant of the remnant montane laurel forests and cloud-saturated high valleys. It is almost arborescent in form, resembling the giant Lobelia spp. (Lobeliaceae) and has leaves up to about 75 cm long which appear to be adapted for the rapid shedding of raindrops. Heterochaenia spp. on Réunion and the extinct Wahlenbergia burchelii A.DC. of St. Helena almost approach this pachycaul condition.

In almost all cases bellflowers are obligate outcrossers (allogamous) (Gadella, 1964) and their flowers show modifications for this purpose (eg. protandry, incompatibility and a unique pollen-transfer mechanism)(Shetler, 1979b). Autogamy is recorded or suspected in, for example Campanula angustiflora Eastwood and C. griffinii Morin (Morin, 1980a) and in 3 species of Githopsis (Morin, 1983) but many genera probably have the potential to be selffertile at least under cultivation. Self-compatibility has been recorded in Campanula rotundifolia L., Platycodon grandiflorum (Jacq.) A.DC. and in Wahlenbergia berteroi (Hook. \& Arn.). Most species are usually chasmogamous and only very rarely
cleistogamous, eg. Githopsis tenella (Morin, 1983), Heterocodon Nutt. (Munz, 1959) and Triodanis Raf. (Torrey 1843, McVaugh 1945b).

The Campanulaceae is predominantly entomophilous, mostly pollinated by bees but also by flies (incl. carrion and pollen-eating hover-flies), beetles and wasps. In many species there are adaptations which appear to orientate insects to the stigma, eg. coloured pollen and/or stigmatic lobes, and stylar glands as in some species of Wahlenbergia. In several unrelated lineages (eg. Codonopsis cardiophylla and Adenophora forrestii) the inner surfaces of the stigmatic lobes are strikingly white in colour and may have some influence on potential pollinators. Frequently the nectary and Pars superior (top end of the gynoecium) are the same colour or may be patterned in contrasting colours (eg. in Codonopsis). The majority of species in the family have nectar domes which effectively exclude most insect visitors from the nectary except the "legitimate" pollinators, bees, especially the genus Bombus L. (bumblebees). Bumblebees have been seen to take the scarlet nectar of Nesocodon in cultivation. Several Aegean species have extremely large cup-shaped flowers which appear to have evolved several times independently as an adaptation to pollination by the giant violet bees of the genus Xylocopa L. (Hymenoptera-Apioidea) although, in Crete, $X$. violacea L. is also a frequent visitor to the open flowers of Petromarula pinnata (L.) A.DC. Those species without nectar domes are pollinated by wasps, flies or birds. The salverform flower of Merciera appears to be adapted to pollination by long-proboscid flies (Diptera: Tabanidae; Nemestrinidae; Bombyliidae) or hawkmoths (Lepidoptera: Sphingidae) while the evolution of aggregated tubular flowers (as in Feeria and Trachelium) would appear to favour butterfly pollination. In Physoplexis and Phyteuma the peculiar flower morphology is perhaps an additional adaptation to increase pollinator specificity (Yeo, 1993). Flowers also act as refugia for insects which may effect pollination (eg. In Zeugandra, a plant of extreme summer temperatures, the flower has lost its nectary and apparently attracts insects by providing shelter).

In tropical regions, birds such as sunbirds (Aves: Nectariniidae) play a role in pollination. Ornithophily is not as important for the Campanulaceae as it is for the Lobeliaceae which have apparently co-evolved in many parts of the world with hovering birds such as
hummingbirds (Aves: Trochilidae) and with less adept hoverers such as sunbirds (eg. Lobelia in the high mountains of East Africa) or hawaiian honeycreepers (Aves: Drepaniidae). On the Juan Fernández Islands the small-billed Firecrown Hummingbirds (Sephaniodes sp.) may possibly be associated with Wahlenbergeria berteroi Hook. \& Arn. but this requires verification. Canarina has many attributes of a bird-pollinated flower but more observations in tropical Africa are needed to verify a close association with birds. The Canary Island species is visited by Sylvia warblers (Aves: Sylviidae) but these predominantly insectivorous birds are not especially adapted to feed on nectar. It may well be that the Canary Islands were inhabited by nectariferous birds in the distant past. On Madeira Musschia is visted by lacertid lizards (pers. obs.; see also Elvers, 1978) which lap the copious nectar but this may just be a fortuitous habit. In general this genus seems to be adapted for fly pollination (as is Azorina) although, as with Canarina, one cannot rule out an ornithophilous connection in the past.

Genera with capitulate inflorescences such as Jasione and Phyteuma show a remarkable convergence to Globularia (Globulariaceae) and Scabious (Dipsacaceae) while Trachelium and Feeria show considerable resemblance to Valeriana (Valerianaceae). Morphological convergence of vegetative parts is even more prevalent, particularly among chasmophytes and taxa of higher elevations. Good examples of this phenomenon are Diosphaera asperuloides which is remarkably like its namesake Asperula (Rubiaceae) and Campanula aizoon which looks very much like a saxifrage (Saxifraga : Saxifragaceae).

Fruit dispersal in the baccate genera is by birds but observations are lacking for the tropical taxa. In the remaining non-baccate genera the capsule usually remains on the plant and it is the seeds which are directly dispersed. However, some taxa of arid regions have accrescent spreading calyx lobes and/or elaborate spines on the capsule and in these cases the whole capsule, on maturity, may be dispersed, perhaps by animals. On the whole, the seeds of the Campanulaceae do not show any adaptations for animal dispersal. Rather, their smooth testas facilitate limited dispersal by surface runoff of rainfall, aided by wind and gravity. Static-electrical discharge from the seeds probably plays a role in immediate emptying of the capsule. Often, all the seeds in a capsule appear to jump out at once upon the slightest touch.

The seeds of the Campanulaceae show considerable morphological differences, even between closely related species, which suggests that they are strongly adapted, probably in their storage capacity, dormancy and germination requirements and imbibition.

### 6.1.3 Geagraplhical Distribuntiom

The Campanulaceae s.s. which comprise about 64 genera with about $600-1000$ species (depending on the author) are to be found on every continent except Antarctica but their areas of greatest diversity are Eurasia and southern Africa. Lammers (1992a) recognised 46 genera, comprising approximately 950 species, $60 \%$ of which were native to Eurasia and $30 \%$ to Africa. They are very poorly represented in South America and Oceania, and only a little less so in Australasia (in terms of diversity of form), and with only moderate diversity in North America. Approximately $9.4 \%$ of the genera are more or less confined to islands while $35.9 \%$ are confined to mountains. Collectively, these two groups represent $43.8 \%$ of the genera and this figure would be even higher if predominantly montane genera were also included. They are neither dominant nor conspicuous elements of tropical or subtropical vegetation. The largest concentration of species and greatest diversity is in the Mediterranean area and the mountain ranges from the eastern Alps to Iran. In the southern hemishere, Campanula is virtually absent. The most widespread genus is Wahlenbergia which is distributed on all southern continents. All other southern hemisphere genera are within a Wahlenbergia alliance, the greatest diversity and concentration of which is in South Africa, particularly western Cape Province.

Many taxa are probably very ancient and show extreme disjunction, eg. Canarina in East Africa and Macaronesia, while others have relict distribution patterns which are more problematical, Musschia in Madeira, and Azorina in the Azores. Many of the endemic taxa of Eurasia such as Campanula: Sect. Pterophyllum, and of southern Africa such as Craterocapsa have distribution patterns which may reflect the changing palaeoclimatic conditions of the past. Others, such as Petromarula which is probably much older than the 5 million years isolation of Crete from the Greek mainland, may reflect ancient paleogeography. It is clear that the numerous lineages of the Campanulaceae have a
considerable distribution both in time and in space but to date there is no fossil evidence which would indicate their age. By inference of the known fossil record of the Asteraceae and Goodeniaceae the age of the Campanulaceae must predate the Oligocene of 40 million years ago (Muller, 1981). The divergence between what are thought to be tribally related genera within the Asteraceae must date back to at least 60 million years (Turner, 1975; 1977) which suggests a late Cretaceous or early Eocene origin for that family. Turner (1977) has suggested that the Asteraceae may be as old as 100 million years and that the distribution has been influenced by continental drift. Certainly, by the Oligocene the Asteraceae were already well developed. This poses several questions about the age of the Campanulaceae since it has generally been botanical orthodoxy for the Campanulaceae to be strong candidates as possible ancestors of the Asteraceae.

The arrival of the genus Wahlenbergia on St. Helena is probably from some time in the Miocene onwards since the island is of volcanic origin and dates from about 14.5 million years ago (Baker, 1973; Cronk, 1990). Wahlenbergia pollen is reported from the Pliocene of New Zealand (Mildenhall, 1980) while the ancestor of the distinctive group of Wahlenbergia on the Juan Fernández Islands is postulated to have colonised the islands subsequent to the evolution of that archipelago some 5.8 million years ago (Lammers, 1996).

Table 2. Genera of the Campanulaceae - percentage distribution worldwide

| No. | AREA | \% | ENDEMICS | WIDES |
| :---: | :---: | :---: | :---: | :---: |
| 1. | Mediterranean Basin to temperate south--central Asia (excluding Himalayas) and northeast Asia | 47 \% | 29 | 1 |
| 2. | Temperate southern Africa | 18 \% | 10 | 1 |
| 3. | Mimalayas to subtropical Japan, S.E. Asia and New Guinea | 18 \% | 9 | 2 |
| 4. | Macaronesia | 11 \% | 2 | 5 |
| 5. | North America | 10 \% | 5 | 1 |
| 6. | Tropical Africa | 6 \% | 0 | 4 |
| 7. | Madagascar, Mauritius, Mascarene Is. | $6 \%$ | 3 | 1 |
| 8. | Tropical South America | $2 \%$ | 0 | 1 |
| 9. | Australia, New Realand, Pacific Islands | 2 \% | 0 | 1 |



Fig. 2. Gemeralised world distributioms of the colpate amd colporate gemera of the Campamulaceme (tribe Platycodomeae). The colpate gemera are boumded by the dashed limes. These imelude Codonopsis, Pseudocodonopsis, Lepprocodom, Ostrowsisia (O), Echimocodon (E) amd Cyamerrethus (solid black). Colporate gemera are fovmed im those areas boumdled by the dotred limes. The disjumet distributiom of Camarina im Airica amd Macaromesia is imdicated loy arrows. The Asiatic mmd Mimesiam colporate gemera are Platycodom, Campermumoea and Cyclocodors.


Fig. 3. Gemeralised woridd distributions of the parate gemera of the Campamulaceae. Well-marked imsular groups are imdicated by
 gemera: Nesocodors, Heterochaeria amd Berenice. Tribe Campamuleae s.l. (comtimunus limes) มre: $\mathbb{A}=A z o r i n a ; \mathbb{M}=\mathbb{M}$ iusschia.


Fig. a. Gemeralised distributioms of emdemic taxa of southerm Africa. The distributiom of Gumallaea is boumded by the dotted lime amd extemds to Madagascar. The distributiom of Namocodon im Namibia is imalieated by diagomal hatchimg. The distributiom of the momtame gemus Croterocapses is boumdled by the daslied limes. Am isolated populatiom of C. zarsodes om Nit. Imyamgami im Zimmalbwe is imdicated by "C". The distribution of Roella im the Cappe Regiom is boumaled by the comtimunous lime, whille that of Prismatocarpus is imdicated by horizomtall hatchimg. The solid black regiom imdicates the distribuntiom of six small emdemic gemera: Merciera, Microcodon, Rhigiophyllum, Siphocodon, Theilera amal Treichelia.


Fig. 5. Gemeralised distriburioms of emdlemic taxa of the Phyteumeo/Asymeumanalliamce im
 may be reppresemted im the E.Aegeam amd Turkey to Lebamom (imdicattod loy?) by the sale species Compamulla cymbellorial burt its relariomships are as yet onmelear. Physoplexis in the European Alps is imelicated by the dorted limes amol Petromurutbo im Crete by solid blacko The distributiom of Cowapowoula trichocollycima is imalicatred loy dlots amal diashes; while Asymeumus comosififarme isclated im Albamia is imdicaterl by the arrow.

|Fig. 6. Gemeralised distributiioms of selected emdenmic tasa im the Miediterramean Basim. The Trachefiusme alliamce is boumdled by the comtimuous Dime. The westerm portiom is Tracheliusmen s.str. The ? imdlicates maturalized extemsioms to the distribution which also extemds to Macaromesia. The easterm portiom is Diosphaera which extemds to Iram. The
 Syouplayavolro (im parti) is lbourmaled by the dotred limes. The daslhed limes imalicate the disjumet distribuntiom of Coumpomulla:Sect.Pterophylloum. The westerm species is C.primusiifolial amoll the easterm species is C.peregrimu. The solid black ramges represemt Feeria (F) im Moracca amd Sicyocodon (S) im smutherm Amatolia.


Fig. 7. Gemeralised distributioms of selected emdemic taxa im Nortlin Amnerica. The distriburiion of Triodumis is boumded by dots amd dashes. Relict taxa im southerm USA are "Campamula" reverchomis ( $\mathbb{R} \mathbb{E}$ ) im cemiral Texas, "Campanasha" floridama (diotted area) amd "Comepanesle" (Rotanothal) robinsiaue ( $\mathbb{R}$ ) im $\mathbb{F l}$ loridla, amod the ammual Califormia group (CA). The "Comparouth" parryi group (mat shows) of the western moumtaims may be allied to these taxa. "Asymenmma" prenamath wides amal "Comparmula" scouteri (mot shown) of the westerm moumtaims may lbe allied ta "Comonpomesla" piperi of the $\mathbb{O l y m p i c}$ Mits. ( $\mathbb{P}$ ), "Campacoula" ausitus (harizamtal hatching) amd Campanaulastrume (vertical hatchimg), disjumet im the east. The swamp harebells of the "Companeula" aparivoides anliamce (which may also imclude the southerm lnarebells gith Edempapasula" divaricatco alliamce)

 limes.

The following major centres of diversity are described in more detail:
6.1.3.1 Mediterramean $\mathbb{B a s i m}$ to temperate south-cemtrall Asial (exclualimg Himalayas) amd mortheast Asia.

The greatest diversity of taxa is to be found in and around the Mediterranean Basin, the European Alps and the mountains from North Africa to the Balkans, from south-central Asia in the mountains of the Caucasus region, and from Anatolia to Iran and Afghanistan. Here a number of campanuloid lineages have diverged, probably as a result of tectonic processes and isolation, although pollinator selection pressure is probably also highly significant especially at higher elevations. Many of these lineages are distinct enough to be placed in separate sections within the genus Campanula although some authors have recognised a number of more or less monotypic genera, eg. Theodorovia Kolak., Sachokiella Kolak, Pseudocampanula Kolak., Hemisphaera Kolak., Annaea Kolak., Mzymtella Kolak., Hyssaria Kolak., Gadellia Serdyukova \& Schulkina, Sergia Fed., Cryptocodon Fed., Cylindrocarpa Fed., etc. The last three generally have found greater acceptance, probably quite simply because they were published in Flora URSS (1957) which is more widely available in its English translation. There is no doubt however that Central and Southern Asia has been and is a major centre of campanulaceous evolution. Despite the questionable status of some of the forementioned taxa there are some very distinctive genera and forms from this region such as Ostrowskia, Michauxia, Zeugandra Davis and the diminutive Muehlbergella Feer.

Further west are subcentres of high diversity in the following regions: Carpathians, where relict species such as Campanula carpatica Jacq. (Subsect. Rotula Fed.) and Phyteuma tetramerum are still to be found on old eroded mountain blocks; the Aegean islands, where isolation and unique conditions have given risen to a mosaic of distinctive species such as those of Sect. Quinqueloculares (Boiss) Phitos; the Balkan peninsula, where Campanula lineages have diverged in a way similar to those of the Caucasus to produce genera such as Symphyandra, Edraianthus and Petkovia Stef. as well as many species of Campanula s.s. (such as C. papillosa Hal.) which have unique suites of characters; the European Alps, where the more ancient "isophylloid" (the "isophylla" group is a well-defined group of taxa
exemplified by C. portenschlagiana, C.poscharskyana, C.pyramidalis, etc. of the western Balkans and Italy) and "asyneumoid" (allied to Asyneuma and species such as Campanula trichocalycina) ancestral taxa have led to genera such as Codonosphaera Buser, Phyteuma and Physoplexis (and to Petromarula in the south in Crete); and in southern Spain and the mountains of North Africa, where ancient "rapunculoid" stock have given way to more advanced forms such as the the Campanula arvatica Lag. group, the "Oreocodon" group exemplified by C. mollis L., and the subgenus Roucela. Of course, this is a rather simplified picture because it is known that many of these ancient lineages once extended far beyond their present distribution. For example, the nearest living relative of the rapunculoid $C$. primulifolia Brot. of southern Portugal is C. peregrina L. from Turkey, Cyprus and Lebanon. The distribution of the diminutive genus Brachycodon suggests a Tethyan association and in general morphology and ecology comes remarkably close to the Californian genus Githopsis. Similarly C. cymbalaria Sm. (Sect. Saxicolae (Boiss.) Charadze) from western Anatolia may have close connections with the "isophylla" group which itself appears to be distantly connected to the cordilleran bellflowers of western North America exemplified by C. piperi T.J.Howell. C. prenanthioides Dur. of W. North America is remarkably similar to Asyneuma and was placed in that genus by McVaugh (1945a). In addition, genera such as the rapunculoid genus Popoviocodonia should be investigated for relationships with North American taxa such as Triodanis.

### 6.1.3.2 Temperate southerm Africa and the Southerm Hemisphere

The highest diversity of Campanulaceae in the Southern Hemisphere is from the elevated highlands of the eastern Cape Province west to Cape Peninsula and the Karroo, and north, through the Drakensbergs to the Chimanimani Mountains of eastern Zimbabwe and to the elevated interior region of Namibia. The dominant vegetation of southern Africa was forest in the past and the present shrubby vegetation has become widespread due to the onset of a Mediterranean type of climate. The Campanulaceae are most diverse in the western Cape and the number of endemic taxa increases to the west within this small subregion. There are also some unique taxa such as Craterocapsa in the more moist mountains facing the Indian Ocean. Many of the Cape taxa are shrubby perennials and grow on poor sandy soils. They frequently have an ericoid appearance with narrow imbricate leaves which reduce
transpiration. The family has speciated considerably in this region. Many are annuals but divergence appears to be the result of selection for more specific pollinators or for changes in dehiscence mechanism of the capsule. One of the best examples of this is to be seen in Merciera which has an indehiscent capsule, a reduction to a single locule and very few ovules. Namacodon from Namibia has unique septicidal dehiscence and appears to be an offshoot from Prismatocarpus L'Herit, as does Gunillaea which is found in Madagascar, Zambia and Zimbabwe. Mauritius possesses the sole genus Nesocodon which, though probably closest to Heterochaenia A.DC. on Reunion, has a flower and form reminiscent of Roella and Craterocapsa. It shares a cumin-like smell from the leaves with the latter genus but its dehiscence mechanism is similar to Wahlenbergia. Heterochaenia and Berenice Tul. on Reunion have probably been long isolated from the main line of Wahlenbergia evolution and probably are not too closely related to one another. Berenice may well be closest to the wide-ranging Cephalostigma A.DC., which is itself very close to Wahlenbergia. In addition to the endemic taxa of the Indian Ocean, there are unique taxa on St. Helena in the Atlantic Ocean and on Juan Fernandez Islands in the Pacific Ocean off the coast of Chile, all within a Wahlenbergia alliance, but further investigation may warrant separate generic status for them. It is known that the species of Wahlenbergia on Juan Fernandez have a chromosome count unique within the genus (Sanders \& Rodriguez, 1983; Spooner, et al., 1987; Crawford, et al., 1990). Their morphology is also a little at odds with the St. Helena group and they may be closer to a small group of 3-valvate wahlenbergioids from Peru and Ecuador, or possibly with the New Zealand species.

### 6.1.3.3 Himalayas to sulbiropical Japam, S. $\mathbb{E}$. Asia amd New Guimea

The diversity of taxa declines further east through the western Himalayan region but there is a second subcentre of high diversity in the eastern Himalayas and southwestern China (Yunnan) where alpine and subalpine genera such as Codonopsis and Cyananthus occur. Other genera such as Peracarpa J.D.Hooker \& T.Thompson, Cyclocodon and Campanumoea extend further south through the mountains of Indonesia as far as New Guinea. These genera are pivotal in our attempts to understand the history of the Campanulaceae in this region and their radiation is no doubt intimately linked to the orogenic processes which led to the uplift of the Himalayan mass. Many of the species and
genera such as Echinocodon Hong and Homocodon Hong are highly localised and/or show adaptations for specific pollinators. This subcentre is distantly connected to western North America where the related endemic genus Heterocodon occurs. The Himalayan-W.North American disjunction can be seen in many other plants and animals.

### 6.1.3.4 Macaromesia

To the west of the main mass of Eurasian taxa there are outliers in Macaronesia (Cape Verde Islands, the Canary Islands, Madeira and the Azores), some of which, such as Azorina, and the laurisylvan and cliff-dwelling Musschia, may have even more ancient connections with the Tertiary floras of Europe and with southern Africa. Certainly Canarina has far-flung connections with tropical Africa and possibly with Asia, a distribution pattern which is repeated often by the floral elements of Macaronesia (eg. Erica L. (Ericaceae) and Aeonium Webb \& Berth. (Crassulaceae). However, with only $11 \%$ of the genera occurring here, two of which are probably palaeoendemics and the rest widely distributed (and probably recent arrivals), Macaronesia displays only a remnant of its former Tertiary flora making it difficult to assess its importance in the evolution of the family. Campanula jacobaea C.Smith from the Cape Verde Islands is closely related to the $2 \mathrm{n}=28$ group of North African campanulas (ie. "Oreocodon") but is shrubbier and shows considerable insular evolution.

### 6.1.3.5 Nortlin America

Most of the taxa occurring in North America are endemic to that continent. Although current convention places some of the species in wide-ranging genera such as Campanula, the situation is more complex and several rather distinct lineages can be discerned, some of which may deserve generic status. There are several relict taxa in southern North America while the more recently evolved forms appear to be linked to the evolution of the western mountain chains. The best known species is Campanulastrum americanum (L.) Small which, on balance, shows features most similar to the "isophylla" group in Europe and to some extent also to Asyneuma and the C.piperi group. However, it possesses so many unique characters that several authors have maintained it in a distinct genus Campanulastrum. The California annual species too cannot be easily fitted into any well-known sections of Campanula although they appear to resemble relict taxa of southern United States such as

Campanula reverchonii and Campanula floridana. Some of the marsh-bellflowers or swampbells such as C. aparinoides Michx. resemble Adenophora (some species of which have a preference for damp habitats) and it may well be that there is an amphiatlantic link as well as an Asia - North American one. This latter group also may be allied to Campanula divaricata, as well as the enigmatic C.robinsiae of Florida which has occasionally been placed in a separate genus, Rotantha Small. Other taxa such as Triodanis and Githopsis Nutt. probably are not as closely related to Legousia as was once thought but evolved from a common ancient stock which spread into North America at an early stage in the evolution of the family. Triodanis may be related to the Asian Popoviocodonia Fed. which has also reputed to show similarities with the North American C. aparinioides Pursh. The widespread genus Campanula s.s. is probably the most recent arrival in North America, mostly in Alaska and the Arctic regions. The harebells of the Subsect. Heterophylla have spread over the continent and radiated to some degree so that many authors prefer to differentiate several species of harebells. However, the North American radiation of the harebells in no way matches the situation to be found in Europe within that subsection.

## 6. 2 The $\mathbb{C}$ mpamulaceae im Comiext

### 6.2.1 Classificatiom of the Higher Taxa

The Campanulales (sensu Cronquist, 1981) has had a varied history as far as its circumscription is concerned especially since its recognition as an order by Lindley (1833) but there is no doubt that it has its most immediate alliances within the Asteridae (sensu Cronquist, 1981; Takhtajan, 1987). Lammers (1992a) has given an extensive review of the classification of the Campanulales so only the essential details with respect to the Campanulaceae are elaborated here. See also Brummit (1992) for a detailed comparison of eight systems of classification. The broadest view of the order is by Wagenitz (1964) who included the Campanulaceae (subfamilies Campanuloideae, Cyphioideae, Lobelioideae), Sphenocleaceae, Pentaphragmataceae, Goodeniaceae, Brunoniaceae, Stylidiaceae (subfamilies Donatioideae, Stylidioideae), Calyceraceae and Asteraceae (subfamilies Asteroideae, Cichorioideae). Takhtajan (1980, 1983) removed the Asteraceae and the Calyceraceae to the Asterales and Calycerales respectively and united the subsequent three orders in his superorder Asteranae within the subclass Asteridae. Brunoniaceae and Pentaphragmataceae together with Sphenocleaceae were treated as subfamilies of the Goodeniaceae and Campanulaceae respectively but the Donatioideae was raised to family rank. These three families were grouped into two suborders, the Goodeninae (Goodeniaceae) and the Campanuliinae (Campanulaceae, Donatiaceae, and Stylidiaceae). The Asteraceae and Calyceraceae were removed because of their possession of involucrate capitulate inflorescences (but see Jasione, Edraianthus), 1-loculed ovaries (see Merciera) and solitary ovules. In a more recent revision (1987) the subfamilies of Campanulaceae were raised to family rank (ie. Pentaphragmataceae, Sphenocleaceae, Campanulaceae, Cyphiaceae, Nemacladaceae, Lobeliaceae and Cyphocarpaceae). Cyphioideae s.s. was kept within the Lobeliaceae while Brunonioideae was raised to family rank within the order Goodeniales.

Cronquist (1981, 1987), unlike Takhtajan, dissociated the Calycerales and Asterales from the Campanulales. Calycerales were considered to be allied to Dipsacales, and Asterales to

Rubiales. Thorne (1968, 1976, 1977, 1981, 1983) also dissociated the Asteraceae and Calyceraceae from the Campanulales. In his scheme Calyceraceae were placed in the Dipsacales while the Donatiaceae and Stylidiaceae were considered to be close to Saxifragaceae (Rosales) and thus removed from the Campanulales. Dahlgren (1975a, 1977, 1980, 1983,) and Dahlgren et al. (1981) also removed Calyceraceae and Asteraceae to Calycerales and Asterales respectively and excluded Donatiaceae and Stylidiaceae to the order Stylidiales (Dahlgren, G. 1989ab). The Brunoniaceae and Goodeniaceae were also removed from the Campanulales to their own order, the Goodeniales and thus Dahlgren's order Campanulales became equivalent to the arrangement of Schönland (1889, see below). These removals were based largely on the distribution of chemical characters, principally the absence of iridoid compounds (monoterpenoid cyclo-pentanoid lactones) from the Campanulales s.s. (Jensen et al., 1975; Dahlgren, 1977, 1983; Dahlgren et al., 1981).

Lammers (1992a) recognised three characters which could be used to separate the Campanulales and Asterales. These were: multinucleate tapetal cells, the absence of endosperm haustoria, and the mevalonate pathway characterise the Asterales, while binucleate tapetal cells, terminal endosperm haustoria, and no mevalonate pathway characterise the Campanulales. The inclusion of the Pentaphragmataceae in the Asterales based on rbcL data necessitates a revision of this scheme. Lammers (1992a) initially included twelve families in the Campanulales for his review, viz.: Asteraceae, Brunoniaceae, Calyceraceae, Campanulaceae, Cyphiaceae, Donatiaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae, Sphenocleaceae and Stylidiaceae. He identified a core group of the following five families: Campanulaceae, Lobeliaceae, Cyphiaceae, Pentaphragmataceae and Sphenocleaceae. He concluded that only nine families should be included in the order Campanulales, viz.: Asteraceae, Calyceraceae, Campanulaceae, Cyphiaceae, Goodeniaceae (including Brunonia), Lobeliaceae, Menyanthaceae, Pentaphragmataceae and Sphenocleaceae. Donatiaceae and Stylidiaceae were assigned provisionally to a position in or near the Ericales. The invaginating hairs were recognised by Lammers (1992a) as being the only apomorphy which would distinguish the Campanulaceae from the other families within the Campanulales complex. He suggested that the Campanulales originated near the ancestry of the Asteridae, in the complex of
families comprising the Cornales and woody Saxifragales (Thorne, 1976; Dahlgren, 1980). De Candolle (1830) and De Candolle (1839) treated the Campanulaceae as distinct from the Lobeliaceae, as did Endlicher (1841), Baillon (1880, 1886), Wettstein (1924), Hutchinson (1973), Dahlgren (1983) and Takhtajan (1987). In contrast these two lineages were treated as subfamilies of the Campanulaceae by Bentham (1876), Dalla Torre \& Harms, 1900-1907, Bessey (1915), Wagenitz (1964), Cronquist (1981) and Thorne (1992a/b).

All families of the Asterales-Campanulales complex with the exception of the Asteraceae: Barnadesiinae share a unique 22 kb inversion in the chloroplast genome (Jansen \& Palmer, 1988; Palmer, et al., 1988). This suggests that the Barnadesiinae are the most primitive members of the complex. Extensive rearrangements of the chloroplast genome distinguish Campanulaceae and, to a lesser extent, Lobeliaceae but have not been noted in other taxa (Lammers, 1992a). Cladistic analyses (Downie \& Palmer, 1992; Olmstead \& Palmer, 1992) indicate the following: Calyceraceae and Goodeniaceae form a clade that is the sister group of the Asteraceae. Menyanthaceae form the sister group of these three families. This is supported by rbcL evidence (Michaels et al., 1993; Olmstead et al, 1992, 1993) and by restriction site comparisons of the cpDNA inverted repeat (Downie \& Palmer, 1992). Collectively these families form what has been termed the "asterad" clade. The Campanulaceae and Lobeliaceae (the "campanulads") form a sister clade of the asterads. The asterad-campanulad major clade was found to be a sister group to a major clade comprising the Apiaceae and Araliaceae ("apiads") and the Adoxaceae, Caprifoliaceae, Dipsacaceae, Valerianaceae and Viburnaceae ("dipsacads"). Many smaller families such as Pentaphragmataceae and Sphenocleaceae were not included in these analyses. Relationships at this level are also supported by restriction site analysis of the cpDNA inverted repeat (Downie \& Palmer, 1992). Interestingly, the rbcL data placed Corokia A. Cunn. (Cornaceae) with the asterads near the Menyanthaceae which would lend some support to Lammers' (1992a) contention that the origin of the Campanulales might be near to the CornalesSaxifragales (Chase et al., 1993; Michaels et al, 1993; Olmstead et al, 1993). However, Corokia's placement in the Cornaceae is still in some doubt (Eyde, 1966). Engler (1930) included Corokia with Berenice in the tribe Argophylleae (Saxifragaceae: Escallonioideae)
but this association seems rather erroneous since Berenice seems to be most easily accomodated in the Campanulaceae.

Cosner, Jansen $\&$ Lammers (1994) examined the cladistic relationships of the Campanulales based on $r b c \mathrm{~L}$ sequences. The results show very strong support for a clade comprising Campanulaceae/Cyphiaceae/Lobeliaceae. This is in accord with their possession of articulated laticifers (Lammers, 1992a). The Cyphiaceae were found to be paraphyletic. Most significantly, the Lobeliaceae and the Campanulaceae were not found to be sister taxa. The clade comprising the Campanulaceae plus the genus Nemacladus Nutt. were found to be a sister group of the Lobeliaceae and collectively these three taxa formed a clade which was a sister group of the Cyphocarpaceae. The "Nemacladaceae", particularly the genus Parishella A.Gray is palynologically close to the genus Cyananthus of the Campanulaceae (Dunbar, 1975a). Despite this, the monophyly of a greater Campanulaceae (include. Nemacladus) was not well supported in bootstrap or decay analyses. At the next two levels of the cladogram the Cyphiaceae and the Stylidiaceae (basal clade) were found to be the next sister groups respectively. Floral development studies of the Stylidiaceae support an association in or near the Campanulales (Erbar, 1992; Leins, 1964) and palynologically the Stylidiaceae (include. Donatiaceae) show affinities with the Campanulaceae (Erdtman, 1952). Pentaphragma Wall. ex G.Don was found to be closer to the Asterales and Sphenoclea Gaertn. to the Solanales. It was suggested that both be treated as monogeneric families.

Gustafsson \& Bremer (1995) also analyzed morphological and chemical data in order to establish the relationships of the Asteraceae with those advanced angiosperm families which are considered to be most closely related, ie. the Calyceraceae, Campanulaceae and Goodeniaceae. Together with the Lobeliaceae, Cyphiaceae, Cyphocarpaceae and Nemacladaceae these families constitute the most consistently recognised families of the Asterales-Campanulales complex. Also considered in their analysis were the Brunoniaceae, Pentaphragmataceae, Sphenocleaceae, Stylidiaceae, and Donatiaceae and other putatively related families. The results indicate that there is a monophyletic group of 14 families comprising those mentioned above plus the Menyanthaceae, see Fig. 9 below. The inclusion
of the Menyanthaceae in the Asterales based on $r b c \mathrm{~L}$ data was well substantiated by this data set.

This ordinal group which was called Asterales by Gustafsson and Bremer is supported by four characters, two of which are homoplastic. Within the order there are two major clades. Menyanthaceae, Asteraceae, Calyceraceae, Brunoniaceae and Goodeniaceae form one comparatively well-supported clade and the other nine families form the other which is less well supported and defined by embryological characters. Strongly supported was a clade which included the Campanulaceae and its closest allies. The Campanulaceae was shown to be a sister group of the subclade which comprised the Nemacladaceae, Cyphiaceae, Cyphocarpaceae and Lobeliaceae. The Lobeliaceae was a sister group of the Cyphocarpaceae. Collectively, these families, plus the Pentaphragmataceae and Sphenocleaceae would have comprised the formerly-recognised Campanulaceae s.l. but were found to be a sister group of a clade which included the Sphenocleaceae, Donatiaceae and Stylidiaceae. The Sphenocleaceae as a sister group of the Stylidiaceae and Donatiaceae was a surprise and contradicted the rbcL findings of Cosner, Jansen \& Lammers (1994). Basal to this major clade was the Pentaphragmataceae which formed the next monophyletic group and is considered to be rather distant from the Campanulaceae. Thus, from these initial cladistic studies, the treatment of the Campanulaceae as a separate family from the Lobeliaceae is strengthened. Since the Cyphocarpaceae formed a sister group to the Lobeliaceae the Cyphiaceae would, under Gustafsson and Bremer's scheme, be paraphyletic if it was included in a broad concept of the Cyphiaceae (as was done by Lammers (1992a) on a provisional basis) because it would then not include the Lobeliaceae. In contrast to the $r b c \mathrm{~L}$ studies, Corokia did not nest within the Asterales complex.

For this study Gustafsson \& Bremer's data were reanalysed phenetically and the results are given below. The immediate usefulness of Bremer and Gustafsson's study is that it highlights certain families which may be useful as outgroups in further cladistic studies. The familial relationships of the Campanulaceae are thus now reasonably well established although their origin remain obscure. An origin near the the Cornales-Saxifragales has been suggested (Hutchinson, 1959; Lammers, 1992a) or perhaps in or near the Cucurbitales
(Hutchinson, 1973) and there is a remote likelihood of a connection with the Gentianaceae (Hutchinson, 1969), Solanales (Cronquist, 1988) or Passiflorales (Hutchinson, 1973). At present, the origin of the family is purely conjectural and it will require more molecular analyses of both the chloroplast and nuclear genomes to give clues as to the ancestral group from which it evolved.


Fig. 8. Campamulales/Asteralles clade based on rbclu amalysis of dataxa (modified fromm Cosmer et al., 1994).


Table.3. Selected classifications of the Campanulales (1839-1995)

| A Summary of Selected Classifications of the Campanulales |  |  |
| :---: | :---: | :---: |
| De Candolle, 1839 Campanulaceae (separate from l ibtilinene) | Endlicher, 1841 <br> Campanulinae <br> Brumoniwecte <br> CRoodeniacelle <br> Lubeliaceac <br> (inimpiniliceat: <br> Songuticat <br> Styliteae: | Benth. \& Hooker, 1873-76 Campanales <br> Stylideae <br> Coodenopiene <br> (2impunilaceate |
| Baillon, 1880-1886 <br> Campanulacées <br> Strie des (AMmpantes <br> Seric des Sphenoclea <br> Serie des lobetie <br> Siril des C Splia <br> Setile der C Coodenli <br> Strile dee l frimanta <br> Strile des Pizylimene | Bessey, 1915 <br> Campanulales <br> (*impannlaceae <br> CYoodenieceee <br> Stylifiaceac <br> © *) yceractal | Wettstein, 1924 <br> Symandrae <br> (A)mpanulaceas <br> ©yphiatecae <br> Liobeliaceac <br> Croodenimeene <br> Silifidiaceae <br> Brumoniaceat <br> Compositae |
| Wagenits, 1964 <br> Campanulales <br> (iampininlicilat <br> Sphienoclenceae <br> Penimphrigmatimcele <br> Coordeniacene <br> Brinomilicelie <br> Stylidiameat <br> (Malyceractie <br> Compositie: | Hatchinson, 1973 <br> Campanales <br> (innjpinulactar Kobeliaceae. | Cronquist, 1981 <br> Campanulales <br> Silicnocleacele <br> Pentaphragmaticelte: <br> (Vinmpinilactas <br> Sty fidiaceae <br> Bonatinceac <br> Brunoniliceat: <br> CWoddenimcene |
| Dahigren, 1983 Campanulales <br> Pentaplrigmanaceack <br> Campanilaceac <br> *obliaiceate | Takhtajan, 1987 <br> Campanulales <br> 18nta phingimataceae <br> splectaeltacere <br> (6an mannilaceat <br> Cyphtaceact <br> Nematindaceae <br> Kobelinceite <br> \$yphocimesaceac | Thorne, 1992 <br> Campanulales <br> Memyanthaceae <br> Pentaphragmataceae <br> Sphenacleaceac <br> (Ampannlacears <br> Gododemaceac |
| Lammers, 1992 C ampanulales <br> Asteraceat: <br> Calycetriceat <br> Goodeniaceat <br> Menyunliacear: <br> Campanulacear <br> (yphiaceae <br> 1, Whetraceat <br> Sphenncleaceas <br>  | Cosner et al., 1994 Campanulales <br> Lobleltaceric <br> CAmpinnlite a! <br> (yyhatea. <br> Stifidiaeeat | Custafs. \& Bremer, 1995 <br> Asterales-C ampanulales <br> Menyanthiceas ( 4 ) <br> 4steraceae ( $\langle$ ) <br> (alyceraceit (4) <br> (Eoodeniaceat (4) <br> Brinonisceae (全) <br> Pentaphramatateat (ㅇ) <br> Sphenocleaceat ( $($ ) <br> Atylidaineat (4) <br> Donatiaceat (ㅇ) <br>  <br> (yphocarpaceac ( $($ ) <br> L. Ohellaceae (C) <br> ©yphaceat (5) <br> Nemachadaceae $(\mathbb{s})$ |

"One cam of course attempt to analyse it, 10 fit it into this system of thought or that, but by its very nature it is bourd to cause a diversion in the neatly-fitted jigsaw. In the end the diversion becomes the deviation that wrecks the system. No wonder those who create systems fear it like the devil."

Neil Gunn, 1956
"The Atom of Delight"

### 6.2.2.1 $184 t h$ amd $194 t h$ Cemturies

Although a few species of the family Campanulaceae are mentioned in pre-Linnaean literature, classification, as with the majority of plant families, really begins with Linnaeus (Carl von Linné, 1707-1778). Linnaeus believed that species were uniquely created, so evolution did not play a role in his system. Linnaeus's system of classification of plants (1753) was artificial because it was influenced by the essentialistic concept of Aristotelian naturalness whereby organisms are placed together in a group only if they embody the essence of the group. Essential characters were those considered to be important to the function of an organism such as reproductive organs. Thus Linnaeus held a priori assumptions of the importance of sexual parts of the flower. The arrangement of Linnaeus's sexual system was essentially a dichotomous one based on the principle of logical division of Theophrastus (c. 370-287 B.C.). However, in fairness, he felt that the existing information and understanding of his time were inadequate for the production of a natural system, and expected his system to be eventually superseded by one (Cronquist, 1988). Thus we can observe that the species recognised in Species Plantarum were also arranged on the basis of overall resemblance (phenetic naturalness) but Linnaeus's concept of the genus was a broad one (Gadella, 1966; Stearn, 1957). In the first edition of 1753 he recognised just 43 species of the Campanulaceae which he placed in 4 genera (Campanula, Phyteuma, Roella and Trachelium) many of which would today be unanimously considered worthy of separate generic status (see Table 4). Genera such as Campanula which were established more than two centuries ago for a small number of species have become depositories for the dumping of newly discovered species which do not obviously fit within segregate genera. Thus the genus Campanula has grown by accretion around its original core.

Table 4. A comparison of species recognised by Linnaeus (1753) with their modern binomials

| Limnaeus's species | Modern treatment |
| :---: | :---: |
| Campanula graminifolia L. | Edraianthus graminifolius (1.) A. DC. |
| C.canariensis li. | Canarina canariensis (1.) Vatke |
| C. speculum 1. | Legousia speculum-veneris (1.) Chaix |
| Cpentagonial. | L.pentagonia (1.) Druce |
| C.capensis l. | Wahlenbergia capensis (1.) A.DC. |
| C. H ederaceal 1. | W. hederacea (1.) Rehb. |
| Phytenma comosal. | Physoplextis comosum (1.) Schur |
| P.pinmatal 1. | Perromarula pinnata |

Alphonse de Candolle (1806-1893), in his monumental treatise Monographie des Campanulées (1830), provided a landmark in the taxonomic treatment of the Campanulaceae s.str. which has served as the basis for all subsequent workers on the family, despite the fact that he only recognised 334 species in 21 genera (see Table 5). His system may be considered as an attempt at a "natural system" based on overall resemblances in contrast to the usage by Linnaeus associated with Aristotelian principles and a belief in Special Creation (Davis \& Heywood, 1963). De Candolle's concept of the genus is especially important and cannot be ignored in any study of the Campanulaceae. In the delimitation of genera, de Candolle did not recognise such units merely because they could be separated by arbitrary characters. To him, a genus was a natural unit, recognisable as such by its own ensemble of features (McVaugh, 1948). He was fully aware that the genera of the Campanulaceae are interrelated in a reticulate pattern and that the ill-defined genus Campanula constitutes the core around which are a number of satellite genera (eg. Symphyandra, Legousia, Michauxia, Adenophora) which are all closer to the core genus than they are to each other. It was, and still is, easier to define which species do not constitute the genus Campanula than those which do. The situation is paralleled by Wahlenbergia and its satellite genera. De Candolle used morphological characters to classify the Campanulaceae and, generally speaking, these served his purpose well. Most of the major divisions recognised today, and even to the generic level, are based on criteria recognised by De Candolle, and subsequently by Boissier, Schönland, Fedorov and almost
all students of this family. One morphological character which de Candolle recognised as of major significance was the method of capsule dehiscence. Using this character he divided the bellflowers into two subtribes, a treatment which was also largely congruent with the separation of Northern and Southern Hemisphere groups of genera (see Table 5).

Table 5. Classification of the Campanulaceae (De Candolle, 1830)

| SUBTRIBE I (WAHL ENBERGEAE) | SUBTRIBE II (CAMPANULEAE) |
| :---: | :---: |
| Capsule with apical (valvate) dehiscence | Capsule with lateral (porate) dehiscence |
| Campanumoea (berry) <br> Canarina (berry) <br> Cephatostigma <br> Codonopsís <br> Jasione <br> Iightfootial'Her. <br> Microcodon <br> Playcodon <br> Prismatocarpus <br> Roella <br> Wahlenbergia | Adenophora <br> Campanula <br> Merciera A. DC. (indehiscent) <br> Michauxia <br> Musschia <br> Petromarula Vent. ex IIedw. f. <br> Phyteuma <br> Specularia A.DC. <br> Symphyandra <br> Trachelium |

Certainly such a division is convenient in the delimitation of taxonomic groups but it may not reflect an ancient split in the evolution of the family. De Candolle's system does not have a structure other than that dictated by overall resemblance. Had he been able to use pollen characters, the association of the colpate/colporate Campanumoea, Codonopsis, Platycodon, and Canarina with the porate Roella, Wahlenbergia and Microcodon, etc. would have immediately been thrown into question. Similarly, had he studied the nature of poricidal dehiscence and capsule ontogeny, the association between Musschia, Merciera and the other genera in this second subgroup would have been deemed unnatural. At a lower level in the taxonomic hierarchy De Candolle grouped species of the genus Wahlenbergia into his Section Nesophylla A.DC. ("island-lovers") based solely on their living on remote islands and shrubby habit. Such a grouping can have profound influence on biogeographic and evolutionary theories for the family. This section included Wahlenbergia species of Saint Helena and Ascension, the Juan Fernandez Islands, W. ensifolia A.DC. (later transferred to the genus Heterochaenia) and several shrubby
perennial species from South Africa. Similarly, the genus Symphyandra may be polyphyletic since it includes species united solely on the possession of connate anthers, a character state which appears to have been expressed independently within several lineages of the Campanulaceae. Merciera seems closely allied to Roella and Prismatocarpus and is clearly out of place within De Candolle's subgroup. It possibly should be with the other South African Wahlenbergeae or the endemic Moroccan genus Feeria Buser despite its indehiscent capsule and Trachelium-like appearance. In Musschia which is an endemic of Madeira, dehiscence is by means of lateral slits, which are probably not homologous with the porate dehiscence of all the other genera in Subtribe II. In Jasione, the capsule is valvate which is probably the basis for its association with Wahlenbergia. However, it its floral morphology it approaches some sections of Campanula. Furthermore, the biogeography of Jasione suggests a closer alliance with Campanula. Its relationships with Feeria have not been clarified nor its relationships with Trachelium. These, then, are just a few of the problems raised with De Candolle's classification. Clearly the family displays homoplasy in many characters which has led to the erection of paraphyletic and polyphyletic taxa, many of which are clearly not justifiable.

In 1839 a summary of all known species was made in the Prodromms Systemnatis Natunralis regmi Vegetabilis (Auguste de Candolle, 1824-1841; completed by Alphonse de Candolle, 1841-1873) but the basic subdivision of the family remained largely unchanged except for the separation of Merciera into a monotypic subtribe, the Merciereae. The compilations of Endlicher (1836-1840), Bentham (1876), and Schönland, (1889-1894; 1900) follow de Candolle's work without any important changes (McVaugh, 1948). Endlicher's "Gemera Plamtarum" followed the Monographie essentially without any change in generic concept (Table 6).

Bentham, (1876) divided the Campanulaceae into three subfamilies, the Campanuloideae, Lobelioideae and Cyphiodeae. Although not a thorough subdivision of the bellflowers, the Campanuloideae were subdivided as shown in Table 7. Petromarula was submerged in Phyteuma by Bentham and by Schönland. The only fully established subdivision of the Campanuloideae was that of Schönland (1889-1894) which generally followed Bentham
and Hooker. Schönland's system was the one most frequently adopted until the modern period. His classification is shown in Table 8.

Table 6. Classification of the Campanulaceae (Endlicher, 1836-1840)

| Subtribus I. Sasioneas |
| :--- |
| Sasione |

Schönland basically followed de Candolle's arrangement but he merged de Candolle's subtribes Merciereae and Wahlenbergeae in his subtribe Wahlenberginae. The subtribe Campanulinae was defined mainly by laterally dehiscent or indehiscent capsules (rarely berries), the Wahlenberginae mainly by apical dehiscence by valves or opercula, rarely berries, and the Platycodinae by the carpels which are as many as,and alternate with the
calyx lobes. In the other two subtribes, the carpels are usually fewer than the calyx lobes or, if isomerous, in an opposite position. The genera within each of Schönland's three subtribes are thus comparatively homogeneous in floral structure but show diversity in fruits and dehiscence. There are also noticable anomalies, perhaps because he included indehiscent fruits in his definitions of two of the subtribes and that his knowledge of lateral dehiscence was scanty. For example, the inclusion of Canarina and Ostrowskia in the subtribe Campanulinae. Ostrowskia has lateral dehiscence, albeit of a unique kind, but Canarina has baccate fruit and is clearly at odds with the rest of his subtribe.

Table 7. Classification of the Campanulaceae (Bentham \& Hooker, 1876)

| Tribus III. CAMPANULEAE |  |
| :---: | :---: |
| Jasione (12) | Rhigiophyllum Hochst. (1) |
| Cephalostigma (7) | Merciera (4) N N |
| Lighyfootia (40) | Siphocoalon (1) |
| Wahlenbergia (80) | Sphenoclea (1) |
| Section Edraiantha | Musschia (2) |
| Cervicina | Michauxía (4) |
| Streleskia Hook. r. | Phyteuma (50) |
| Microcodon (4) | Section Sjuntoma C. Don |
| Platycodon (1) | Hedraianthum C., Don |
| Heterochaenia (1) | Podanthus C., Don |
| Leptocodon (Hook. f.) Lem. (1) | Campanula (230) |
| Codonopsis (12) | Campanula (230) |
| Campanumoea (5) | Section Melium |
| Canarina (1) | Eircodon |
| Peracatpa (1) | Specularia (8) |
| Pentaphiragma (3) | Adenophora (15) |
| Roella (11) | Symphyandra (7) |
| Prismatocatpus (15) | Section Melanocalyx |
| Githopsí! (1) | Sericodon |
|  | Trachelium (5) |

Table 8. Classification of the Campanulaceae (Schönland, 1889-1894)

| Tribe CAMPANULEAE |  |  |
| :---: | :---: | :---: |
| Subtribe Campanulinae | Subtribe Wahlenberginae | Subtribe Platycodinae |
| 1. Aidenophora | 11. Campanumoea | 28. Microcodon |
| 2. Cimmanuta | 12. Cephatostigma | sect. Eumicrocodon A. DC. |
| sect. Melium Tourn. | 13. Codonopsis | sect. Caelotheca A.DC. |
| sect. Rapunculus Boiss. | 14. Cyananthus Wall. | 29. Musschia |
| 3. Canarina | 15. Githopsis | 30. Platycodon |
| 4. Heterocodon | 16. Hedracanthus A.DC. |  |
| 5. Michauxia | 17. Heterochaenia |  |
| 6. Ostrouskia | 18. Jasione |  |
| 7. Peracarpa | 19. Leptocodon |  |
| 8. Phyteuma | 20. Lightfootia |  |
| sect. CVİndrocarpa Rgl. | 21. Merctera |  |
| sect. Hedranthum C. Don | 22. Prismatocarpus |  |
| sect. Petromarula | 23. Rhigiophyllum |  |
| sect. Podanthum | 24. Roella |  |
| seeti. Synotoma | 25. Siphocodon |  |
| 9. Symphyandra | 26. Treichelia |  |
| 10. Trachelium | 27. Wahlenbergia |  |

Before dealing with developments in the 20th Century, mention should be made of subdivisions within the large core genus Campanula. De Candolle divided the genus into two large sections based on presence or absence of calyx appendages, ie. sect. Eucodon (appendages absent); sect. Medium (appendages present). However, Boissier $(1875,1888)$ placed greater reliance on the mode of dehiscence of the capsule, ie. whether the pores were at the top or apical end of the capsule, the middle (median) or at the base (basal). On account of this character, Boissier divided the genus also into two sections: Rapunculus (dehiscence apical); Medium (dehiscence basal). Confusion by the literature is possible since the valvate dehiscence of the Wahlenbergia and Codonopsis alliances are often referred to as apical. The pores in Campanula capsules are always lateral, ie. below the
level of the calyx and these may be positioned apically, medially or basally, but they are never above the calyx, on the top end of the capsule as in Wahlenbergia or Codonopsis. Also, because the pores in some species of Campanula rupture leaving a flap or operculum, they are sometimes described as valvate. Although further research is required to determine the physiology of dehiscence in many species of Campanula, for convenience and, to distinguish them from the strictly valvate dehiscence of Wahlenbergia, their dehiscence should be termed porate.

Table 9. Composition and numbers of genera of the Campanulaceae (1753-1997)

| AUTHOR | DATE | GENERA | SPECIES | MEAN | MONOSP. |  |  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Linnaeus | 1753 |  |  |  | 4 |  |  |  | 43 |  |  |

Table 9. shows a comparison between the number of species and genera recognised from 1753 until the present day. From the fairly steady increase in species numbers one can assume that the differences are due, at least partly, to more species being discovered but one cannot say this also for genera since it is most unlikely that the frequency of discovery of distinctive forms, especially monospecific taxa, would actually increase with time. The mean number of species per genus can also be misleading due to the skewness in the distribution of genus size (Cronk, 1989). It is highly likely that the lower numbers in earlier classifications reflect the conservatism of the authors as well as the fact that a phenetic (aggregate similarity) approach to classification was used. In addition, taxa were mostly widespread, temperate European forms. Little, if any influence would be given to biogeographical, cytological or evolutionary aspects in earlier classifications which is not the case with the unpublished data (1997). Therefore, with these figures, one cannot make simple conclusions about the information content in a classification. Probably there are large measures of psychohistorical artifact and biological reality in all of these classifications (see Cronk, 1989) and this must be borne in mind in the reclassification
process. The statements of Corner (1981) and Anderson (1974) are probably unduly pessimistic for the creation of an efficient information system, at least as far as the Campanulaceae are concerned.

### 6.2.2.2 20th Cemtonry

Taxonomy of the Campanulaceae in the 20th Century has centred on monographic revisions, particularly of individual genera. These have varied in scope and complexity and many have only been partial revisions for floral works such as that of Fedorov (1957). Other significant works, many of which have keys, include, those of Badré (1976); Damboldt \& Phitos, in Davis, ed. (1978a,1988); Fedorov \& Kovanda (1976); Kao \& Devol (1978, see also 1974); Moeliono \& Tuyn (1960); Pignatti (1982); Quézel (1953); Rechinger \& Schiman-Czeika (1965); Thulin (1983) and Van Thuan (1969). Taxonomic accounts (mostly of a limited number of species) exist for a few genera, eg. Aldén (1976); Ayasligil (1984); Badré et al.(1972-1975); Carlström (1986); Carolin (1964); Charadze (1949, 1970, 1976); Contandriopoulos (1964-1984); Contandropoulos et al. (1972-1984); Damboldt (1962-1978); Davis (1950-1973); Davis \& Sorger (1979); Eddie (1984); Esfandiari (1980); Hedberg (1961); Hilliard \& Burtt (1973); Hong (1980); Hong \& Ma (1991); Lakusic (1973); Lobin (1986); McVaugh (1941); Miller \& Whitcombe (1983); Morin (1980-1983); Nakai (1909); Parnell (1980-1987); Phitos (1963-1966); Rechinger (1980-1984); Richardson (1978); Shetler (1979-1982); Skottsberg (1953); Smith (1976-1992); Tan (1982); Tan \& Yildiz (1988); Thulin (1974-1987); Turrill, (1920); van Royen (1978). Somewhat older monographs, keys and miscellaneous taxonomic notes exist for other genera, which are no less valuable for future revisions, viz. Adamson (1946-1955); Anthony (1926); Buser (1894); Chipp (1908); Erdtman \& Metcalfe (1963); Feer (1890); Lambinon \& Duvigneaud (1961); McVaugh (1945-1948); Nannfeldt (1931); Schmeja (1931); Schulz (1904); Stojanov (1926); von Brehmer (1915); von Wettstein (1887);

After Schönland there were no further major reclassifications of the Campanulaceae s.s. until the work of Fedorov (1957) whose system differed considerably from that of Schönland. What merits it may have had were weakened by the fact that he only considered genera which occurred within the boundaries of the former Soviet Union and that it was not
used for his account of the Campanulaceae in Flora Europaea. Fedorov's system is as follows:

Table 10. Classification of the Campanulaceae (Fedorov, 1957)

| TRIBES AND GENERA |  |  |
| :---: | :---: | :---: |
| 1. CAMPANULEAE | 3. JASIONEAE | 7. PHYTEUMATEAE |
| Adenophora <br> Astrocodon Fed. <br> Brachycodon Fed. <br> Campanula <br> Symphyandra <br> Popoviocodonia Feal. | Jasione | Asyneuma <br> Cryptocodon <br> Culindrocarpa <br> Legousía <br> Phyteuma <br> Sergía Fed. |
|  |  |  |
|  | 4. MICHAUXIEAE |  |
|  | Michauxia |  |
|  |  |  |
|  | 5. OSTROWSKIEAE |  |
|  | Osirowstia |  |
| 2. EDRAIANTHEAE |  | 8. WAHLENBERGEAE |
| Edraianthus | 6. PERACARPEAE | Codonopsis |
|  | Peracarpa | Platycodon <br> Wahlenbergia |

Fedorov erected 5 new genera and resurrected Sect. Cylindrocarpa Rgl. of Schönland to generic status. Certainly these taxa apparently deserve separate status but lack of access to living material of many of Fedorov's central Asian genera has prevented any critical appraisal. It remains to be seen whether his monotypic genera will be subsequently merged with Adenophora, Campanula or Asyneuma or even associated with these genera. Sergia regelii (Trautv.) Fed., for example, has basal dehiscence, unlike the majority of species in Asyneuma. It is difficult to understand what was achieved by placing Edraianthus, Jasione, Michauxia, Ostrowskia and Peracarpa in independent tribes within the Campanulaceae other than to highlight their uniqueness, for it broke up the cohesion of more natural clusters of genera and made their phylogeny even more difficult to understand. Michauxia (certainly) and Peracarpa (doubtfully) are satellite genera of Campanula, as perhaps Edraianthus is, while Jasione may be better placed in association with Campanula or Wahlenbergia, and Ostrowskia with Platycodon. The association of Brachycodon with Campanula was laudable but the placing of Legousia with Phyteuma in his tribe Phyteumateae Fed. possibly destroyed the cohesion of a closely related assemblage of genera. Fedorov's treatment of the genus Campanula is no less problematical. He divided
the genus into 2 sections (Sect. Campanula DC. and Sect. Rapunculus Dum.). The former was subdivided into 23 subsections based on the morphology of the capsule. Although these subsections are all homogeneous in terms of branching pattern and ontogeny, they are certainly not so in terms of their life-forms, due to divergent adaptive radiation and convergence (Schulkina, 1980c). Furthermore, Gadella (1964) was of the opinion that many subsections recognised by Fedorov are unnatural because he was able to hybridise species belonging to different subsections, eg. C. trachelium L. (subsect. Eucodon (DC.) Fed.) X C. glomerata L.(subsect. Involucratae (Fomin) Fed. ) or with C. alliariifolia Willd. (subsect. Latilimbus Fed.).

The only complete attempts to revise Schönland's (1889) classification in the latter half of the 20th Century are those of Kolakovskii (1987) and Hong (1995). Kolakovskii has studied carpology in great detail and there is no doubt that this approach could be extremely profitable but it remains to be seen how valid many of his monotypic genera will be. Hong based his classification on the distribution patterns of 44 of the recognised genera.

Students of the Campanulaceae such as De Candolle, Adamson, Charadze, Fedorov, Feer, Fomin, Buser and many others who studied the genera in great detail in contrast to students of major groupings such as Schönland have made perhaps the most significance progress towards an understanding of phylogenetic relations and a more satisfactory classification. Ironically many of their findings are still ignored, perhaps because of a reluctance to split large genera such as Campanula. De Candolle's monograph of 1830 remains a starting point for all students of the family and it is likely that more genera will have to be recognised if any progress is to be made. With the advent of molecular systematics the challenge to unravel the mysteries of these plants has increased dramatically.

### 6.3 Homolagy, Tax@m@mic Characters amd Tramsformatiom Series

"Every description exists on a background of biological theory, to which it is intimately related - whether
this relationship is expressed or merely understood"
Agnes Arber, 1954.

### 6.3.1 Homology

Some understanding of homology is necessary for the practitioner of biological systematics since it forms the basis for the reconstruction of phylogenetic history with morphological and molecular methods. The following discussion is an attempt to clarify some of the major contributions towards this rather complex topic during the last few decades, and to provide a rationale for the methods adopted during the course of this study of the Campanulaceae.

### 6.3.1.1 Definitioms of Homology

The relationship between developmental and evolutionary processes was an issue of central importance in Roth's (1984) discussion of homology and for her a necessary component of homology is the sharing of a common developmental pathway. Wagner (1986) phrased this to mean that homology implies the historical acquisition of genetically regulated developmental constraints. It may also be considered to be "the possession by two or more species of a trait derived, with or without modification, from their common ancestor" (Futuyma, 1986) but this begs the question as to what defines ancestry. Van Valen (1982) defined homology simply as "resemblance caused by a continuity of information". Much of the original literature on homology was contributed by zoologists in the 19th century and, in the original meaning of the term from comparative anatomy, homology refers to a correspondence between parts of the body, regardless of form or function. The supracellular building blocks (of higher animals) are "homologues", ie. the same organ is found in different animals under every variety of form and function (Owen, 1848, cited in Mayr, 1982). Wagner's (1989) thesis was that the evolutionary origin, maintenance and modification of these building blocks of "higher" animals is equivalent to the biological content of the homology concept. Presumably Wagner's thesis was also meant to include such building blocks in plants although nowhere does he explicitly state this. According to Wagner, the homology relation has the formal properties of an equivalence relation and
defines a class of characters. A homologue is "an intensional concept that corresponds to the class of characters among which the homology relation holds and which are thus equivalent in some sense". The biological basis of this equivalence is the biological basis of homology. The following three biological properties that must be explained by a biological concept of homology were recognised by Wagner:

1. Conservation: lemologues mast share certaive features which remaim conserved in spite of changes in form furnction.

## 2. Inalividuality: individually named parts moust be developmeratally inodividualised to

 express their own characteristic features.3. Uniquueness: the arigin of an individualised complex of features, must be sufficiently pare that the features can characterise monophyletic groups.

Wagner (1989) concluded that a homologous structure is a "heritable semi-autonomous unit of the phenotype that gains its individuality with respect to the rest of the body by its unique developmental organization avad has been acquired only once in the history of the group (of animals) possessing this character". Wagner (1986) listed a number of invariant features which could be used to determine historical contingency of characters and their states and thus true homologues, but mostly these are conservative features which have limited value in phylogeny reconstruction. All vascular plants exhibit a certain homology of organisation which transcends systematic boundaries (Wardlaw, 1965). Therefore the concept of homology, to be useful in systematics, requires that organisms display a degree of variation or "individuality" (Wagner, 1989). There are thus different levels and different degrees of homology. Since most taxonomic groups under analysis at any given time usually possess the same principal parts it is usually necessary to consider homology between character states, eg. in the case of plants, the possession of a campanulate corolla may be due to common descent (ie. homologous) or to convergent evolution (ie. analogous). Used in this way the term "homology" is more or less synonymous with synapomorphy (Patterson, 1982) although Patterson (1988) found the distinction between characters and character
states neither useful nor necessary in the discussion of homologous features. Also, it should be borne in mind that plesiomorphic characters, although usually less suitable for cladistic analyses, can also be homologous.

### 6.3.1.2 The Detectiom of Morphological amd Molecular Homology

Meeuse (1984) believed that fruitless theoretical considerations (of homology) do not help us much when it comes to practical applications of the concept in morphological, systematic and phylogenetic botany. All this may be intellectually stimulating, but how is homology detected, especially since it is not necessary for homologues to display congruence between phenotype and genotype? Meeuse was in favour of an empirical or operational approach to the problem. Only by using a comparative approach and experience of the organisms in question may we hope to have a knowledge of homologous relations. There are no methodological shortcuts for the determination of homology. The detection of homology has been considered most frequently to require heuristic similarity criteria such as structure or position (topographic correspondence) (Remane, 1952; Riedl, 1978; Cain, 1982), coincidence (Remane, 1952), ontogenetic transformation and transitional forms (Westheide \& Rieger, 1987). In comparative morphology, similarity is the traditional means of testing for homology whereas discordance of characters (which is tantamount to incongruence) is a test for convergence (Le Quesne, 1972). Cracraft (1981; see also Stevens, 1984) has argued that similarity should be regarded merely as a postulate of simnilarity. It is therefore a weak test of homology due to its "low resolving power" (Bock, 1977). Where characters have greater complexity and display greater similarity a higher level of confidence in homologous relations is inferred (Riedl, 1978). The concept therefore is defined operationally (Kaplan, 1984) and provides an a priori postulate of homology which can then be tested a posteriori. Tests such as congruence should determine whether this postulated similarity is due to genealogical relationships (including "latent homology"; see Cain, 1982) or to convergence. Ontogenetic criteria undoubtedly play a major role in the detection of homology but, although "there is often a lack of correspondence between anatomical, embryological and genetic levels of organization" (Wagner, 1989), not all aspects of development have equal importance. Only those aspects of the developmental system that have been historically acquired (ie. are unique in the sense of being synapomorphies) and
cause a biased or restricted range of phenotypic variation in response to genetic variation are important. Development only matters to the extent that it causes developmental constraints on the further evolutionary modification of characters, ie. there are highly biased patterns of heritable phenotypic variation (Maynard-Smith et al., 1985) although Wagner (1989) believed that there is no need to expect homologues to have similar developmental pathways (contra Roth, 1984).

For this study of the Campanulaceae an operational or comparative approach was employed as outlined above. Characters were postulated a priori to be homologous purely on the basis of homology of organisation before any attempt was made to discriminate them phylogenetically. This is equivalent to the term paralogy of Hunter (1964) but should not be confused with the use of that term in molecular systematics. A posteriori evaluation of the characters ("reciprocal illumination") using some of the tests outlined below was made on the basis of provisional results and corrected where necessary by removal or by change of coding status.

Patterson (1982) proposed three tests to determine homology: congruence tests, similarity tests and conjunction tests but not all of these can be completed a priori. He concluded that the distinction between homology and non-homology (for morphological data) depends most decisively on congruence tests (ie. congruence with other homologies). True homology will pass on all three tests whereas non-homology (or homoplasy) will fail in at least one them. For molecular data the determination of homology depends largely on similarity tests. He also recognised paralogy (Fitch,1970a) as the molecular equivalent of serial homology which he called homonomy. Conjunction is the test which Patterson recommends to disprove homology if the two putative homologues occur in the same organism. Obviously homonomy and paralogy would fail this test because they occur as copies in a single individual. Parallelisms pass on similarity but fail the congruence test whereas convergences usually fail on both. A complement situation, where one of the homologies is absent altogether, passes both the congruence test and the conjunction test but obviously fails the similarity test. See Patterson (1988) for further discussions on parallelism and convergence.

Table 11. Tests to determine relations of morphological and molecular characters (modified from Patterson, 1988)

| RELATION | TEST |  |  |
| :---: | :---: | :---: | :---: |
|  | CONGRUENCE | SIMILARITY | CONJUNCTION |
| Homology | pass | pass | pass |
| Orthology | pass | pass | pass |
| Homonomy | pass | pass | fril |
| Paralogy | pass | pass | fail |
| Complement | pass | fail | pass |
| Parallelism | fail | pass | pass |
| Convergence | fail | fail | pass |

The situation regarding homology is a little different in molecular systematics. Fitch (1966) used the term "structural similarity which is greater than might be anticipated by chance" in order to detect homology among proteins. Fitch (1970a) also argued that discrimination of analogous from homologous similarity between two groups of sequences could be accomplished by constructing putative ancestral sequences and asking whether the inferred ancestors are more or less similar than the observed descendants. Similarity in sequence data may be analysed by statistical methods (Fitch, 1966, 1970b) which would eliminate randomness as the cause. However, non-random similarity ("homology" in a broad sense) for sequence data must be determined as either orthology or paralogy (Fitch, 1970a). Orthology is homology reflecting the descent of species and paralogy is homology reflecting the descent of genes (Patterson, 1988). Molecular sequence homology can be detected if the sequences can be aligned to give a score for the match as $=($ or $>) 3.0$ SDs above the score of scrambled versions of the same sequences (Doolittle, 1981).

Orthology and paralogy may be distinguished theoretically by the conjunction test but orthologs are normally present in multiple copy genes and the conjunction test will fail. See Patterson (1988) for a possible resolution of this dilemma. One must use "operationally orthologous" sequences without being sure that all are strictly orthologous (Goodman, 1976). The similarity test is the best means of distinguishing orthology and paralogy from the complement situation. Convergence in molecular sequence data has been elusive to demonstrate. Woese (1987) has stated that the number of possible functional configurations for a given gene are enormous and that similarity at the genotypic level can never reflect
convergent evolution. Convergence between sequences are considered too improbable to occur which recalls the argument from complexity, that if two structures are complex enough and similar in detail, probability dictates that thay must be homologous (Patterson, 1988). The usual method of determining similarity of molecular sequences has been the alignment procedure using several alignment algorithms and the limit between homology and non-homology is determined by the statistical procedures used. There are, however, alternative methods available such as the MALIGN program (Wheeler \& Gladstein, 1992) which utilises parsimony. Due to time constraints these have not been used during the course of this study.

### 6.3.2 Classes of Evidlence (Taxomomic Characters) and Trmmsformmation Series

In the early and middle part of the 20th Century, taxonomy declined as biological research centred on genetics and population biology, but the application of the new techniques of genetics, and equipment such as the scanning electron microscope, to taxonomy enabled existing classifications to be tested and refined. The search for new characters which might improve existing classifications dominated much taxonomic endeavour. Cain (1982) has made useful comments on the influence of natural selection on characters and distinguished three classes of characters which need to be recognised in systematic work. Applying his concept to plants, it can be argued that these are :

## 1. Those characters which are basic to all planets and vital for the complete functioning

 and well-being of the organism. Examples of such characters in plamis moust surely incluade those associated with physiological mechamisms such as phorosymethesis, respirarion, transpiration, etc. The genes which control the development and function of these systems must alsa be highly conserved and theus of limited application in systematics.2. Those which have responded to different evironmental selection pressures and which oullow uas to measure the tempo aved mode of evoluaion. Such charracters meay incluode flower shape, pollivation mechownisws, vegetative adoptorions, etc. but, ironically, it is those very characters which prove to be mosi problematical when it comes to differentiating between those which are homologous and those which are convergent.

Three such characters ine particular (chromosome ramber, pollen and seed-coat morphology) rave held sway among taxonomisis over the last three decades in an attempt to improve the existing classification of the Campanulaceae. All involved the use of laborainy proceedures, two of whic extensively employed scanming eleciron microscopy.
3. Those characters which do not seem to be under selection pressure and possibly display ramadom variation such as parts of the geveric code. Presumably variation at the individual level could also be classed here. In such cases frequency of polymorpheism is too right to be usefull for systemautic stuodies.

In this study, data sets which were subjected to cladistic analyses included morphological (flowers \& fruits; pollen; seeds) and molecular characters. Determination of the relative advancement of the former characters could only be achieved by long experience of the Campanulaceae and other groups, both in tropical regions and at higher latitudes. For molecular characters one has to resort to statistical techniques in the choice of nucleotide substitution. There is always the danger of circularity in these approaches and it is for these reasons that different data sets, including molecular ones, and other methods of analysis such as the use of phenetics were employed. The final arbiter must be congruence of these data sets in the determination of the accuracy of phylogenetic reconstructions. After each heading there is a short discussion about their use in systematics and possible transformation series.

### 6.3.2.1 Floral amd froit characters

Generally speaking, character states which are common in the family are probably primitive states and therefore it follows that taxa characterised primarily by such states are considered to be relatively primitive. Generally, inflorescence architecture has been considered to be of little value in delimiting higher taxa of flowering plants (Stebbins, 1974). In a sense the majority of species in the Campanulaceae except the perennial shrubby taxa may be considered to consist almost entirely of inflorescence in their mature state. Terminal flowers resulting in determinate main and lateral axes are very common features of the Campanulaceae (Parkin, 1914; Philpson, 1953; Troll, 1964). Twining genera such as Canarina and Campanumoea and those with sprawling growth such as Cyananthus,

Codonopsis and some of the rapunculoid species of Campanula have a determinate axis and terminal flowers as well as solitary flowers in the axils of the leaves (hapaxanthic). The branching system is therefore sympodial. Accrescent or indeterminate inflorescence axes appear to be more advanced than determinate inflorescence axes. The loss of the terminal flower is evident in Phyteuma and Jasione while a tendency for the axis of the inflorescence to continue growing exists in genera such as Jasione and Merciera. Several capitate species of Wahlenbergia such as $W$. verbascioides Thulin may also have lost the terminal flower. The panicle with acropetal maturation of the terminal flowers is therefore the most primitive type of inflorescence in the family, a conclusion also reached by Philipson (1953). Sympodial growth in such inflorescences sometimes makes the terminal flower difficult to distinguish due to overtopping. However, in the Campanulaceae the boundaries between a strictly acropetal maturation of the terminal flowers and basipetal maturation of lateral flowers become blurred and there is a tendency towards pleiochasia (Parkin, 1914). The thyrse, which shows more pronounced cymoid branching of the partial inflorescences is more advanced than the panicle, and the corymb more advanced still. In general, long pedicels are more primitive than short pedicels and the sessile flowers forming spikes are more advanced. Contraction of partial inflorescences to form spikes is a more advanced condition than the panicle or the thyrse. Spikes can also have reductions in the number of sessile flowers as in Triodanis and Brachycodon and appear quite frondose. Some spicate inflorescences are, in reality, congested, elongated glomerules (eg. Campanula spicata L., C. thyrsoides). Arrested internodes giving rise to fascicled inflorescences is a frequent trend in the family although studies of Campanula glomerata have shown that this may be correlated with latitude (Gadella, 1964). Glomerules (fore-shortened panicles) appear to be more advanced than panicles or thyrses, while umbels (shortened internodes and pedicellate flowers) and capitula (shortened internodes and sessile flowers) more advanced than glomerules. As stated above, the solitary axillary flower is more primitive than the inflorescence but care has to be exercised because an inflorescence may be reduced to a solitary flower, eg. Wahlenbergia pusilla or Campanula oreadum Boiss. \& Heldr.). In the Campanulaceae primarily solitary flowers are found mainly in genera such as Cyananthus, Canarina, Nesocodon, etc. The most common condition is for an inflorescence to be present.

Reduced size, especially of flower parts, is a derived character state often associated with floral aggregation, and taxa with small flowers are probably derived taxa, unless polyploidy has caused a reversal of this trend. Nodding, bell-shaped flowers are probably more primitive than upright star-shaped flowers and tend to be associated with cloudier, wetter climates whereas the latter are associated with floral aggregation as well as sunnier, drier climates. Transformations from the typically campanulate form through cupulate or tubular forms to rotate or stellate forms are discernible in many independent lineages. Some floral shapes are unique and highly derived, eg. in Campanula excisa Murith or C. zoysii and in Phyteuma and Physoplexis. Similarly corolla lobes show trends from being broad and rounded and shallowly incised to being narrow and pointed and deeply incised. The most derived corolla lobes are either ligulate or very lanceolate and either very reflexed or erect. A balloon-shaped or clavate flower bud is probably primitive while a slender or attenuate one is derived. Other corolla characters such as awned lobes, inter-lobe sinuses or the presence of a domatium are clearly derived. Probably the most primitive flower colours are yellows, oranges, reds or greens (often with very distinct vein markings) associated with tropical genera, whereas the various blue or violet hues (usually fairly uniform or occasionally with "honeyguides" or "eyespots") displayed by the bulk of the temperate genera are associated with bee-pollination and represent a more advanced condition. The corolla closing at night in Legousia and a few rapunculoid species of Campanula is a uniquely derived condition. The colouration of other floral parts, such as the petaloid calyx lobes of Musschia, is clearly integrated with the totality of the flower's attractiveness to pollinators. Many different lineages have coloured styles or presenter regions but the presence of highly distinctive coloured patterns in the nectary region at the base of the floral cup is associated most clearly with those taxa which lack a nectar dome and have broad receptacles. The presence of coloured pollen is also clearly a derived state as is the unique scarlet nectar of Nesocodon, the stylar glands of Wahlenbergia, or the absence altogether of a visible nectary in Zeugandra.

The number of floral parts is commonly five but there are frequent departures from this. Stamen number is usually five but occasionally is reduced to four or more commonly increased to six as in Canarina or eight or more in Michauxia. Connate anthers (may be
connate only at the base as in Jasione) are derived in several independent lineages. The ancestral state is probably for the anthers to be separate as is the presence of an appendage protruding between the tips of the thecae. The exact function, if any, of this structure is unknown. Sessile anthers (as in Petromarula and Sergia) represent an advanced condition and the presence of ciliated margins to the filaments is more advanced than the glabrous state. There are trends in basal broadening of the filaments, associated with ciliated margins, culminating in the development of the nectar dome. This finds its greatest expression in the fused dome of Zeugandra and the long tubular dome of Petromarula. The most simple, shield-like segments of the nectar-dome are less advanced than the auriculate ones.

Styles are rather broad, not exserted and the stigmatic lobes thick and short in the most primitive taxa and the presenter region during the male phase appears club-shaped. In marked contrast, the long slender, exserted styles and thin, filiform stigmatic lobes are to be found in more advanced taxa. There are several deviations or combinations of these trends such as the very short, square-shaped stigmatic lobes of Trachelium and Jasione. The unfolding sequence of the stigmatic-lobes most primitively begins from the apex but in some rapunculoid species of Campanula it begins at the middle or the base. The presence of mucilage on the stigmatic lobes (as in Wahlenbergia) is considered to be a primitive character. This is lacking in the majority of genera which have dry stigmas. The Campanulaceae have not been fully investigated for the presence of invaginating stylar hairs. It is suspected that some genera such as Phyteuma have collapsing hairs which may represent a more ancestral state.

In the more primitive genera there are clearly apparent transitions from a completely superior ovary (Cyananthus) through a intermediate state to an inferior ovary (Codonopsis). An inferior ovary is almost the norm for much of the family but there are occasional surprises such as the half-inferior ovary of Campanula barbata L. Interpretation of the ovary position is confounded by many taxa possessing a conical bulge above the level of the calyx lobes. This is particularly prevalent among the southern African species of Wahlenbergia and allied genera. In some this bulge or cone blends imperceptibly with the base of the style. In such cases, however, the ovules are usually below the level of the calyx. The inferior
ovary in the Campanulaceae is axillar in origin, ie. it is derived by fusion of axillar appendages (calyx lobes) to form a hypanthium which in turn is fused to the ovary wall. In Cyananthus the hypanthium is free from the ovary wall and merely forms a partly fused globular sack surrounding the superior ovary. In Codonopsis, Campanumoea and Cyclocodon W.Griffith various degrees of fusion with the ovary wall can be discerned. In most cases the point of origin of the corolla coincides with the top of the inferior ovary (completely encased in a fused hypanthium) and the free lobes of the calyx but in some taxa the hypanthium grows above the level of the calyx lobes. Protection of the ovary has continued in some taxa such as Campanula and Michauxia which possess calyx appendages (clearly a derived condition). Here the calyx lobes recurve to completely enclose the ovaries in a "pseudo-capsule". This condition is found in those taxa inhabiting seasonally dry climates. In other species from dry or Mediterranean climates there is often an elaboration of spiny hairs on the capsule and fruit and/or accrescence of the calyx lobes. These features may aid dispersal of the whole capsule rather than act as a deterrent to herbivorous animals. In any case these features are clearly advanced. Five fused carpels appears to be the most primitive condition but the most common number is three or two. The number of carpels usually directly affects the shape of the capsule in transverse section although the capsules of those genera such as Phyteuma which have densely compact inflorescences show some degrees of compression. Rarely (as in Michauxia and Canarina) is this number increased, or as in the case of Merciera, reduced to a unilocular ovary by abortion of the septum. Consequently, it is difficult to assess the symmetry of the ovules in relation to the calyx lobes or the number of veins. Vein number is particularly confusing. In some cases 10 veins are clearly symmetrically disposed with five main veins entering the calyx lobes. In other cases, the number of veins is reduced to eight or five, some of which bifurcate between the calyx lobes. In other cases the number of veins is reduced to three, some of which then bifurcate and act as main veins in the five calyx lobes. Placentation is axile in the primitive condition and the most primitive arrangement is for numerous ovules to be distributed along much of the axis. A more derived condition is where the ovules are confined to the top end or, as in Merciera, basally. The partially parietal condition in Triodanis appears to be derived.

If it is accepted that the ancestors of the Campanulaceae were forest plants of tropical regions it is not an unreasonable assumption to hypothesise that animals were both principal pollinators of the flowers and vectors of the seeds. From this perspective, a berry should be viewed as more primitive than a capsule. Among extant taxa of the Campanulaceae the berry is only associated with tropical/subtropical taxa, as is the retention of caducousness of the corolla. The evolution of the capsule from berries may have occurred more than once since the capsule type in Peracarpa seems rather anomalous. The mode of dehiscence in the Campanulaceae shows quite definite trends which appear to be correlated by the evolution of the inferior ovary. Basically, the most primitive situation is to be found in those platycodonoid and wahlenbergioid taxa which have the capsule opening by five valves at the apex of the ovaries above the calyx lobes. This then may be reduced to three or two valves or occasionally increased to six. In the wahlenbergioid lineages the valvate arrangement appears to be elaborate in several directions. In a few genera such as Gunnilaea the capsule is completely indehiscent, the seeds being liberated simply by decay, or, as in Merciera, dehiscence is achieved by means of periodic fire in the environment. In Roella, the regular valvate arrangement is replaced by a situation where the style is caducous and the tissue at the apex of the ovaries breaks down to form a fairly regular hole, whereas in Craterocapsa the apical tissue separates as a circumscissile lid or chalice. In Prismatocarpus and Heterochaenia, the capsule splits loculicidally into five or three segments respectively, whereas in Namacodon the splits are septicidal.

The temperate campanuloid genera of the Northern Hemisphere are essentially porate but this condition is probably derived from an ancestral valvate condition. Genera such as Githopsis display indehiscence or irregular rupture of the capsule apex. In this respect they are paralleled by a similar mode of dehiscence in Edraianthus but the two taxa do not seem particularly close. The most primitive porate dehiscence is probably to be seen in the rapunculoid species of Campanula, Brachycodon and Legousia where the pore is at the apex of the capsule, but lateral and where the flower is upright in orientation. The pore in the middle may also represent the most primitive condition and is to be found in diverse genera such as Phyteuma, Physoplexis, the "Isophylla" lineage of Campanula, and in many North American taxa. It need not be associated with an upright flower. The most advanced
condition appears to be with the pore (often a flap) at the base of the capsule. This is usually associated with taxa which have nodding flowers and/or capsules. Changes in the position of the lateral pores in Campanula and allied genera appear not to have occurred sequentially, ie. apical to mid to basal positions. A change to lateral dehiscence has meant, for many taxa, a change in the number, symmetry and disposition of the main veins in the capsule. For example, a five- or ten-veined capsule with three pores between the main veins would probably display some asymmetry or loss of secondary veins. This is an area of anatomy where much more research is needed.

### 6.3.2.2 Seed characters

Netolitzky (1926), who summarised the literature on seed anatomy of angiosperms almost 70 years ago, noticed that the structure of the seed coat is characteristic of a family in general, and it is, therefore, of taxonomic value. Takhtajan (1991) pointed out that even for phylogenetic correlations between families and genera, the structure of the seed coat might be important, while, according to Barthlott (1984), seed surface features are little affected by environmental conditions and seem to reflect genetic-phylogenetic differences in the plants concerned (Haridasan $\&$ Mukherjee, 1987). Seed surface characters in the Campanulaceae are complex and clearly many of the characters are highly adaptive for dormancy, dispersal, water-uptake, etc. but the adaptive significance of seed-coat sculpturing and ornamentation has been little studied. Shetler \& Morin (1986) concluded that the seeds of the family Campanulaceae in North America show different tendencies of specialisation in the seedcoat although it was not clear whether these tendencies have evolved in North America in response to ecological or other selective factors, or represent tendencies to be found elsewhere in the family. Many authors believe that SEM data are useful only to delimit taxa at the species level and sometimes as indicators of suprageneric groupings (Behnke \& Barthlott, 1983, Barthlott, 1981, 1984, ). In his brief summary of seed characteristics in the family Campanulaceae, Corner (1976) listed previous literature on seed studies for this family, but there has been no systematic study of seed surface morphology in this family as a whole. Limited studies of selected species or genera have been surveyed, eg. Gunnilaea, Namacodon and Wahlenbergia (Thulin, 1974, 1975), 38 species of North American Campanulaceae (Shetler \& Morin, 1986), and 28 species of the family from India (Haridasan
\& Mukherjee, 1987). The occurrence of character states is thus rather reticulate, making cladistic analysis difficult. Nevertheless, it would appear that rather vague transition series can be distinguished. Large dark-coloured or blackish seeds appear to be primitive, small whitish or pale coloured seeds being rather advanced. Similarly, shininess appears correlated with the annual habit and with dormancy and is clearly a derived character since the surface features on such seeds can often be seen very faintly. Symmetry on the long axis appears to be regular in primitive seeds and the regularly ovoid or elliptical seed is more primitive than the conical, round or turbinate types. In cross-section, the round seed is more primitive than the flattened type, and the trigonous and quadrangular types or clearly derived. Also a regular tapering hilum is more primitive than the irregular or angular types. Rugose ornamentation, surface projections (as in Rotantha, s.s.) or upturned ends of the radial walls (as in Campanulastrum) are derived whereas the reticulate pattern is more primitive, especially those seeds with isodiametric cells. Polygonal-reticulate patterns are more primitive than rectangular-reticulate (the reticulate type could be subdivided into six subtypes: polygonal-reticulate, trapezoid-reticulate, irregularly-reticulate, rect-angularreticulate with broad areoles, rectangular- reticulate with narrow areoles, and scalariformreticulate). Striated arrangements are more advanced than reticulate but in themselves show transitions, mainly associated with the length of the cells and the prominence of the walls. The longest cells and the narrowest wall are the most advanced. Beaded cell walls are clearly derived but are rather primitive in a global context. Secondary ornamentation of the cell wall is also a derived character. Seed wings appear to be rather primitive on the whole but appear to be derived independently several times. For example, the large single wing appears to be unique to Platycodon while a rounded "winglike" margin is quite characteristic of Azorina.

### 6.3.2.3 Pollem characters

The use of pollen analysis by Scandinavian workers in the early part of the 20 th century as an instrument for the investigation of Quaternary changes of vegetation and climate stimulated its use in the field of taxonomy. In particular the numerous works of Erdtman from 1921 onwards promoted pollen analysis as an important taxonomic tool. This use was accelerated by the invention of the scanning electron microscope which allowed much greater detail of the surface features of pollen grains to be observed. The pollen of the

Campanulaceae were surveyed by Erdtman (1952) using light microscopy and by Dunbar, (1973). Erdtman's 1971 publication also contains a list of the literature pertaining to all previous microscopy studies of the pollen of the family. He examined about 75 species from 35 genera. A correlation of the pollen morphology with the taxonomy of the Campanulaceae s.l. was made by means of light microscopy by Chapman (1967) who studied 31 species from 21 genera and by Avetisjan (1967, 1973). Lines of evolution have proceeded in Campanuloideae as indicated by the shape, number and position of the apertures (Avetisjan, 1967, 1973). Avetisjan (1967) gave a schematic presentation of evolution based on the development of apertures from pollen with many colpi to pantoporate pollen grains. Avetisjan stated that colpate, colporate and colpate-porate pollen grains are typical of genera of the Campanulaceae s.l. found in tropical zones, and that porate apertures constitute one of the most important characters in the new type of pollen of the family distributed in temperate zones. Evolution in Campanula pollen can thus be seen in the decrease in length of spinules in association with an increase in numbers of pores. By far, the greatest contribution to our knowledge of Campanulaceae s.l. pollen has been through the works of Dunbar (1973a,b,c, 1975a, 1975b, 1976 (with Wallentinus), 1978a,b, 1979, 1981, 1984 ). From these studies Dunbar concluded that the family Campanulaceae s.l. (as traditionally conceived) is very heterogeneous. The suggestion by Avetisjan (1967) that tropical colpate/colporate pollen is the most primitive, while pollen from temperate zones show more specialised characters is supported partially by Dunbar (1984) where a complex exine structure occurs among some of the porate pollen. There are, however, other porate pollen with a more simple structure. Badré et al. (1972) studied the three species of the endemic genus Heterochaenia and, interestingly, concluded that an evolutionary progression in the pollen within the genus could be determined.

### 6.3.2.4 Cytolagical characters

In the search for generic criteria, one would expect chromosomal features to provide very strong characters because their evolution is often conservative. However, this conservatism limits the usefulness of the most common feature considered, namely the basic chromosome number. The possession of a common basic number does not mean that a taxon is primitive. Many genera that appear to be dibasic are really monobasic with dysploid reduction in
number. Most of the apparently polybasic genera constitute polyploid complexes. The taxonomic literature for Astereae tends towards the concept espoused, for example by Löve (1963) that presumes genera to be monobasic, although Löve does accept the possibility of dysploid and alloploid changes of number within a genus. We must look for correlations between chromosomal features and gross morphology. Gadella (1964) used the criterion of chromosome number to establish the possible relationships which exist between the genera of the Campanulaceae, but principally the relationship between species within the genus Campanula. He proposed a new classification which took into account chromosome number and size, morphological characters (eg. presence/absence of calyx appendages, glabrous/hairy styles, carpel number, capsule orientation, apical/basal dehiscence, etc.) and the life cycle. Contandriopoulos (1984) continued and refined Gadella's pioneering efforts. She published a paper on the differentiation and evolution of the genus Campanula in the Mediterranean region but her results have implication for the delimitation of genera in the family as a whole. She classified the species by subgenera and sections in relation to cytotaxonomy, life cycle and geographic distribution. In all she studied 317 taxa whose chromosome numbers were known (about $3 / 5$ of known taxa in the genus Campanula). There have been numerous chromosome studies of individual species or sections of the genus Campanula (Podlech, 1962, 1965; Podlech \& Damboldt, 1964; Bielawska, 1983; Böcher, 1964) and a few other genera such as Jasione (Parnell,1980-1987); Wahlenbergia (Thulin 1974-1987); Chromosome doubling is reported as having occurred in two species or several times in a third species of Githopsis (Morin, 1980-1981; 1983) with associated chromosome loss; Musschia (Bramwell et al., 1976); Azorina (Mesquita-Rodrigues, 1954) etc. Many of these studies were detailed and exacting and have provided a wealth of data for the more generalised studies of Gadella and Contandriopoulos, mentioned above. The chromosomal evolution of the genus Campanula is very complex and diverse. It is the most studied genus of the family from a cytological viewpoint and may well serve as a more generalised model for chromosomal evolution for the family in general. For this reason, the diagrams of Gadella (1964) (with modifications) and Contandriopoulos (1984) is reproduced below.

Table 12. Schematic system of chromosome evolutiom im the gemus Camparaula s.l. (modified from Gadella, 1964 amd Comtamalriopoulos, 1984).


## Group I. Camparouldas sulbgem. Rappumeulus

Group II. Campawoulta: sulbgem. Rappuncullus
Group IIII. Camapavaula: sulbgem. Rappunculius
Group IV. Campanoullas: subbgem. Rappunnculluas; Gaudellia, Campanoulla: sect. Pteroplayllum; Roucela

Group V. Campanoulla: sect. Oreocodon, Compamaula: sect. Medium
Group VII. Campansulla: sect. Oreocodos: Roscela
Group VII. Companoulla: sect. Camparmulla, Qusinquelocullares, Tulipella, etc.
"We unite all things by perceiving the law which pervades them; by perceiving the superficial differences and the profound resemblances. But every mental act, - this very perception of identity or oneness, recognises the difference of things. Oneness and otherness. It is impossible to speak or to think without embracing both."

Ralph Waldo Emerson, 1850
"Plato; or the Philosopher"

### 7.1 Plhemeties Sectiom

### 7.1.11 Imaroductiom

As an initial procedural step for systematic study and classification there must be groupmaking based on overall resemblances (Davis \& Heywood, 1963; Heywood, 1964) which provide first approximations of relationships within a larger systematic strategy. The rigorous idea of equal weighting of characters (isocratic, sensu Burtt, 1964) is rejected as unrealistic. The "neo-classical" approach suggested by Heywood (1964), in which those characters which are selected (as opposed to potentially available) are given equal weight, is adopted in this study. This allows for taxonomic experience of the available evidence and a rejection of a priori notions that all characters have the same information content. Phenetic methodology as a starting point allows for the greater scrutiny of taxonomic characters and their correlation, while phenograms, as well as ordination analysis, give us starting points in the assessment of the structure of the data sets. It is not an endorsement of phenetic methodology for the reconstruction of phylogeny.

### 7.1.2 Comstructiom of the Plnemetic $\mathbb{D}$ ata Sets

Data files were initially created for all morphological data sets using the $\mathbb{D E L T A}$ format (Dallwitz, 1980), and these were edited using the " $\mathbb{D E D I T} \mathbb{T}^{\prime \prime}$ program of the $\mathbb{P A N K E Y}$ package (Pankhurst, 1995). DELTA is now accepted as an international standard for encoding taxonomic data and the advantages of using it are that it is versatile, has a free format and there are no restrictions on the kinds of characters (eg. quantitative or qualitative; ordered or unordered, multistate and binary) or the description of variability. Allowance is also made for character dependencies (Pankhurst, 1991) and characters may be weighted. Table. 13 summarises the 14 data sets and subsets which were constructed plus the total
number of taxa (items) and characters in each. None of the subsets contains any additional characters or taxa. All characters are unweighted.

Table 13. Data sets and subsets used in phenetic analyses.

| DATA SET/SUBSET |  | TAXA (ITEMS) | CHARACTERS |
| :---: | :---: | :---: | :---: |
| 1. a. | Asterales (G\&B.DAT) | 23 . | $W^{46}$ |
| b. | Campanulales subset | 14 | 46 |
|  |  | 65 | 50 |
|  |  | 38 | 50 |
|  |  | 12 | 50 |
|  |  | 22 | 50 |
| 3. a. <br> b. <br> c. <br> d. | Pollen (Camplal.DAT) | 38 | 9 |
|  | Campanuleae subset | 21 | 9 |
|  | Platycodoneae subset | 11 | 9 |
|  | Wahlenbergeae subset | 15 | 9 |
| 4. a. <br> b. <br> c. <br> d. | Seeds (CampSeed. DAT) | 53 | 11 |
|  | Campanuleae subset | 43 | 11 |
|  | Platycodoneae subset | 6 | 11 |
|  | Wahlenbergeae subset | 13 | 11 |

Table 14. Characters used in the Asterales (G\&B.DAT) data set for phenetic analyses (after Gustaffson \& Bremer, 1995). State changes are listed below each character. The scoring for the full data matrix is given in the Appendix 12.1.1.1-2.

| CHARACTERS USED IN THE ASTERALES DATA SET |  |  |
| :---: | :---: | :---: |
| 1. Iridoins | 17. Petal Wings | 33. Carpels/s |
| 1. present <br> 2. absent | 1. absent <br> 2. present | 1. four to five to many <br> 2. three <br> 3. two |
| 2. Higher lnufins | 18. Petal Lateral Veins | 34. Siyles |
| 1. absent | 1. absent | 1. free |
| 2. present | 2. present | 2. fused |
| 3. Liatieffers | 19.Petal Lateral Veins | 35. Stylar Indusium |
| 1. absent | 1. end subapically | 1. present |
| 2. present | 2. apically confluent | 2. absent |
| 4. Resin Cells | 20. Lateral Veins | 36. Style |
| 1. absent | I, free 4 MAMA | 1. glabrous |
| 2. present | 2. fused with adjacem lateral | 2. with unicellular hairs |
| 5. Vessel Perforations | 21. Stamens | 37. Late Style Clongation |
| 1. scalariform | H. four to five to mam | 1. absent |
| 2. simple | 2. two to three | 2. present |
| 6. Heflcal Thickeninge | 22. Anthers | 38. Placentation |
| 1. present | 1. torsificed | 1. central |
| 2.absent | 2. busifficed | 2. parietal |
|  |  | 3. apical |
|  |  | 4. basal. |
| 7. Trich. Element Pits | 23. Lower Part of Thecae | 39. Ovaies |
| 1. bordered | 1. ffee | 1. few to many |
| 2. simple | 2. fused wilh connectuve | 2. one |
| 8. Nodes | 24. Anther Dehiscence | 40. Partetal Iissue. |
| 1. tri- to multilacunar | t. immorie | 1. present |
| 2. unilacunar | 2. evtrorse | 2. absent |
|  |  |  |
| 9. Sclerench. diobiasts | 25. Anther Fusion | 41. Hypostase |
| 1. absent | 1. free"s | 1. absent |
| 2. present | 2. commute | 2. present |
| 10. Plants | 26. Pollen Presentation | 42. Endosperm Developil. |
| 1. woody |  | 1. cellular |
| 2. herbaceous | 2. from apical pore (pollen pump) <br> 3. from the stule | 2. nuclear |
| 11. leayes | 27. Tapetum Cells | 43. Micropylar Haust. |
| 1. alternate | 1. muthuidente | 1. present |
| 2. opposite | 2. binucleale | 2. absent |
| 12. Stipules | 28. Cell No. in Pollen | 44. Chalazal Haust. |
| 1. absent | 1. tho | 1. present |
| 2. present | 2. tiree | 2. absent |
| 13. Caly ${ }^{\text {a }}$ | 29. Tectum | 45. Terminal (ell (Proemb) |
| 1. actinomorphic | 1. imperforateifine perforate | 1. div. by longitudinal wall |
| 2. zygomorphic(odd sepal dorsal) | 2. wilh lumina femitectate) | 2. div. by transverse wall |
| 3. zygomorphic(odd sepal ventral) |  |  |

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Table 14. continued

| 14. Corolla | 30. Columellae | 46. Basal Cell |
| :---: | :---: | :---: |
| 1. actinomorphic | 1. unbranched | 1. contrib. sign. to embryo |
| 2. bilabiate $\boldsymbol{A}(3+2)$ | 2, bifurcate | 2. forming suspensor only |
| 3. bilabiate $\boldsymbol{B}(1+4)$ |  |  |
| 4.bilabiate $C(1+1)+3$ |  |  |
| 15. Corolla Vernation | 31. Spinules or Verrucae |  |
| 1. imbricate |  |  |
| 2. valvate | 2. present |  |
| 16. Petal Fission | 32. Ovary |  |
| 1. choripetaly | 1. Superior |  |
| 2. sympetaly | 2. inferiorsem-inferior |  |

Table 15. Characters used in the Flowers \& Fruits data set (Flowers.DAT) for phenetic analyses. State changes are listed below each character. The scoring for the full data matrix is given in the Appendix 12.1.1.3-6.

CHARACTERS USED IN THE FLOWERS AND FRUITS DATA SET

| CHARACTERS USED IN THE FLOWERS AND FRUITS DATA SET |  |  |
| :---: | :---: | :---: |
| 1. Inflorescence type | 7. Corolla lobe Ofientation. | Corolla Colour contd. |
| 1. monotelic (ferninal flower) | 1. usually erect, not spreading | \% * irraw yellow or sercant <br> 8. sulphum yettom <br> 9. gollien syellow |
| 2.2 potitetic (ino terminal flower) | 2. usually spreading |  |
| 3. sunctromous tevetopment | 3. usually reflexed |  |
| 2. Synflorescence | 8. Corolla Lobe Sliape | i0. greenish or gtaucercent |
| 1. a primarib soliany fower | 1. tapering and lanceolate |  |
| 2. 4 simpte cime | 2. ligulate | 12. vermilion |
| 3. a secondarily solitary flower | 3. ovate or rounded | 13. brich red |
| 4. a parmite | 4. cucullate | 14. iromze or copper |
| 5. a glomerute or giomerules | 9. Lobe Tips | 15. maroon or crimsan |
| 6. as sitie or verticllisiter | 1. more or less pointed | 16, puyple |
| 7. a hivre | 2. more or less rounded | 17. Colour Distribution |
| 8. a corsmb | 10. Disfinct Mucro at Tip | 1 hiore or lest mitiorn |
| 9. ant unibel | 1. present | 2. pate at baste. darker lobtes |
| 10. a capitulim | 2. absent | 3 pote evespolt at base |
| 3. Inflorescence Axis | 11. Distinct Interlobular Sinus | 4. durk eyespot at base |
| 1. accrescent (after flowerme) | 1. present | 5. coltured buind artourd mindite |
| 2. not acerresent | 2. absent | 6. tosselated or : itit spors it torthes |
| 4. Flower Orientation | 12. Coronal IIairs / ppendages | 18. Reticulated Corolla-veins |
| 1. erect or notiling | 1. present | 1. distinctioften a different colour) |
| 2. pendent | 2.absent | 2. indtitinct |
| 5. Flower Bud Shape | 13. Corolla Domatium | 19. Distinet Long. Main Veins |
| 1. bathoon-like or clavate | 1. present | 1. present(may appear as graoves) |
| 2. attenuate or cotinulricat | 2. absent | 2. absemt |
| 6. Corolla Shape | 14. Corolla Lobe Division | 20. Corolla Behaviour |
| I. rotate | 1. more or less divided to base | 1. closes at night |
| 2. Infundithutar | 2. divided > one third | 2. does not close at night |
| 3. campanulate (incl. cupulate) | 3. divided < one third | 21. Corolla Accrescence |

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Table 15. continued

| 4. hypocrateriform | 15. Iolee Colierence | 1. murked |
| :---: | :---: | :---: |
| 5. sylindrical (Iabes inconspic.) | 1. free and expand normally | 2. Hot markeit |
| 6. obiconical or finnel-shaped <br> 7 stellate | 2. temporarily coherent at tips <br> 3. permanently coherent at tips | 22. Stamen Fusion and No. <br> 1. apostemonous and 5 |
| 8. ureeotate | 16. Corolla Colour | 2. apostemonous and 6 |
| 9. ungnicutute | 1. snowy white (no trace ofpink) | 3ipelatostemonous and 5 |
| 10. twhinate: | 2. whitish,pinkinsh-white or pink | 4. apostemomous indi 4 |
| 11. long mbitar (expmatil lobest | 3. violet | 5. apostemman sila |
| 12. shorn tubutor expmati. tobest | 4. lilac, lavender or azure | 6. apostemorrus and? |
| 13. tubie glatoss al base | 5. ultramarine, indigo, blue-black 6.gentian blue |  |
| 23. Anther Appendage | 33. Disi Shape | 40. Style Insertion/Exsertion |
| I. present (may he wery shom) | 1. disklike/ annular (no swellings) | i, inserted 4 ansansand |
| 2. absent (often comeave at ip) | 2. continuous penta-/hexagonal | 2. erserted |
| 24. Anther Attachment | 3. continuous, lobed (swollen) | 41. Style Accrescence |
| 1. sessille or evaremely short | 4 .interrupted(separate arcs/lobes) | \%.present |
| 2. wirh discorminte filaments | 5.cylindrical or cup-shaped | 2. absent |
| 25. Filament Cilia (At Base) | 6. conical | 42. Stylar Glands/Papillae |
| 1 pretent | 7. pubescent | 1. present |
| 2. itsient | 8. club-shaped glands | 2. absent |
| 26. Base of Filament (Shape) | 9. two-lobed | 43. Style Base |
| 1. Hol illited for neimin dome) | 34. Disk * 010ur | I. a sotid plughall or tissue fayer. |
| 2is sightly iliared (weak dome) | 1. orange or yellow | 2. iop of ovary relaively thin |
|  | 2. red | 3. a Mollour cone at ion of avary |
| 4: illated (amiculatefenerifate) | 3. lime green | 44. Closed Stigma Shape |
| 27. Stamens after Anthesis | 4. purple | I/ stub-rinjed (broad at iop) |
| 1. Andilums | 5. black or blackish-violet | 2. Shorf ant capitute |
| 2. persistent hut withereit | 6. colourless (leaf-green/brown) | S. SHehty thickencil for "ctup) |
| 3. persistent ami mirgil | 7. pinkish maroon | 4. ilenter and flifom |
| 28. Nectar Dome Shape | 8. crimson | S. shorf and scarcely itevitoped |
|  | 9. dark green | 45. Stigma Lobes/Presenter |
| 2. hemispherical (ongestort) | 15. Disk Accrescence | \%. ilue \#r whlet (outer surface) |
| 29. Nectar Dome Fusion | 1. present | 2. no distinctly colmurid |
|  | 2. absent | 46. Stigmatic Lobe Number |
| 2. aimosi comptety, fuseit | 36. Nectar Colour | 1. trio to five |
| 30. Anthers at Maturity | 1. colourless | 2. sit to eight |
| \%/fee: ustally wilhering quicky | 2. orange red (scarlet) | 3, eight to ten |
| 2. coherent along edges finbetike) | 3\%. Receptacle Wirilh | 47. Open Stigmatic Lobes |
| 3. colteremin Haser onty | 1. broad | 1. long and thin (petatoid) |
| 4. coulescent foi coheremi) | 2. intermediate | 2. moderately tirch |
| 31. Pollen Colour | 3. narrow | 3. very thick |
| 1. bright azure blue or hilae | 38. Style Sliape | 4. short, thick and square-ended |
| 2. purple or purplist hrown | 1. straight | 5i. frome a shorr commatre tubt |
| 3. oramge-hroun or brichited | 2. gently curved (usually upwards) | 6. Short and scarcely teteloped |
| 4. yellow, cream or white | 3. a distinct $S$-shaped curve | 7. short and rather thin |
| S. violer or pinktsh-violet | 4. abruptly angled at stigma | 48. Lobe Opening Sequence |
| 6. crimson | 39. Style Thickiness | I, from the ajex |
| 7. Aull green | 1. long and filiform (not tapered) | 2. From the base or midltle |

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Table 15. continued

| 32. Disk <br> f. present, usually quite instinct <br> 2. absent or mor teveloped | 2. long, +/- thick (not tapered) <br> 3. short and filiform (not tapered) <br> 4. short and thick (not tapered) | 49. Stigmatic Surface <br> 1. dy with one-celled popillae <br> 2. wet, muctiaginous |
| :---: | :---: | :---: |
|  | 5. long and tapering | 50. Collective Hairs |
|  | 6. short and tapering | I. invaginate |
| 51. Stylar Protective Hairs | 62. Petaloid Calyx Lohes | 2. Io not invaginate |
| 1. present | 1. present | Dehiscence contd. |
| 2. absent | 2. absent | 13. septicidal fseptat processes) |
| 52. Top of Ovary before Fert. | 63. (aly) L Lobes on Fruit | 14. capsule tertiches |
| 1. flat or concave | 1. erect andor convergent | 15. irregntar rupture of wall |
| 2. conver or conicat | 2. stellate patent or accrescent | 16. 3 spliting papery segments |
| 53. Ovary Position | 3. little or no change | 17. apically hy a caducous plug |
| 1. supertor | 4. reflexed or recurved | 18. rupure of thim pericom |
| 2. semi-superior | 5. occas. caducous when mature | 70. Valvate Dehiscence |
| 3. infertor | 64. Calyx Bracts | 1. twa valves |
| 54. Carpel Number | 1. present | 2. three valves |
| 1. one | 2. absent | 3. five vatues |
| 2. mo | 65. Fruil Orientation | 4. valvote but indehiscent |
| 3. thice to five | 1. upright or nodding | 71. Porate Dehiscence |
| 4, stito etigh: | 2. pendent | 1. al aper |
| S. Sthit to ten. | 66. (apsule Shape in IS | 2. il middle |
| 55. Carpel:Calyx Rel.Position | 1. distinctly prismatic | li. it buse |
| I, ilfirnite | 2.angular but not sulcate | 4. betour midalte (rol at base) |
| 2. Ais int alternate | 3. more or less terete ( $+/$ ribbed) | 72. Pore |
| 3indelerminate | 4. angular, markedly sulcate | 1. regular from mital depression: |
| 56. Placentation | 5. compressed or flattened | 2. with a flap on topsitie |
| 1. inilim | 67. C apsule Yeins | 3. Imegutar tear |
| 2. basal | 1. 10 veins symmetrically disposed | 4. it hase herween septa (regular) |
| 3. purtatly partetal | 2. 8 veins asymmetrically disposed | 73. Capsule in Fruit |
| 4, penditions:4.s. | 3. 6 veins asymmetrically disposed | I/ acmescent lengilinise |
| 57. Ovule Number | 4. 5 veins symmetrically disposed | 2. \#ot uccrescht lenginvise |
| 1. mumerous in eadh lochle | 5.3 veins | 74. Corolla (post-flowering) |
| 2. Fer in each tocule | 6. 10 veins asymmetrically disp. | \%. weally chlinims |
| 58. Top of Ovary after Fert. | 7.8 veins symmetrically disposed | 2. persilim |
| i. Ilat | 68. Pedicels | 75. Pollen |
| 2. conver | 1. elongating in fruit | 1. molpate |
| 59. Fruit | 2. not elongating in fruit | 2 is colporate |
| 1. " berry | 6\%. Dehiscence | 3. porate |
| 2. a capsule | 1. tardy,often by decomposition | 76. Capsule at Upper End |
| 60. Calyx Fusion | 2. irregular rupture of apex | \%, not eonstricted"/4.4. |
| 1. lobes form a slobutar sae | 3. operculate (lid or chalice) | 2. constricted |
| 2. Inhesf fee ir partly fused | 4. apical valves between septa | 77. Filament Insertion |
| 3. Ioher partiy fiseld (feetine\%) | 5. lateral pores between septa | 1. low amil near base |
| 61. Calyx Appendages | 6. lateral vertical slits | 2. high and near corolta mouth |
| 1. absent | 7. irregular horizontal slits |  |
| 2. mimute or lestigiat | 8. loculicidal |  |
| 3. small and simple | 9. splitting into three hard facets |  |
| 4. medium large: iften etaborate | 10. short apical slits or pores |  |
| 5. accrescent, embracing capsute. | 11.apical hole |  |
| 6. Iobules in intertobutar simusers | 12.5 vertically splitting segments |  |

Table. 16. Characters used in the Pollen data set (CampPal.DAT) for phenetic analyses. State changes are listed below each character. The scoring for the full data matrix is given in the Appendix 12.1.1.7-10.


Table 17. Characters used in the seeds data set (CampSeed.DAT) for phenetic analyses. State changes are listed below each character. The scoring for the full data matrix is given in the Appendix 12.1.1.11-14.

| CHARACTERS USED IN THE SEEDS DATA SET |  |  |
| :---: | :---: | :---: |
| 1. Degree of Symmetry | 5. Seed Surface | 12. Discontinuous Thickening |
| 1. High | 1. shiny | 1. present |
| 2. Viedilim | 2. dull | 2. absent |
| 3. Low | 6. Testa Surface (Scutpturing) | 13. Beaded Longitudinal Walls |
| 2. Seed Shape (ratio) | 1. shallowly furrowed2. smooth | 1. present |
| \%. elliptical ( $2: 173: 2)$ |  | 2. absent |
| 2. narrow elliptical (6.133.1) | 3. tuberculate | 14. Second.Orn. Radial Walls |
| 3. broad alliptical (0.5) | 4. pebbled |  |
| 4. transverse elliptical (2:3.122) | 5. striate | 2. wrrted |
| 5. narrow trantvieltiplic (1:311:\%) |  | 3. stippled |
| 6. bromd transverse , elliptic (5.6). | 6. shallowly colliculate 7. reticulate | 4. idged <br> 5. channeled |
| 7. circuiar (1)1) | 7. reticulate 8. rugose |  |
| 8. ovite (2:13\% 2 ) | 7. Striation: <br> 1. incomplete <br> 2. fine <br> 3. ribbed | 15. Second. Orn. Tang. Walls |
| 9. Atrrom arate (6.133) |  | 1. alveotate <br> 2. Ingulosely strinte <br> 3. chamieled <br> 4. ridged <br> 5 sitipled <br> 6. warted <br> 7. keeled |
| 10. hroat orite 66.5 s$)$ |  |  |
| 11. Framsurse onme (2:31:2) |  |  |
|  | 8. Reticulations |  |
| 13. obnaver (2:13:32) | 1. polygonal2. trapezoid |  |
| 14. natran obovate (6, 1011) |  |  |
| Si. broal obinvale (ta:3) | 3. irregular |  |
| 10. inmmerse abomate (2:30.22) | 4. rectangular with broad areoles | 16. Seed Wings |
| 1. hroal tran\#whovate (1/15\%t\%) | 5. rectangular with narrow areoles <br> 6. scalariform | 1. Ilevetop, both sifles long aris |
| 13. quatrangutar |  | 2. ievilop.one sitle long ints |
| 19. fusiform | 9. Sliape of Testa Cetls | 3. vesigial both sittes long nxil |
| 20. turbinate | 1. fibriform | 4. yestiginl one side lo ng ands |
| 21. conicat |  | 5. Ievetop. hillum enti ontl. |
| 3. Seed Shape (Cross-Section) | 3. isodiametric <br> 4. irregular | 6. vestigint hilum ent anly |
| I tercte |  | 7. tevelog termunl end only |
| 2. semilerete | 5. fusiform | \& vestigint iemmat end only |
| 3 isuate | 10. Lumen of Testa Cells | 9. teveloped ani continuous |
| 4. shovate | 1. narrow | 10. vestigtal ind eomimums |
| 5. triangular | 2. medium | 11. ahsent |
| 6. Flatterter | 3. large | 17. Hilum |
| 7. Ieniticular | 4. broad | 1. Iruncate amiflattened in TS |
| 8. etlipitical | 5. wide | 2. Impered <br> 3. Iruncate and round in TS |
| \%. quiatrangutar | 11. Wall Thickness (Iesta) |  |
| 4. Seed Colour |  | 4. irregular |
| 1. blach or blockish | 2. medium |  |
| 2. dirth brown or ehesthut | 3. thin |  |
| 3. tight brown or pate tawny | 4. variable |  |
| 4. cream. vellom or whitte |  |  |

### 7.1.3 Character Analyses and Similarity Coefficients

The characters in these data sets were then investigated for information content in and between characters in order to assess their distribution and possible correlation. This was done by the "CHANAL" (Character Analysis) program of PANKEY. The information statistic H, (Estabrook, 1967), was calculated for each character and the conditional information of character $a$ on character $b(H(a / b))$ and vice-versa $(H(b / a))$ plus the information held by both $a$ and $b(H(a . b))$ was also calculated. Generally, a high value for $H$ corresponds to characters which are fully scored in the data set, have well distributed states and which do not vary within species (Pankhurst, 1995). Multi-state characters usually have a higher value than binary characters. For further details of this procedure, see Pankhurst (1991, 1995). The value $S$, which is a measure of the correlation between two characters, was also calculated for all character-pair permutations. When two characters have $S=1.0$ they are exactly correlated and when $S=0$ they are independent. Character pair summaries from the output files of CHANAL are given in Tables 18-21. and the results of each analysis are discussed below. Matrices of similarity coefficients were then obtained for each data file from the program "SC3" of PANKEY. This program reads data in DELTA format and then outputs a file with a lower triangular matrix of similarity coefficients.

### 7.1.4 Ordination Methods

Since clustering methods will always find clusters even if they do not actually exist in the data, a check was made first on the presence of clusters in each data set by using several ordination methods such as principal coordinates analyses and non-metric multidimensional scaling (Kruskal, 1964a, 1964b) with the programs "EIGEN" and "MDSCALE" respectively, and viewing with the graphics programs "MOD3D" and "MXPLOT" of the NTSYS v. 1.7 package (Rohlf, 1992). The resultant plots were then visually inspected for the presence of clusters. The 3-dimensional plots are best interpreted on a computer screen since they can be rotated to reveal the exact position of each point. Pins which connect each point to the base have been provided in each text figure in order to help locate their positions. The results of these procedures are shown below. The similarity matrix files from PANKEY were first double-centred by the program "DCENTER". When the matrices are double-centred, the row and column means are subtracted from each element and the grand
mean is added on (Rohlf, 1992). This program therefore transforms the symmetric similarity matrices to scalar product forms in order to compute eigenvalues and eigenvectors for a principal coordinates analysis of each dataset. The ouput file from the DCENTER program was then factored by the program EIGEN using the default scaling (SQRT:LAMDA) and the elements of the eigenvectors corresponding to positive eigenvalues can be interpreted as the coordinates of each point in cartesian space. The data is not normalised, therefore the correct relationships among the points are shown. According to Rohlf (1982), when there are missing values in the data sets, principal coordinates analysis performs better than principal component analysis. In any case principal components analysis was inapplicable in this study since it can only be applied to strictly quantitative characters (Pankhurst, 1991).

Multidimensional scaling can correct for distortion in principal coordinates plotted in 3dimensional space because it tends to preserve the interpoint (taxonomic) distances more faithfully (Rohlf, 1992), ie. greater or lesser distances are preserved. The position of the points in $k$-dimensional space is scaled by using the differences between actual distances and the transformed distances (= "stress"). Stress is therefore a measure of the fit of the distances in the configuration space to the monotone function of the original distances. In the multidimensional scaling analyses the eigenvectors from the principal coordinates output files (.EVE) were used as initial configuration matrices. Final stress values for 3 dimensions using a maximum of 40 iterations and the default stress coefficient (2) are given in each table. These give a measure of fit of the data to the 3 -dimensional plot. A value of 0.00 is a perfect fit while values $>0.20$ are considered poor.

### 7.1.5 Clustering Methods

A minimum-spanning tree, which simply connects each taxon with the most similar taxon, is another way of assessing clusters and, if plotted on to ordinations, is useful in the detection of points which may seem close but are actually far apart when other dimensions are considered. A minimum spanning-tree for each of the data sets was calculated using the program "MST" and these were projected on to the principal coordinates plots.

The output files were then converted into phenograms for each of the data files (including subsets of each file) by the SAHN clustering programs in NTSYS. It is essential that some consideration be given to the characters used because the way in which the similarity coefficient is calculated depends on the type of character and the nature and degree of its variation (Dunn \& Everitt, 1982). Different coefficients estimate different aspects of the taxonomic relationship (Sneath \& Sokal, 1973). Many characters are presence/absence type and scoring them as binary is straightforward. However, many morphological characters show a range of states which may be quite subtle whether ordered or unordered. Treating such characters as binary is far too crude and would affect the accuracy of the similarity measures as well as, ultimately, the phenogram. The Simple Matching Coefficient (Sokal \& Michener, 1958) which is the ratio of the total number of matches to the total number of characters, and the Jaccard Coefficient (Jaccard, 1908) which is the ratio of the number of positive matches to the total number of characters minus the number of negative matches, may only be used with binary characters which are not variable within the OTUs being compared. The SC3 program scores characters in four different ways and uses the Gower Coefficient (Gower, 1971) which allows both quantitative and qualitative data with more than two states to be used in the same set. Allowances are also made for character variation within OTUs and a modified Gower Coefficient is then used. See Pankhurst (1991) and Dunn \& Everitt (1982) for full details of similarity measures in phenetic analyses.

Various clustering algorithms were used, eg. Complete/Single/Average Linkage (the latter is also known as UPGMA) (Rohlf, 1992; see also Sneath \& Sokal, 1973; Dunn \& Everitt, 1982). Single-linkage, Complete Linkage and UPGMA clustering methods were tried in order to determine the distinctness of the clusters. If results are similar then the clusters are usually distinct ("ball" clusters). Strict Consensus trees were also obtained by the program NT-SYS using the program "CONSENSUS". "Ball clusters" can be confirmed particularly by the use of strict consensus methods. Consensus indices were obtained for each permutation of the three clustering methods (see below for discussion on consensus indices). Clustering methods used in this study were agglomerative. For a discussion of these and the pros and cons of different linkages methods, see Cormack (1971). In general single linkage tends to exaggerate similarity between groups and links groups in a chain-like tree topology
but it may fail to resolve relatively distinct groups if a number of intermediate OTUs are present (Dunn \& Everitt, 1982). Complete linkage shows the more cohesive clusters but may not capture less obvious cases. Average linkage is a compromise between the other two and is generally favoured among phenetic systematists.

The goodness of fit of the data to the phenograms produced by the UPGMA clustering method of the SAHN programs of NTSYS was assessed by means of the Cophenetic Correlation Coefficient (Sokal \& Rohlf, 1962). This is a measure of the similarity between the common nodes linking two taxa in the dendrogram and is used because the dendrogram tends to distort the true relation between individual pairs of taxa (Pankhurst, 1991). This similarity is often lower than direct similarity between two taxa and the higher the correlation, the better is the fit of the data with the phenogram. UPGMA usually gives the highest values so only these were calculated for each data set. To obtain these, cophenetic matrices were first produced by using the program "COPH" of NTSYS and the cophenetic correlation coefficients computed with the program "MXCOMP". Values given by Rohlf (1992) are as follows: $0.9=($ or $<) r \ldots$ very good fit; $0.8=($ or $<) r<0.9 \ldots$ good fit; $0.7=($ or $<) r<0.8 \ldots$ poor fit and $\mathrm{r}<0.7 \ldots$ very poor fit ( $r=$ product-moment correlation). Values which are $>0.8$ are usually sufficient to reject the null hypothesis.

### 7.1.5.1 Testing heterogeneity of the rival trees using consensus

The different clustering methods usually produce different trees from the same data set which have varying degrees of agreement of their subsets. If two or more trees which are being compared are identical in their subset relations, the resulting consensus tree is fully bifurcating (Rohlf, 1992). Otherwise incompatible subset relationships result in multifurcating branches. It is necessary to evaluate such heterogeneity in order to determine which of the rival phenograms best represent the data set and to identify the most distinct clusters. The comparison of phenograms by consensus is thus a method for evaluating taxonomic congruence or, in other words, the extent to which independent phenograms for the same set of taxa support the same groupings. The most commonly used approach is the consensus tree that summarises areas of agreement among the conflicting trees. Consensus techniques were originally designed to handle the problem of different data sets rather than
the problem of multiple trees from a single data set Carpenter (1988). Consensus indices of given trees give a numerical measure how well resolved they are (ie. fully bifurcating or not) ie. the amount of structure retained by a consensus tree provides a measure of congruence among the conflicting trees. A highly resolved consensus tree $=$ high congruence. Conversely, the consensus tree also can provide an index of how each phenogram differed (degree of incongruence) from the consensus. In situations where different phenograms are produced from different data sets (but with identical taxa) consensus methods give equal weight to each data set. Thus the potential for data sets with relatively large numbers of characters to swamp data sets with fewer characters is reduced (Kluge, 1983). The Strict Consensus is conceptually the simplest (Swofford, 1991) and was defined by Sokal and Rohlf (1981) as the unique tree that contains only those groups that appear on all the rival trees. Of all the consensus methods the strict consensus is most likely to yield a result that is consistent with a tree produced from a combined analysis. However, it has a serious flaw. When two trees being compared have identical topology except for one terminal placement, the consensus tree is completely unresolved (Swofford,1991). To overcome this limitation and when several trees are being compared, a majority-rule consensus may be preferred. Those groups that occur on a predetermined proportion of the conflicting trees are retained, eg. more than $50 \%$ or more than $75 \%$. Consensus indices for the phenograms are shown in Table 24.

### 7.1.6 Results

### 7.1.6.1 Character Analyses

Tables 18.-21. show the results for a selection of the ten most informative characters in the G\&B.DAT data set for the Asterales, Flowers.DAT for flowers and fruit characters, CampPal.DAT for pollen characters and CampSeed.DAT for seed characters respectively. All are selected from output files of the character analysis program CHANAL in the PANKEY package. Correlated characters were not subsequently removed from the data set because correlation is a continuous variable and removal of certain characters would amount to a purely arbitrary process. In addition, it was also desirable to record how such characters behaved in the cladistic analyses.

Table. 18 Information in characters of the Asterales data set (G\&B.DAT), plus character pair summaries. (10 highest values).

| Char. | Inf. Stat. (H) |  | Pair <br> a | H(a) | H(b) | H(a/b) | H(b/a) | H(a.b) | S |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 5 | 0.3557 | 10 | 2 | 0.2134 | 0.5138 | 0.0237 | 0.0316 | 0.1897 | 0.7142 |
| 10 | 0.5138 | 19 | 9 | 0.1304 | 0.0791 | 0.0000 | 0.0119 | 0.0237 | 0.6667 |
| 13 | 0.4150 | 20 | 9 | 0.1304 | 0.0632 | 0.0000 | 0.0119 | 0.0237 | 0.6667 |
| 18 | 0.3320 | 20 | 19 | 0.0791 | 0.0632 | 0.0000 | 0.0000 | 0.0632 | 1.0000 |
| 23 | 0.3557 | 37 | 26 | 0.4901 | 0.4743 | 0.0751 | 0.0593 | 0.4150 | 0.7554 |
| 26 | 0.4901 | 43 | 19 | 0.0791 | 0.1423 | 0.0000 | 0.0000 | 0.0395 | 1.0000 |
| 29 | 0.3557 | 43 | 20 | 0.0632 | 0.1423 | 0.0000 | 0.0000 | 0.0316 | 1.0000 |
| 36 | 0.4427 | 43 | 27 | 0.0949 | 0.1423 | 0.0000 | 0.0198 | 0.0593 | 0.7500 |
| 37 | 0.4743 | 44 | 43 | 0.1423 | 0.1383 | 0.0237 | 0.0198 | 0.1186 | 0.7317 |
| 38 | 0.6482 | 46 | 45 | 0.1186 | 0.1186 | 0.0198 | 0.0198 | 0.0988 | 0.7143 |

From Table 18. it can be seen that Character 38 (placentation) has the highest information statistic while character 10 (woody versus herbaceous) has the next best score. The S values (similarity coefficient) indicate that characters 20 (lateral-vein fusion), 19 (confluence of lateral vein-endings) and 43 (micropylar endosperm haustoria) are exactly correlated. Characters 19 and 20 also show a moderate degree of correlation with character 9 (sclerenchymous idioblasts) while character 43 also has a high correlation with character 27 (tapetal cell nuclei) and naturally, character 44 (chalazal endosperm haustoria); character 10 (woody versus herbaceous) has a high correlation with the presence/absence of higher inulins (character 2); character 37 (late style elongation) is highly correlated with character 26 (pollen presentation mechanism); and character 46 (basal cell contribution to embryo) has a high correlation with character 45 (method of division of the terminal cell of the proembryo).

Table 19. Information in characters of the flowers \& fruits data set (Flowers.DAT), plus character pair summaries. ( 10 highest values).

| Char. | Inf.Stat. <br> (H) |  | Pair <br> a | H(a) | H(b) | H(a/b) | H(b/a) | H(a.b) | S |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 0.4587 | 3 | 2 | 0.0308 | 0.0308 | 0.0000 | 0.0000 | 0.0308 | 1.0000 |
| 7 | 0.4111 | 15 | 2 | 0.0308 | 0.0308 | 0.0000 | 0.0000 | 0.0308 | 1.0000 |
| 9 | 0.4750 | 15 | 3 | 0.0308 | 0.0308 | 0.0000 | 0.0000 | 0.0308 | 1.0000 |
| 19 | 0.6327 | 23 | 5 | 0.3058 | 0.3212 | 0.0303 | 0.0447 | 0.2755 | 0.7860 |
| 20 | 0.4269 | 29 | 18 | 0.0010 | 0.4769 | 0.0000 | 0.0005 | 0.0010 | 0.6667 |
| 26 | 0.4813 | 35 | 12 | 0.0293 | 0.0308 | 0.0000 | 0.0014 | 0.0293 | 0.9531 |
| 27 | 0.4663 | 37 | 18 | 0.0010 | 0.1918 | 0.0000 | 0.0000 | 0.0010 | 1.0000 |
| 29 | 0.4769 | 4 | 14 | 0.0880 | 0.0880 | 0.0014 | 0.0014 | 0.0865 | 0.9677 |
| 31 | 0.6183 | 46 | 18 | 0.0010 | 0.0630 | 0.0000 | 0.0000 | 0.0010 | 1.0000 |
| 45 | 0.4678 | 48 | 7 | 0.4111 | 0.1226 | 0.0303 | 0.0332 | 0.0678 | 0.5165 |

From Table 19. it can be seen that character 19 (filament bases) has the highest information statistic while character 31 (style/presenter shape) has the next highest score. Characters 2 (flower symmetry), 3 (presence/absence of resupination) and 15 (presence/absence of fused staminal column) are exactly correlated, as are characters 37 (ovule number) and 18 (level of filament insertion). Character 18 is exactly correlated with character 46 (mode of apical dehiscence) and moderately correlated with character 29 (style accrescence). Characters 41 (fruit type) and 14 (presence/absence of a weakly caducous corolla), and characters 35 (placentation) and 12 (presence/absence of distinct main veins) are almost exactly correlated. Characters 23 (pollen aperture type) and 5 (flower bud shape) are highly correlated, while character 48 (mode of porate dehiscence) is moderately correlated with character 7 (presence/absence of non-campanulate corollas).

Table 20. Information in characters of the pollen data set (CampPal.DAT), plus character pair summaries ( 10 highest values)

| Char. | Inf.Stat. <br> (H) |  | $\begin{aligned} & \text { Pair } \\ & \text { a } \end{aligned}$ | H(a) | H(b) | H(a/b) | H(b/a) | H(a.b) | S |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 0.0526 | 8 | 7 | 0.0085 | 0.0939 | 0.0028 | 0.0057 | 0.0057 | 0.4000 |
| 2 | 0.2802 | 10 | 4 | 0.3841 | 0.0370 | 0.0071 | 0.0185 | 0.0185 | 0.4194 |
| 3 | 0.0797 | 10 | 7 | 0.0085 | 0.0370 | 0.0000 | 0.0014 | 0.0014 | 0.5000 |
| 4 | 0.3841 | 10 | 9 | 0.0384 | 0.0370 | 0.0000 | 0.0199 | 0.0171 | 0.4615 |
| 5 | 0.0725 | 12 | 4 | 0.3841 | 0.0256 | 0.0028 | 0.0085 | 0.0171 | 0.6000 |
| 8 | 0.0939 | 12 | 8 | 0.0939 | 0.0256 | 0.0043 | 0.0100 | 0.0156 | 0.5238 |
| 9 | 0.0384 | 12 | 10 | 0.0370 | 0.0256 | 0.0171 | 0.0043 | 0.0128 | 0.3750 |
| 10 | 0.0370 | 13 | 4 | 0.3841 | 0.0256 | 0.0100 | 0.0100 | 0.0156 | 0.4400 |
| 12 | 0.0256 | 13 | 7 | 0.0085 | 0.0256 | 0.0000 | 0.0014 | 0.0014 | 0.5000 |
| 13 | 0.0256 | 13 | 10 | 0.0370 | 0.0256 | 0.0156 | 0.0043 | 0.0213 | 0.5172 |

From Table 20. it can be seen that character 4 (aperture type) has the highest information statistic and that character 2 (equatorial shape) has the next highest score. No characters show exact correlation although characters 12 (division of the footlayer) and 4 (aperture type) show a moderate correlation. Character 4 also has a rather weak correlation with character 10 (bacula) and character 13 (endexine). Character 12 also has a moderate correlation with character 8 (sculpturing) and a weak correlation with character 10 , while character 8 also has a rather weak correlation with character 7 (number of colpi). Characters 7,10 and 13 all have a moderate degree of correlation with each other while 10 has a rather weak correlation with character 9 (tectum).

Table 21. Information in characters of the seed data set (CampSeed.DAT), plus character pair summaries ( $\mathbf{1 0}$ highest values)

| Char. | Inf.Stat. <br> (H) |  | ir | H(a) | H(b) | H(a/b) | H(b/a) | H(a.b) | S |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 0.2917 | 8 | 4 | 0.4913 | 0.3099 | 0.2438 | 0.0624 | 0.2475 | 0. 4469 |
| 2 | 0.5029 | 9 | 2 | 0.5029 | 0.6618 | 0.1546 | 0.2895 | 0.3483 | 0.4396 |
| 3 | 0.3077 | 9 | 4 | 0.4913 | 0.6618 | 0.1611 | 0.3316 | 0.3302 | 0.4012 |
| 4 | 0.4913 | 111 | 4 | 0.4913 | 0.3665 | 0.2504 | 0.1255 | 0.2409 | 0.4012 |
| 5 | 0.1067 | 6 | 4 | 0.4913 | 0.3403 | 0.2583 | 0.1074 | 0.2329 | 0.3891 |
| 6 | 0.3403 | 4 | 2 | 0.5029 | 0.4913 | 0.2431 | 0.2032 | 0.2598 | 0.3679 |
| 7 | 0.2954 | 11 | 6 | 0.3403 | 0.3665 | 0.1662 | 0.1923 | 0.1742 | 0.3270 |
| 8 | 0.3099 | 4 | 3 | 0.3077 | 0.4913 | 0.1132 | 0.2968 | 0.1945 | 0.3217 |
| 9 | 0.6618 | 11 | 8 | 0.3099 | 0.3665 | 0.1466 | 0.2032 | 0.1633 | 0.3182 |
| 10 | 0.1509 | 8 | 6 | 0.3403 | 0.3099 | 0.1858 | 0.1553 | 0.1546 | 0.3119 |

From Table 21. it can be seen that character 9 (seed wings) has the highest information statistic and character 2 (seed shape) the next highest score. No characters show exact correlation and most characters are relatively independent. The highest similarity coefficient $(\mathrm{S})$ is 0.4469 for characters 8 (secondary ornamentation of radial walls) and 4 (testa surface sculpturing) which is rather low.

### 7.1.6.2 Ordination analyses

The transformed variables are shown in Table 22. for the first 3 eigenvectors. The cumulative percentage variations are $53.57 \%, 32.64 \%, 56.58 \%$ and $31.68 \%$ respectively for each data set which means that the plots in Figs.10-13;14-17 and 18-21 are based on only those percentages of the total data in each set. The very low value for the Flowers \& Fruits and Seed data sets can perhaps be explained by the amount of missing data in the set, the large number of taxa and the unevenness of scoring. Nevertheless, even with only about $32 \%$ of the total data both plots look remarkably congruent with those from the other datasets.

Table 22. Eigenvalues (1st three) for the data sets (G\&B.DAT, Flowers.DAT, CampPal.DAT and CampSeed.DAT)

| DATA SET | i | Eigenvalue | Percent | Cumulative |
| :---: | :---: | :---: | :---: | :---: |
| Asterales (G\&B.DAT) | 1 | 2.74980 | 29.92 | 29.92 |
|  | 2 | 1.33221 | 14.50 | 44.42 |
|  | 3 | 0.84127 | 9.15 | 53.57 |
| Flowers \& Fruits (Flowers.DAT) | 1 | 3.49224 | 16.71 | 16.71 |
|  | 2 | 1.74019 | 8.33 | 25.04 |
|  | 3 | 1.58840 | 7.60 | 32.64 |
| Pollen (CampPal.DAT) | 1 | 5.12421 | 34.91 | 34.91 |
|  | 2 | 1.67833 | 11.44 | 46.35 |
|  | 3 | 1.50077 | 10.23 | 56.58 |
| Seeds (CampSeed.DAT) | 1 | 3.92407 | 12.52 | 12.52 |
|  | 2 | 3.57162 | 11.39 | 23.91 |
|  | 3 | 2.43699 | 7.77 | 31.68 |

Figs. 10-11, 14-15 and 18-19 show the principal coordinates and multi-dimensional scaled distances projected in 3-dimensional space respectively, while Figs.12-13, 16-17, 11-12 and 20-21 show plots of the new variables 1 against 2, and 1 against 3 respectively.

## a. The Asterales (G\&B.DAT) data sets

In the MOD3D plot (Fig.10) there is a loose cluster of the 7 families: Sambucaceae (7), Viburnaceae (8), Pittosporaceae (6), Aquifoliaceae (1), Araliaceae (2), and Bruniaceae (3), with the Aquifoliaceae, Bruniaceae and Viburnaceae clustering most closely. The Pittosporaceae are closest to the Araliaceae while the Sambucaceae are closest to the Viburnaceae. The best cluster is that formed by the 5 families: Campanulaceae (18), Lobeliaceae (22), Cyphiaceae (19), Cyphocarpaceae (20) and Nemacladaceae (23). Within this cluster the Lobeliaceae is closer to the Cyphiaceae and Cyphocarpaceae and rather less so to the Campanulaceae. The Nemacladaceae are most distant. The Campanulaceae clusters most closely with the Lobeliaceae. Collectively this cluster is closest to the Goodeniaceae (21) which itself is a little more distant from the Brunoniaceae (16). The Calyceraceae (17) is closest to the Brunoniaceae and the Asteraceae (15) is next closest. These four families form a very loose cluster which also includes the Menyanthaceae (11). Finally, there is a rather loose cluster formed by the Stylidiaceae (14) and Sphenocleaceae (13) and more distantly with the Donatiaceae (10). Pentaphragmataceae (12) is rather distant from Cyphiaceae and closest to Argophyllaceae (9) and Escalloniaceae (4) which are closest to each other and collectively a little less so to the Griseliniaceae (5). The MDSCALE (Fig.11) plot is essentially very similar to the MOD3D plot apart from minor differences in interpoint distances.

List of Taxa and Numbers for the Asterales (G\&B.DAT) data set

1. Aquifoliaceae
2. Araliaceae
3. Bruniaceae
4. Escalloniaceae
5. Griseliniaceae
6. Pittosporaceae
7. Sambucaceae
8. Viburnaceae
9. Argophyllaceae
10. Donatiaceae
11. Menyanthaceae
12. Pentaphragmataceae
13. Sphenocleaceae
14. Stylidiaceae
15. Asteraceae
16. Brunoniaceae
17. Calyceraceae
18. Campanulaceae
19. Cyphiaceae
20. Cyphocarpaceae
21. Goodeniaceae
22. Lobeliaceae
23. Nemacladaceae


Fig. 10. Principal coordinates and superimposed minimum-spanning tree for the Asterales (G\&B.DAT) data set projected in 3-dimensional space. For explanation of the point numbers, see opposite. For analysis, see text.

List of Taxa and Numbers for the Asterales (G\&B.DAT) data set

1. Aquifoliaceae
2. Araliaceae
3. Bruniaceae
4. Escalloniaceae
5. Griseliniaceae
6. Pittosporaceae
7. Sambucaceae
8. Viburnaceae
9. Argophyllaceae
10. Donatiaceae
11. Menyanthaceae
12. Pentaphragmataceae
13. Sphenocleaceae
14. Stylidiaceae
15. Asteraceae
16. Brunoniaceae
17. Calyceraceae
18. Campanulaceae
19. Cyphiaceae
20. Cyphocarpaceae
21. Goodeniaceae
22. Lobeliaceae
23. Nemacladaceae

## Aster ales (MDSCALE)



Fig.11. Multi-dimensional scaled taxonomic distances and superimposed minimumspanning tree for the Asterales (G\&B.DAT) data set projected in 3-dimensional space. For explanation of the point numbers, see opposite. For analysis, see text.

List of Taxa and Numbers for the Asterales (G\&B.DAT) data set

1. Aquifoliaceae
2. Araliaceae
3. Bruniaceae
4. Escalloniaceae
5. Griseliniaceae
6. Pittosporaceae
7. Sambucaceae
8. Viburnaceae
9. Argophyllaceae
10. Donatiaceae
11. Menyanthaceae
12. Pentaphragmataceae
13. Sphenocleaceae
14. Stylidiaceae
15. Asteraceae
16. Brunoniaceae
17. Calyceraceae
18. Campanulaceae
19. Cyphiaceae
20. Cyphocarpaceae
21. Goodeniaceae
22. Lobeliaceae
23. Nemacladaceae


Fig. 12. Principal coordinates 1 and 2 for the Asterales (G\&B.DAT) data set and superimposed minimum-spanning tree. For explanation of the point numbers, see opposite.

List of Taxa and Numbers for the Asterales (G\&B.DAT) data set

1. Aquifoliaceae
2. Araliaceae
3. Bruniaceae
4. Escalloniaceae
5. Griseliniaceae
6. Pittosporaceae
7. Sambucaceae
8. Viburnaceae
9. Argophyllaceae
10. Donatiaceae
11. Menyanthaceae
12. Pentaphragmataceae
13. Sphenocleaceae
14. Stylidiaceae
15. Asteraceae
16. Brunoniaceae
17. Calyceraceae
18. Campanulaceae
19. Cyphiaceae
20. Cyphocarpaceae
21. Goodeniaceae
22. Lobeliaceae
23. Nemacladaceae


Fig.13. Principal coordinates 1 and 3 for the Asterales (G\&B.DAT) data set and superimposed minimum-spanning tree. For explanation of the point numbers, see opposite.

## List of Taxa and Numbers for the Flowers and Fruits (Flowers.DAT) data set

1. Adenophora
2. Astrocodon
3. Asyneuma
4. Azorina
5. Berenice
6. Brachycodon
7. Campanula
8. Campanulastrum
9. Campanumoea
10. Canarina
11. Cephalostigma
12. Codonopsis
13. Craterocapsa
14. Cryptocodon
15. Cyananthus
16. Cyclocodon
17. Cylindrocarpa
18. Diosphaera
19. Echinocodon
20. Edraianthus
21. Feeria
22. Gadellia
23. Githopsis
24. Gunillaea
25. Hanabusaya
26. Heterochaenia
27. Heterocodon
28. "Himalcodon" (Obconicapsula)
29. Homocodon
30. "IsophyIta" group (C.garganica etc.)
31. Jasione
32. Legousia
33. Leptocodon
34. Merciera
35. Michauxia
36. Microcodon
37. Muehlbergella
38. Musschia
39. Namacodon
40. Nesocodon
41. Ostrowskia
42. Peracarpa
43. Petkovia
44. Petromarula
45. Phyteuma
46. Physoplexis
47. Platycodon
48. Popoviocodonia
49. Prismatocarpus
50. Lobelia
51. Pseudocodonopsis
52. Rapunculus
53. Rhigiophyllum
54. Roella
55. Roucela
56. Sergia
57. Sicyocodon
58. Siphocodon
59. Symphyandra
60. Theilera
61. Trachelium
62. Treichelia
63. Triodanis
64. Wahlenbergia
65. Zeugandra


Fig.14. Principal coordinates and superimposed minimum-spanning tree for the Flowers \& Fruits (Flowers.DAT) data set projected in 3-dimensional space. For explanation of the point numbers, see opposite. For analysis, see text.

## List of Taxa and Numbers for the Flowers and Fruits (Flowers.DAT) data set

1. Adenophora
2. Astrocodon
3. Asyneuma
4. Azorina
5. Berenice
6. Brachycodon
7. Campanula
8. Campanulastrum
9. Campanumoea
10. Canarina
11. Cephalostigma
12. Codonopsis
13. Craterocapsa
14. Cryptocodon
15. Cyananthus
16. Cyclocodon
17. Cylindrocarpa
18. Diosphaera
19. Echinocodon
20. Edraianthus
21. Feeria
22. Gadellia
23. Githopsis
24. Gunillaea
25. Hanabusaya
26. Heterochaenia
27. Heterocodon
28. "Himalcodon" (Obconicapsula)
29. Homocodon
30. "Isophylla" group (C.garganica etc.)
31. Jasione
32. Legousia
33. Leptocodon
34. Merciera
35. Michauxia
36. Microcodon
37. Muehlbergella
38. Musschia
39. Namacodon
40. Nesocodon
41. Ostrowskia
42. Peracarpa
43. Petkovia
44. Petromarula
45. Phyteuma
46. Physoplexis
47. Platycodon
48. Popoviocodonia
49. Prismatocarpus
50. Lobelia
51. Pseudocodonopsis
52. Rapunculus
53. RhigiophyIlum
54. Roella
55. Roucela
56. Sergia
57. Sicyocodon
58. Siphocodon
59. Symphyandra
60. Theilera
61. Trachelium
62. Treichelia
63. Triodanis
64. Wahlenbergia
65. Zeugandra


Fig.15. Multi-dimensional scaled taxonomic distances and superimposed minimumspanning tree for the Flowers \& Fruits (Flowers.DAT) data set projected in 3dimensional space. For explanation of the point numbers, see opposite. For analysis, see text.

## List of Taxa and Numbers for the Flowers and Fruits (Flowers.DAT) data set

| 1. Adenophora | 34. Merciera |
| :---: | :---: |
| 2. Astrocodon | 35. Michauxia |
| 3. Asyneuma | 36. Microcodon |
| 4. Azorina | 37. Muehlbergella |
| 5. Berenice | 38. Musschia |
| 6. Brachycodon | 39. Namacodon |
| 7. Campanula | 40. Nesocodon |
| 8. Campanulastrum | 41. Ostrowskia |
| 9. Campanumoea | 42. Peracarpa |
| 10. Canarina | 43. Petkovia |
| 11. Cephalostigma | 44. Petromarula |
| 12. Codonopsis | 45. Phyteuma |
| 13. Craterocapsa | 46. Physoplexis |
| 14. Cryptocodon | 47. Platycodon |
| 15. Cyananthus | 48. Popoviocodonia |
| 16. Cyclocodon | 49. Prismatocarpus |
| 17. Cylindrocarpa | 50. Lobelia |
| 18. Diosphaera | 51. Pseudocodonopsis |
| 19. Echinocodon | 52. Rapunculus |
| 20. Edraianthus | 53. Rhigiophyllum |
| 21. Feeria | 54. Roella |
| 22. Gadellia | 55. Roucela |
| 23. Githopsis | 56. Sergia |
| 24. Gunillaea | 57. Sicyocodon |
| 25. Hanabusaya | 58. Siphocodon |
| 26. Heterochaenia | 59. Symphyandra |
| 27. Heterocodon | 60. Theilera |
| 28. "Himalcodon" (Obconicapsula) | 61. Trachelium |
| 29. Homocodon | 62. Treichelia |
| 30. "Isophylla" group (C.garganica etc.) | 63. Triodanis |
| 31. Jasione | 64. Wahlenbergia |
| 32. Legousia | 65. Zeugandra |
| 33. Leptocodon |  |

33. Leptocodon


Fig.16. Principal coordinates 1 and 2 for the Flowers \& Fruits (Flowers.DAT) data set
and superimposed minimum-spanning tree. For explanation of the point numbers, see
opposite.

## List of Taxa and Numbers for the Flowers and Fruits (Flowers.DAT) data set

1. Adenophora
2. Astrocodon
3. Asyneuma
4. Azorina
5. Berenice
6. Brachycodon
7. Campanula
8. Campanulastrum
9. Campanumoea
10. Canarina
11. Cephalostigma
12. Codonopsis
13. Craterocapsa
14. Cryptocodon
15. Cyananthus
16. Cyclocodon
17. Cylindrocarpa
18. Diosphaera
19. Echinocodon
20. Edraianthus
21. Feeria
22. Gadellia
23. Githopsis
24. Gunillaea
25. Hanabusaya
26. Heterochaenia
27. Heterocodon
28. "Himalcodon" (Obconicapsula)
29. Homocodon
30. "Isophy/fa" group (C.garganica ete.)
31. Jasione
32. Legousia
33. Leptocodon
34. Merciera
35. Michauxia
36. Microcodon
37. Muehlbergella
38. Musschia
39. Namacodon
40. Nesocodon
41. Ostrowskia
42. Peracarpa
43. Petkovia
44. Petromarula
45. Phyteuma
46. Physoplexis
47. Platycodon
48. Popoviocodonia
49. Prismatocarpus
50. Lobelia
51. Pseudocodonopsis
52. Rapunculus
53. Rhigiophyllum
54. Roella
55. Roucela
56. Sergia
57. Sicyocodon
58. Siphocodon
59. Symphyandra
60. Theilera
61. Trachelium
62. Treichelia
63. Triodartis
64. Wahlenbergia
65. Teugandra


Fig.17. Principal coordinates 1 and 3 for the Flowers \& Fruits (Flowers.DAT) data set opposite.

List of Taxa and Numbers for the Pollen (CampPal.DAT) data set

| 1. Adenophora | 20. Leptocodon |
| :--- | :--- |
| 2. Asyneuma | 21. Michauxia |
| 3. Campanula | 22. Musschia |
| 4. Campanulastrum | 23. Namacodon |
| 5. Campanumoea | 24. Nesocodon |
| 6. Canarina | 25. Ostrowskia |
| 7. Codonopsis | 26. Peracarpa |
| 8. Cyananthus | 27. Phyteuma |
| 9. Echinocodon | 28. Physoplexis |
| 10. Edraianthus | 29. Platycodon |
| 11. Gadellia | 30. Prismatocarpus |
| 12. Githopsis | 31. Pseudocodonopsis |
| 13. Gunillaea | 32. Rapunculus |
| 14. Hanabusaya | 33. Roella |
| 15. Heterochaenia | 34. Roucela |
| 16. Homocodon | 35. Symphyandra |
| 17. "Isophylla" | 36. Trachelium |
| 18. Jasione | 37. Wahlenbergia |
| 19. Legousia | 38. Lobelia |

## Pollen (PCOORDA + MST)



Fig. 18. Principal coordinates and superimposed minimum-spanning tree for the Pollen (Camppal.DAT) data set projected in 3-dimensional space. For explanation of the point numbers, see opposite. For analysis, see text.

List of Taxa and Numbers for the Pollen (CampPal.DAT) data set

1. Adenophora
2. Asyneuma
3. Campanula
4. Campanulastrum
5. Campanumoea
6. Canarina
7. Codonopsis
8. Cyananthus
9. Echinocodon
10. Edraianthus
11. Gadellia
12. Githopsis
13. Gunillaea
14. Hanabusaya
15. Heterochaenia
16. Homocodon
17. "Isophylla"
18. Jasione
19. Legousia
20. Leptocodon
21. Michauxia
22. Musschia
23. Namacodon
24. Nesocodon
25. Ostrowskia
26. Peracarpa
27. Phyteuma
28. Physoplexis
29. Platycodon
30. Prismatocarpus
31. Pseudocodonopsis
32. Rapunculus
33. Roella
34. Roucela
35. Symphyandra
36. Trachelium
37. Wahlenbergia
38. Lobelia

## Pollen (MDSCALE)



Fig.19. Multi-dimensional scaled taxonomic distances and superimposed minimumspanning tree for the Pollen (Camppal.DAT) data set projected in 3-dimensional space. For explanation of the point numbers, see opposite. For analysis, see text.

List of Taxa and Numbers for the Pollen (CampPal.DAT) data set

1. Adenophora
2. Leptocodon
3. Asyneuma
4. Campanula
5. Campanulastrum
6. Campanumoea
7. Canarina
8. Codonopsis
9. Cyananthus
10. Echinocodon
11. Edraianthus
12. Gadellia
13. Githopsis
14. Gunillaea
15. Hanabusaya
16. Heterochaenia
17. Homocodon
18. "Isophylla"
19. Jasione
20. Legousia
21. Michauxia
22. Musschia
23. Namacodon
24. Nesocodon
25. Ostrowskia
26. Peracarpa
27. Phyteuma
28. Physoplexis
29. Platycodon
30. Prismatocarpus
31. Pseudocodonopsis
32. Rapunculus
33. Roella
34. Roucela
35. Symphyandra
36. Trachelium
37. Wahlenbergia
38. Lobelia

## Pollen (PCOORDA + MST)



Fig.20. Principal coordinates 1 and 2 for the Pollen (Camppal.DAT) data set and superimposed minimum spanning tree. For explanation of the point numbers, see opposite.

List of Taxa and Numbers for the Pollen (CampPal.DAT) data set

| 1. Adenophora | 20. Leptocodon |
| :--- | :--- |
| 2. Asyneuma | 21. Michauxia |
| 3. Campanula | 22. Musschia |
| 4. Campanulastrum | 23. Namacodon |
| 5. Campanumoea | 24. Nesocodon |
| 6. Canarina | 25. Ostrowskia |
| 7. Codonopsis | 26. Peracarpa |
| 8. Cyananthus | 27. Phyteuma |
| 9. Echinocodon | 28. Physoplexis |
| 10. Edraianthus | 29. Platycodon |
| 11. Gadellia | 30. Prismatocarpus |
| 12. Githopsis | 31. Pseudocodonopsis |
| 13. Gunillaea | 32. Rapunculus |
| 14. Hanabusaya | 33. Roella |
| 15. Heterochaenia | 34. Roucela |
| 16. Homocodon | 35. Symphyandra |
| 17. "Isophylla" | 36. Trachelium |
| 18. Jasione | 37. Wahlenbergia |
| 19. Legousia | 38. Lobelia |



[^0]Taxa and Numbers for the Seeds (Campseed.DAT) data set (data matrix compiled from the species listed in brackets)

1. Adenophora (A. bulleyana, A. confusa, A. hakusanensis, A. liliifolia)
2. Asyneuma (A. japonica, A. michauxioides, A. canescens)
3. Azorina (A. vidalii)
4. Brachycodon (B. fastigiata)
5. Campanulastrum (C. americanum)
6. "Iberocodon" (C. arvatica)
7. Scapiflorae (C. bellidifolia)
8. Symphyandriformes (C. betulifolia, C. troegerae)
9. Involucratae (C. cervicaria, C. spicata)
10. Rupestres (C. coriaceae, C. bornmuelleri, C. heterophylla, C. calaminthifolia)
11. Quinqueloculares (C. crispa, C. tomentosa)
12. "Oreocodon" (C. mollis, C. jacobaea, C. edulis, C. alsinoides)
13. Campanula formanekiana
14. Megalocodon (C. incurva)
15. Campanula lanata
16. Campanula lingulata
17. Spinulosae (C. mirabilis)
18. Tulipella (C. punctata var. hondensis)
19. Campanula sartorii
20. Codonosphaera (C. thyrsoides)
21. Codonopsis (C. bulleyana, C. clematidea, C. pilosula)
22. Craterocapsa (C. congesta)
23. Cyananthus (C. Iobatus)
24. Cylindrocarpa (C. sewertzowii)
25. Diosphaera (D. rumelianum)
26. Edraianthus (E. graminifolius, E. serbicus)
27. Gadellia (G. Iactiflora)
28. Githopsis (G. diffusa)
29. "Isophylla" (C. tommasiniana, C. waldsteiniana, C. versicolor, C. zoysii, C. fenestrellata)
30. Jasione (J. heldreichii, J. humilis, J. crispa ssp. crispa, J. laevis)
31. Legousia (L. falcata, L. speculum-veneris)
32. Leptocodon (L. gracilis)
33. Michauxia (M. tchihatchewii, M. laevigata)
34. Musschia (M. wollastoni, M. aurea)
35. Nesocodon (N. mauritianus)
36. Peracarpa ( $P$. circaeoides)
37. Petkovia (C. orphanidea)
38. Petromarula (P. pinnata)
39. Phyteuma (P. pyrenaicum)
40. Platycodon (P. grandiflorum)
41. Rapunculus (C. hawkinsiana, C. aizoon, C. trichocalycina)
42. Melanocalyx (C. unicolor)
43. Pterophyllum (C. primulifolia)
44. Roucela (C. drabifolia, C. erinus)
45. Roella (R. maculata, R. ciliata)
46. Sergia (S. regelii)
47. Symphyandra hoffmannii
48. "Otocalyx" (S. armena)
49. Symphyandra wanneri
50. Trachelium (T. caeruleum)
51. Wahlenbergia (W. gloriosa, W. androsacea, W. congesta)
52. "Helenacodon" (W. angustifolia)
53. "Fernandeziocodon" (W. berteroi, W. grahamae, W. larrainii)

## Seeds (PCOORDA + MST)



Fig.22. Principal coordinates and superimposed minimum-spanning tree for the Seed (Campseed.DAT) data set projected in 3-dimensional space. For explanation of the point numbers, see ooposite. For analysis, see text.

Taxa and Numbers for the Seeds (Campseed.DAT) data set (data matrix compiled from the species listed in brackets)

1. Adenophora (A. bulleyana, A, confusa, A. hakusanensis, A. liliifolia)
2. Asyneuma (A. japonica, A. michauxioides, A. canescens)
3. Azorina (A. vidalii)
4. Brachycodon (B. fastigiata)
5. Campanulastrum (C. americanum)
6. "Iberocodon" (C. arvatica)
7. Scapiflorae (C. bellidifolia)
8. Symphyandriformes (C. betulifolia, C. troegerae)
9. Involucratae (C. cervicaria, C. spicata)
10. Rupestres (C. coriaceae, C. bornmuelleri, C. heterophylla, C. calaminthifolia)
11. Quinqueloculares (C. crispa, C. tomentosa)
12. "Oreocodon" (C. mollis, C. jacobaea, C. edulis, C. alsinoides)
13. Campanula formanekiana
14. Megalocodon (C, incurva)
15. Campanula lanata
16. Campanula lingulata
17. Spinulosae (C. mirabilis)
18. Tulipella (C. punctata var. hondensis)
19. Campanula sartorii
20. Codonosphaera (C. thyrsoides)
21. Codonopsis (C. bulleyana, C. clematidea, C. pilosula)
22. Craterocapsa (C. congesta)
23. Cyananthus (C. Iobatus)
24. Cylindrocarpa (C. sewertzowii)
25. Diosphaera (D. rumelianum)
26. Edraianthus (E. graminifolius, E. serbicus)
27. Gadellia (G. lactiflora)
28. Githopsis (G. diffusa)
29. "Isophylla" (C. tommasiniana, C. waldsteiniana, C. versicolor, C. zoysii, C. fenestrellata)
30. Jasione (J. heldreichii, J. humilis, J. crispa ssp. crispa, J. laevis)
31. Legousia (L. falcata, L. speculum-veneris)
32. Leptocodon (L. gracilis)
33. Michauxia (M. tchihatchewii, M. laevigata)
34. Musschia (M. wollastoni, M. aurea)
35. Nesocodon (N. mauritianus)
36. Peracarpa (P. circaeoides)
37. Petkovia (C. orphanidea)
38. Petromarula (P. pinnata)
39. Phyteuma (P. pyrenaicum)
40. Platycodon (P. grandiflorum)
41. Rapunculus (C. hawkinsiana, C. aizoon, C. trichocalycina)
42. Melanocalyx (C. unicolor)
43. Pterophyllum (C. primulifolia)
44. Roucela (C. drabifolia, C. erinus)
45. Roella (R. maculata, R. ciliata)
46. Sergia (S. regelii)
47. Symphyandra hoffmannii
48. "Otocalyx" (S. armena)
49. Symphyandra wanneri
50. Trachelium (T. caeruleum)
51. Wahlenbergia (W. gloriosa, W. androsacea, W. congesta)
52. "Helenacodon" (W. angustifolia)
53. "Fernandeziocodon" (W. berteroi, W. grahamae, W. larrainii)


Fig.23. Multi-dimensional scaled taxonomic distances and superimposed minimumspanning tree for the Seed (Campseed.DAT) data set projected in 3-dimensional space. For explanation of the point numbers, see opposite. For analysis, see text.

## Taxa and Numbers for the Seeds (Campseed.DAT) data set (data matrix compiled from the species listed in brackets)

1. Adenophora (A. bulleyana, A. confusa, A. hakusanensis, A. Iiliifolia)
2. Asyneuma (A. japonica, A. michauxioides, A. canescens)
3. Azorina (A. vidalii)
4. Brachycodon (B. fastigiata)
5. Campanulastrum (C. americanum)
6. "Iberocodon" (C. arvatica)
7. Scapiflorae (C. bellidifolia)
8. Symphyandriformes (C. betulifolia, C. troegerae)
9. Involucratae (C. cervicaria, C. spicata)
10. Rupestres (C. coriaceae, C. bornmuelleri, C. heterophylla, C. calaminthifolia)
11. Quinqueloculares (C. crispa, C. tomentosa)
12. "Oreocodon" (C. mollis, C. jacobaea, C. edulis, C. alsinoides)
13. Campanula formanekiana
14. Megalocodon (C. incurva)
15. Campanula lanata
16. Campanula lingulata
17. Spinulosae (C. mirabilis)
18. Tulipella (C. punctata var. hondensis)
19. Campanula sartorii
20. Codonosphaera (C. thyrsoides)
21. Codonopsis (C. bulleyana, C. clematidea, C. pilosula)
22. Craterocapsa (C. congesta)
23. Cyananthus (C. Iobatus)
24. Cylindrocarpa (C. sewertzowii)
25. Diosphaera (D. rumelianum)
26. Edraianthus (E. graminifolius, $E$. serbicus)
27. Gadellia (G. lactiflora)
28. Githopsis (G. diffusa)
29. "Isophylla" (C. tommasiniana, C. waldsteiniana, C. versicolor, C. zoysii, C. fenestrellata)
30. Jasione (J. heldreichii, J. humilis, J. crispa ssp. crispa, J. Iaevis)
31. Legousia (L. falcata, L. speculum-veneris)
32. Leptocodon (L. gracilis)
33. Michauxia (M. tchihatchewii, M. laevigata)
34. Musschia (M. wollastoni, M. aurea)
35. Nesocodon (N. mauritianus)
36. Peracarpa ( $P$. circaeoides)
37. Petkovia (C. orphanidea)
38. Petromarula (P. pinnata)
39. Phyteuma (P. pyrenaicum)
40. Platycodon (P. grandiflorum)
41. Rapunculus (C. hawkinsiana, C. aizoon, C. trichocalycina)
42. Melanocalyx (C. unicolor)
43. Pterophyllum (C. primulifolia)
44. Roucela (C. drabifolia, C. erinus)
45. Roella (R. maculata, R. ciliata)
46. Sergia (S. regelii)
47. Symphyandra hoffmannii
48. "Otocalyx" (S. armena)
49. Symphyandra wanneri
50. Trachelium (T. caeruleum)
51. Wahlenbergia (W. gloriosa, W. androsacea, W. congesta)
52. "Helenacodon" (W. angustifolia)
53. "Fernandeziocodon"(W. berteroi, W. grahamae, W. larrainii)


Fig.24. Principal coordinates 1 and 2 for the Seed (Campseed.DAT) data set and superimposed minimum spanning tree. For explanation of the point numbers, see opposite.

Taxa and Numbers for the Seeds (Campseed.DAT) data set (data matrix compiled from the species listed in brackets)

1. Adenophora (A. bulleyana, A. confusa, A. hakusanensis, A. Iiliifolia)
2. Asyneuma (A. japonica, A. michauxioides, A. canescens)
3. Azorina (A.vidalii)
4. Brachycodon (B.fastigiata)
5. Campanulastrum (C.americanum)
6. "Iberocodon" (C. arvatica)
7. Scapiflorae (C. bellidifolia)
8. Symphyandriformes (C. betulifolia, C. troegerae)
9. Involucratae (C. cervicaria, C. spicata)
10.Rupestres (C. coriaceae, C. bornmuelleri, C. heterophylla, C. calaminthifolia)
11.Quinqueloculares (C. crispa, C. tomentosa)
12."Oreocodon" (C.mollis, C. jacobaea, C.edulis, C.alsinoides)
10. Campanula formanekiana
14.Megalocodon (C. incurva)
11. Campanula lanata
12. Campanula lingulata
17.Spinulosae (C.mirabilis)
18.Tulipella (C. punctata var. hondensis)
19.Campanula sartori
20.Codonosphaera (C. thyrsoides)
21.Codonopsis (C.bulleyana, C. clematidea, C. pilosula)
22.Craterocapsa (C.congesta)
23.Cyananthus (C.lobatus)
24.Cylindrocarpa (C.sewertzowii)
25.Diosphaera (D.rumelianum)
26.Edraianthus (E.graminifolius, E. serbicus)
27.Gadellia (G.lactiflora)
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28.Githopsis (G.diffusa)
29."Isophylla" (C. tommasiniana, C. waldsteiniana, C. versicolor, C. zoysii, C.
fenestrellata)
30.Jasione (J. heldreichii, J. humilis, J. crispa ssp. crispa, J. laevis)
31.Legousia (L.falcata, L.speculum-veneris)
32.Leptocodon (L. gracilis)
33.Michauxia (M. tchihatchewii,M. laevigata)
34.Musschia (M.wollastoni,M.aurea)
35.Nesocodon (N. mauritianus)
36.Peracarpa (P. circaeoides)
37.Petkovia (C.orphanidea)
38.Petromarula (P.pinnata)
39.Phyteuma (P.pyrenaicum)
40.Platycodon (P. grandiflorum)
41.Rapunculus (C. hawkinsiana, C. aizoon, C. trichocalycina)
42.Melanocalyx (C. unicolor)
43.Pterophyllum (C. primulifolia)
44.Roucela (C. drabifolia, C. erinus)
45.Roella (R. maculata, R. ciliata)
46.Sergia (S.regelii)
47.Symphyandra hoffmannii
48."Otocalyx" (S. armena)
49.Symphyandra wanneri
50.Trachelium (T.caeruleum)
51.Wahlenbergia (W.gloriosa, W. androsacea, W. congesta)
52."Helenacodon" (W. angustifolia)
53. "Fernandeziocodon" (W. berteroi, W. grahamae, W. Iarrainii)
```



Fig.25. Principal coordinates 1 and 3 for the Seed (Campseed.DAT) data set and superimposed minimum-spanning tree. For explanation of the point numbers, see opposite.

## b. The Flowers \& Fruits (Flowers.DAT) data sets

From Fig. 14 showing the results of principal coordinate analysis for flower and fruit data (FLOWERS.DAT) projected in 3-dimensional space and with a mininum spanning tree superimposed, it can be seen that there is some structure to the scatter of points. There is one large rather tight cluster comprising two tight subclusters which include most of the genera in both campanuloid and wahlenbergioid alliances. This is about three times larger than the smaller loose cluster which comprises most of the genera in the platycodonoid alliance plus some wahlenbergioids. Within this smaller loose cluster are also a number of subcluster comprising one or two genera, eg. Cyclocodon (16), Campanumoea (9) and Codonopsis (12) are extremely close and only a little less so to "Himalcodon" (28) and Canarina (10). Ostrowskia (41) and Platycodon (47) are next closest to this subcluster but both are somewhat isolated. Leptocodon (33) is also rather distant from Codonopsis and only a little closer to Cyananthus (15), while Echinocodon (19) is very remote from all but Cyananthus. Pseudocodonopsis (50) is rather distant from "Himalcodon". Some of these platycodonoid genera connect with taxa which appear somewhat intermediate between the two clusters. For example, the genera Nesocodon (40), Heterochaenia (26), Azorina (4), Roella (53) and Craterocapsa (13) all show a fairly close association, with a more distant link with Berenice (5), Wahlenbergia (63) and Cephalostigma (11) and Adenophora (1) and Musschia (38).

Within the large cluster there is a subcluster formed by genera such as Edraianthus (20) which also links to Roella (53). Other genera include Hanabusaya (25), Sicyocodon (56), Petkovia (43), Symphyandra (58) and Cryptocodon (14). These cluster fairly close to Campanula (7), Zeugandra (64) and Michauxia, and more distantly with Muehlbergella (37). Another subcluster is formed by Roucela (54), Astrocodon (2), "Isophylla" (30), Petromarula (44), Rapunculus (51) and Gadellia (22). This cluster then links with the subclusters formed by Sergia (55), Phyteuma (45), Physoplexis (46), Triodanis (62) and by Popoviocodonia (48), Campanulastrum (8) and Asyneuma (3). Slightly more remote from the latter subcluster is Cylindrocarpa (17). Homocodon (29) is very close to Heterocodon (27). Finally, there is a very tight subcluster of South African wahlenbergioid genera with taxa such as Jasione (31) and Feeria (21) peripheral to this massing. Relationships within
this subcluster are rather difficult to entangle but included here are campanuloids such as Trachelium (60) and Legousia (32), as well as lobelioids such as Lobelia (65).

## c. The Pollen (CampPal.DAT) data sets

Figs. 18-19 show even more the polarisation between one large tight cluster composed of wahlenbergioid and campanuloid genera and a smaller loose cluster composed of platycodonoid taxa. Within the smaller cluster the tightest subcluster is formed by the three genera, Homocodon (16), Peracarpa (26) and Physoplexis (28). All the other genera are rather distant from each other although Canarina (6) with Platycodon (29) and Codonopsis (7) with Leptocodon (20) show a somewhat closer alliance. The MDSCALE plot brings the genera, Ostrowskia (25), Cyananthus (8), Echinocodon (9), Lobelia (38), Codonopsis (7), Canarina (6), Leptocodon (20), Platycodon (29), Pseudocodonopsis (31) and Campanumoea (5) into a much tighter cluster, with Ostrowskia and Campanumoea most peripheral. The larger cluster comprises a number of small subclusters of 2-4 genera, eg. Heterochaenia (15), Symphyandra (35),Roucela (34) and Gadellia (11), or Gunnillaea (13), Roella (33); Phyteuma (27) and Rapunculus (32). Adenophora (1), Hanabusaya (14) and Jasione (18) are rather peripheral. Edraianthus (10) shows a close alliance with Michauxia (21) while Legousia (19) is allied with Githopsis (12), and Asyneuma (2) and Campanula (3) with Wahlenbergia (37). In marked contrast to the MDSCALE, the principal coordinates plot actually makes this large cluster much tighter. Otherwise both plots are essentially similar.

## d. The Seeds (CampSeed.DAT) data sets

In the MOD3D plot (Fig.22) the separation of distinct clusters is much less clear but there is a loose minor cluster formed by "Iberocodon (6), Roella (45), Craterocapsa (22) and Edraianthus (26) and by C. lingulata (16), Nesocodon (35) and "Helenacodon" (52). These contrast with the main mass of genera. Within this main mass there are a few minor clusters discernible. These are formed by Symphyandriformes (8), C. formanekiana (13), Megalocodon (14), Petromarula (38) and Symphyandra wanneri (49); by Cyananthus (23), Githopsis (28), Michauxia (33) and Peracarpa (36); and by Jasione (30), Sergia (46) and Roucela (44). The MDSCALE plot (Fig.23) clarifies the situation and several other minor
clusterings are to be seen. For example Trachelium (50) and Pterophyllum (43); Legousia (31), Rapunculus (41) and Melanocalyx (42); "Oreocodon" (12) and Cylindrocarpa (24).

Although one has to interpret these results with some caution (Pankhurst, 1991), they nevertheless confirm that clusters are present within the data sets and that the composition of these clusters obtained by the various permutations of the new variables plus that of the 3dimensional plots are fairly consistent. One can therefore proceed with the cluster analyses with some degree of confidence that clusters do exist and that their composition seems reasonably correct.

### 7.1.6.3 Cluster Analyses

a. The Asterales (G\&B.DAT) data sets

## (i). The Asterales full dataset.

Fig. 26 shows the phenogram for the Asterales full data set (G\&B.DAT) using the UPGMA clustering method. From Table 23. it can be seen that the Cophenetic Correlation Coefficient is 0.82932 which indicates a very close fit of the clustering to the data set. Although there is no satisfactory statistical test for significance of the correlation, a value of 0.8 or more is considered acceptable (Pankhurst, 1991). The phenogram is well balanced (ie. in the number of clusters which merge at each step) and comprises two major clusters which diverge at the - 0.1 phenon level.. Each of the two major clusters in turn comprise two major subclusters which diverge at about the 0.00 level. The first of these subclusters comprises the Aquifoliaceae, Araliaceae, Bruniaceae, Griseliniaceae, Viburnaceae, Sambucaceae, Escalloniaceae, Argophyllaceae and Pittosporaceae, while the second subcluster comprises the Donatiaceae, Stylidiaceae, Sphenocleaceae and Pentaphragmataceae. The third subcluster comprises the Menyanthaceae, Asteraceae, Brunoniaceae, Calyceraceae and Goodeniaceae, while the fourth subcluster comprises the Campanulaceae, Cyphocarpaceae, Lobeliaceae, Cyphiaceae and Nemacladaceae.

The Brunoniaceae and Calyceraceae are closest to each other and cluster at about the 0.3 phenon level. The Cyphocarpaceae and Lobeliaceae and the Cyphiaceae and Nemacladaceae respectively are the next closest to each other. Both groups clusters at about the 0.28 phenon
level. The most similar family to the Brunoniaceae and Calyceraceae collectively is the Asteraceae and the most similar family to the collective group formed by the Cyphocarpaceae, Lobeliaceae, Cyphiaceae and Nemacladaceae is the Campanulaceae which clusters at about the 0.18 phenon level. The collective group formed by the Asteraceae, Calyceraceae and Brunoniaceae also cluster with the Goodeniaceae at the 0.18 level. The Menyanthaceae are more dissimilar to the last-mentioned group and cluster at the 0.16 phenon level.

A comparison was then made with the results obtained by the Single and Complete Linkage clustering methods. The single linkage method produced similar results for the third subcluster but clustered more closely with the fourth subcluster instead of with the Menyanthaceae. The fourth subcluster produced a closer linkage with Cyphiaceae and Nemacladaceae and with Lobeliaceae and Cyphocarpaceae respectively, while the Campanulaceae diverged at a more distant level. Also the resolution of four subclusters collapsed to just three with subclusters 3 and 4 united and with the Pentaphragmataceae isolated. The complete linkage method restored 4 subclusters but the composition of each had changed. The third subcluster was now united with the first, while the second was united with the fourth. However, within each subcluster, the clustering of families remained similar. This was especially the case for the families in the fourth subcluster. Strict consensus trees of the UPGMA and single linkage methods and of the UPGMA and complete linkage methods were then obtained in order to discover the most distinct clusters among the closest allies of the Campanulaceae. For the strict consensus tree of the UPGMA and Single-linkage, the most distinct cluster was formed by the Campanulaceae and Goodeniaceae. The CIm index for this consensus tree is 0.3 which is rather poor. For the strict consensus tree of the UPGMA and Complete-linkage the CIm index is even poorer at 0.01 . The only distinct cluster in the Campanulaceae alliance was formed by the Cyphiaceae and Lobeliaceae. See Table 24. for consensus indices.

## (ii). The Campanulales subset.

It is known that the ratio of the number of characters to the number of taxa in a data set can substantially affect the topology of the resultant phenogram. In order to resolve the
conflicting results obtained for the Campanulaceae alliance, a subset (Campanulales) of the original data was then analysed by UPGMA procedures (Fig.29). The Cophenetic Correlation Coefficient was 0.85519 . The topology of the subcluster containing the Campanulaceae alliance was very similar to that obtained in the full data set analysis.

## Asterales (UPGMA)

-0
0.12
0.00
0.12
0.24
0.36


Fig.26. Phenogram for the Asterales full data set (G\&B.DAT): UPGMA Method


Fig.27. Phemograms for the Asterales full data set (G\&B.DAT): Simgle amd Complete Limkage Methods


Fig.28. Phemograms for the Asteralles fund data set (G\&B.DAT): Comsemsus Trees of combined UPGMIA amm Simgle/Complete Limkage Methods


Fig.29. Phemogram fior the Asteralles data sulbset (G\&B.BAT), "Campamulalles" s.l.: $\mathbb{U P G M A}$ Method

Th. The $\mathbb{F l}$ lowers \& Frunits ( $\mathbb{F l l o w e r s . D A T \text { ) data sets. }}$
(i). The Flowers \& Frunits fulll data set

Fig. 30 shows the phenogram for the Flowers \& Fruits full data set (Flowers.DAT) using the UPGMA clustering method. From Table 23. it can be seen that the Cophenetic Correlation Coefficient is 0.50576 which is a very poor fit of the clustering to the data set. The phenogram is reasonably well balanced and there are two major clusters which diverge at the -0.05 phenon level. The smaller of the two clusters comprise all the colpate and colpate genera plus the porate Azorina and Berenice. The porate genera Nesocodon, Heterochaenia, Roella and Craterocapsa form the other cohesive subcluster. Nesocodon clusters most closely with Heterochaenia at the 0.16 phenon level, while Roella with Craterocapsa and Azorina with Berenice at about the 0.15 level. Campanumoea and Cyclocodon are very close, clustering at 0.48 (maximum value) and diverging from Canarina at about 0.35 . Within the colpate subcluster Codonopsis is most close to Himalcodon, Cyananthus with Leptocodon and Echinocodon with Pseudocodonopsis. Rather surprisingly, Platycodon clustered most closely with Ostrowskia.

Within the larger cluster several traditionally close associations can be observed although much of the topology remains in conflict with conventional classifications. Cephalostigma is most close to Wahlenbergia and there is a cohesive cluster formed by the endemic Cape genera such as Theilera, Microcodon, Rhigiophyllum, Siphocodon and Treichelia. The genus Asyneuma seems to be correctly clustered with Cylindrocarpa, Campanulastrum, Triodanis, Popoviocodonia and Sergia and fairly close to Rapunculus, Gadellia and Isophylla. Also within this grouping are subcluster formed by Phyteuma, Physoplexis and Petromarula. Jasione is, rather surprisingly, also included here. The composition of the cluster which includes Campanula s.str. is much in accord with conventional classifications. The position of Sicyocodon with Zeugandra and Michaxia is interesting. The clustering of Homocodon, Heterocodon and Peracarpa seems reasonable but their association with Muehlbergella and Astrocodon is problematical. Brachycodon is most closely clustered with Legousia and collectively with Githopsis. At a lower level this trio unites with the African genera Gunillaea, Namacodon and Prismatocarpus. Feeria clusters most closely with Trachelium and collectively both of these unite with Diosphaera, while at a lower level they join with

Merciera. Finally, this grouping diverges at about the 0.04 phenon level with a cluster which, oddly, comprises Musschia and Lobelia. There is thus a mixture of expected and unexpected results. Much of this is probably due to the unevenness of the scoring, the size of the data set and the ratio of characters to taxa. Single-linkage, Complete-linkage methods were therefore tried to help resolve these ambiguities.

Fig. 31 shows the phenogram obtained from the Complete-linkage method. The topology at the lower level has substantially changed but the clustering at the higher level is remarkably consistent with the UPGMA results. Again there are two major clusters. For the smaller cluster Azorina and Berenice more logically unite with the porate subcluster separate from the colpate and colporate genera. In the phenogram for the Single-linkage method (Fig.32) Adenophora diverges at a very low level from all other taxa. There are then two major subclusters at a slightly higher level but the composition of these is radically different from that obtained by the UPGMA and Complete-linkage methods. The colpate and colporate genera nest within a very heterogeneous subcluster containing both campanuloid and wahlenbergioid elements and the overall topology of the phenogram seemed very unacceptable.

A strict consensus tree (Fig.33) of the UPGMA and complete-linkage trees gave a CIm index of 0.03 which is very poor indeed. The most distinct clusters on this tree were a strange alliance of Adenophora with Cephalostigma and Asyneuma with Wahlenbergia. More acceptable were the clusters formed by Canarina with Codonopsis, Heterochaenia with Roella, Heterocodon with Roucela and Himalcodon with Ostrowskia. The data was therefore divided into subsets comprising the traditionally circumscribed tribes, Campanuleae, Wahlenbergeae and Platycodoneae and were then reanalysed with UPGMA methods.

## (iii) The Campamuleae subsset

From the phenogram of the Campanuleae data subset using the UPGMA method (Fig.34) it can be seen that the topology has a much better balance than the trees from the full data set. The Cophenetic Correlation Coefficient is 0.72468 which, while still a poor fit, is a substantial improvement over the values obtained from the full data set. There are two major
clusters at the -0.03 phenon level. The smaller cluster is more homogeneous than the larger cluster and comprises those genera in a "rapunculoid" alliance such as Asyneuma, Campanulastrum, Rapunculus, Phyteuma and Isophylla, etc. Jasione is also included in this cluster and diverges from Petromarula, Phyteuma and Physoplexis at the 0.07 phenon level. Cylindrocarpa is closest to Asyneuma, and Triodanis is closest to Campanulastrum, while Popoviocodonia is closest to Sergia. Gadellia is closest to Rapunculus and Phyteuma is closest to Physoplexis. All these results are not discordant with traditional classifications except for the position of Jasione which traditionally has been associated with the Wahlenbergeae.

The second cluster is more heterogeneous and contains two subclusters which diverge at the 0.02 phenon level. Again, one is smaller and more homogeneous and comprises those genera typically associated with the genus Campanula s.str. Hanabusaya is most close to Symphyandra s.l. and collectively they are closest to Campanula. Edraianthus is closest to Petkovia and collectively they are closest to Cryptocodon. Sicyocodon is closest to Zeugandra and collectively they are closest to Michauxia. Finally, Roucela, alone, diverges at a low level of 0.02 from all these genera. The larger more heterogeneous subcluster has a further two subclusters. The smaller is formed by Heterocodon and Homocodon which are most similar and at a lower level with Peracarpa. At an even lower level they unite with Muehlbergella, which is an interesting result. Finally, the last subcluster again is rather heterogeneous but contains taxa which seem related, eg. Trachelium, Feeria with Diosphaera and Brachycodon and Legousia with Githopsis and Prismatocarpus (Wahlenbergeae, but added as an outgroup). Adenophora clusters with Azorina and collectively they cluster with Musschia which does seem a little odd.

## (iiii) The Platycod omeae sulbset

From the phenogram of the Platycodoneae subset using UPGMA methods (Fig.35) two main clusters are evident. The phenogram is well balanced overall and within the two main clusters. The Cophenetic Correlation Coefficient is 0.84131 which is a good fit. The larger of the two containing seven taxa shows that Campanumoea and Cyclocodon are closest to each other at the 0.16 phenon level and collectively with Canarina at the 0.09 level.

Codonopsis is closest to Himalcodon at about the 0.07 level and joins the Campanumoea/Cyclocodon/Canarina cluster at the 0.04 level. Finally within this main cluster Ostrowskia and Platycodon cluster together at about 0.06 and join the remaining taxa at 0.00 level. The main cluster containing five taxa is slightly surprising since it contains the outgroup Lobelia nested within the subcluster comprising Cyananthus and Leptocodon. The latter two genera are closest at the 0.10 level. Echinocodon and Pseudocodonopsis cluster at the 0.08 level and join the other subcluster at about the 0.03 phenon level. Apart from the placement of Lobelia and the levels of the nodes, the topology of the phenogram in the subset is virtually identical to that obtained from the full set.
(iv) The Walnlembergeac sulbset.

From the phenogram obtained for the Wahlenbergeae subset (Fig.36) it can be seen that the tree is reasonably well balanced and that there are two major clusters, each with two major subclusters. The Cophenetic Correlation Coefficient is 0.78550 which is not too bad a fit. The larger cluster contains 12 taxa including Feeria and Musschia which were included as putative outgroups, while the smaller contains 10 taxa including Lobelia as an outgroup and three other putative outgroups, Legousia, Githopsis and Jasione. In the larger cluster Craterocapsa and Roella cluster most closely at the 0.14 phenon level and Heterochaenia and Nesocodon at the 0.16 level. Both groups unite at the 0.08 level and collectively with Musschia at about the 0.03 phenon level. Rhigiophyllum clusters most closely with Siphocodon at the 0.16 level, both genera nesting within a subcluster formed by other Cape genera such as Microcodon, Treichelia and Theilera. This subcluster unites with the cluster formed by Feeria and Merciera at the 0.00 level. In the smaller main cluster Wahlenbergia, Cephalostigma and Berenice form a cluster which joins Jasione and Lobelia at the 0.00 level. At about the -0.02 level this subcluster, in turn, joins the remaining subcluster which shows Namacodon as closest to Gunillaea at the 0.15 level. Collectively these two taxa join Prismatocarpus at about the 0.09 level. This subcluster then joins the putative outgroups Githopsis and Legousia at the 0.08 level. Altogether, this tree is very much in accord with conventional classifications and presents a clearer picture of relationships within the Wahlenbergeae than the full data set.


Fig.30. Phemogram for the Flowers \& Fruits full data set (Flowers.DAT): UPGMA Method


Fig.31. Plnemogram for the Flowers \& Fruits funll data set (Flowers.DAT): Complete Limkage Method


Fig.32. Phemogram for the Flowers \& Frwits full data set (Flowers. $\mathbb{D} A T$ ): Single Limkage Method


Fig.33. Plhemogramn for the Flowers \& Froits funll data set (Flowers.DAT): Comsemsus Tree of combimed UPGMA amd Complete Limkage $\mathbb{M}$ Iethods


Fig.34. Phemagran for the Flowers \& Fruits diata subset (Fiowers.iDAT), "Campamulleme" amal putative autgroups: UPGMIA Methoal


Fig.35. Phemogram for the Flowers \& Fruits data sulbset (Flowers.DDAT), "PPlatycodlomeae" amd puntative outgroups: UPGMIA Micthod


Fig.36. Phemogram Tior the Flowers \& Fruits data sulbset (Flowers.DDAT), "WWalnlembergeae" amd putative outgroups: UPGMAA Method

(i). The $\mathbb{P}$ ollem fulll data set.

Analysis of the pollen full data set produced using the UPGMA method yielded 2 tied trees which were then used to produce a strict consensus tree (Fig.37). The fit of this consensus tree was naturally very poor, the Cophenetic Correlation Coefficient being just 0.53206 . The CIm index for this tree is 0.22807 . This consensus tree is relatively unbalanced with one small and one large major cluster. The smaller cluster is well balanced and contains traditionally allied genera as well as the outgroup Lobelia. Cyananthus and Echinocodon cluster most closely at the 0.60 phenon level and collectively with Leptocodon at the 0.70 level. This subcluster joins Pseudocodonopsis and Lobelia at about the 0.80 level. The other main cluster has a lack of resolution at midlevels and contains several subclusters. The first of these to diverge at the 0.80 level is the small cluster formed by Codonopsis and Platycodon. This is followed at the 0.70 level by Canarina alone. There is a well resolved subcluster containing wahlenbergioid and campanuloid genera although the cluster formed by Phyteuma and Roella and Hanabusaya with Prismatocarpus are odd results.

The Single-linkage method also yielded two tied trees and from these a strict consensus tree was obtained (Fig.38). The CIm index is 0.53509 . This is a slightly better balanced tree than the UPGMA strict consensus tree and was more resolved but the colpate and colporate genera such as Codonopsis and Canarina were nested more within subclusters. The following minor clusters were noteworthy: Adenophora with Asyneuma; Campanulastrum with Legousia; Codonopsis with Platycodon; Cyananthus with Echinocodon; Edraianthus with Namacodon; Gunillaea with Nesocodon, and Heterochaenia with Musschia and Trachelium.

The Complete-linkage method again yielded two tied trees from which a strict consensus tree was obtained (Fig.39). The CIm index is 0.31579 . Again, this tree is fairly unbalanced and shows a relative lack of resolution at higher levels. Like the UPGMA method, the colpate and colporate genera diverge at low levels. The tree is on the whole remarkably similar to the UPGMA tree but is marginally more resolved at the higher levels. It does conflict with the UPGMA tree in some of the minor clusters. In order to resolve the
ambiguities between the three methods, strict consensus trees were then obtained of several permutations and from them it was hoped to identify the most distinct clusters. The results are shown in Figs.40-42. The minor clusters which consistently appear to be most distinct are : Adenophora with Asyneuma; Codonopsis with Platycodon; Cyananthus with Echinocodon and Leptocodon; Pseudocodonopsis with the outgroup Lobelia, and Legousia with Rapunculus. These results are much in accord with published studies of Campanulaceae pollen. Other minor clusters which appear consistently distinct but which are more difficult to interpret are : Phyteuma with Roella; Campanumoea with Physoplexis and Ostrowskia with Peracarpa; and Musschia with Namacodon. Therefore, as with the Flowers and Fruits data set, the Pollen data set was divided into three subsets comprising the traditionally circumscribed tribes and then reanalysed in the same manner.

## (iii) The Campamulleac sunbset

Two tied trees were found for the UPGMA method applied to the Campanuleae subset. Both of these trees are shown in Fig. 43 and the strict consensus of these is shown in Fig.44. The Cophenetic Correlation Coefficient for the two trees is marginally poor at 0.77290 , while the CIm index is 0.28000 . Both trees are rather similar and well balanced. They each have two main clusters, the larger of the two being identical for the two trees. Asyneuma and Campanula cluster most closely and collectively with Adenophora and Rapunculus at the 0.2 phenon level. The next level at about 0.05 unites this subcluster with Campanulastrum, Githopsis and Legousia. They finally link up at the -0.05 level with Edraianthus, Isophylla, Jasione and Hanabusaya with Michauxia. This main cluster accords well with traditional studies of pollen relationships. The smaller main cluster differs considerably in topology at lower levels in both trees and consequently is unresolved in the strict consensus tree. The subclusters formed by Homocodon, Peracarpa and Physoplexis and by Musschia and Phyteuma are consistent in both trees. The cluster formed by Gadellia, Symphyandra, Roucela and Trachelium show minor shifts in the relative position of the taxa. In the strict consensus tree where there is resolution there are some realignments. Adenophora clusters most closely with Asyneuma, Campanulastrum with Rapunculus, Edraianthus with Legousia and Githopsis. Apart from Jasione clustering with Hanabusaya, these groupings in the consensus tree do again do not depart radically from traditional arrangements.
(iiii) The $\mathbb{P l l a t y c o d}$ meac subset
The phenogram shown in Fig. 45 for the Platycodoneae using UPGMA methods is reasonably well balanced, forms two major clusters and is fully resolved. The Cophenetic Correlation Coefficient is 0.76705 . There are a few surprises, eg. Campanumoea, a colporate genus, clusters with the colpate Pseudocodonopsis at about the 0.18 phenon level. Canarina clusters most closely with Platycodon, which is not unexpected. There is a slightly odd alliance formed by the outgroup Nesocodon and Ostrowskia, with Leptocodon joining at a lower level. In the smaller main cluster Codonopsis aligns most closely with Cyananthus, while the outgroup Lobelia nests within a larger subcluster which also includes Echinocodon. Overall, the tree doesn't depart too radically from traditional arrangements but some alliances are difficult to interpret.
(iv) The Walnlembergeae sulbset

The phenogram shown in Fig. 46 for the Wahlenbergeae using the UPGMA method is well balanced if one ignores the early branching of the two outgroups, Canarina and Lobelia. The tree is also fully resolved and, apart from the outgroup cluster, forms two major clusters. The Cophenetic Correlation Coefficient is 0.69685 . The smaller of the two contains just four genera, Gunillaea with Namacodon at about the 0.30 phenon level and Musschia with Nesocodon at the 0.20 level. Musschia was added as an outgroup. In the larger cluster, the two outgroups, Jasione and Edraianthus cluster most closely while a fourth outgroup, Trachelium clusters with Prismatocarpus. The final two outgroups, Legousia and Githopsis cluster with Wahlenbergia and collectively this subcluster unites at the 0.005 level with Heterochaenia and Roella. As with the Platycodoneae, some alliances are difficult to interpret but the broader associations do not seem to be too unreasonable.
Pollen (Str.Consensus 2 Tied Trees: UPGMA)

| 1.00 | 0.75 | 0.50 | 0.25 | 0.00 |
| :--- | :--- | :--- | :--- | :--- |


 died trees: UPGMA Method

## Pollen (Str.Consensus 2 Tied Trees: SINGLE)


 tied $\mathbb{H}$ rees: Simgle Limkage Method

Pollen (Str.Consensus 2 Tied Trees: COMPLETE) 2.00 3.00

Fig.39. Phemogram for the Pollem full data set (CampPall.DAT): Strict Comsensus of 2 tied trees: Complete Limkage Mlethod


Fig. A0. Phemogram for the Pollem fuhl data set (CampPall.DAT): Strict Comsemsus of the combimed UPGMIA amd Simgle Limkage Methods


Fig. 11 . Phemagram for the $\mathbb{P o l l e m}$ fund data set (Camp Pal.DAT): Strict Comsemsus $\mathbb{1}$ of 2 tied trees (comblbimed UPGMA amd Complete Limkage Mrethods)


Fig. 42. Phemogramn for the Pollem funl data set (CampPPal.DAT): Strict Comsemsus 2 of 2 tied trees (combined UPGMA amd Complete Limkage Methods)


Fig.43. Phemagrams for the Pallem data subset (CampPad.DAT), "Campamunleae" amd putative outgroups. 2 tied trees: UPGMA Niethmals

 putative outgroups. Strict Comsemsus of 2 tied trees: UPGMA Methods


Fig. 45 . Plhemogram fior the Pollem daua sulbset (CampPPal.DATI), "Platycodomeae" amd putative outgroups: UPGMIA Miethods


Fig.46. Plhenogram for the Pollem data sulbset (CamplPal. DAT), "Walulembergeae" mmal putative outgroups: UPGNA $\mathbb{M}$ ethods
d. The Seeds (CampSeed.IDAT) data sets
(i). The Seedls funll data set

Analysis of the full dataset using the UPGMA method yielded a single tree (Fig.47). The Cophenetic Correlation Coefficient is 0.71253 . The tree is well balanced and most of the major bifurcations occur at lower phenon levels. There are two major clusters each of which have two subclusters and several minor clusters. On the whole the tree is extremely difficult to interpret and appears exceedingly unsatisfactory. One subcluster however, comprising Symphyandra and numerous sections of Campanula s.str. seems fairly homogeneous. It represents those taxa with seeds which have high surface relief and well-marked striations of the testa. Several 2-4 taxa-clusters appear to reflect traditional alignments more accurately. These include: "Oreocodon" with Cylindrocarpa and collectively with Legousia, Rapunculus and Melanocalyx; Asyneuma with Campanulastrum, Phyteuma and Jasione; Leptocodon with Platycodon; Diosphaera with Trachelium; and Craterocapsa with Roella and Edraianthus. Many of the minor clusters appear completely nonsensical. This can probably be explained by the high levels of homoplasy in seed characters due to intense selection pressures in what must be an exceedingly narrow adaptive landscape.

The Single-linkage and Complete-linkage methods (Figs.48-49) were equally poor, particularly the single-linkage where there was an even greater loss of resolution. Consensus trees of UPGMA/Single (Fig.50) (CIm index $=0.03994$ ) and UPGMA/Complete (Fig.51) $($ CIm index $=0.04734)$ yielded several more distinct minor clusters. The most resolved include clusters formed by Megalocodon and Petromarula; Cylindrocarpa with Legousia; and Adenophora with "Oreocodon", Wahlenbergia, Cylindrocarpa, Legousia and Rapunculus. Wahlenbergia appears out of place in this cluster. Less resolved clusters include Quinqueloculares with Tulipella and C.sartorii; and C.lingulata with Petkovia, Craterocapsa, Edraianthus, Isophylla, Nesocodon and "Helenacodon". The analyses were then repeated with subsets of the full data set.
(iii) The Campamuleae subset

The phenogram shown in Fig. 52 is well balanced and has a Cophenetic Correlation Coefficient of 0.74386 . As in the full data set, it forms two main clusters and has several
subclusters branching at the lower phenon levels. The subclustering is essentially identical to that of the main set.
(iiii) The Platycodoneae sulbset
This small phenogram (Fig.53) is unbalanced but is fully resolved. The Cophenetic Correlation Coefficient is 0.84818 which is much more satisfactory. Several traditional alliances are picked up in this tree. Codonopsis clusters most closely with Cyananthus at about the 0.03 phenon level, while Leptocodon and Platycodon are extremely close at almost the 0.24 level. The outgroups formed by the genera Nesocodon and Roella cluster together at about 0.00 level and nest within the first-mentioned subcluster. This is a fairly acceptable result.
(iv) The Wallilembergeae subset

The phenogram shown in Fig. 54 has a Cophenetic Correlation Coefficient of 0.77952; is quite well balanced, and fully resolved. There are two main clusters, each with two subclusters and several minor clusters. The outgroup Azorina clusters with the outgroup Githopsis, which is not too surprising, but they unite at about the 0.10 level with "Fernadeziana" which is a bit odd. Jasione clusters closely with Wahlenbergia and collectively, they unite with the outgroups Legousia and Trachelium at the 0.05 phenon level. In the second major cluster Nesocodon clusters most closely with "Helenacodon" which is not unexpected and together they join Musschia at the 0.03 level, which is interesting. Edraianthus clusters extremely closely with Roella which is exceedingly interesting, if not a little surprising, while they both join Craterocapsa at the 0.12 level. This is also a fairly satisfactory result but still with several tantalising anomalies.


Fig.47. Plhemogrom for the Seeds fund data set (CampSeed.IDAT): UPGMA Method


Fig. 48. Phemagram for the Seeds fun data set (CampSeed. DATT): Simgle Limkage
Method


Fig. 49 . Phemogram for the Seeds full data set (CampSeed.DAT): Complete Limkage Method


Fig.50. Phemogramn for the Seeds fiull data set (CampSeed.DAT): Comsemsus tree of the combimed UPGMA amd Simgle Limkage Methodls


Fig.51. Phemogram for the Seeds funi data set (CampSeed.DAT): Consensus tree of the combimed UIPGMA am@l Complete Limkage Miethodls


Fig.52. Phemøgram for the Seedls data sulbset (CampSeed.IDAT), "Campamuleae" amd puntative outgroups: $\mathbb{U P G M A} \mathbb{M}$ ethod





Fig.54. Plnenogrann for the Seeds data subset (CampSeed.IDAT), "Walhiembergeae" amd putative oungroups: UPGMA Method

Table 23. Cophenetic correlation coefficients for UPGMA methods.

## DATA SETS

Correlation Coefficient

| 1.a. Asterales full set (G\&B.DAT) <br> b. Campanulales subset | $\begin{aligned} & 0.82932 \\ & 0.85519 \end{aligned}$ |
| :---: | :---: |
| 2.a. Flowers \& Fruits full set (Flowers.DAT) | 0.50576 |
| b.Campanuleae subset | 0.72468 |
| c. Platycodoneae subset | 0.841 .31 |
| d. Wahlenbergeae subset | 0.78550 |
| 3.a. Pollen full set(CampPal.DAT) | 0.53206 |
| b. Campanuleae subset | 0.77290 |
| c. Platycodoneae subset | 0.76705 |
| d. Wahlenbergeae subset | 0.69685 |
| 4.a. Seeds full set (CampSeed.DAT) | 0.71253 |
| b. Campanuleae subset | 0.74386 |
| c. Platycodoneae subset | 0.84818 |
| d. Wahlenbergeae subset | 0.77952 |

Table 24. Consensus indices for Strict Consensus Trees of G\&B.DAT, Flowers.DAT, CampPal.DAT and CampSeed.DAT.

| DATA SETS | CIc | CIm | $N$ | CIsf |
| :---: | :---: | :---: | :---: | :---: |
| Asterales data sets (G\&B.DAT) |  |  |  |  |
| 1. IPPGMA + Single Linkage (full set) | $\begin{aligned} & 0.42857 \\ & 0.09524 \end{aligned}$ | $\begin{aligned} & 0.31405 \\ & 0.01653 \end{aligned}$ | 9 | 311 |
| 2. IPCMM + Complete linkage (full set) |  |  | 2 | 2 |
| Flowers \& Fruits data sets (Flowers.DAT) | 0.15873 | 0.03125 | 10 | 1558 |
| 3. IPCMA + Complete I İnkage (fill set) |  |  |  |  |
| Pollen data sets (CampPal.DAT) | 0.69444 | 0.22807 | 25 | 1935 |
| 4. UPGMA: 2 fied trees (fall set) |  |  |  |  |
| 5. Single Linkage: 2 tied trees (full set) | 0.97222 | 0.53509 | 35 | 1404 |
| 6. Complete linkage: 2 tied trees (full set) | 0.77778 | 0.31579 | 28 | 2240 |
| 7. UPGMA + Single linkage (full set) | 0.13889 | 0.01754 | 5 | 7 |
| 8. UPGMA + Complete linkage: tree I (full set) | 0.41667 | 0.13743 | 15 | 1833 |
| 9. IUPCMA + Complete linkage: tree 2 (full set) | 0.44444 | 0.14035 | 16 | 1834 |
| 10. UPCMA: 2 tied trees (Campanuleae subset) | 0.47368 | 0.28000 | 9 | 89 |
| Seeds data set (CampSeed.DAT) |  |  |  |  |
| 11. IPGMA + Single linkage (full set) | 0.19608 | 0.03994 | 10 | 66 |
| 12. IPGMA + Complete linkage (fill set) | 0.31373 | 0.04734 | 16 | 69 |

### 7.2 Cladistics Section

"Neither lumping nor splitting leads consistently to well-defined, conceptually useful genera, and the fruits of a determined pursuit of absolute monophylesis are equally poisonous."

## A. Cronquist, 1985

The phenetic analyses of the previous section has shown that a series of similar patterns in the similarity relations of the taxa is beginning to emerge. The overall picture is still very blurred but it does provide useful reference points for the construction of classifications albeit with very poorly substantiated evidence for phylogenetic relations. A more refined analysis is required which will take into account hypotheses concerning the evolutionary transformation of characters and algorithms which will impose a hierarchical relationship on the existing phenetic relations. The use of cladistic methods in this study does not imply that a cladogram represents actual or hypothetical genealogy or is the best method to represent relationships between taxa. Because of autapomorphies and heterochrony, it is not always possible to assign taxa to monophyletic groups. The transformation of character states rarely presents a simple pattern and is frequently confounded by hybridisation events as well as parallel and convergent evolution. In addition, the heuristic algorithms usually cannot find the most parsimonious tree in large data sets. Cladistic analyses therefore represent another way of looking at evolutionary problems but should not, in themselves, be considered superior. Nevertheless, it is worth quoting in full the following three guiding principles behind the cladistic methodology adopted in this study of the Campanulaceae (see Wiley, 1981):

1. Natural supraspecific taxa are genealogical entities and they are historically unique. Observed or inferred genealogy is both necessary and sufficient to include an entity in a group. Certain characters (apomorphies) are biologically connected to the concept of genealogy and thus can provide justification for the group in the absence of directly observed genealogy.
2. Characters hypothesised to justify unique genealogical groups must be those which indicate that the descendant members of the group share a common ancestral species not
shared with another taxon. The only characters that justify such groups are synapomorphies employed at their correct level of universality.

## 3. Unique genealogical groups corroborated by synapomorphies are monophyletic groups.

If natural taxa exhibited Aristotelean essences, then characters alone could be used to place them in a hierarchy. Because of descent with modification, such criteria are often inadequate. For example, "secondary pollen presentation mechanism present" would exclude Pentaphragma and Sphenoclea from the Campanulaceae s.l., yet it may be possible to discover that these two taxa are united with the Campanulaceae on other characters. Therefore, characters alone are insufficient to define natural taxa. Such taxa have to be viewed in a relative manner, their known genealogies and their cladistic patterns compared with those of other taxa. Characters cannot be divorced from evolutionary principles that tie characters to genealogy. For these reasons then it is desirable to use data sets of characters in a cladistic analysis and observe how the resultant cladograms compare with the results obtained by aggregate similarity methods (phenetics) and then integrate known data on wellestablished relationships (eg. as obtained by cytological methods or breeding experiments).

### 7.2.1 Construction of the Cladistic Data Sets

All types of characters were used and multistate characters were both ordered and unordered, additive and non-additive. They are more or less identical to those used in three of the four phenetics data sets and subsets (G\&B.DAT was omitted because a cladistic analysis has already been done by Gustafsson \& Bremer, 1995) but were modified to reflect polarity of the character states and their suitability for cladistic analyses (see Appendices). The characters were polarised according to the outgroup comparison methods of Watrous \& Wheeler (1981); Stevens (1980) and Maddison, Donoghue and Maddison (1984). This is tantamount to statements about the evolutionary pathways of the various characters but is not necessarily an endorsement of the view that evolution always proceeds most parsimoniously. A discussion of character polarity and tranformation series is given above in Sect. 6.3.2. A summary of the transformation series is given below. Most ordered multistate characters were straightforward morphoclines. Inapplicable data was treated as missing and
represented by a "-", while characters found to be highly homoplastic in baseline runs were excluded in the later phylogenetic reconstructions. The cladistics programs MacCLADE (v. 3.06; Maddison \& Maddison, 1992) and PAUP (v. 3.1.1; Swofford, 1993) both allow for parallelisms and reversals (homoplasy), and provide an option for encoding missing data.

### 7.2.2 A SUMIMAR $\mathbb{O F}$ THIE EVOLUTIONARY TRANSFORMATION $\mathbb{O F} \mathbb{C H} A R A \mathbb{C T E R S} \mathbb{I N} T H I E ~ C A M I P A N U L A C E A E$

A. Gemeral Observatioms

1. Character states which commonly occur throughout the fomily are probably primitive stoutes.
2. Taxa charocierised mostly by primitive stotes are probably fprimitive taxa.
3. Polyploidy is a derived stoue (apmmorphic) and polyploid taxa are alerived taxa. Ancient polyploidly mast be tolken ivato accound.
4. Reduced size, especially of flower parts, is a derived character state and town with small flowers ave usually derived traxa, unaless polyploidy has coused a reversal of theis tremd.
5. The busic chromosome numbers have changed from 7 to 8 or 1 , from which the groups witl $x=17$ arce derived.
B. Vegetative Clnaracters amd Habits
6. Within certain limiturions, arborescence and the presence of woody stems and caudices suggest primitiveness. Shubls, therefore, are probably more primitive than herbs.
7. Tropical climbers are possibly more primitive than woody shrubs of moarked seasonal climates but may not be more primitive tham tropical shrubs.
8. Peremials are more primitive than biennials, and anmuals have been derived frome both.
9. Among perennials and biemmiols, absence of a tapmoor is a derived condition. Rhizomes or storage caudices are more aduanced conditions.
10. Succullence is a specialisation.
11. Spinimess, hairimess ar ann elmborote ivodumentum are speciolisations. Glabrousness is more pprimitive.
12. A waxy shivay cusicle is a leighly derived condition from a primitive "rommal" cuticle.
C. Imfilorescemce
13. The solitary flower is primarily more primitive than the inflorescence (which may be reduced to a solitary flower). In most cases a solitary flower is highly derived. This care often be deduced by comparison with congeners.
14. Glomerules are more advanced than pancicles and thyrses while umbels anod coppitula are more advanced than glomeralles.
15. Long ppedicels are usuadly more primaitive than short pedicels.
16. An indeterminate flowering axis is more advanced than a determinatite one.
D. Flowers
17. Actinomorphy is mere primeitive tham zygomorphy.
18. Clowate flower buds are more primitive tham attenuate ones.
19. Pendlown flowers are more primitive than apright or nodding flowers
20. Broad corolla lobes are more primitive thave varrow ligulare anes and departures in the number of floral parts from the mosit common number of five are derived.
21. The campanulate corolla is more primitive than a non-campanalate corolla.
22. Patterned corollas, especiolly those showing pronoumced reticulate patterns annd/or eyespots are more primitive than umpatierned corollas.
23. Corollas closing at might or in cloudy conditions are clearly highly derived.
24. Separate stamens are more primitive than connate stamens and presence of an anther appendoge is more primitive than the absence.
25. Glabrous filamenês and umexpanded fillament bases (no nectar dome) are more primaitive than ciliated filaments and expanded bases (nectar dome).
26. Epippetaly is a derived condition. High placement in the corolla tube is the most derived condition.
27. Broud, colourless and/or inserted presenters are more priwitive than filiform, colourced andior exserted ones.
28. Glamads on the presenter region are probably primitive.
29. Synchronous pollen transfer is more primitive than osynchronous or pseudo-inedusial types.
30. A brood recepracle is more primitive than a nourrow one.
31. A open patrerned necrary region is more primitive than a concealed unporterned one.
32. Colourless nectar and yellow pollen are more primitive than scarlet nectar amd blue/puarple pollem resprecively.
33. Pollen grains have evolved from long-mudticalpal to short-mudticolpal, then to meultiporout.
E. Fronits amd Seeds
34. Hypogyny is the primitive condition, and from it perigyny and epigyny have been derived.
35. An monfused loypamothiom is more primitive than a partially or completely fused bypownthium.
36. Polycarpy is more primoitive than oligocarpy
37. Axile placentution is primitive while partioully parietal conditions are derived.
38. The ovules at ar above the midalle of the ovaries are primitive while pendavat or basal positions are most derived.
39. A five loculed ovary is the most primitive condition. Deppartures from theis nomber arre derived.
40. Capsules and bractis unoited as dispersall umits is a olerived condition.
41. Calyx appendages are more derived than their absence anad the presence of an elaborate pseudo-capsulle is the mosit derived condition of all.
42. A berry is more primitive thave the dehiscent capsule.
43. Apical valvate dehiscence is the most primitive mode of capsulle dehiscence while irreguldur rapturing anol challice-type modes are more advanced. Iredelriscent and lateral porate modes are also more advanced.
44. Among the porate modes of dehiscence, the upper and medially-placed pores are more primitive than the basall pores.
45. Seeds which are regular in symmerry, lack wings aved have pronownced rericulations with high rellief are more primitive tham those more irregular seeds which are rather smooth or striarted amed possess wivegs.

In the main data sets a hypothesised outgroup and/or Lobelia were used but for the subsets putative outgroups from within the main data sets were used. Lobelia was chosen because the Lobeliaceae was one of four terminal taxa which formed a sister group to the Campanulaceae in the cladistic analyses of Gustafsson \& Bremer (1995). In certain cases some putative outgroups were used in several subsets. For the Flowers \& Fruits full data set (Flowers.DAT), 66 terminal taxa were used, including Lobelia and the hypothetical outgroup "HYPOTH._EUDICOT" and 50 characters were used. This was then broken into three subsets restricted to Campanuleae (38 taxa), Platycodoneae (12 taxa), and Wahlenbergeae ( 22 taxa) (all in their approximate traditional circumscription) using the same character set. This procedure was repeated for the Pollen full data set (CampPal.DAT) with 38 terminal taxa and 14 characters, and for the Seeds full data set CampSeed.DAT) with 53 terminal taxa and 11 characters. The Pollen data subsets were Campanuleae ( 21 taxa), Platycodoneae ( 11 taxa) and Wahlenbergeae ( 15 taxa). The Seeds data subsets were Campanuleae (43 taxa), Platycodoneae (6 taxa) and Wahlenbergeae (13 taxa).

These twelve data sets were converted to NEXUS format and constructed in the data editor of the MacClade program on a Macintosh Quadra 610. They were initially evaluated and uninformative characters were excluded. The characters were given equal weight using procedures suggested in Maddison \& Maddison (1992) and Swofford (1993). Thus, in the character lists, the different weights accorded to each character correlate to the number of states in each character. The most parsimonious topology for each tree was then found by invoking the "full-search above" strategy of MacClade. Various statistics and indices were also computed from the shortest trees and character distribution on the cladogram was observed using the "Trace Character" option. This data was later used for the phylogenetic reconstructions. The data sets were then transferred to the program PAUP and rooted by outgroup which was treated as a monophyletic sister group of the ingroup (except where indicated). The ingroup was considered to be monophyletic. Multiple states were interpreted
as polymorphisms. For phylogenetic analyses, the ordered (Wagner) and unordered (Fitch) characters were optimised by selecting both the ACCTRAN and DELTRAN options (the former favours single origin followed by reversal, while the latter favours parallelisms). MAXTREES was set at 100-550 depending on the size of the dataset and the computing time required. Topological searches for the most parsimonious trees were invoked by using heuristic search algorithms. For the initial searches several options were tried in order to avoid local optima or "islands" of suboptimal topologies (Maddison, 1991; Page, 1993). The search strategies used were essentially those given in Appendix 1. of Olmstead $\&$ Palmer (1994). As a general procedure the "keep minimal trees only" option was selected, the ancestral states option set for the outgroup "on", and the "collapse zero-length branches" off. The latter option was selected in order to maximise the number of trees found on each local optimum. For each initial heuristic search branch swapping was initiated on the starting trees which were imported from MaClade, the NNI (nearest-neighbour interchange) option was selected with MULPARS "off" and STEEPEST DESCENT "on". For each data set 5 independent runs using 1000 addition sequence replications were made with the Random Addition option selected. During each of the 5 runs no more than 5 MPRs (most parsimonious reconstructions) were retained and these were used as the seed for each subsequent run. The shortest tree from the five runs was then used as the starting tree for a full search using the TBR (tree-bisection-reconnection) option and MULPARS and COLLAPSE options "on". In some cases multiple trees were found and in these instances consensus trees were constructed. Where a large number of most-parsimonious trees were found an arbitrary choice based on the best apparent fit was made. The trees in these subjective subsets differed only by 1-2 symmetric-difference units from each other. For all trees found, tree lengths and consistency indices were obtained, while, for the consensus trees consensus indices were also obtained. See Tables 25 . and 26 . Bootstrap values (the bootstrap p-value; Felsenstein, 1985) were calculated from PAUP for all baseline subsets using 2000 replicates (Hedges, 1992), and bootstrap consensus trees (Figs.59;65;70;73 and 78 ) constructed for groups compatible with the $50 \%$ majority-rule consensus. Due to computational cost, only pruned subsets lacking putative outgroups and taxa which have much missing data were used. For subsets less than or $=10$ taxa the Branch and Bound search option was used but for all other subsets the Heuristic search option was employed.

Only included and informative characters were used in the Bootstrap analyses. The swapping algorithm was the TBR and the addition sequence was Simple (ie. corresponding the the "advancement index" of Farris, 1970). For a discussion on the use of the Bootstrap see below.

### 7.2.3 Clunsterimg algarithms

Under parsimony, the optimality criterion is to minimise tree length (ie. the number of character steps required) which is considered to represent an historical reconstruction with the minimum number of evolutionary changes. However, we do not know if and when evolution proceeds parsimoniously. The strongest argument for using parsimony is that it is the method which explains the data to the greatest degree while minimising ad hoc (eg. evolutionary) assumptions (Farris, 1983). Parsimony analysis assumes that characters are independent of each other and this allows for independent models of evolution for each character. Such an approach (which also parallels the maximum-likelihood method) would then be to find the tree(s) for which the length summed over all the data sets is a minimum. Under simple parsimony, length is computed for each character independently and in the same manner for all characters. The tree that minimises the sum of lengths of two data sets is also the tree with minimum length for the combined data set. This approach does not account for different stochastic processes affecting the characters. When these differ, it is doubtful whether simple addition of tree lengths is appropriate. A reasonable solution to this problem is differential character weighting but in this study it is too premature to give differential weights to characters. In the phylogenetic reconstruction some experimentation with character weighting was made, principally the implied weighting (Goloboff, 1993) procedure using the programs SPA and PIWE but have not been implemented in this study.

### 7.2.4 Measures of firt

### 7.2.4.1 Tree Lemgths

Tree length $(s)$ is a statistic that gives an indication of how well the tree fits the data Camin \& Sokal (1965). The longer the tree length, the worse the fit. Tree length is simply the weighted sum, over all the characters, of the number of evolutionary steps in each character of the tree but it is also dependent on the number of states. As these variables increase, so
too does the length. Tree length is also a measure of the amount of evolutionary change required by a tree, therefore indicating the amount of convergence and reversal. The actual value depends on whether the characters are weighted or not, and the models of character evolution (and hence the cost of the reconstruction) which are invoked. The most parsimonious reconstruction of ancestral states implies a minimum number of steps in each character of the tree. For the formulae used in the calculation of tree lengths and for consistency indices, see Maddison \& Maddison (1992).

### 7.2.4.2 Comsistemey, Retemtiom amd Homoplasy Imdices

The Consistency Index ( $C I$ ) indicates how well a tree fits a data set and is derived by scaling the number of steps ( $s$ ) required by a tree by the minimum $m$ (the minimal amount of change that the character may show on any conceivable tree) and/or maximum ( $g$ ) conceivable number of steps the character could have in any possible tree (Kluge \& Farris, 1969; Maddison \& Maddison, 1992), ie. $C I=m / s$. More simply, it can be viewed as the minimum possible tree length divided by the observed tree length. The $C I$ can be calculated in PAUP and in MacCLADE for individual characters and for the whole tree (the "ensemble" index) and is appropriate only for the included characters in any given analysis. However, autapomorphies may be included in the $C I$ if so desired. For all of the baseline analyses used in this study uninformative characters were excluded. The $C I$ is a reliable estimate of phylogeny if homoplasy is low. If the characters in the data set are perfectly congruent and there is no homoplasy, then the $C I=1$. As homoplasy and the number of steps increases, so the value of the $C I$ approaches but never reaches zero. $C I$ has also been used to measure homoplasy since $s$ will exceed by the amount of extra steps or homoplasy in order to account for the character on the tree but it does not always increase as homoplasy decreases. A high value for the $C I$ is considered desirable but it can be negatively correlated with the number of taxa and characters in the data set. Autapomorphies and symplesiomorphies also cause the $C I$ to increase without providing extra support for groupings of taxa. The Rescaled Consistency Index ( $R C$ ) (Farris, 1988), which is essentially a refinement of the $C I$, achieves a value of zero and is calculated by multiplying the values of the Consistency Index and Retention Index. It suffers from similar weaknesses as the CI. See Siebert (1992) for futher details.

The Retention Index (RI) (Archie, 1989) is derived in the same way as the Consistency Index and as with that index, it provides a reliable estimate of phylogeny when homoplasy is low. When a character fits the tree as poorly as possible, its retention index $=0$ (Swofford, 1991). However, it is designed to express the amount of synapomorphy by examining the actual amount of homoplasy as a fraction of the maximim possible homoplasy. In this respect it may be considered a better measure of support for groupings than the Consistency Index. The RI is high when state changes occur predominantly on internal nodes and low when changes occur mainly on terminal branches. The formula for the calculation of this index may be found in Maddison \& Maddison (1992).

The Homoplasy Index $(H I)$ is calculated by the formula $1-C I$ and is a measure of the amount of homoplasy in individual characters and, as a summation, for the whole tree. For multistate taxa which are considered polymorphic (as in this study) the $H I$ will have a different value from multistate taxa which are "uncertain" (Swofford, 1991).

### 7.2.4.3 The $\mathbb{B}$ ootstrap

This procedure is designed to give measures of confidence to a cladogram or a phylogenetic reconstruction. The bootstrap method (Felsenstein, 1985) involves sampling the original data set with replacement, thus constructing a series of replicates of the same size. The variation among these replicates is regarded as a measure of the error when estimates are made from the original data set. The taxa are held constant in the resampling but the characters are sampled with replacement to build a series of new replicates (the bootstrap replicates). These are then subject to the same search strategies as for the original data set and a majority-rule consensus tree is constructed showing the percentage of occurrences of a particular component among the trees (the bootstrap value). It is considered that for a data set to have $95 \%$ (or greater) confidence in the bootstrap values, at least 2,000 replicates are required (Hedges, 1992). For this study, bootstrap analyses were conducted on pruned, unrooted trees using included characters only, 2000 bootstrap replicates, simple weighting and simple addition sequence. Depending on the size of the data set, the search option was either branch and bound or heuristic.

### 7.2.5 Comsemsus Niethodls

Details of consensus methods can be found in Section 7.1.5.1. The following two methods were used only with the cladistic analyses:

## a. Adamms-2 Consemsus

This predates all other consensus methods (Adams 1972). This method often preserves more structure than the strict consensus. Any taxonomic statement shared by the trees being compared are included in the consensus, regardless of whether they constitute completely uncontradicted components. Adams (1972) stated that the Adams-2 consensus tree satisfies the following conditions: 1) any nesting found in all of the rival trees must also occur in the consensus tree; and 2) any nesting that reflects clusters of the consensus tree (ie. a nesting involving the inclusion of one within a larger group) must be found in all of the rival trees. This method may produce consensus trees containing clusters not found on any of the rival trees. It may be valuable in pin-pointing taxa that are responsible for incongruence (Funk, 1985; Hillis, 1987).

## b. Combinable-compomemt (Semi-strict comsensus)

Hillis devised a consensus method, formalised by Bremer (1990) as the "combinable component consensus" or "semi-strict consensus". When one or more of the rival trees is not fully dichotomous, groups that are never contradicted may occur on some, but not all, of the trees. Two groups are combinable (Nelson, 1979) if either i) they have no taxa in common ("exclusion") or ii) they are identical ("replication"); or iii) one group is a proper subset ("further resolution") of the other ("inclusion"). The combinable-component consensus is defined by the set of all combinable groups (ie. each group retained in the consensus is equal to or combinable with all groups of every rival tree). When all rival trees are fully dichotomous, the strict and combinable-component consensus methods.

### 7.2.5. I Comsemsus Imdices...measures of heterogemeity of rival cladograms.

Consensus methods provide less parsimonious explanations of the character data but they are most useful when used in congruence testing. In cladistic studies, the use of consensus methods applies mainly to independent cladograms produced in the same cladistic analysis.

In phylogenetic reconstruction, the use of consensus methods can be used to determine congruence between trees produced from different data sets and different methods (but with the same terminal taxa). Consensus trees are not estimates of phylogeny but are simply statements about areas of agreement among trees (Swofford, 1991). A consensus index provides a quantitive measure of congruence. In Table 26. only the CIs which which strictly measure agreement between trees are shown. Consensus indices usually vary between 0 (implying no agreement among rivals) and 1 (maximum agreement). This means that if an index has a value of 0.8 the rival trees share $80 \%$ as much information on relationships as does a set of identical, maximally asymmetrical trees but there are problems of interpretation as to what this actually means. It may be useful to test, using Monte Carlo methods, whether a given consensus index is greater than that expected for a set of randomly chosen trees (Simberloff, 1987).

The various indices which are briefly described below are generated by the program PAUP. The simplest consensus index is the Component Information of Nelson (1979) which is the number of informative (ie. non-trivial groups which comprise at least two terminal taxa) clusters present on the tree. The Schuh-Farris Levels Sum (Schuh \& Farris, 1981) is a measure of the number of times distinct pairs of terminal taxa occur together on the same informative cluster. The resolution of the consensus tree can be further quantified by the CIc or Colless Consensus Fork Index (Colless, 1980) which is the component information divided by the maximum possible such number ( $t-2$, where $t=$ number of terminal taxa). The degree of resolution of a tree does not necessarily reflect the amount of information it contains (Swofford, 1991). The most favourable consensus index which combines information content and congruence is the Mickevich index, CIm, (Rohlf, 1982; Mickevich, 1978). A property of these indices is that they are sensitive to tree symmetry or balance (Swofford, 1991) and that the normalised total-information measure and the levels sum can achieve their maximum value only when the consensus tree is fully resolved and maximally asymmetrical. Asymmetry bias in a consensus index can result in two different asymmetrical trees achieving a higher score than two identical symmetrical trees. The CIm however, can achieve its maximum value on a tree that is maximally symmetrical (Swofford, 1991).

Therefore, where it is desirable to reflect only agreement it would be preferable to use the CIm.

Indices which are not sensitive to excessive asymmetry bias are Rohlf's $C I(1)$ and $C I(2)$. The $C I(1)$ (Rohlf, 1982) always has a maximum value of 1 (ie. fully resolved) and reflects both information content and resolution. The $C I(2)$ (Rohlf, 1982) is the proportion of all possible binary trees that contain the clusters found in the consensus tree.

A legitimate criticism of these "one-dimensional" (Swofford, 1991) consensus indices is that they depend only on the consensus tree; once this tree has been calculated, all contact with the original rival trees is abandoned. Thus, for example, it is not possible to determine whether a consensus index is low because there was substantial disagreement among a set of well resolved trees or because there was substantial disagreement among a set of poorlyresolved trees.

### 7.2.6 Results of the Baselime Cladistic Amalyses

The results of the baseline cladistic analyses are given in Figs. 55-78 and the consistency and consensus indices are shown in Tables 25. and 26.

### 7.2.6. 1 The Campamulaceac full data set

The Flowers and Fruits full data set for the Campanulaceae yielded a single tree (Fig.55) with a length of 5576 and a $C I$ of 0.602 . This was constructed from 40 characters ( 8 characters were excluded), 6 of which were unordered. $25 \%$ of the characters had a $C I$ 口 0.750 while $15 \%$ (No.s $12,13,15,37,38$ and 39) had a $C I=1.000$. The tree is fully resolved apart for a major trichotomy at about mid level and a minor one comprising three small clades characterised by genera such as Asyneuma, Legousia, Gadellia and Rapunculus. The greatest weakness of the tree is the fact that the colporate and colpate genera do not form a single monophyletic group but branch off singly forming a chain of sister groups or minor clades such as those formed by Campanumoea, Cyclocodon and Canarina and by Platycodon and Ostrowskia which are nevertheless very plausible groupings. Heterochaenia, Nesocodon and, rather surprisingly, Azorina are basal to all other genera which comprise the
largest single clade. Within this large clade Adenophora is basal and a sister group of all other taxa. There are many minor clades which appear to support traditional groupings such as the clade formed by Asyneuma, Phyteuma, Petromarula and Physoplexis. Most interestingly, this clade also included Campanulastrum, Sergia, Popoviocodonia and Triodanis. Another such clade included genera such as Brachycodon, Legousia, Prismatocarpus, Gunillaea, Namacodon and Cylindrocarpa. Most of the South African endemic genera grouped in expected places but the presence of Githopsis with Roella and Craterocapsa seemed anomalous as did Leptocodon and Cyananthus with Musschia. Although the majority of the Campanuleae form clades separate from the Wahlenbergeae there are interpolations of taxa such as Legousia and Trachelium into two largely separate groups of the Wahlenbergeae which suggests that both tribes are less homogeneous entities than previously thought. Because of the size of this data set no attempt was made to obtain bootstrap values.

The Pollen full data set for the Campanulaceae also yielded a single tree (Fig.56) with a length of 1260 and a $C I=0.852$. This was constructed from 13 characters ( 4 excluded), 3 of which were unordered and 2 were irreversible. $69 \%$ had a $C I$ ロ 0.750 while $38 \%$ had a $C I=$ 1.000. The tree is unbalanced and poorly resolved which is not surprising given the small number of characters. One or two interesting features can be seen however. The colpate and colporate genera are basal to the porate genera. Asyneuma again forms a clade with Phyteuma although Physoplexis now unites with Jasione and Campanulastrum on a separate clade. Roella, Nesocodon, Musschia and Craterocapsa unite on an unresolved clade as do Legousia, Prismatocarpus and Githopsis.

The Seeds full data set for the Campanulaceae yielded a single tree (Fig.57) with a length of 4622 and a $C I=0.886$. This was constructed from a mere 12 characters (none excluded), 4 of which were unordered. $83 \%$ had a $C I$ ロ 0.750 while $8 \%($ no. 4$)$ had a $C I=1.000$. It is a moderately resolved tree and quite well balanced but there are several polytomies at lower levels. This tree conflicts in many ways with those obtained for flowers \& fruits and for pollen although it is not strictly comparable because of a very different suite of taxa. The colporate and colpate genera do not group basally to the porate genera. Instead genera such C.lingulata with the latter genera is quite anomalous. There seems to be a fairly acceptable grouping of taxa in the campanuloid clade comprising Symphyandriformes, Quinqueloculares, Michauxia, etc. Other minor clades do not appear to conflict with the other data sets. For example, Campanulastrum groups with Phyteuma and Jasione with Trachelium. However, overall these results are remarkably confusing and this is compounded by the nesting of genera such as Platycodon and Cyananthus, etc. within campanuloid or wahlenbergioid lineages.


Fig.55. Baselime cladogramn of the Campamonlaceae (Flowers \& Fruits funl set). A simgle tree was obtaimed.


Fig.56. Banselime cladogranm of the Campamullaceae (Pollem finll setr). A simgle tree was - btaimed.


Fig.57. Baselime cladagram of the $\mathbb{C}$ ampamulaceae (Seedls full set). A simgle tree was olbtaimed.

In order to obtain better resolution, cladograms based on subsets comprising the traditional tribal groupings of Campanuleae, Platycodoneae and Wahlenbergeae were obtained.

### 7.2.6.2 The Campamuleae sulbset

The Flowers and Fruits subset for the Campanuleae yielded a single tree (Fig.58) with a length of 3288 and a $C I$ of 0.662 . This was constructed from 30 characters ( 18 characters were excluded), 5 of which were unordered. $43 \%$ had a CI 口 0.750 while $13 \%$ (No.s 4,18 , 37 and 43) had a $C I=1.000$. It is fairly well resolved apart from a trichotomy within the "rapunculoid" clade and another within the "campanuloid" clade. This subtree is naturally very similar to major portions of the tree obtained with the full data set. Azorina and Adenophora are basal with the latter being the sister group of all other taxa. Hanabusaya and Symphyandra both diverge early as does the minor clade comprising Edraianthus, Petkovia, Roucela and Githopsis. The remainder of the taxa form two large subclades, the first comprising what might be losely called a "rapunculoid/legousioid" clade (including genera such as Petromarula, Phyteuma and Campanulastrum, etc.), while the second forms what might be losely called a "campanuloid/trachelioid" clade (including genera such as Musschia, Feeria, Jasione, etc.). An unrooted bootstrap consensus tree (Fig.59) gave weak or very modest support for the monophyly of some of the minor clades. The strongest support was for the clade No. 1 which had a $p$-value $=68 \%$ while the subclade of this (No. 2) had a $p$-value $=55 \%$. Clade No. 3 had a $p$-value $=60 \%$ and clade No. 4 had a $p$-value $=$ 54\%.

The Pollen subset of the Campanuleae yielded 6 trees, 4 of which were saved (Fig.60). These were chosen arbitrarily and were $<($ or $=) 20$ symmetric-difference unitsfrom tree No.1. The length of these trees was 642 and the $C I=0.903$. This was constructed from 8 characters ( 9 excluded), 3 of which were unordered and 1 irreversible. $86 \%$ had:a $C I>$ ( or $=$ ) 0.750 while $50 \%$ had $C I=1.000$. The 4 trees are poorly resolved and not very symmetrical. There are a few interesting, though unresolved clusters formed by Adenophora, Azorina and Campanula, and by Asyneuma, Phyteuma and Physoplexis,etc. Consensus trees (Fig.61) were then obtained in order to ascertain the best-supported groups (see also Consensus Indices in Table 26.). The Strict Consensus shows an unresolved minor clade comprising

Githopsis, Hanabusaya and Legousia and this is confirmed by the Semistrict Consensus which gives a value $=100 \%$. The branch with Prismatocarpus joins this clade with a value of $25 \%$. This minor clade then forms part of a larger, also unresolved, polytomy which includes Homocodon, Peracarpa and Prismatocarpus which has a value $=100 \%$. The remainder of the cladogram for Strict and Semistrict Consensus is completely unresolved. In the Majority Rule Consensus the genera Adenophora, Azorina and Campanula form a subclade in 3 out of 4 trees (75\%) as do Homocodon and Peracarpa. The subclade formed by Githopsis, Hanabusaya and Legousia are found in all trees. Both subclades form a single larger clade in all 4 trees ( $100 \%$ ). A bootstrap consensus tree (not shown) yielded no support for any of these clades (the highest p-value obtained was $40 \%$ for Homocodon with Peracarpa).

The Seeds subset of the Campanuleae yielded a single tree (Fig.62) with a length of 3949 and a $C I=0.877$. This was constructed from 11 characters ( 1 excluded), 2 of which are unordered. All characters had a $C I>($ or $=$ ) 0.750 while $9 \%$ had a $C I=1.00$. This is a moderately well-resolved tree although it is not very symmetrical. Similar groupings to those in the full data set are present and Musschia (and the anomalous C.lingulata) is basal to all other taxa. The "Isophylla" group also is low on the cladogram. As with the full data set, many of the groups are difficult to reconcile with traditional arrangements or with the other two data sets. A bootstrap consensus (not shown) yielded no support for any of these clades (the highest p-value obtained was $37 \%$ for Azorina with C. lanata), 3 of which were unordered.


Fig.58. Baselime cladlogram of the Campamuleae (Flowers \& Fruits subset). A simgle tre was obtaimed.


Fig.59. Bootstrap comsemsus tree for the Campamuleae sulbset (Flowers \& Fruits data). Groups compatible with the $50 \%$ Najority $\mathbb{R} u l l e$ comsemsus are also shown. Numbered triangles refer to the modes which are memtiomed im the text.

-Fig.60. Basclime cladiagrams of the Campamuleae (Poilem sublbet). 4 trees which were $<$ (or $=$




Fig. G1. Baselime claclograms of the Campamuleae (Pablem sulbset̂). Comsemsus trees from 4 saved trees.


Fig.62. Baselime clandogramn of the Campamunleae (Seēdls subset). A simgle tree was obtainecd.

### 7.2.6.3 The Platycodomeae sulbset

The Flowers and Fruits subset for the Platycodoneae yielded 13 trees (Fig. 63), 4 of which were saved. These were chosen arbitrarily and were $<($ or $=$ ) 2 symmetric-difference units from tree No.11. The 4 trees had a length of 1356 and a $C I=0.617$. The data set was constructed from 23 characters ( 25 excluded), 3 of which were unordered. $35 \%$ had a $C I>$ ( or $=$ ) 0.750 , while $26 \%$ (No.s $4,5,7,12,38$ and 47) had a $C I=1.000$. The trees are all fully resolved and very symmetrical. The colporate genera Campanumoea, Cyclocodon and Canarina form a clade in all four trees and are basal. Cyananthus forms a clade with Leptocodon in all 4 trees as does Musschia with Platycodon. Consensus trees were obtained and are shown in Fig. 64. (see also Consensus Indices in Table 26.). Both Strict and Semistrict are completely unresolved except for the clade comprising Cyananthus and Leptocodon (100\%). In the Majority Rule Consensus Campanumoea, Canarina and Cyclocodon have a value of $62 \%$ while the clade formed by all other taxa occur in $100 \%$ of the trees. Within this clade Musschia and Platycodon have a value of $85 \%$. An unrooted bootstrap consensus (Fig.65) gave strong support (70\%) for the clade (No. 2) formed by Codonopsis, Cyananthus, Leptocodon, Echinocodon, Pseudocodonopsis, Platycodon and Ostrowskia. Rather weaker support ( $56 \%$ ) was given to an enlarged clade (No.1) which had Canarina as basal to the above-mentioned taxa, and to the subclade (No.3) which comprised Cyananthus and Leptocodon.

The Pollen subset for the Platycodoneae yielded 38 trees, 4 of which were saved (Fig.66). These were chosen arbitrarily and were < (or =) 3 symmetric-difference units from tree No.38. The 4 trees had a length of 432 and a $C I=0.875$. The data set was constructed from just 6 characters ( 11 excluded), 2 of which were unordered and 2 were irreversible. $83 \%$ of the characters had a $C I>($ or $=$ ) 0.750 while $50 \%$ (No.s 4,14 and 15) had a $C I=1.00$. The trees are fully resolved but not very symmetrical. Cyananthus and Leptocodon are basal in all 4 trees while the latter form a sister group to all other taxa. Canarina forms a clade with Codonopsis in all 4 trees, as does Musschia with Platycodon. Pseudocodonopsis consistently separates from Codonopsis. Consensus trees were obtained (Fig. 67) which supports these results (see also Consensus Indices in Table 26.). The Strict Consensus shows Musschia with Platycodon and Canarina with Codonopsis. This is confirmed by the Majority Rule

Consensus which also gives $100 \%$ support to the clade comprising Echinocodon, Musschia, Platycodon, Ostrowskia and Pseudocodonopsis. Despite these results an unrooted bootstrap consensus (not shown) failed to provide any strong support for these clades. The highest values obtained were $52 \%$ for Clade No. 1 ( $40 \%$ support for Echinocodon with Platycodon, and $40 \%$ for Canarina with Codonopsis).

The Seeds subset for the Platycodoneae yielded 3 trees (Fig.68) with a length of 660 and a $C I=0.864$. It was constructed from 9 characters ( 3 excluded), 1 of which was unordered. $78 \%$ of the characters had a $C I=1.000(4,6,7,8,9,11$ and 12$)$. All 3 trees are fully resolved but considerably asymmetrical. Roella was consistently basal in all 3 trees while Cyananthus formed a clade with Codonopsis in 2 of the trees. A Strict Consensus (Fig.69) (see also Consensus Indices in Table 26) showed Roella to be basal to all other taxa but the remainder formed an unresolved polytomy. In the Majority Rule Consensus, Roella, as a basal taxon and sister taxon of the others, has a value of $100 \%$. Likewise, at a higher level Platycodon is the sister taxon of Cyananthus, Codonopsis, Nesocodon and Leptocodon. An unrooted bootstrap consensus (Fig.70) gave 100\% support for the clade formed by Platycodon and Leptocodon.


Fig.63. Baselime cladograms of the Platycod omeae (Flowers \& Fruits subset). \& trees which were < (or $=) 2$ symmetric- $d$ lifferemce wnits fromn tree $\mathbb{N}$ ©. 11 were saved from 13 trees.

 trees from 4 saved urees.

Codonopsïs s.s.



Fig.66. Baselime cladlograms of the Platycodlomeac (Poxlem sulbset). 4 trees which were $<$ (or $=$ ) 3 symmetric-differemce umits fromn tree $\mathbb{N} \omega .38$ were saved fromm 38 trees.


Fig.67. Baselime cladiograms of the Platycodomeae (Pollem sulbset). Comsemsus trees of 4 saved trees.


2


Fig. 68. Baselime chadimgrams of the Platycodomeae (Seeds subset). 3 trees were obtaimed.


Majority rule


Adams


Fig. 69 . Baselime cladlograms of the $\mathbb{P l a t y c o d}$ meae (Seeds subset). Comsensus trees of 3 saved trees.


Fig.70. Bootstrap comsemsus tree for the $\mathbb{P l a t y c o d m a e r e ~ ( S e e d l s ~ s u b o s e t ) . ~ G r o u p s ~ c o m p m a t b l e ~}$ with the $50 \%$ Majority $\mathbb{R}$ unle consensuds are allso shown.

### 7.2.6.4. The Wailnlembergeae sulbset

The Flowers \& Fruits data subset for the Wahlenbergeae yielded 2 trees (Fig.71) with a length of 2262 and a $C I=0.698$. It was constructed from 38 characters ( 20 excluded), 4 of which were unordered. $34 \%$ had a $C I>($ or $=$ ) 0.750 while $16 \%$ (No.s $2,11,13,15,29$ and 39) had a $C I=1.000$. Both trees are well resolved and highly symmetrical. Nesocodon and Heterochaenia are both basal and the latter genus is sister taxon of all the remainder. There are two major clades in each tree, one comprising Roella, Prismatocarpus and closely related South African endemic genera plus the putative outgroups such as Legousia, Githopsis and Edraianthus. The other clade comprises Wahlenbergia, Berenice and other South African endemic genera such as Microcodon, Merciera, etc., plus putative outgroups such as Trachelium, Feeria, Jasione and Musschia. The two trees differ mainly in the arrangement of groups within the latter clade. The Strict and Semistrict Consensus trees (Fig.72) (see also Consensus Indices in Table 26.) hardly improve the situation by each producing producing a polytomy within which the grouping of Feeria, Merciera and Theilera remains unresolved. A pruned bootstrap consensus tree (with putative outgroups removed) is shown in Fig.73. Bootstrap p-values of 53\% were found for clade No.1, $62 \%$ for clade No.2, $74 \%$ for clade No.3, $64 \%$ for clade No. 4 and $87 \%$ for clade No. 5 .

The Pollen data subset for the Wahlenbergeae yielded 372 trees, 4 of which were saved (Fig.74). These were chosen arbitrarily and each was < (or =) 4 symmetric-difference units from tree No.1. The length of the 4 trees was 328 and the $C I=0.963$. The dataset was constructed from only 5 characters ( 12 excluded), 2 of which were unordered and 1 was irreversible. All characters had a $C I>0.750$ while $80 \%$ (No.s $5,6,10$ and 16) had a $C I=$ 1.000. The 4 trees are well balanced but contain a few polytomies, particularly the clade comprising Heterochaenia, Musschia, Nesocodon, Prismatocarpus and Roella. Githopsis and Legousia consistently formed a single clade while a basal position varied between the bulk of the genera and Edraianthus (tree 1 and 147), Trachelium (tree 138) or Gunillaea (tree 280). Semistrict and Majority Rule Consensus trees (Fig.75) (see also Consensus Indices in Table 26.) gave a support value of $75 \%$ for the clade comprising Githopsis, Legousia, Heterochaenia, Musschia, Nesocodon, Prismatocarpus, Roella, Wahlenbergia
and Jasione. A pruned bootstrap consensus tree (not shown) failed to provide any support for these clades.

The Seeds data subset for the Wahlenbergeae yielded 32 trees, 5 of which were saved (Fig.76). These were chosen arbitrarily and each was < (or =) 3 symmetric-difference units from tree No.15. The length of the trees was 1260 and the $C I=0.881$. The data set was constructed from 9 characters ( 3 excluded), all of which were ordered. $89 \%$ had a $C I>$ (or $=$ ) 0.750 while $44 \%$ (No.s 4, 6, 7 and 11) had a $C I=1.000$. The trees are not well balanced and 2 (No.s 6 and 10) have minor polytomies. Craterocapsa and Roella are most consistently basal, while Musschia and "Helenacodon" also remain close to the outgroup (HYPOTH.-EUDICOT). Edraianthus forms a a clade with Trachelium in all 5 trees. The consensus trees (Fig.77) (see also Consensus Indices in Table 26.) show $100 \%$ support for the clade formed by Roella and Craterocapsa and by Edraianthus and Trachelium. A pruned bootstrap consensus tree (Fig.78) gave considerable support for several of these minor clades. Clade No. 1 had a p-value of $81 \%$ while clade No. 2 had a p-value of $74 \%$.

These baseline cladograms have yielded a series of descent patterns based on the hierarchic distribution of characters in the three data sets. These patterns show varying degrees of concordance with the patterns obtained in the phenetic analysis. Some of the groupings obtained by cladistic means show striking similarities with phenetic results while others are rather poor, particularly those obtained from the Pollen and Seeds data sets. This is not surprising given the very low numbers of characters used in the construction of the cladograms. By analysing subsets of data based on the three traditional tribal groupings a somewhat improved resolution was obtained but the problem of a high taxa:character ratio remained. Pruning these data sets still further for bootstrap consensus trees only marginally improved the situation. In conclusion of this section, these baseline studies have provided data which will be integrated with the results from molecular studies and component analysis. Further manipulation and testing of the data and results (such a iterative weighting, T-PTP tests and selective removal of poorly scored taxa) could possibly provide further support for selected clades in a phylogenetic construction. In addition the combining of datasets could provide better phylogenetic signal.


2


Fig. 71. Baselime claulograms of the Wamlembergeae (Flowers \& Fruits subset). 2 trees were obtaimed.

Strict


Semistrict


Fig. 72. Baselime cladograms of the $\mathbb{W}$ alhlembergeae $\{$ (Flowers \& Fraits sulbset). Comsemsus trees from 2 saved trees.


Fig.73. Bootstrap comsemsus tree for the Walmlembergeae (Flowers \& Fruits subset). Groups compratible with the $50 \%$ Niajority $\mathbb{R} u$ le comsemsus are also shown. Numblered triamgles refier to modes memtiomed im the text.


Fig.74. Baselime cladagrams of the $\mathbb{W}$ almlembergeae (Pollem subset). 4 trees which were $<$ (or $=) 4$ symmetric-differemce umits from Tree No. 1 were saved from 372 đrees.


Fig. 75. Baselime clandograms of the Wamlembergeae (Pollem sulbset). Comsemsus trees of 4
saved trees.


Fig.76. Baselime claollggromns of the Wainlembergeae (Seedls subset). 5 trees which were $<$ (or $=$ ) 3 symmetric-differemce mats from Tree $N$. 15 were saved from 32 trees.


Strict


Majority rule


Fig. 77. Baselime cladiograms of the Walhlembergeac (Seeds subset). Comsemsus trees of 5 saved trees.


Fig. 78. Bootstrap comsemsus tree for the Walhlembergear (Seeds sulbset). Groups compatible with the $50 \%$ Majority $\mathbb{R}$ unle comsemsuss are also showm. Numnbered triamgles refer to the monles memtioned im the text.

Table 25. Tree lengths and consistency indices (Baseline Analyses)

| DATA SET | LENGTH | CI | III | RI | $R C$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Flowers and Fruits - full set (Campanulaceae) | 5576 | 0.602 | 0.831 | 0.682 | 0.410 |
| Flowers and Fruits - subset 1 (Campanuleae) | 3288 | 0.662 | 0.775 | 0.655 | 0.434 |
| Flowers and Fruits - subset 2 (Platycodoneae) | 1356 | 0.617 | 0.586 | 0.640 | 0.395 |
| Flowers and Fruits - subset 3 (Wahlenbergeae) | 2262 | 0.698 | 0.718 | 0.639 | 0.446 |
| Pollen - full set (Campanulaceae) | 1260 | 0.852 | 0.768 | 0.880 | 0.750 |
| Pollen - subset 1 (Campanuleae) | 642 | 0.903 | 0.695 | 0.956 | 0.863 |
| Pollen - subset 2 (Platycodoneae) | 432 | 0.875 | 0.694 | 0.795 | 0.696 |
| Pollen - subset 3 (Wahlenbergeae) | 328 | 0.963 | 0.646 | 0.983 | 0.947 |
| Seeds - full set (Campanulaceae) | 4622 | 0.886 | 0.924 | 0.788 | 0.698 |
| Seeds - subset 1 (Campanuleae) | 3949 | 0.877 | 0.919 | 0.762 | 0.668 |
| Seeds - subset 2 (Platycodoneae) | 660 | 0.864 | 0.545 | 0.793 | 0.685 |
| Seeds - subset 3 (Wahlenbergeae) | 1260 | 0.881 | 0.793 | 0.801 | 0.705 |

Table 26. Consensus Indices (Baseline Analyses)

| DATA SET | CIc | CIm | Pm | Csf | CI(1) | CI(2) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| F.\&F.(subset P) S | 0.333 | 0.286 | 0.367 | 0.418 | 0.372 | 16.643 |
| F.\&F.(subset P) MR | 0.833 | 0.690 | 0.622 | 0.533 | 0.939 | 27.501 |
| F.\&F.(subset P) A | 0.500 | 0.429 | 0.465 | 0.453 | 0.473 | 22.596 |
| F.\&F.(subset W) S | 0.909 | 0.561 | 0.549 | 0.465 | 0.949 | 62.695 |
| F.\&F.(subset W) A | 0.955 | 0.583 | 0.564 | 0.468 | 0.971 | 64.305 |
| Pollen (subset C) S | 0.136 | 0.061 | 0.116 | 0.134 | 0.115 | 18.305 |
| Pollen (subset C) MR | 0.227 | 0.083 | 0.135 | 0.136 | 0.133 | 25.746 |
| Pollen (subset C) A | 0.409 | 0.295 | 0.331 | 0.319 | 0.385 | 48.231 |
| Pollen (subset C) CC | 0.227 | 0.098 | 0.142 | 0.138 | 0.140 | 25.746 |
| Pollen (subset P) S | 0.778 | 0.640 | 0.685 | 0.673 | 0.750 | 18.103 |
| Pollen (subset P) MR | 0.889 | 0.760 | 0.833 | 0.842 | 0.925 | 19.201 |
| Pollen (subset W)S | 0.333 | 0.262 | 0.289 | 0.286 | 0.301 | 15.796 |
| Pollen (subset W) A | 0.417 | 0.357 | 0.400 | 0.409 | 0.425 | 19.629 |
| Pollen (subset W) CC | 0.411 | 0.381 | 0.389 | 0.385 | 0.411 | 19.292 |
| Seeds (subset P) S | 0.400 | 0.333 | 0.550 | 0.714 | 0.600 | 4.595 |
| Seeds (subset P) MR | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 9.249 |
| Seeds (subset P) A | 0.800 | 0.667 | 0.800 | 0.829 | 0.800 | 8.150 |
| Seeds (subset W)S | 0.667 | 0.643 | 0.611 | 0.588 | 0.681 | 24.793 |
| Seeds (subset W)MR | 0.917 | 0.929 | 0.856 | 0.813 | 0.971 | 28.600 |
| Seeds (subset W) CC | 0.750 | 0.786 | 0.689 | 0.646 | 0.768 | 25.892 |

S =Strict Consensus $\quad$ MR = Majority-Rule $\quad \mathrm{A}=$ Adams-2 $\quad \mathrm{CC}=\mathbf{C o m b i n a b l e ~ C o m p o n e n t ~}$ CIc = Consensus Fork Index $\quad$ CIm $=$ Mickevich's Index $\quad$ Pm = Colless weighted consensus fork
CIsf $=$ Schuh-Farris Levels Sum Index
CI(1) \& CI(2) = Rohlf's Consensus Indices, 1 \& 2

The data sets for Flowers \& Fruits, Pollen and Seeds were combined into a grand data set (Combined.DAT) using a reduced set of 49 taxa and a total of 67 characters. Uninformative characters were excluded and all characters were unweighted. The parameters used for the baseline searches were again used for the combined sets. Subsets of the Campanuleae, Platycodoneae and Wahlenbergeae were also constructed using this combined character set. The results for the combined data set of the Campanulaceae (Fig.79) agree with the baseline cladogram of the flower \& fruits data in that it yields a small basal monophyletic clade consisting of Canarina, Cyclocodon and Campanumoea. There is more resolution among the taxa of the Platycodoneae compared to the baseline cladogram and the taxa are closer to each other. However the Platycodoneae do not form a single monophyletic group. Cyananthus and Leptocodon form a minor clade as do Platycodon, Pseudocodonopsis and Echinocodon. Unlike the baseline cladogram, Ostrowskia does not link up with Platycodon. The clades formed by Canarina, Campanumoea and Cyclocodon, and Echinocodon, Platycodon and Pseudocodonopsis were confirmed by the results of the subset searches (Figs.81-82). Codonopsis and Cyananthus were, sequentially, sister groups to all other taxa (other than the clade which included Canarina). Ostrowskia was the sister group of the clade which included Echinocodon, Platycodon and Pseudocodonopsis, while Leptocodon, surprisingly did not link with Codonopsis but formed a clade with the outgroups Musschia and Microcodon.

The Wahlenbergeae show more resolution in the combined analysis and their position on the cladograms (Figs.83-84) as well as the minor clades formed by the taxa agree much more closely with traditional arrangements in comparison with the baseline analysis. Nesocodon forms a minor clade with Roella and Craterocapsa and this is the most basal clade for the Wahlenbergeae. Wahlenbergia is the sister group of all the remaining taxa which show a mixing of traditionally "wahlenbergioid" taxa with "campanuloid" taxa. The remaining taxa are largely divided into two major clades. In the smaller clade Microcodon, Rhigiophyllum and Siphocodon form a sister group of the remaining taxa. Berenice forms a a clade with Heterochaenia (and surprisingly with Peracarpa), while Merciera and Theilera collectively form the sister group of Feeria, Legousia, Trachelium, Jasione and Musschia. In the larger
clade Adenophora and Azorina form the sister group of the remaining taxa. Githopsis, Gunillaea, Namacodon and Prismatocarpus form the next sister group of the residue of "campanuloid" taxa and the lone "wahlenbergioid" genus Treichelia which also forms a minor clade with Triodanis. The Campanuleae in the combined analysis (Fig.80) are divided into two broad groupings which is much in accord with the baseline analysis as well as the phenetic analysis. The clade which includes Musschia, Jasione, Feeria, Legousia, Peracarpa and Trachelium is the sister group of the larger clade which includes Campanula and its closest allies. The most basal clade is that formed by Azorina and Adenophora and this is the sister group of all remaining taxa in the larger clade. Not surprisingly Petromarula, Asyneuma, Phyteuma and Physoplexis form a monophyletic group (with Rapunculus as the sister group) as do Hanabusaya, Symphyandra, Michauxia and Zeugandra, and Heterocodon with Homocodon.


Fig.79. Combimed cladlogram of the Campamulaceae (Fwll set). A simgle tree was obraimed.


Fig.80. Combimed cladogram for the Campamuleae (subset). A simgle tree was obtaimed.


2


Fig.81. Combimed cladlagranm for the Platycodmmeae (subset). 2 trees were obtaimed.


Fig.82. Combimed cladogram for the Platycodomeac (subset). Comsemsus trees of 2 saved trees.


Fig.83. Combimed ciadogranns for the $\mathbb{W}$ alllembergeae (subset). 4 trees were obtained.

Sirict


Majority rule


Fig.84. Combimed clanlograms for the Wahlembergeat (sulbset). Comsemsus trees of 4 saved trees.
"Detailed understarnding of an organism will only be achieved when every gene has been identified and its
transcript and the timing of transcript synthesis Anown."
"An surderstanding of evolution will require comparative analysis of entire genomes pather than individual genes."

## S. $\mathbb{B}$. Primrose, 1995

### 7.3.11 Imtroductiom

Many of the taxa used in this study could, by orthodox opinion, be considered as valid genera. At most, some of the taxa would probably be more acceptable as subgenera or sections of genera. However, there is little or no evidence of equivalency between these taxa and the criteria used to establish rank cannot be applied generally. There are neither generic exemplars within the Campanulaceae nor known rates of evolution within different lineages. In the selection of a gene which will display sufficient polymorphism between taxa and generate useful phylogenetic signal it is necessary to select one which is not too conservative in its evolution and which will allow the discrimination of taxa at the lower levels of the taxonomic hierarchy. The rbcL gene was considered and rejected as too conservative. It was also rather large for manual sequencing techniques which were, by necessity, the only methods available when this study commenced. $R b c L$ sequences for a small number of taxa have already been obtained for the Campanulaceae (Cosner et al., 1994) and it is to be hoped that the number of such sequences will increase. This will be most desirable in elucidating the relationships of the higher taxa, particularly at the tribal level, and will be useful in congruence studies with other genes or spacers such as ITS. There is some evidence to suggest that there is conflict between cpDNA and other lines of evidence (Rieseberg \& Soltis, 1991).

For the genera of the Campanulaceae, a gene, or region of DNA which is easily amplifiable, rapidly evolving and unambiguously alignable was required. Examination of the results of Baldwin $(1992,1993 a, 1993 b, 1994)$ suggested that the most suitable region of DNA could be the internal transcribed spacers (ITS) of the $18 \mathrm{~S}-26 \mathrm{~S}$ nuclear ribosomal DNA (nrDNA). The ITS region comprises the ITS1 spacer, the 5.8 S subunit and the ITS2 spacer (See Fig. 85). This region forms part of the transcriptional unit of nrDNA but the spacers are not incorporated into the mature ribosomes. The mature cytoplasmic $18 \mathrm{~S}, 5.8 \mathrm{~S}$ and 26 S rRNAs
are cleaved from a larger precursor, the $37 \mathrm{~S}-45 \mathrm{~S}$ nRNA (Venkateswarlu \& Nazar, 1991). The spacer regions appear to partly function in the maturation of nrRNAs. Vedman et al. (1980; 1981) have shown that the deletion of the spacer regions can prevent the accumulation of mature ribosomal RNAs, while the studies of Nazar et al. (1987) suggest they maintain processed sites in close proximity. Therefore, although the ITS region is less conservative that its flanking coding regions, it is not without some evolutionary constraints. For extensive discussion of the utility of the ITS region in the reconstruction of angiosperm phylogeny, see Baldwin et al. (1995).

## ITS5 Primer



Fig. 85. Diagram of the ITS region of nuclear ribosomal 18S-26S DNA tandem repeat units. The small arrows indicate the primer sites.

The ITS region possesses several important properties which make it favourable for use in molecular systematic studies. It is highly repeated within the nuclear genome at multiple loci (Rogers \& Bendich, 1987) and thus facilitates easier amplification and sequencing. The small size of the ITS region ( $<654 \mathrm{bp}$ in the Campanulaceae) and the highly conserved flanking subunits makes it relatively easy to amplify and for many angiosperm families even herbarium material can be used (although the Campanulaceae are recalcitrant in this latter respect). Most importantly, this multigene family is subject to concerted evolution via unequal crossing-over at meiosis and thus undergoes a homogenisation process. This is vital if these tandem repeats are to be useful in the reconstruction of phylogenetic relationships. It is considered that the homogenisation is so complete and so rapid that pooled DNA from several independent samples can be used (Baldwin et al., 1995) and that intrapopulation sampling may be minimised. The possibility that divergent paralogues (ie. those ITS regions at different chromosomal loci) remain should not be overlooked (Sanderson \&

Doyle, 1992). Usually this kind of intragenomic variation or misreplication (usually one indel) can be detected fairly rapidly in direct sequences and can be seen clearly on automated sequencer electropherograms. For this study of ITS variation in the Campanulaceae the presence of paralogues was not considered to be a major problem although the small sample sizes and the possibility of such products being sampled must be borne in mind. The Tbr polymerase used in the amplification reactions has a very low error rate and thus the signal for the correctly replicated sequences will predominate (see Baldwin, et al., 1995).

### 7.3.2 Gemomic $\mathbb{D N A}$ extractiom amd purificatiom.

Fresh leaf tissue was obtained from living plants cultivated at ICMB (University of Edinburgh) or the Royal Botanic Garden Edinburgh (RBGE). Identification to the generic level was straightforward but, in a few instances, identification to the species level proved more problematical and the sample was then labelled with the specific epithet "sp." Voucher specimens were prepared for all the material analysed (see Appendices). Where possible, 1-3 g of fresh leaves from each sample were used in preference to dried herbarium or field collected material since it was determined empirically that these yielded qualitatively better DNA. For some samples, material collected in the field and stored on silica gel (Chase \& Hills, 1991) was used. Ideally, the leaves were undamaged, free from fungal attack and relatively young since, in this condition, the highest yield of genomic DNA was usually obtained. The leaves were gently washed with sterile water and dried on lint-free tissue and the weight assessed on a bench balance. They were then placed in aluminium foil and plunged into liquid nitrogen for about 15 minutes before being ground in a mortar. The grinding process was aided by a pinch of fine acid-washed sand and the sample was kept frozen by the addition of small quantities of liquid nitrogen. The mortar was previously cooled by placing it in a $-20^{\circ} \mathrm{C}$ freezer for about 30 minutes before use in order to prevent it cracking when the liquid nitrogen is added. Also, prior to the grinding, 1 -several (depending on the number of samples) labelled 50 ml centrifuge tubes containing 25 ml of Doyle \& Doyle 2xCTAB Isolation Buffer (Doyle \& Doyle, 1987) and $50 \mu$ l of 2-mercaptoethanol were placed in an incubator at $65^{\circ} \mathrm{C}$ for about 30 minutes. Depending on the sample, various modifications to the basic D. \& D. formula were used. The Campanulaceae proved to be particularly troublesome as far as contaminants such as polysaccharides were concerned.

Usually $1-4 \%$ PVP-40 was added to the isolation buffer and occasionally the CTAB was increased to $3 \%$. Often these methods still proved ineffective and experiments on the purity of DNA extractions are still continuing. It is to be hoped that methods involving the use of diatomaceous earth and alcohol-free CTAB precipitation may prove more successful (see Murray \& Thompson, 1980). Caesium chloride centrifugation was tried but proved to be ineffective as well as hazardous and time-consuming. As a routine method it was quickly abandoned.

When the samples were finely ground they were quickly tranferred to the centrifuge tubes, sealed and gently agitated for about 20-30 seconds before being placed in the incubator at $65^{\circ} \mathrm{C}$ for another 30 minutes. After this time 25 ml of SEVAG (Iso-amyl alcohol:Chloroform in the ratio $1: 24$ ) was added to each sample. The tubes were gently agitated to ensure adequate mixing and placed on a rotary agitator at room temperature for 30 minutes after which they were centrifuged in a Mistral 2000 benchtop centrifuge at 3600 rpm for 5 minutes. The supernatant aqueous layer was removed using a wide-bore pipette and the contents placed in a new labelled sterile 50 ml centrifuge tube. Usually the yield at this stage was about $20-25 \mathrm{ml}$. Care was taken to ensure that no contaminating fragments of the sample were transferred with the supernatant. To each sample 1 volume of $100 \%$ isopropanol (kept at $-20^{\circ} \mathrm{C}$ ) was added and the contents gently mixed. At this stage long threads of precipitated DNA were usually visible. However, not infrequently the precipitate was finely particulate or not visible and the tube had to be placed in a freezer at $-20^{\circ} \mathrm{C}$ to aid precipitation. The samples were then centrifuged again at 1000 rpm for 3 minutes and the excess liquid poured off. Each tube was inverted over dry lint-free tissue and allowed to drain for 1 hour-overnight and care was taken to ensure that the DNA pellets remained at the base of the inverted tubes. This latter stage was substituted by the use of a vacuum drier which dried the DNA pellets more rapidly and efficiently ( 1000 rpm at $25^{\circ} \mathrm{C}$ for 30 min .).

The DNA pellets were then transferred to a wash buffer ( $76 \% \mathrm{EtOH}$ ) for approximately 1 hour and again drained and vacuum dried. They were then redissolved in sterile distilled water and placed in a refrigerator at $-20^{\circ} \mathrm{C}$ until used. Initially the samples were stored in
$1 \times T E$ and stored at $4^{\circ} \mathrm{C}$ but this may have contributed to amplification problems encountered during the PCR stage. $20 \mu \mathrm{l}$ aliquots of each sample were diluted to 1.0 ml with distilled water and analysed by UV spectrophotometry using a Beckmann DU-64 Spectrophotometer in order to obtain a crude measure of the total DNA concentation and quality. This can be assessed by the peak wavelength obtained (which should be A260) and the quality of the graph. The following formula was used to find the concentration of DNA in the stock solutions:


At this stage a check was occasionally made for the presence of polysaccharide contaminants in the genomic DNA. 5 M stock of NaCl was added to the samples to give a final concentration of 2 M . Using a UV scan of A230-A320 the ratio of the values for A260/A230 should be equal to or $>2.0$ if polysaccharides are in low concentration.

Ribonuclease A (RNAse: Sigma Chemical Co.) was then added to each sample ( $10 \mathrm{mg} / \mathrm{ml}$ ) and incubated for 30 minutes at $37^{\circ} \mathrm{C}$. The samples were then diluted with 2 volumes of sterile distilled water and 7.5 M ammonium acetate added to a final concentration of 2.5 M . 2.5 volumes of cold absolute EtOH were then added and gently mixed to precipitate the DNA. The samples were then spun again at 1000 rpm for 3 minutes and the EtOH poured off. They were then washed twice in $76 \% \mathrm{EtOH}$ wash buffer and finally vacuum dried before being resuspended in sterile distilled water (usually $200 \mu \mathrm{l}-1 \mathrm{ml}$ ). All samples redissolved in this manner were stored in a freezer at $-20^{\circ} \mathrm{C}$. When required, small aliquots (usually $5-10 \mu \mathrm{l}$ ) of the samples were tested by electrophoresis using $1 \%$ agarose mini-gels and 1 x TAE buffer. $30-45$ minutes at 80 V for a 1.5 litre electrophoresis tank was sufficient to obtain good mobility of the DNA across the gel. A standard DNA marker was also incorporated to assess to size of the DNA or any fragments. The gel was stained in ethidium bromide and examined under UV light. The performance of the RNAse could also be assessed at this stage.

### 7.3.3 Amplification and PCR (Polymerase Chain Reaction).

The complete ITS region was required for analysis. The purity of the genomic DNA template often affects the ability of the target sequence to be amplified. Usually the concentration of DNA in the genomic template was between $50-250 \mu \mathrm{~g} / \mu \mathrm{l}$ but for amplification of some samples the concentration of the template was determined empirically by a dilution series. Some samples required a concentration as low as $5-10 \mu \mathrm{~g} / \mu \mathrm{l}$. A $50.0 \mu \mathrm{l}$ PCR mix was prepared for each sample. This mix was usually very close to the following formula but sometimes had to be varied depending on the sample:

Table 27. Formula for PCR Mix used in the sequencing analyses

| COMPONENT | VOLUME in $\mu \mathrm{L}$ |
| :---: | :---: |
| 1. Sterile distilled water | 35.5 |
| 2. 10x buffer ( $\mathbf{3 m M}$ ) | 5.0 |
| 3. dNTPs ( 10 mM ) | 1.0 |
| 4. Forward primer (ITS5) | 2.5 |
| 5. Reverse primer (ITS4) | 2.5 |
| 6. Polythermase enzyme ( $T b r$ *) | 0.5 |
| 7. Genomic template | 3.0 |
| IOTAI. | 50.0 |
| * Thermus brockianus |  |

The thermal profile for each PCR run was usually determined empirically and rerun if necessary. Usually the optimal settings were as follows:

Table 28. Thermal profile for PCR

| STEP | TEMP. ${ }^{\circ} \mathrm{C}$ | SECONDS | CYCLE |
| :---: | :---: | :---: | :---: |
| 1. Initial Denaturation | 94.0 | 60 | x 1 |
| 2. Denaturation | 94.0 | 2 |  |
| 3. Annealing | 48.0 | 2 | x 35 |
| 4. Extension | 72.0 | 20 |  |
| 5. Final Extension | 72.0 | 120 | x 1 |

The amplifications were all completed on an Idaho RAPIDCYCLER (Idaho technologies) using manufactured oligonucleotides obtained from Oswell DNA Service and from Applied

Biosystems Division of Perkin-Elmer. The primer sequences were those of White et al. (1990) and are as follows:

ITS5 (firward): $5^{\prime} \mathbb{G} \mathbb{G A A G T A A A A G T C} \mathbb{G} \mathbb{A} \mathbb{C A A G G} 3^{\prime}$
ITSA (reverse): $5^{\prime}$ TCCTCCGCTTATTGATATGC $3^{\prime}$

Several modifications (Yokota et al., 1989) to these basic ITS primers were kindly suggested by Dr. M. Möller (Royal Botanic Garden, Edinburgh) and were used successfully on some recalcitrant samples. These were as follows:

ITS8P (reverse): $5^{\prime} \mathbb{C A C G C T T C T C C A G A C T A C A} \mathbb{3}^{\prime}$

When each run was completed a small aliquot of each double-stranded amplicand was tested electrophoretically in the manner described above. A PCR marker (Sigma BioSciences) whose ranges included the size of the target sequence was included. If the band of DNA was the correct size (ie. in terms of the number of base pairs and hence its migration on the gel) it was excised from the gel using sterile scalpels and placed in a fresh Eppendorf tube. Each sample was then cleaned using either Promega Wizard PCR Preps DNA Purification System (Promega Corporation) or the similar QIAquick gel extraction kits (Qiagen Ltd.) kits, eluted with sterile distilled water, and the final recovery concentration estimated using a GibcoBRL Low DNA Mass Ladder (Life Technologies). Ideally this was about 20-50 $\mathrm{ng} / \mu \mathrm{l}$ but frequently was as low as 5ng. This problem could often be alleviated by increasing the $p \mathrm{H}$ of the distilled water by using a small amount of 1 xTE . The samples were then ready for the cycle-sequencing reactions.

### 7.3.4 Cycle-Sequencing

For the cycle-sequencing reactions the ABI Prism Dye Terminator Cycle Sequencing Kit with AmpliTaq DNA Polymerase (Applied Biosystems Division of Perkin Elmer) was used and the amplifications were again carried out on the Idaho RAPIDCYCLER.

Table 29. Formula and reaction conditions for cycle sequencing


Each reaction was then subjected to ethanol precipitation. The entire $20 \mu \mathrm{~L}$ contents of each Eppendorf tube from the cycle-sequencing stage were transferred to a fresh 0.75 mL tube containing $2 \mu \mathrm{~L}$ of 3 M Sodium acetate ( pH 4.6 ) and $50 \mu \mathrm{~L}$ of $95 \%$ ethanol. This was briefly vortexed and placed on ice for 10 minutes before being centrifuged at 13000 rpm for 20-30 minutes. The ethanol solution was then carefully aspirated with a micropipette and the pellet was rinsed with $250 \mu \mathrm{~L}$ of $70 \%$ ethanol. This solution was again carefully aspirated to remove as much as possible before the pellet was dried in a vacuum centrifuge for about 10 minutes. The dried pellet was then supplied to the automated sequencer technician for the sequencing runs. The machine used was the ABI 377 Prism Automatic DNA Sequencer Perkin Elmer, Applied Biosystems Division). For each taxon, forward and reverse reactions were obtained. The sequencing primers were those used in the PCR amplification reactions. The results were saved to floppy disks both as text files and as electropherograms which could be viewed and edited using the Apple Mackintosh programs such as ABI PRISM and SEQUENCE NAVIGATOR.

### 7.3.5 Aligmment amd lnomalogy.

The underlying assumption when two or more sequences are being compared is that they are homologous. If they are not homologous then it is not legitimate to try to extrapolate phylogenetic signal from them. If they are homologous they must first be aligned in order to maximise their homology and before any differences in the compared sequences can be scored. The resultant trees obtained from sequence data are only as good as the alignment. It is therefore crucial that the best alignment possible be obtained. To align a pair of sequences one must firstly know the boundaries of the sequences to be aligned and secondly have some criterion of optimality with which to evaluate the alignment. There are complete ITS sequences published for more than twenty angiosperm families (Baldwin, et al. 1995) but none for the Campanulaceae or its most closely allied families. The boundaries for the ITS region were obtained by comparison with published ITS sequences of Nicotiana rustica: Solanaceae (Venkateswarlu \& Nazar, 1991), Krigia: Asteraceae (Kim \& Jansen, 1994), Madiinae :Asteraceae (Baldwin, 1992) and Gentiana: Gentianaceae (Yuan, et al.,1996). There are several alignment computer programs available and many of them use the dynamic programming algorithm of Needleman $\&$ Wunsch (1970). The majority of these programs however suffer from both theoretical and practical limitations and only the simplest of data sets can be aligned in this way (Wheeler \& Gladstein, 1994). Therefore, all multiple alignment approaches make use of heuristic algorithms. In each case a distance measure is calculated from pairwise alignments (Feng \& Doolittle, 1987; 1990; Higgins and Sharp, 1989) and a Fitch-Margoliash tree (Fitch \& Margoliash, 1967) or a NeighbourJoining tree (Saitou \& Nei, 1987) is determined for these distances. This "alignment tree" or "guide tree" is specified in order to allow the ordered accumulation of aligned sequences into a multiple alignment. The topology of the guide tree determines the order of construction and the multiple alignment is built up progressively by a series of pairwise alignments. This is essentially the method used in the PILEUP program of the GCG package and CLUSTALW. However, as Wheeler \& Gladstein (1994) point out, all these algorithms simply produce a result or have a stopping rule but lack a criterion of optimality. All the problems of using distance measures are inherent in these methods (Swofford, 1981). One solution to the problem of optimality is to use parsimony in the alignment of sequences. Wheeler \& Gladstein (1994) used this method in their alignment program MALIGN which
minimises cost instead of maximising benefit and which uses the minimum number of steps required to explain the observed variation among the sequences. The best alignment is that which yields the most parsimonious cladogram. This option was considered but not used due to the time constraints imposed on this study. It may yield results which differ from distance-based alignment procedures and should be borne in mind for future studies.

All the above-mentioned programs also suffer from the difficulties in determining parameters for the alignment. This problem was considered by Thompson et al. (1994) to be at least as serious as the local minimum problem. When the data set consists of very similar sequences almost any weight matrix will produce an approximation to the correct alignment. When there are very divergent sequences present the weights given can be critical and more mismatches will be produced. Different weight matrices are optimal for different evolutionary distances. The range of gap penalties that will find the best alignment can be wide for similar sequences (Thompson et al., 1994). Again, as more divergent sequences are used the exact values of gap penalties become critical for success. An equally serious problem is the selection of a model of nucleotide substitution.

Multiple sequence alignments obtained by distance methods are far from robust. New data added to the alignment procedure are not allowed to modify the previously-generated incomplete alignment. Since the optimality criterion is purely mathematical and not biological the subsequent analyses often produces a tree with a topology identical to the topology of the guide tree. In practice, with the programs which use distance-based progressive pairwise methods and in cases where sequences are closely related the quality of the alignment apparently is surprisingly excellent (Thompson, et al., 1994) while in more difficult cases (ie. $<25-30 \%$ identity) the alignment can be the starting point for manual refinement. Manual alignment is based on subjective (aesthetic) criteria and carries the risk that the result is incorrect. Throughout this study final manual alignment was avoided where possible. The program GeneDOC provides a combination of alignment editing and analyses using sum-of-pairs scoring and weighted parsimony scoring. For this study it was necessary to refine alignments using several methods as shown in Fig. 30.

Talble 30. Diagrammatic represemtatiom of the aligmmemt, refimememt amd playlogemy recomstructiom strategies used for the molecular data.


The multiple alignment used in this study was created by CLUSTALW, ver. 1.6, in several stages using the Slow/Accurate dynamic programming option. The major block of taxa comprising the Campanuleae s.s. was first aligned and then manually adjusted several times. The gap penalty was set at 10.0 (default) and gap extension penalty was 5.0 (default). Divergent sequences $>40 \%$ were delayed in the alignment procedure. The scoring matrix used in ver. 1.6 of ClustalW is shown below (a modification of this is now used in ver. 1.7 but was not available when the alignments were made).

|  | $\mathbb{A}$ | $\mathbb{C}$ | $\mathbf{G}$ | $\mathbb{T}$ |
| :--- | :--- | :--- | :--- | :--- |
| $\mathbb{A}$ | $\mathbf{3}$ | 0 | 1 | 0 |
| $\mathbb{C}$ | 0 | 3 | 0 | 1 |
| $\mathbb{G}$ | 1 | 0 | 3 | 0 |
| $\mathbb{T}$ | 0 | 1 | 0 | 3 |

Fig. 86. Scorimg Matrix for CLUSTALW, ver. 1.6 as used in the Multiple Aligmment

To the first multiple alignment was added sequentially the sequences for Jasione crispa and Craterocapsa congesta and the subsequent multiple alignments were again manually
adjusted. The Platycodoneae s.s. was also aligned and adjusted in a similar manner and a profile alignment was then carried out to align both aligned groups. The final grand multiple alignment was manually adjusted and rerun several times using the same guide tree (produced by the neighbour-joining algorithm of Saitou \& Nei, 1987) until a consistent result was obtained. The aligned sequences for all the taxa are shown in Fig. 87.

Adenophora divaricata Petromarla pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Michauxia tchihatchewii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Jasione crispa Craterocapsa congeata Codonopsis lanceolata Leptocodon gracilis Cyanamthus sp. Canarina canariensis platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica
$31030 \quad 30 \quad 40 \quad 50$ TCGAA-CCCTG-CA-TA-GCA-TAACAACCCGCAAA-CACATTGAAAAACACA--TT-TG TCGAATTCCGG-CA-TA-GCAG-AACAACCCGGGGA-CACGTTGAAAAACACAT-TTATG TCGAA-CCCGG-CACTAT-CAG-AACGACCCACGAA-CACGTTGAAAAACACA--TTC-G TCGAA--CCTG-CA-CA-GCAG-AACGACCCGCGAA-CACGTTGAAAAACACA--TTC-G TCGAA--CCTG-CA-CA-GCAG-AACGACCCGCGAA-CACGTTGAAAAACACA--TTC-G TCGAAACCCTG-CA-TATGCA-TAACAACCCGGGAAACACGTTGAAAAACACAAAT-A-G TCGAA-CCCTG-CA-TA-GCAG-AACAACCCGCGAA-CACGTTGAAAAACACA-ATT-TG TCGAA-CCCTG-CA-TA-GCAG-AACAACCCGGGAA-CACGTTGAAAAACACAT-TTCTG TAAAAA-CCTG-CACTAT-CAG-AACGACCCGCGAA-CACGTTGAAAAACACA--TT-TG TCGAA--CCTGGCA-TA-GCA-TAACGACCCGCGAA-CACGTTGAAAAACACA--TTC-G TCGAA-CCCTG-CA-TA-GCAG-AACAACCCGCGAA-CACGTTGAAAAACACA-TT-TG TCGAA-CCCTG-CA-TATGCAG-AACAACC-GGGAA-CACGTTGAAAAACACA--TTATG TCGAA--CCTG-CA-CA-GCAG-AACGACCCGCGAA-CACGTTGAAAAACACA--TTC-G TCGAA--CCTG-CA-TAT-CAG-AACGACCCGCGAA-CACGTTGAAAAACACA--TTC-G TCGAA-CCCTG-CA-TATGCA-TCACGACCCGGGAAATACATTGAAAAACACA--TTC-G TCGAA-CCCTG-CA-TATGCA-TAAC-ACGCCAGGAACACATTGAAAA-CACATATTTTG TCGAA--CCTG-CA-TA-GCAG-AACGACCAGCGAA-CACGTTGAAAAACACA--TT-TG TCGAA--CCTG-CA-TA-GCAG-AACGACCCGCGAA-CACGTTGAAAAACACA--TCC-G TCGAA--CCTG-CA-TA-GCAG-AACAACCCGCGAA-CACGTTGAACAACACA--TT-TG TCGAA-CCCTG-CAATA-GCAG-AACAACCCGCGAA-CACGTTGAAAAACACA-ATT-TG TCGAA--CCTG-CA-CA-GCAG-AACGACCCGCGAA-CACGTTGAAAAACACA--TTC-G TCGAA- CCTG-CA-TA-GCAG-AACGACCCGCGAA-CACGTTTAAA - CA-AAAT-C-G TCGAA- CCTG-CA-CATGCAGTAACGACCCGCGAA-CACGTTGAAAAACAC--ATTCTG TGGAAA-CCTG-CAC-A-GC-A-G-TAAC-‥-GA---CCGG-GAAAA-AA-G--T--GA TCGAAA-CCTG--AC-A-GC-A-G--AG--.-GA---CCGGCGGAAA-AG-G--G-GA TCGAAA-CCTG-CAC-A-GC-A-G-TAAC---GA--CCC----GCAAC-ACG--TC-AA TCGAAA-CCTG-CAC-A-GC-A-G--AAC-.--GA--CCC-- GCGAAC-AC---GT-AA

TGGAAAACCTGG-AT-AAGCCAAGG-AAAACG-GA--CCCCGGGGAAACAATG--GT-AA TCGAAA-CCTG-CA--AAGC--AG--AA--CG--A--CCC-GC-GAA-C--TTG-TTTAA

Adenophora divaricata Petromarula pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Michauxia tchihatchewii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Jasione crispa Craterocapda congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica
$7080 \quad 90 \quad 100 \quad 110 \quad 120$
$\begin{array}{cccccc}70 & 80 & 90 & 100 & 110 & 120\end{array}$
GGGG--ATGCGTGCAC-GGGACAA-GG-CGACAGCCCCCC-GT-G--CATGCGGCCCC-T GGGGG-ATGTGTGTTTCGGAATTA-GG-CAATA-CCCCCCCGT-G--CACGCAGCCC-T GGGGG-ACGTGGGTTT-GGGATAA-GGGTGAAAGCCCCCC-T-GCCCATG--GCCCC-T GGGGG-ACGTGGGTTT-GGGATAA-GGGCGATAGCCCCCC- - T-GCCCATG--GCCCC-T GGGGG-ACGTGGGTTT-GGGATAATGG-CGAAAGCCCCC--T-GCCCATGT--CCCC-T GGG---ATGTGTGCTT-GGGATAA-GG-TGAAAGCCCCCC-GT-G--CAT-CAGCCCC-T GGGG--ACGTGTGCTC-GGGACAA-GG-CGTCAGCCCCCC-GT-G--CATGCAGCCCC-T GG-- TATGTGTGTTTCGGGATTA-GG-CGATAGCCCCCC-GT-G--TACGCAGCCCC-GGGGG-ATGTGGGTTC-GGGATAA-GGGCGACAGCCCCCC--T-GCCCATGGTGCCC--T GGGGGGACGCGTGCGA-GGGACAA-GGGC-AT-GCCCCCC--T--CCCGCGG--CCCC-T GGGG--ATGCGTGCAC-GGGACAA-GG-CGACAGCCCCCC-GT-G--CATGCGACCCC-T GGG--TATGTGAGTTC-GGGACTA-GG-CAATAGCCCCCCC-TTG--CACGCAGCCCC--GGGGGT-CGTGGGCTC-GGGATAA-GGGCGAGAGCTCCCCC-T-GCCCATGT--CCCC-T GGGGG-ACGTGGGTTT-GGGATAA-GGGCGACAGCCCCCC--T-GCCCATGGA-CCC-T GGGGG-ACGTGTGCGA-GGGACAA-GGGC-AT-GCCCCCCC-T--CCCGCGG--CCCC-T AGGGGTATGTGTGCTC-GAGACAA-GG-TGAAAGCCCCCC-GT-G--CATGCAACCCC-T GGGGGT-CGTGGGTTT-GGGATAA-GGGCGACAGCCCTCC--T-GCCCATGG--CCCCTT GGGGG-ACGTGGGTTT-GGGATAA-GGGCGATAGCCCCCCCG--GCCCATGGG-CCC--T AGGGG-ACGTTTGTAT-GGGACAA-GGCTTAT--CCCCCCCGT-A--CATTCGACCCC--GGGG--ATGTGTGCT--GGGACAA-GG-CGAAAGCCCCCCC-T-G--CATGCAGCCCC-C GGGGG-ACGTGGGTTT-GGGATAA-GGGCGTCAGCCCCCC-T-GCCCATGG--CCCC-T GGGGG--CGC-TGCAGCGGGAGAA-GGGCGAAAGCCCCC--A-AACCCCTGCAĆTCTCCC

A-AACTCCGGGGACCGCGGGCT--TG-CCCGTGGCCCCTTG--.--CCGTCGGACCGC--ACAACACCGGGGGGAGC-GGCT--TG-CCCGTGGCCCTTT-....-.TTGT-GGG-CGC- -GGAACACTGGGAAA-AC-GGGC-ATG-CCCGT-CGCCCCT------TG-T-CGGTG-C--- AAACATCGAAGGA-TCGGGGT- - TGTCGCG-GGCCTCCT--...-CCGT-CGG-AGC- -
 GGAACAAGGGGGGACGCGGGGCAATGCCCCGTGGGTTCAT-.....-TG-T-TGA-A-C--ACA-C-T--GGGGAGT-GGCGCGGC--CGGGGTGC-TTCG---. - - GCCTCCGCCCGTG-

Fig. 87. Sequence data matrix of aligned $\mathbb{I T S}$ region of nuclear ribosomal $\mathbb{D N A}$ from 29 taxa of the Campanulaceae and $\mathbb{1}$ taxon (outgroup) of the Solanaceae. Input order is partly randomised. The sequences are in 5 , to 3 , orientation and in IUPAC code. The ITS1 region spans sites $1-313$, the 5.8 S coding region spans sites $314-478$, and the ITS2 region spans sites 479-722. Alignment gaps are indicated by hyphems. The numbers in square brackets at the end of the matrix indicate the total length of $\mathbb{T}$ SI, 5.8 subunit and ITS2, minus alignment gaps. Continues overleaf.

Fig. 87. contimured

Adenophora divaricata petromarula pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Michausia tchihatchewii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Jasione crispa Craterocapsa congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica

Adenophora divaricata Petromarula pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Michauxia tchihatchewii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoidea Jasione crispa Craterocapsa congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis Platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica
$130 \quad 140$
150
160
170
T-CCTTGTGGTGTCGGAGCAATCGAGCGAAAGC- - - -GCGTGAGCTTCGG-CC--CC -AGCCTTGTGGTGTCTTAGCGAGCGATCGAAAGC-----CCGTGAGCTTAGG-CC--CCC TGC-TTG-GGTGCCGAAGCGAGTGAGCGAAAGC---- GACCTAACTCCAG-C-G-CC-TGC-TTG-GGCGCCGAAGTGAGGGAGCGAAAGC-----GACCTAACTCCGG-C-G-CG-TGC-TTGTGGCGCCGGAGTGAGGGAGCGAAAGC-----GAGCGAGCTTCGG-C-G-CC--GCCTTGTGGTGTCGCAGCAAGCAAGCGAAAGC-----GCGTGAGCTCTGG-CC--CC-A -GCATTGTGGTGCCGCAGCGAGCAAGCGAAAGC-----ACGTGAGCTTCGG-CC--CC-A AGCCTTGTGGTGCCGTAGCGAGCGAGCGAAAGC--..-CCGTGAGCTCTGG-C---CC--TGC-TTG-GGCGTCGAAGCGAGGTAGCGAAAGC---- GACCCAACTCCGG-C-G-CC-T-CCTTGCGGCGTCGGTGCGAGCTCGCGAATGC-----GAGTGCGTGCCGGA--G-CC-T-CCTTGTGGTGCCGGAGCAATCGAGCGAAAGC-- - -GCGTGAGCTTCGG-CC--CC -ATCCTTGTGGTGCCGTAGCGAGCGAGCGAAAGC-----GCGTGAGCTCCG--TC--CC-TGC-TTGGGGCGCCGAAG-GAGGGAGCGTGAGC--.--GAACCGGCTCCGG-C- ACC-TGC-TTGG-GCGCCGAAGCGAGGGAGCGAAAGC---- -GACCTAACTCCGG-T-G-C--G TGC-TTGCGGCATCGGTGTGCGCTCGCAAATGC-----AATTGCGTTTCGGA--G-CC-T-CCTTGTAGTGTCAAAGCAAGCAAGTGAATGC---.-CTGTGAGCTTTGG-C---CC-A TGC-TTGCGGTGCTGAAGTGAGCGAGCAAAAGC-----GAACAAACTCTGG-CT--CC-TGC-TTG-GGGGCCGAAACGAGGGAGCGAAAGC-- - - GACCCAACTCCGG-C-G-CC-TTCCTTGTTGTGTTGAAGCAAGCAAGCGAGAGC-----TCGTGAGCTTCGG-C---CC-G - GCCTTGTGGGGTCGTAGCAAGCGAGCGAAAGC---- GCGCGAGCTTTGG-CT--CC-A TGC-TTGT-GCGCCGAAGCGAGGGAACGAAAGC-----GACCTAACTCCGG-C-G-CC--TTCCTTGCGGTTTCGGTGCGAGCGAGCGTAAGC-----GAGC-AACTGCCG--TGACC-------GCGGCGCCGGTGCCCGC---C-T---C---C-GG-TGCC--CCGG-- $-\ldots$ ----GCG-CCCGCCCAA-CCA-CTC-T-GGTGGCA---GGG-G-A--GCG-T-G-C-G ----GGG-CCTGCCCGG-CCATTTTGTGGGAGGGA---GGGTGCG-TGCGT-TCGTTTGG ----GTG-CGC-CCT----T------T-GG--------GAGTGC---GCG--T----CGG ----GCG-CCT-CCGAATCGATTCT-TGGGC--C--- -GGACGT--CGCG--T---CAA ----AT--TTT-CCG----G-------GGG--------GGGTGT---GCG--C---CGG ----GCG-GGC-CCT----T------TGGG--------GAGTGC---GCG--T---CGG -----CGCTCTCTCCTA-TCCCCGG-C--GCGCGCGTCGGCTGGCTGCTG----- - - -

CAAGAAAC-AAACCCCGGCGCAA--TTCGCGCCAAGGAAAT-CTTTAAACT-CAAGGGCG CAAGTAAC-TAACCCCGGCGCAA--TTCGCGCCAAGG-AAAACTTTAAACT-CAAGGGTG CAAGAAAC-GAACCCCGACGCAA--TCCGCGTCAAGG-AAAACATTTAACT-CGAGGGCG CAAGAAAC-GAACCCCGACGCAA--TCCGCGTCAAGG-AAAACATTTAACT-CGAGGGCG CAAGAAAC-GAACCCCGACGCAA--TCCGCGTCAAGG-AAAACATACAACT-CGAGGGCG CAATTAAC-CAACCCCGGCGCAA--TTCGCGCCAAGG-AGAACTTTAAACT-CAAGGGTG CAATTAAC-TAACCCCGGCGCAA- -TTCGCGCCAAGG-AAAACATTAAACT-CAAGGGCG CAAGTAAC-TAACCCCGGCGCAA--TTCGCGCCAAGG-AAAAATTTAAACT-CAAGGGCA CGAGAAAC-AAACCCCGACGCAA--TCCGCGTCAAGG-AAAACATTTAACT-CGAGGGCG CGAGAAAC-GAACCCCGGCGCAA--TCTGCGCCAAGG-AAAACTTTAAACT-CGAGGGCG CAAGAAACAAAACCCCGGCGCAA--TTCGCGTCAAGGGAATACATTAAACT-CAAGGGCG CAAGTAAC-TAACCCCGGCGCAA--TTCGCGCCAAGGGAAAAATTTAAACT-CAAGGGCG CAAGAAAC-GAACCCCGACGCAA--CCCGCGTCAAGGGAAAACATTTAACT -CGAGGGCG CAAGAAAC-GAACCCCGACGCAA--TCCGCGTCAAGG-AAAACATTTAACT-CGAGGGCG CAAGAAAC-AAACCCCGGCGCAA--TCTGCGCCAAGG-AAAACATTAAACT-CAAGGGCG CAAGAAAC-TAACCCCGGCGCAA--TTCGCGCCAAGGGAAAACATTAAACT-TAAGGGTG CAAGAAAC-GAACCCCGACGCAA--TTCGCGTCAAGG-AAAACATTTAACT-CGAGAGCG CATGAAAC-GAACCCCGACGCAT - TCCGCGTCAAGG-AAAACATTTAACT-CGAGGGCG CAAGAAAC-TAACCCCGGCGCAA--TTCGCGTCAAGGAAAA-CTTTAAACT-CAAGGGTG CAATTAAC-TAACCCCGACGCAA--TTCGCGTCAAGG-AAAACTTTAAACT-CAAGGGTG CAAGAAAC-GAACCCCGACGCAA- TCCGCGTCAAGG-AAAACAATTAACT-CGAGGGCG CAAGAAAC-GAACCCCGGCGCAAAATCCGCGCCAAGG-AAAACTTTAAACT-TGAGAGCG ---GAAAC-GAACCCCGGCGCGAA--CCGCGCCAAGGGAAAACTCCAAACT-CGAGGGCG TGCCAAAC-GAACCCCGGCGCGA--TCCGCGCCAAGG-AAAACTTAACTC--AAAGAGCG CGCCAAAC-GAACCCCGGCGCGA--TCCGCGCCAAGG--AAACATAACT---GAAGGGCA CA-CAAAC-GAACCCCGGCGCGG--TCTGCGCCAAGG-AAAACATAACTC-A-AAGAGCG TGCCAAACGGAACCCCGGCGCGA--TCCGCGCCAAGG-AAAACATAACTCT--AA-AGCA CGCAAAAC-GAACCCCGGCGCGA- -TCCGCGCCAAGG-AAAACATAACTCTAGAAGAGCG CACCAAAC-GAACCCCGGCGCGA--TCCGCGCCAAGG-AAAACCTAACTC---GAGAGCG TGATTAAC-GAA-CCCGGCGTGGA--AAGCGCCAAGG-- AATACTAAATT - -GAAAGCC

Comtimues overleaf

Fig. 87. contimured

Adenophora divaricata petromarula pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Michauria tchihatchewii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Jasione crispa Craterocapsa congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica

Adenophora divaricata Petromarula pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Michauxia tchihatchewii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Jasione crispa Craterocapsa congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp.
Canarina canariensis Platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica

TGCTCTCCTCACGTTGCCCCCGTTTGCGGGTGCGCGACTGGGTG-- TTTGCCCGCTCCT TGTTATCTCCTTGTTGCCCCCGTTTTCGGGTGTGTGACTGGGTG-- TTTGCCCGCTCCT TGCTGTCGTCCCGTCGCCCCCGTTCGCGGGTTGGCGCGCGGGCT---GACGGCCGCTTCT TGCTGTCGTCCCGTCGCCCCCGTTCGCGGGTTGGCGCGCGGGCT---GACGGTCGCTTCT TACTGTCGTCCCGTCGCCCCCGTTCGCGGGTGTGCGCGCGGGCT - - GACGGCCGCTTCT TGCCATCATCCCGTCGCCCCCGTTCGCGGGTGCTCGATTGGGTG--TTTGGTCGCTTCT TGCCGTCATCCCGTTGCCCCCGTTAGCGGGTGCGCGATTGGGTG---TTTGGCCGCTTCT TGCTATCCTCTTGTTGCCCCCGTTTTCGGGTGTGTGACTGGGTG-- -TATGGCAGCTTCT TGTTGTCGTCCCGTCGCCCCCGTTCGCGGGTTGGCGCGCGGGCT---GACGGCCGCTTCT CGCTGTCATCCCGTCGCCACCGTTCGCGGATGCGTGTGCGGGTT---GTCG-CCGCTTCT TGCTCTCCTCACGTTGCCCCCGTTTGCGGGTGCGCGACTGGGTG-- TTTGCCTGCTCCT TGCTATCCTCTTGTTCCCCCCGTTTTCGGGTGTGTGACTGGGTG---TTTGGCCGCTTCT TGTTGTCGTCCCCTCGCCCCCGTCCGCGGGTGAGCGCG-GGGCC-- -GACGGCCGCTTCT TGCTGTTGTCCCGTCGCCCCCGTTCGCGGGTTGGCGCGCGGACT---GACGACCGCTTCT CGCTGTCATCCCGTCGCCGCCGTTCGCGGATGCTTGTGCGGGCT---GTCC-CCGCTTCT TGCTATCCTCATGTTGCCCCCGTTTGCGGGTGCGTGACTGGGTG-- TTTGGCCGCTCCT TGCTGTAGCCTTGTCGCCCCCGTTCGCGGGTGAGCGCACAGGCT---GATGGCCGCTTCT CGCTGTCATCCCTCCGCCCCCGTTCGCAGGTTGGCGCGCGGGCT-- -GACCGCCGCTTCT TACCATTTCCATGTTGACCCCGTTTGCGGGTGCGCGACTGG-TG-- - ATTGATCGCTCCT TGCCATCACAAGGTTTCCCCCGTTAGCGGGTGTGTGATCCGGTG---CTTGGCCGCTTCT TGTTGTTGTCCCGTCGCCCCCGTTCGCGGGTTGGCGCGCGGGCT---GACGGACGCTTCT TGCTGCCGGCCCATCGCCCCCGTTCGCGGGTGCGCGTT-GGGTG---GCTG-CCGCTTCT AACCGTACTCCCGCCGCCCCCGTCCGCGGGTGCGCGCGCGGGAT---GCCGGCCGCCTCT CCCCGTCCTCCCGTCGCC-CCGTTCGCGG-TGTGCGCA-GGTT--G-GGCGGTCGCTTCT GTACGTCC-ACCGTCGCC-CCGTTCGCGG-TGCGCGCGCGGTT--G-GGCTGTTGCTTCT CCTCG-CCTGCTGTCACC-CCGTTCGCGG-TGCGTGCATGGTC----AAC-GTCGCCTCT TCTCACCCTCCCGTCGCC-CCGTTCGCGG-TGTGC-C-CGGTT--G-GGTGGCCGCTTCT CCCCGTCCTCCCGTCGCC-CCGTCCGCGG-TGCGCGTGCGGCTGGGCGGTGGCCGCTTCT CCTCGTCCTGCCGTCGCC-TCGTTCGCGG-TGCGCGCGCGGTT--G-GACGGTCGCTTCT TGCC-----CCTCGCGCC-CCGTTCGCGG-TGCGCGCGTGG----G-GACTTGTGCTTCT 5.85
$310 \quad 330 \quad 340 \quad 350 \quad 360$
TAGTGAAAA--CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAA--CACAAA-TGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAAACA-AAAACGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAAA-CA-AAAACGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAAA-CA-AAAACGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAA - CACAAAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAA - CACAAAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAA - CACAAAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAA-CACAAA-CGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGTAAAAACACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAA - CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TATTGAAAA- -CACAAAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAA-CA-AAAACGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAAA-CA-AAAACGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TATTGTAAAAACA-AAAACCACTCTCGGCAACGGATATCTCGGCTCTCGCATCAATAAAG TAGTGAAAA - TACAAA-CGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAAA-CATAAA-CGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAGAAA-CA-AAAACGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAA - CA-AAAACGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAA- CACAAAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAA-CAAAAA-CGACTCTCGGCAACGGATATCTTGGCTCTCGCATCGATGAAG TAGTGAAAA- CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAA- -CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAA-CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAA-CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAA-CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTG-AAAA-CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG CGGTG-AAAA-CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG TAGTGAAAAA-CACAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG T-TTG-AAA- CATAAA-CGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAG

Fig. 87. contimured

Adenophora divaricata Petromarula pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Michauria tchihatchewii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Jasione.crispa Craterocapea congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica

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$370 \quad 380$
390
AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTATCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTACCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTACCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTT AACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCGCGTGAACCATCGAGTCTTT
$430 \quad 440 \quad 450 \quad 460 \quad 470 \quad 3$

GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCAAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCTTTTAGACCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTTAGGCTGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCTAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACCCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCTGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTAGGTTGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCTTTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCGTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCGTTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCATGGGCGTCACGCAT GAACGCAAGTTGCGCCGGAAGCCATTAGGCCGAGGGCACGTCTGCCTGGGCGTCACGCAT

Comtimues overleaf

Fig.87. comtimured

Adenophora divaricata
Petromarula pinnata
Campanula barbata
Campanula petraea
Diosphaera rumelianum
Campanulastrum americanum
Legousia falcata
Phyteuma spicatum
Campanula lanata
Musschia aurea
Hanabusaya asiatica
Physoplexis comosus
Roucela erinus
Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Michauxia tchihatchewii Jasione crispa
Craterocapsa congesta
Codonopsis lanceolata
Leptocodon gracilis Cyananthus sp. Canarina canariensis platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica

Adenophora divaricata Petromarula pinneta Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma apicatum Campanula lanata Musachia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Camppanula persicifolia Azorina vidalii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Michauria tchihatchewii Jasione crispa Craterocapsa congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis Platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica
$490 \quad 500$
500510
CG-CATCGCCCCCCC-AA--G-CAT-CTT-GCACCTCCAAGTGCCTGCTTG-CTTGG-T-CG-CGTCGCCTCCC--AAA-A-CAT-CAT-GCACTTTCCAGTGCTTGCTTG-CTTGA-T-CG-CGTCGCCCCCCCCAAA---CAC-TGA-ACCCCCCAAATTGCTCTTTGG-CTTGG-T-CG-CGTCGCCCCCCC-AAA---CAC-TGA-GCACCT-AAAGTGCTCTCTGG-CTTGG-T-CG-CGTCGCCCCCCC-AAAA - -CAT-TTG-GC-CCTTACATTGCCCCCTGG-CTTGGG-CG-CGTCGCCTCCC--AAA-G-CAT-CTTT-CACTTCCAAGTGCTTTGTGC-TTTGA-T-CG-CGTCGCCTCCC--AAA-G-CAT-CTC-GCACCTCCGAGTGCTTGCTTG-CTTGA-C CG-CGTCGCCCCC-- AAAAAACAT-CTT-GCACTTCCATGTGCTTGCTTG-CTTGA-T-CG-CGTCGCCCCCC--AAA---CAC-TTA-GCACCCAAAAGTGCTATCTAG-CTTGG-T-CG-CGTCGCCCCCCC-AAAA--CAACGA- GCACCTCAAAGTTCTCGGTTG-CTTGG-C CG-CGTCGCCCCCCC-AA--G-CAT-CTT-GCACCTCCAAGTGCCTGCTTG-CTTGG-T-CG-CGTCGCCCCC---AAAAA-CTT-CTT-GCACTTCCATGTGCTTGCTTG-CTTGA-T-CG-CGTCGCCCCCCCCAAA---CAA-TGC-GTACCTAACGGTGCTCCATGG-CTTGG-T-CG-CGTCGCCCCCCC-AA-A--CAC-TGA-GCACC-CACAGTGCTCTCTGG-CTTGG-T-CG-CGTCCCCCCCCC-AAAA- - CAAAAA- - GCACCTCAAAGTGCTCTGTTG-CTTGG-C-CG-CGTCGCCCCCC--AA--G-CA--TCTTGCACTTCCAAGTGCTCGCTTG-CTTGA-T-CG-CGTCGCCCCCC--AAA---CA- TTGTGCACCTAG-AGTGCTCTCTTG-CTTGG-T-
 CG-CGTCGCCTCCT- -AAAAG-CA- - TCCCGCACTTCCGAGTGCCGGCTTG-CTTGA-T-CG-CGTCGCCCCCCC-AA-A--CAC-TGA-ACACC-CCAAATTCTCTCTGG-CTTGG-T-CG-CGTCGCCCCCCCCAAAAATTAAACTC----CCCATAATTCTCTCCTTGCCTTGGGTG CG-CGTCGCCCCC----AACTTAAATCGTGCACCC--AGGTGCACTGCT--TTTGG-T-
 CG-CGTCGCCCCCCTCAACTTA-- ATTGTTTACA--AAA-CAAGTCAAGG-AAAG-. -CGTCGTCGCCTCCCTTAACCTA---ATTGTTTGAA--AAAACGA-TGGGGG-AAAG-- -CG-CGTCGCCCCCCCCTTCCCG---AC----AC---AAAACAAGGGAAGA-GGGG-- - G CG-CGTCGCCCCCCCAAACAAC-- ACAGAGCAAA--GAAAC-TTTGGCTG-GTTG--CG-CGTCGCCCCCCCAAACAAACAAACAAACAAAC--CAAACGTTTG-TCG-GTTGTTCA
 CG-CGTCGCCCCCG---.-.--CACAC--CGCGCCC--ATTCTCATGATTGCGGTGGTGT
55056057050000

GGGGAG-CGTACATTGGCTTCCC--GTGCCTCGCAG--TTCGGTT-GGCTCAAAA-TGGA GTGGAG-CGTACATTGGCCTCCC--GTGCCTTGTCG--TACGGCA-GGCTCAAAA-TGGA GGGAA--CGAATATTGGCCCCCC--GTGCCTTCCGG--CCCGGTT-GGTTCAAAC-TTAA GGGGGAACGGATATTGGCCTCCC--GTGCCTTTCAG--TGCGGCT-GGCTCAAAC-TTGA GGGAA-CCGAATATTGGCCCCCC--TTCCCTTCGGG--C-CGG-T-GGCCCAAAC-TTAA GGGGAA-CGTACATTGGCCTCCC--GTGCCTTTTCC--C-CGGTT-GGTTTAAAA-TGGA GGGGAG-CGTACATTGGCCTCCC--GTGCCTAACCG--TGCGGCT-GGTTTAAAA-TGGA GGGGAG-CGTACATTGGCCTCCC--GTGCCTCTCCG--TGCGGCT-GGCTCAAAA-TGGA GGGGAG-CGGATATTGGCCTCCC--GTGCCTTTCGG--CGCGGCT-GGCTTAAAC-TTGA GGGGAAACGGATATTGGCCTCCC--GTGCCTTGTCGC-CTCGGCTTGGCTCAAAA-TGGA GGGGAG-CGTACATTGGCCTCCC--GTGCCTCGCAG--TTCGGTT-GGCTCAAAA-TGGA GGGGAAGCGTACATTGGCCCCCC--GTGCCTCGCCG-TGCGGTT-GGCTCAAAA-TGGA GGGGAG-CGGATATTGGCCTCCC--GTGCCTCGCGG--CGCGGCT-GGCTCAAAC-TTGA GGGGAA-CGGACATTGGCCTCCC--GTGCCTTTCGG--CGCGGCT-GGCTCAAAC-TTGA GGGGAAACGGATAATGGCCTCCC--GTGCCTTGCG-- CGCGGCT-GGCTCAAAA-TGGA GGGGAG-CGTATATTGGCCTCCC--GTGCCTTGCCG--CGCGGTT-GGCTCAAAA-TGGA GGGGAG-CGGATATTGGCCTCCC--GTGCCTTGCGG--CGTGGTT-GGCTCAAAC-TAGA GGGGAG-CGTACATTGGCCTCCC--GTGCCTAACCG-TGCGGCT-GGCTCAAAA-TAGA GGGGAG-CGGACATTGGCCTCCC--GCGCCTTGCAG--TGCGGCT-GGTTTAAAA-TGGA GGGGAA-CGGATATTGGCCTCCC--GTGCCTTTCGG---GCGGTT-GGCTCAAAC-TTGA GGGGAACCGCATTTTTGCCTCCCCTTTGCCTTTTGGGCCCCGGGTGGGTCCAAACCTTGA GGGGA--CGGATATTGGCCTCCC--GTGCCTCCTGG--TGCGGGT-GGCTGAAAA-TGGA GGGGAG-CGGACATTGGCCTCCC--GCGCCTCGCGG--CGCGGCT-GGCTCAAAA -TGGA -GGGGAGCGGATACTGGCCTCCC--GTGCCTTGCGG--CGCGGCT-GGCTCAAAA-CGGA -GGGGAGCGGATAGTGGCCTCCC--GTGCCTTGCGG--CGCGGAT-GGCTGAAAA-CGGA GAGAGTACGTATATTGGCCTCCC--GTGCCTCGTGG--TGCGGGT-GGCTAAAAA-AGGA -GGGGAGCGGAT---GGCCTCCC--GTGCCTCACGG--TGCGG-T-GGCTCAAAA-CAGA GGGGGAGCGGATACTGGCCTCCC--GTGCCTCGCGG--CGCGGCT-GGCTCAAAA-CGGA -GGGGAGCGGATACTGGCCTCCC--GTGCCTCGCGG--CGCGGCT-GGCTCAAAA-CGGA CGTGGGACGGATACTGGCCTCCCGTGTGCCTCGAGCG-TGCGGTT-GGCCTAAATGCG-A

Fig. 87. comtimured

Adenophora divaricata Petromarula pinnata Campanula barbata Campanula petraea Dioaphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Michauria tchihatchewii Jasione crispa Craterocapsa congesta Codonopsis lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis platycodon grandiflorum Codonopsis dicentrifolia Nicotiana rustica G-TCCCC-GG-T-GA-AGGACGCACGACAAGTGATGG-TTGAATAATAACGGCCCTCG---TTCCCCTG-CTTGG-AACCC-CACAAAAAGTGGTGG-TTAA-TAACAAAGGCCCCCCC A-TCCCC-TC-C--GT-AGGACGCACGACAAGTGGTGG-TTGA-TAACAA-AGGCCTCG---TTCCCCTG-C- -TA-AGGACCCCCAAAAATTGGTGG-TGAA-TAACAA-GGCCCCC-G-TCCAC-CG--TTGA-ACGACGCACGACAAGTGGTGG-TTGA-TAATAAGGGCCTCC- -G-TCCCC-TG-C--GA-AGGACGCACGACAAGTGGTGG-TTGA-TAACAA-GGCCCTCG-G-TCCCT-CG--T-GA-AGGACGCACGACAAGTGGTGG-TTGA-TAATAA-GGCCCTCG-G-TCCCC-TG-C--GT-AGGACGCACGACAAGTGGTGG-TTGA--AACAA-GGCCCTCG---TCCCCCTG-C--GA-AAGACGCACGACAAGTGGTGG-TTGAATAAACAAGGCCCTCG-G-TCCCC-TG-T-GA-AGGACGCACGACAAGTGGTGG-TTGA-TAATAA-GGCCCTCG-G-TCCCC-CC--TTGA-AGGACGCACGACAACTGGTGG-TTGAACAACGAGGGCCCTCGC G-TCCCC-TG-C--GT-AGGACGCACGACAAGTGGTGG-TTGA-TAACAA-GGCCTTCG-A-TCCCCCTG-C--GT-AGGACGCACGACAAGTGGTGG-TTGAATAACAAGGGCCCTCG-C-TCCCC-TG-CC-GA-AGGACGCACGACAAGTGGTGG-TTGA-TAACAAGG-CCCTCG-G-TCCC--TG-T-GA-AGGACGCCCGACAAGTGGTGG-TTGA-TAA--- -GGCCCTCG-G-TCCCC-TG-C--GTTAGGACGCACGACAAGTGGTGG-TTGA-TAACAA-GGCCTTCG-G-TCCGC-TG--TTGA-AGGACGCAGGACAAGTGGTGG-TTGA-AAATAA-GGGCCTCG-G-TCCCC-CG--T-GA-AGGACGCACGACAAGTGGTGG-TTGA-TAATAA-GGCCCTCG-A-TCCCC-TG-C--GTT-GGACGCCCGACAAGTGGTGG-TTGA-TAACAA-AGGCCTCC -AGTCCCCCTG---GCC----T-TT-GGCAAA-G----CC--.-- CAAAACTTTTTG-G-ACCCC-TGGC--GA-AGGATGCACGACAAGTGGTGG-TTGA-TAATAA-GGGCCTCG-G-TCCCC-TG-C--GA-AGGACGCACGGCAAGTGGTGG-TTGA-TAAAAA-GGCCCTCG-GTCCCCCGCG----AA--GGACGCACGACAAGTGGTGG-TTGA-TAACAA-GGCCCTCG-GTCCCCTGCG----AA--GGACGCACGACAAGTGGTGG-TTGA-TAACAA-GGCCCTCG-CTCCCCTGTG---AA--GGACCCACTACTAGTGGTGG-TTGA-CAACGA-GGCCCTCG-GTCCCCCGCG--- GA--GGACGCACGACAAGTGGTGGGTTGA-TAACAA-GGCCCTCG-GTCCCCCGCG---AA--GGACGCACGGCAAGTGGTGG-TTGA-TAACAA-GGCCCTCG-GTCCCCCGCG--- AA--GGACGCACGACAAGTGGTGG-TTGA-TAACAA-GGCCCTCG-GTCC-ACGGC---GACGGACGTCACGACAAGTGGTGG-TTGAAACTCAA - .-. CTC-

$$
\begin{array}{llllll}
670 & 680 & 690 & 700 & 710 & 720
\end{array}
$$

Adenophora divaricata Petromarula pinnata Campanula barbata Campanula petraea Diosphaera rumelianum Campanulastrum americanum Legousia falcata Phyteuma spicatum Campanula lanata Musschia aurea Hanabusaya asiatica Physoplexis comosus Roucela erinus Campanula punctata Gadellia lactiflora Campanula persicifolia Azorina vidalii Campanula pyramidalis Legousia speculum-veneris Campanula thyrsoides Michauxia tchihatchewii Jasione crispa Craterocapsa congesta Codonopais lanceolata Leptocodon gracilis Cyananthus sp. Canarina canariensis platycodon grandiflorum Codonopais dicentrifolia Nicotiana rustica
-CGTTCT-G--TC-GTGC-TTGAGTCCTTTGC--CGG---TTTTGG----CTCT-TC-G-CCGTTTTCG- -TCCGTGCGGGTCAACCCCTCT--CGAGGAATTTGGG---CCCC-CCCA -CC-TTCCCCGTTCCT-GGGGGAAATCCCTTGCGG-GGAAATT--GGG---CCCT-CTCAC -C-TTCCCG--TCCTTGCGGGAA-TCCTCCTTG--GGAA-TTT-GGG---CTC-GTTTAC CC-TTCCCG-TTCTT-GCGGGAATCCCTCCTT---GGGAATTT-GG----CTCT-TC-A-CCGTTTT-G--TCGTTGTGGGTACCCCTT---G-CGGAA-TTT-GG-..-CTC-GTTTA--CGTTAT-G--TC-TTGC-GGTAATCCTTC--G-CGGGA-TTT-GG----CTC-GTT-G--CGTTTT-G--TCGTC-C-GGTAATCCTTT--G-CGGGA-TTT-GA----CTC-GTT-G--CGTCCC-G--TCGT-GC-GGCAATCCTTC--G-CGGGA-TTT-GG----CTC-GTC--CCGTCCC-G--TCCT-GCCGTCAATAATCTCCG-TGGGGATCT-GG--.-CTCCGTCCAC -CGTTCT-G--TCGT-GC-TTGAATCCTTTGC-- GGG--TTTTGG--- CTCT-TC-G-СT-TTTCTGG-CCCTC-CGGGTAATCCCTC-CG-CGGAGGAAT--A---C-C-ACCCG--CGTCCC-G--TCGT-GC-GGCAATCCTCCG-- TGGG--TTT-GG--- CTC-GTC - -CC-TCCC-G--TCTT-GC-CGCAATCCCTCC-GGCGGGA-TTT-GGG-- CTCC-TCC-CC-TCCCCG- -TTGT-GT-GTCAATA--CTCCG-CGGGGATCT-GG----CTCC-CCCAC -CATTAT-G--TCAT-GCCGGAAATCCTTTAC-ATGA--TTT-GA---CTC-AT--G--CGTCCC-G--TCGT-GC-GAATATCCTTCG---TGGGA-TTT-GGG---CTC-GTC---CGTTTT-G--TTGT-GCCGAAAAATGGTTT--ATGGGA-TTT-GGGGGGTTC-ATTTA--CGTTTT-G--TCGT-GC-GATAATCCTCTGC---GGGA-TTTTGA--- CTC-GTTCA--CGTTCC-G--TCCTTGC-GGGAATCCTTTGC--TGGA--TTT-GGG-- TCCT-CCCA----TT---GG-.-.--GTCGGAAAAAA-..-C--CAAG-...-.-GGG---CCCT-CCTTC
 -CGTCCC-G--CCGT-GCGGCAA-TCC-TCC-G-CGGGA-TCC-GG--- - CTCT-CCCAC - CGT-CCCGT-TCGT-GCGCACG-TCCTGCGC--TGGG-TT--GG---CTCT-CT-. --CGT-CCCG--TCGT-GCGCACG-TCCTGCGC--TGGG---CC-GG---CTCA-C-GT -CAT-CTTG--TGGT-GCGCTCG-TCCCTTA-G-TGGGA-T---GGG---CTCT-C--AC -CGT-CATG--TCGT-GTGCACG-TCCTGCGC--TGGAG-T---AGG---CTCT-C-GT -CGTACCCG- -TCGT-GCGCAAG-TCCTGAGCGATGGTG--C-AGG---CTCT-C-GT -CGT-CCCGT-CTGC-GCATGT--TCCTTG-CGCTGGGG-TT--GGG---TCT---AT TC-GTAATGTG----GC-TACAACCCGTCGCA-TG---TTT-GGGC---TCC-CC-G-

Fig. 87. comtinued


### 7.3.6 Results of the Molecular Analyses

7.3.6.1 Sequence Analysis

Basic statistics for the aligned sequences were calculated using MacCLADE, MEGA and by visual inspection and the results are given in Table 31. below.

Table 31. Sequence parameters for the ITS1 and ITS2 spacer regions and the 5.8 S subunit of ribosomal DNA.

|  | ITS1 | 5.8 Subunit | ITS2 | ITS1 + ITS2 |
| :---: | :---: | :---: | :---: | :---: |
| Aligned Length | 313 | 165 | 244 | 557 |
| Invariant Sites | 80 | 148 | 59 | 139 |
| Variable Sites | 233 | 17 | 185 | 418 |
| Bp Length (min. - max.) | 208-279 * | 164-165 | 179-213 | 390-488* |
| Mean length (bp) | 265.3 * | 164.2 | 197.9 | 462.9 * |
| $\mathrm{C}+\mathrm{C}$ content (\%) | 50.5-67.3 * | 53.0-55.5 | 51.8-68.2 | 52.0-67.7 |
| Mean G + C content (\%) | 59.1 * | 54.2 | 58.8 | 58.9 |
| Transitions (mín.-max.) | 370-405 | 15-15 | 340-369 | 717-786 |
| Transversions (min.-max | 287-322 | 11-11 | 252-281 | 550-619 |
| Unambig. Transitions | 279 | 13 | 240 | 503 |
| Unambig. Transversions | 157 | 7 | 152 | 295 |
| Ts/Ts ratio | 1.8 | 1.9 | 1.6 | 1.7 |
| Number of indels | 20-44 * | 0-1 | 18-35 | 18-44 |
| Mean No. of indels | 28.2 * | 0.87 | 29.2 | 28.8 * |
| Size of indels | 1-8 ** | 1 | 1-12 | 1-12 ** |
| Informative sites | 177 | 5 | 136 | 313 |
| Seq. diverg.(C) (\%) Ts + T \% | 0.95-85.36 | 0.00-5.97 | 2.27-76.85 | 3.18-66.05 |
| Seq.diverg.(C) $\%$ \%) Ty | 0.00-37.70 | 0.00-4.70 | 0.00-42.00 | 0.51-24.81 |
| Seq.diverg.(PW)(\%) TV | 3.70-52.34 | 0.00-4.70 | 1.05-66.18 | 0.65-45.41 |
| $\mathrm{C}=$ Complete deletion PW = Pairwise deletion. Ts $=$ Transitions Tv = Transversions <br> * $\mathrm{n}=29$ (not including Platycodon) $k+29$ (not including Crateracapsa) |  |  |  |  |

The multiple alignment of the 30 taxa produced a data matrix of the complete ITS region consisting of 722-bp (see Fig.87). Removal of alignment gaps gives a mean value of 265.3bp for ITS1, 164.2-bp for 5.8 S subunit and 197.9-bp for ITS2. The alignment required a maximum of 44 gaps for ITS1 ranging in size from 1-8 bp (Craterocapsa not included in size range), 1 gap for the 5.8 S subunit of size $1-\mathrm{bp}$, and 35 gaps for ITS2 ranging in size from 1-12 bp.. The ITS1 sequence for Platycodon was not included in the statistical calculations since it was incomplete. Craterocapsa had a massive deletion of 63-bp (interrupted at position 97 by the ClustalW alignment of three cytosines). From a total of

318, the number of variable sites for ITS1 was 233 , of which 177 were potentially parsimoniously informative; for the 5.8 S subunit the number of variable sites was 17 , of which 5 were potentially parsimoniously informative; and for ITS2 the number of variable sites was 185 of which 136 were potentially parsimoniously informative. ITS1 had about 23 \% more parsimoniously informative sites than ITS2. Base pair lengths and G + C content for ITS1 and ITS2 are very similar to the figures given for other angiosperm families by Baldwin et al. (1995). It has been suggested by Baldwin et al. that the similarity in G + C content in ITS 1 and ITS2 reflects the co-evolution of both spacer regions.

Reconstruction of molecular phylogeny depends on some knowledge of the evolutionary distance between a pair of sequences which is usually measured by the number of nucleotide substitutions per site (d) between them (Kumar, Tamura and Nei, 1993). Pairwise distances are calculated for each combination of taxa pairs and a distance matrix is built up. The actual method used to calculate such distance depends on the pattern of nucleotide substitution and subsequently the model used. If the rate of all evolutionary lineages was the same then the simple proportion ( $p$ ) of nucleotide sites at which two sequences differ would probably suffice. This, however, is rarely what we find or should expect in natural circumstances. The choice of a substitution model is exceedingly difficult. Statistical criteria should theoretically aid the choice of the appropriate model for a given data set (Bulmer, 1991; Goldman, 1993; Tamura, 1994). Kumar, Tamura \& Nei (1993) have supplied some guidelines for choosing distance measures which were used in the choice of substitution model for this study. As a baseline measure, the Jukes-Cantor model was used and the range found for the combined ITS1 and ITS2 data set with gap sites and missing information removed (complete deletion) was $0.0308<d<0.4561$. The range found for the same data set with pairwise deletion was $0.0284<d<0.6526$. The pairwise values predominantly gave $d>0.05$, thus suggesting the choice of a different model. For the ITS1 data set the range found for complete deletion was $0.0094<d<0.5364$ and for pairwise deletion $0.0300<d<0.7647$. For the ITS2 data set the range found for complete deletion was $0.0221<d<0.5532$ and for pairwise deletion $0.0261<d<0.7346$. The transition/transversion ratio was also calculated for the same combined data set and found to be both wide ranging and high (0.3750-7.000 for complete deletion and 0.6623-4.200 for pairwise deletion). With 557 nucleotides in the combined

ITS data set, 313 or 244 in the ITS1 or ITS2 data sets respectively, the suggested option was the Kimura 2-parameter model (K2P). It seems reasonable to assume that the rate of nucleotide substitution differs for each nucleotide site and therefore the gamma distances were also used in conjunction with the K2P model (Uzzell \& Corbin, 1971; Tamura \& Nei, 1993; Wakeley, 1993). For pairwise distances for the combined ITS1 and ITS2 data using the K2P model and gamma distribution, see Fig.88. The gamma distribution can be specified by the parameter $a$ which is the inverse of the coefficient of variation of the substitution rate (ë). With the K-2 model the program MEGA gives a default value of $a=1.0$.

| Taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 |  | 0.1586 | 0.3363 | 0.2609 | 0.3907 | 0.2021 | 0.1373 | 0.1589 | 0.2414 |
| 2 | 0.0352 |  | 0.4107 | 0.3377 | 0.4302 | 0.1857 | 0.1453 | 0.1102 | 0.2962 |
| 3 | 0.0665 | 0.0779 |  | 0.1055 | 0.1230 | 0.3323 | 0.2776 | 0.3323 | 0.1126 |
| 4 | 0.0523 | 0.0641 | 0.0277 |  | 0.1754 | 0.2892 | 0.2398 | 0.2587 | 0.0488 |
| 5 | 0.0754 | 0.0797 | 0.0296 | 0.0384 |  | 0.4131 | 0.3493 | 0.3995 | 0.1837 |
| 6 | 0.0435 | 0.0408 | 0.0647 | 0.0569 | 0.0789 |  | 0.1191 | 0.2081 | 0.2710 |
| 7 | 0.0320 | 0.0336 | 0.0544 | 0.0480 | 0.0662 | 0.0300 |  | 0.1310 | 0.2230 |
| 8 | 0.0354 | 0.0278 | 0.0647 | 0.0513 | 0.0761 | 0.0463 | 0.0313 |  | 0.2609 |
| 9 | 0.0488 | 0.0572 | 0.0291 | 0.0172 | 0.0399 | 0.0542 | 0.0456 | 0.0523 |  |
| 10 | 0.0398 | 0.0452 | 0.0452 | 0.0329 | 0.0500 | 0.0470 | 0.0435 | 0.0458 | 0.0308 |
| 11 | 0.0135 | 0.0376 | 0.0583 | 0.0460 | 0.0662 | 0.0464 | 0.0298 | 0.0340 | 0.0460 |
| 12 | 0.0341 | 0.0298 | 0.0620 | 0.0523 | 0.0718 | 0.0504 | 0.0326 | 0.0189 | 0.0558 |
| 13 | 0.0511 | 0.0617 | 0.0319 | 0.0214 | 0.0395 | 0.0618 | 0.0493 | 0.0518 | 0.0182 |
| 14 | 0.0476 | 0.0586 | 0.0261 | 0.0145 | 0.0367 | 0.0555 | 0.0438 | 0.0468 | 0.0135 |
| 15 | 0.0414 | 0.0513 | 0.0517 | 0.0406 | 0.0569 | 0.0524 | 0.0421 | 0.0518 | 0.0343 |
| 16 | 0.0306 | 0.0286 | 0.0665 | 0.0542 | 0.0722 | 0.0466 | 0.0362 | 0.0313 | 0.0523 |
| 17 | 0.0573 | 0.0603 | 0.0417 | 0.0324 | 0.0540 | 0.0627 | 0.0556 | 0.0488 | 0.0339 |
| 18 | 0.1055 | 0.1086 | 0.0481 | 0.0431 | 0.0549 | 0.0837 | 0.0837 | 0.0976 | 0.0448 |
| 19 | 0.0336 | 0.0388 | 0.0766 | 0.0582 | 0.0779 | 0.0459 | 0.0363 | 0.0446 | 0.0603 |
| 20 | 0.0425 | 0.0401 | 0.0761 | 0.0605 | 0.0864 | 0.0403 | 0.0339 | 0.0417 | 0.0558 |
| 21 | 0.0531 | 0.0612 | 0.0283 | 0.0156 | 0.0370 | 0.0596 | 0.0491 | 0.0523 | 0.0144 |
| 22 | 0.0435 | 0.0544 | 0.0452 | 0.0410 | 0.0555 | 0.0481 | 0.0441 | 0.0505 | 0.0381 |
| 23 | 0.0534 | 0.0729 | 0.0573 | 0.0430 | 0.0583 | 0.0633 | 0.0505 | 0.0569 | 0.0446 |
| 24 | 0.0610 | 0.0761 | 0.0677 | 0.0461 | 0.0662 | 0.0686 | 0.0596 | 0.0693 | 0.0513 |
| 25 | 0.0709 | 0.0854 | 0.0779 | 0.0564 | 0.0845 | 0.0718 | 0.0601 | 0.0779 | 0.0591 |
| 26 | 0.0845 | 0.0854 | 0.0876 | 0.0673 | 0.0854 | 0.0923 | 0.0789 | 0.0864 | 0.0685 |
| 27 | 0.0636 | 0.0771 | 0.0627 | 0.0511 | 0.0733 | 0.0745 | 0.0549 | 0.0624 | 0.0505 |
| 28 | 0.0609 | 0.0831 | 0.0756 | 0.0565 | 0.0821 | 0.0749 | 0.0536 | 0.0695 | 0.0633 |
| 29 | 0.0671 | 0.0837 | 0.0693 | 0.0474 | 0.0702 | 0.0783 | 0.0632 | 0.0761 | 0.0509 |
| 30 | 0.0930 | 0.1118 | 0.1107 | 0.0797 | 0.1158 | 0.0797 | 0.0856 | 0.0874 | 0.0761 |

Fig. 88. Pairwise distamces for the combined ITS1 amd ITS2 sequence data sets (557 mucleotides). Gamma distances are used with the $\mathbb{K i m u r r a} 2$-parameter model ( $a=\mathbb{1}$ ). Gap sites amd missing imformatiom were removed from the subset dlata (Complete deletion optiom). Distamces are im the upper-right matrix. Stamdard Errors are im the lower-left matrix. Taxa labels are as follows:

| 1.Adenophora divaricata | 11.Hanabusaya asiatica | 21.Campanula thyrsoides |
| :---: | :---: | :---: |
| 2.Petromarula pinnata | 12.Physoplexis comosus | 22.Jasione crispa |
| 3.Campanula barbata | 13.Roucela erinus | 23.Craterocapsa congesta |
| 4.Campanula petraea | 14.Campanula punctata | 24.Codonopsis lanceolata |
| 5.Diosphaera rumelianum | 15.Gadellia lactiflora | 25.Leptocodon gracilis |
| 6.Campanulastrum america | 16.Campanula persicifolia | 26.Cyananthus sp. |
| 7.Legousia falcata | 17.Azorina vidalii | 27. Canarina canariensis |
| 8.Phyteuma spicatum | 18.Michauxia tchihatchewii | 28.Platycodon grandiflorum |
| 9.Campanula lanata | 19.Campanula pyramidalis | 29.Obconicapsula dicentrifolia |
| 10.Musschia aurea | 20.Legousia speculum-veneris | 30.Nicotiana rustica |

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Fig. 88. comtinused

| Taxa | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 0.1783 | 0.0318 | 0.1514 | 0.2522 | 0.2330 | 0.1922 | 0.1249 | 0.2780 | 0.5271 |
| 2 | 0.2167 | 0.1737 | 0.1233 | 0.3191 | 0.3057 | 0.2587 | 0.1164 | 0.3094 | 0.5596 |
| 3 | 0.2167 | 0.2923 | 0.3264 | 0.1323 | 0.0979 | 0.2536 | 0.3363 | 0.1823 | 0.2285 |
| 4 | 0.1440 | 0.2238 | 0.2668 | 0.0722 | 0.0370 | 0.1905 | 0.2710 | 0.1285 | 0.1957 |
| 5 | 0.2500 | 0.3423 | 0.3828 | 0.1829 | 0.1667 | 0.2892 | 0.3693 | 0.2586 | 0.2725 |
| 6 | 0.2205 | 0.2191 | 0.2336 | 0.3128 | 0.2800 | 0.2551 | 0.2141 | 0.3148 | 0.4389 |
| 7 | 0.2021 | 0.1233 | 0.1384 | 0.2425 | 0.2136 | 0.1990 | 0.1556 | 0.2742 | 0.4389 |
| 8 | 0.2178 | 0.1511 | 0.0597 | 0.2597 | 0.2313 | 0.2597 | 0.1310 | 0.2414 | 0.5013 |
| 9 | 0.1301 | 0.2238 | 0.2868 | 0.0545 | 0.0318 | 0.1518 | 0.2609 | 0.1363 | 0.2048 |
| 10 |  | 0.1944 | 0.2087 | 0.1378 | 0.1298 | 0.0599 | 0.1932 | 0.2048 | 0.2787 |
| 11 | 0.0425 |  | 0.1511 | 0.2157 | 0.1982 | 0.1932 | 0.1256 | 0.2383 | 0.4636 |
| 12 | 0.0441 | 0.0340 |  | 0.2676 | 0.2567 | 0.2425 | 0.1523 | 0.2686 | 0.5208 |
| 13 | 0.0323 | 0.0448 | 0.0526 |  | 0.0542 | 0.1762 | 0.2831 | 0.1072 | 0.2126 |
| 14 | 0.0307 | 0.0417 | 0.0504 | 0.0180 |  | 0.1667 | 0.2697 | 0.1199 | 0.1857 |
| 15 | 0.0191 | 0.0419 | 0.0493 | 0.0388 | 0.0367 |  | 0.1990 | 0.2521 | 0.3323 |
| 16 | 0.0419 | 0.0310 | 0.0346 | 0.0569 | 0.0536 | 0.0421 |  | 0.2466 | 0.5186 |
| 17 | 0.0448 | 0.0500 | 0.0531 | 0.0286 | 0.0305 | 0.0536 | 0.0512 |  | 0.2938 |
| 18 | 0.0549 | 0.0914 | 0.0988 | 0.0459 | 0.0408 | 0.0647 | 0.1054 | 0.0617 |  |
| 19 | 0.0540 | 0.0333 | 0.0452 | 0.0656 | 0.0577 | 0.0562 | 0.0353 | 0.0549 | 0.1126 |
| 20 | 0.0536 | 0.0421 | 0.0425 | 0.0647 | 0.0572 | 0.0575 | 0.0395 | 0.0569 | 0.1111 |
| 21 | 0.0339 | 0.0468 | 0.0562 | 0.0189 | 0.0144 | 0.0401 | 0.0542 | 0.0328 | 0.0431 |
| 22 | 0.0293 | 0.0464 | 0.0513 | 0.0378 | 0.0392 | 0.0363 | 0.0499 | 0.0435 | 0.0596 |
| 23 | 0.0380 | 0.0525 | 0.0569 | 0.0374 | 0.0381 | 0.0482 | 0.0655 | 0.0579 | 0.0695 |
| 24 | 0.0417 | 0.0603 | 0.0678 | 0.0500 | 0.0453 | 0.0468 | 0.0669 | 0.0604 | 0.0917 |
| 25 | 0.0544 | 0.0626 | 0.0845 | 0.0596 | 0.0558 | 0.0577 | 0.0743 | 0.0695 | 0.1144 |
| 26 | 0.0526 | 0.0795 | 0.0845 | 0.0647 | 0.0669 | 0.0596 | 0.0826 | 0.0878 | 0.1241 |
| 27 | 0.0561 | 0.0600 | 0.0677 | 0.0475 | 0.0475 | 0.0552 | 0.0745 | 0.0561 | 0.0955 |
| 28 | 0.0481 | 0.0573 | 0.0677 | 0.0531 | 0.0552 | 0.0512 | 0.0687 | 0.0628 | 0.0991 |
| 29 | 0.0476 | 0.0639 | 0.0769 | 0.0465 | 0.0496 | 0.0549 | 0.0761 | 0.0665 | 0.0938 |
| 30 | 0.0709 | 0.0876 | 0.0974 | 0.0766 | 0.0801 | 0.0831 | 0.0938 | 0.0754 | 0.1294 |
| Taxa | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
| 1 | 0.1453 | 0.1999 | 0.2686 | 0.2021 | 0.2459 | 0.3110 | 0.3736 | 0.4329 | 0.3169 |
| 2 | 0.1762 | 0.1893 | 0.3247 | 0.2776 | 0.3642 | 0.3995 | 0.4583 | 0.4583 | 0.4018 |
| 3 | 0.3933 | 0.3995 | 0.1112 | 0.2167 | 0.2780 | 0.3525 | 0.4107 | 0.4631 | 0.3148 |
| 4 | 0.2985 | 0.3165 | 0.0426 | 0.1913 | 0.2009 | 0.2299 | 0.2946 | 0.3585 | 0.2522 |
| 5 | 0.4107 | 0.4506 | 0.1673 | 0.2800 | 0.2923 | 0.3493 | 0.4483 | 0.4583 | 0.3718 |
| 6 | 0.2126 | 0.1846 | 0.3080 | 0.2341 | 0.3098 | 0.3544 | 0.3828 | 0.4815 | 0.3746 |
| 7 | 0.1608 | 0.1459 | 0.2478 | 0.2142 | 0.2451 | 0.3080 | 0.3155 | 0.4131 | 0.2725 |
| 8 | 0.2099 | 0.1982 | 0.2668 | 0.2510 | 0.2831 | 0.3629 | 0.4184 | 0.4606 | 0.3207 |
| 9 | 0.3094 | 0.2868 | 0.0369 | 0.1747 | 0.2099 | 0.2587 | 0.3068 | 0.3612 | 0.2451 |
| 10 | 0.2586 | 0.2637 | 0.1509 | 0.1177 | 0.1593 | 0.1982 | 0.2776 | 0.2676 | 0.2692 |
| 11 | 0.1447 | 0.1990 | 0.2313 | 0.2191 | 0.2438 | 0.3094 | 0.3276 | 0.4071 | 0.2960 |
| 12 | 0.2167 | 0.1999 | 0.2941 | 0.2587 | 0.2831 | 0.3598 | 0.4564 | 0.4564 | 0.3525 |
| 13 | 0.3342 | 0.3323 | 0.0597 | 0.1741 | 0.1680 | 0.2500 | 0.3080 | 0.3390 | 0.2271 |
| 14 | 0.2972 | 0.2962 | 0.0369 | 0.1822 | 0.1747 | 0.2223 | 0.2868 | 0.3508 | 0.2271 |
| 15 | 0.2815 | 0.2906 | 0.1893 | 0.1608 | 0.2177 | 0.2313 | 0.2972 | 0.3080 | 0.2672 |
| 16 | 0.1487 | 0.1829 | 0.2710 | 0.2437 | 0.3149 | 0.3508 | 0.3955 | 0.4363 | 0.3746 |
| 17 | 0.2725 | 0.2892 | 0.1341 | 0.2021 | 0.2674 | 0.3033 | 0.3566 | 0.4480 | 0.2692 |
| 18 | 0.5594 | 0.5739 | 0.1957 | 0.3080 | 0.3566 | 0.4884 | 0.5996 | 0.6394 | 0.4884 |
| 19 |  | 0.2148 | 0.3290 | 0.2831 | 0.3005 | 0.3612 | 0.4302 | 0.4884 | 0.3544 |
| 20 | 0.0444 |  | 0.3366 | 0.3224 | 0.3289 | 0.3755 | 0.4223 | 0.5415 | 0.4246 |
| 21 | 0.0632 | 0.0636 |  | 0.1982 | 0.1990 | 0.2563 | 0.3141 | 0.3682 | 0.2500 |
| 22 | 0.0569 | 0.0632 | 0.0417 |  | 0.1823 | 0.2510 | 0.2985 | 0.3442 | 0.2077 |
| 23 | 0.0619 | 0.0661 | 0.0421 | 0.0417 |  | 0.1905 | 0.2609 | 0.3224 | 0.2466 |
| 24 | 0.0685 | 0.0718 | 0.0502 | 0.0505 | 0.0406 |  | 0.0786 | 0.1972 | 0.1126 |
| 25 | 0.0797 | 0.0797 | 0.0594 | 0.0582 | 0.0523 | 0.0226 |  | 0.2481 | 0.1399 |
| 26 | 0.0917 | 0.1044 | 0.0685 | 0.0671 | 0.0632 | 0.0437 | 0.0544 |  | 0.2400 |
| 27 | 0.0686 | 0.0841 | 0.0500 | 0.0436 | 0.0512 | 0.0291 | 0.0333 | 0.0508 |  |
| 28 | 0.0733 | 0.0813 | 0.0613 | 0.0430 | 0.0403 | 0.0283 | 0.0353 | 0.0512 | 0.0263 |
| 29 | 0.0837 | 0.0951 | 0.0488 | 0.0500 | 0.0464 | 0.0286 | 0.0374 | 0.0362 | 0.0362 |
| 30 | 0.1075 | 0.1050 | 0.0826 | 0.0664 | 0.0693 | 0.0647 | 0.0586 | 0.0787 | 0.0639 |

Comtimued averleaf

Fig. 88. comtinued.

| Taxa | 28 | 29 | 30 |
| :---: | :---: | :---: | :---: |
| 1 | 0.2982 | 0.3442 | 0.4912 |
| 2 | 0.4299 | 0.4389 | 0.5845 |
| 3 | 0.3702 | 0.3629 | 0.5639 |
| 4 | 0.2760 | 0.2385 | 0.4223 |
| 5 | 0.4056 | 0.3719 | 0.5931 |
| 6 | 0.3825 | 0.4043 | 0.4223 |
| 7 | 0.2697 | 0.3290 | 0.4509 |
| 8 | 0.3566 | 0.3995 | 0.4709 |
| 9 | 0.3098 | 0.2579 | 0.3995 |
| 10 | 0.2285 | 0.2330 | 0.3736 |
| 11 | 0.2780 | 0.3305 | 0.4631 |
| 12 | 0.3525 | 0.4087 | 0.5177 |
| 13 | 0.2568 | 0.2307 | 0.3933 |
| 14 | 0.2672 | 0.2491 | 0.4156 |
| 15 | 0.2466 | 0.2787 | 0.4299 |
| 16 | 0.3412 | 0.3995 | 0.5015 |
| 17 | 0.2965 | 0.3363 | 0.3907 |
| 18 | 0.4965 | 0.5015 | 0.6605 |
| 19 | 0.3718 | 0.4389 | 0.5661 |
| 20 | 0.4184 | 0.4797 | 0.5518 |
| 21 | 0.3053 | 0.2472 | 0.4363 |
| 22 | 0.2009 | 0.2500 | 0.3566 |
| 23 | 0.1846 | 0.2248 | 0.3629 |
| 24 | 0.1112 | 0.1072 | 0.3323 |
| 25 | 0.1537 | 0.1580 | 0.3057 |
| 26 | 0.2466 | 0.1556 | 0.4202 |
| 27 | 0.0939 | 0.1556 | 0.3305 |
| 28 |  | 0.1459 | 0.3508 |
| 29 | 0.0339 |  | 0.3508 |
| 30 | 0.0669 | 0.0669 |  |

Fig. 89 shows the distribution of changes at each site across the entire ITS region. Pairwise sequence divergence (with the KTP model) using the complete deletion option varied within ITS1 from $0.95-85.36 \%$ and from $2.27-76.85 \%$ in ITS2 (see Table.31). Thus ITS2 was slightly less variable (but see data for transversion-only events). The highly conserved 5.8 S subunit diverged from $0.00-5.97 \%$. For the combined data sets, the smallest sequence divergence was $3.18 \%\left(0.65 \%^{*}\right)$ between Adenophora and Hanabusaya and between Campanula punctata and Campanula lanata (1.11\%* between Campanula punctata and Campanula petraea in the transversion-only with pairwise-deletion data), whereas the greatest divergence was $66.05 \%(45.41 \%$ *) between Michauxia tchihatchewii and the outgroup, Nicotiana rustica. Within the Campanuleae s.s. (including Jasione) the sequence divergence ranged from $3.18 \%\left(0.065 \%^{*}\right)$ among the taxa mentioned above to $57.39 \%$ between Michauxia tchihatchewii and Legousia speculum-veneris $(20.92 \%$ * between Petromarula and Michauxia in the transversion-only with the pairwise-deletion data), with a mean divergence of $26.7 \%\left(9.93 \%{ }^{*}\right)$. Sequence divergence between Michauxia and the rest of the Campanuleae was 19.57-57.39 \%; mean $=37.2 \%(7.12-20.92 \%$; mean $=13.24$ $\%$ *). Sequence divergence between Jasione and the rest of the Campanuleae was 11.8 $32.2 \%$ (9.41-17.10 \%; mean $=12.09 \%$ *). Between Jasione and Craterocapsa sequence divergence was $18.23 \%(6.77 \%$ *). Between Jasione and the Platycodoneae s.s. sequence divergence was $20.10-34.4 \%$; mean $=25.87 \%(19.44-28.85$; mean $=22.98 \% *$ ). Within the Platycodoneae the sequence divergence ranged from $7.86-24.81 \%$ with a mean divergence of $15.62 \%\left(2.96-14.13 \%\right.$; mean $\left.=8.30 \%^{*}\right)$. Finally, the sequence divergence between the outgroup Nicotiana and the ingroup was 30.6-66.1 \%; mean $=44.51 \%$ ( 22.37 - $45.41 \%$ mean $=34.41 \%^{*}$ ). These sequence divergence values are higher than those given for a selection of angiosperm families by Baldwin, et al. (1995), in many cases more than double the highest values recorded. By 1995 the family-wide analysis of the Polemoniaceae by Porter (1993) held the record for taking the use of ITS for phylogenetic reconstruction to its limits. The very high divergence values obtained for the Campanulaceae are probably a direct consequence of the phylogenetic distances of the taxa used in this study. In many investigations which have used the ITS region to reconstruct phylogeny, the taxa used have usually been more closely related, often with species within a single genus. However, if the amount of divergence is high combined with a high transition/transversion
ratio, the sequences could be saturated with transition differences which have the effect creating "noise" (Goldstein \& Pollock, 1994) and inflating the variance of evolutionary distance estimates. This appears to be the situation with the data obtained for the Campanulaceae. For this reason, pairwise distances and percentage sequence divergences were recalculated for transversion events only but otherwise retaining the same parameters as for the original distance matrix. Pairwise distances were also recalculated for transversion events only but with pairwise deletion (not shown). Greater relaxation of contraints on the information content of the data set combined with the elimination of transition bias might yield a compromise (and more realistic) set of sequence divergence values. This set of parameters gave values which were much closer to those calculated for Polemoniaceae (Baldwin et al., 1995). The recalculated sequence divergences based on transversion events only for the examples given above but with relaxed pairwise-deletion have been re-entered in brackets (see above *). It should be noted, however, that average pairwise distance values may not be an adequate measure of relative evolutionary rates (Baldwin, et al.,1995) and that the relative rate tests of Muse \& Weir (1992) should be used instead. Furthermore, within subregions of both ITS1 and ITS2 there is a possibility of rate heterogeneity which complicates a simple model of evolutionary rates based on pairwise sequence divergence values (Gaut \& Weir, 1994).

| Taxal | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 |  | 0.7866 | 1.8501 | 1.3625 | 1.5993 | 1.9469 | 1.0025 | 0.9414 | 1.1862 |
| 2 |  |  | 1.3223 | 1.0126 | 0.9934 | 1.9877 | 1.3375 | 1.2154 | 0.9702 |
| 3 |  |  |  | 2.9875 | 0.7944 | 1.4841 | 1.0753 | 1.4841 | 3.2572 |
| 4 |  |  |  |  | 1.3341 | 1.2989 | 0.9061 | 1.0566 | 3.7623 |
| 5 |  |  |  |  |  | 1.4618 | 1.0817 | 1.3808 | 1.4443 |
| 6 |  |  |  |  |  | 2.7111 | 3.7595 | 1.4544 |  |
| 7 |  |  |  |  |  |  | 1.3442 | 1.0194 |  |
| 8 |  |  |  |  |  |  |  | 1.3625 |  |
| 9 |  |  |  |  |  |  |  |  |  |


| Tヵxめ | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 2.1909 | 5.2633 | 0.8488 | 1.4480 | 1.2617 | 1.5574 | 1.8568 | 2.3952 | 2.3163 |
| 2 | 1.4412 | 0.8129 | 0.9846 | 1.2481 | 0.9237 | 1.0566 | 0.8725 | 1.3133 | 1.7207 |
| 3 | 1.4412 | 1.6465 | 0.9455 | 2.0261 | 2.0517 | 1.6467 | 1.8501 | 3.8167 | 2.0414 |
| 4 | 0.7584 | 1.1723 | 0.8795 | 1.7298 | 1.3821 | 1.1461 | 1.4544 | 5.1351 | 2.5034 |
| 5 | 1.1182 | 1.4116 | 1.0557 | 1.2336 | 1.0364 | 1.2989 | 1.7609 | 2.4412 | 1.6451 |
| 6 | 2.2155 | 1.9154 | 3.1816 | 1.6505 | 1.3728 | 1.8740 | 2.8331 | 1.8503 | 1.4813 |
| 7 | 1.9469 | 0.9846 | 1.4767 | 1.3536 | 0.8101 | 1.2419 | 2.5597 | 1.8618 | 1.4813 |
| 8 | 1.6603 | 0.7022 | 0.3655 | 1.2007 | 0.9600 | 1.2007 | 1.3442 | 1.1862 | 1.8342 |
| 9 | 0.8972 | 1.1723 | 1.0206 | 2.5046 | 5.2633 | 1.0197 | 1.3625 | 5.5063 | 2.6660 |
| 10 |  | 2.1282 | 1.5494 | 1.2170 | 0.7278 | 1.2654 | 1.8179 | 2.6660 | 1.2158 |
| 11 |  |  | 0.7022 | 1.2513 | 1.0690 | 1.8179 | 2.3201 | 2.1709 | 2.0837 |
| 12 |  |  |  | 1.0005 | 0.7074 | 1.3536 | 1.2210 | 1.1351 | 1.4128 |
| 13 |  |  |  |  | 1.5874 | 1.5699 | 1.7481 | 5.8946 | 2.4206 |
| 14 |  |  |  |  |  | 1.0364 | 1.2855 | 3.5335 | 1.9877 |
| 15 |  |  |  |  |  |  | 1.2419 | 3.0563 | 1.4841 |
| 16 |  |  |  |  |  |  |  | 2.0122 | 2.6537 |
| 17 |  |  |  |  |  |  |  |  | 3.2850 |
| 18 |  |  |  |  |  |  |  |  |  |
| T2xa | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
| 1 | 1.3375 | 1.4413 | 1.1351 | 1.9469 | 3.9448 | 1.4726 | 1.2265 | 1.8799 | 2.0758 |
| 2 | 1.5699 | 0.8377 | 0.7439 | 1.0753 | 2.2977 | 1.3808 | 1.1236 | 1.1236 | 1.5279 |
| 3 | 1.7708 | 1.3808 | 1.9384 | 1.4412 | 2.3952 | 1.3449 | 1.3223 | 1.3652 | 1.8503 |
| 4 | 1.2316 | 0.9914 | 1.0321 | 1.3361 | 1.6736 | 0.6198 | 0.7559 | 0.9252 | 1.4480 |
| 5 | 1.3223 | 1.2394 | 1.2266 | 1.3728 | 1.6465 | 1.0817 | 1.2897 | 1.1236 | 1.9561 |
| 6 | 2.4206 | 1.6923 | 1.1700 | 1.4435 | 2.4900 | 1.4971 | 1.0557 | 1.5858 | 2.1741 |
| 7 | 1.5877 | 1. 6124 | 0.7461 | 0.9393 | 1.7613 | 1.1700 | 0.8804 | 1.4618 | 1.6451 |
| 8 | 1.7929 | 1.0690 | 0.8795 | 1.2731 | 1.7481 | 1.2835 | 1.0343 | 1.2394 | 1.3974 |
| 9 | 1.3133 | 1.0206 | 0.7632 | 1.1338 | 1.7929 | 1.0566 | 1.0408 | 1.1530 | 1.7613 |
| 10 | 2.4412 | 1.7527 | 0.5754 | 1.6916 | 5.0227 | 1.0690 | 1.0753 | 1.0005 | 2.5823 |
| 11 | 1.1104 | 1.2419 | 0.9600 | 1.9154 | 3.3633 | 1.3133 | 1.0611 | 1.8682 | 2.0898 |
| 12 | 1.4412 | 1.4413 | 0.6628 | 1.0566 | 1.7481 | 1.0340 | 1.0168 | 1.0168 | 1.3449 |
| 13 | 1.6570 | 1.4841 | 0.5773 | 0.9618 | 1.4506 | 1.1182 | 1.1700 | 1.1330 | 1.7744 |
| 14 | 1.0942 | 0.9702 | 0.3953 | 1.0528 | 1.1338 | 0.8840 | 1.0206 | 1.2070 | 1.7744 |
| 15 | 1.5491 | 1.4627 | 0.8377 | 1.5877 | 3.9790 | 0.9600 | 1.0942 | 1.1700 | 2.2638 |
| 16 | 2.9290 | 1.2336 | 1.4544 | 1.5437 | 3.1908 | 1.2070 | 1.1241 | 1.3432 | 2.1741 |
| 17 | 1.6451 | 1.2989 | 3.1781 | 1.9469 | 4.3777 | 1.7469 | 1.6657 | 1.9800 | 2.5823 |
| 18 | 2.3339 | 1.6592 | 2.5034 | 1.1700 | 1.6657 | 1.2631 | 1.4164 | 1.5768 | 1.9111 |
| 19 |  | 1.0853 | 1.1882 | 1.7481 | 2.6701 | 1.1530 | 0.9934 | 1.2631 | 1.4971 |
| 20 |  |  | 0.9028 | 1.5634 | 2.1919 | 1.3623 | 1.2677 | 1.6329 | 2.1747 |
| 21 |  |  |  | 1.0690 | 1.2419 | 0.6128 | 0.6869 | 0.7903 | 1.1182 |
| 22 |  |  |  |  | 3.8167 | 1.2731 | 1.2316 | 1.5735 | 1.3402 |
| 23 |  |  |  |  |  | 1.1461 | 1.3625 | 1.5634 | 2.0122 |
| 24 |  |  |  |  |  |  | 1.9699 | 2.9651 | 3.2572 |
| 25 |  |  |  |  |  |  |  | 4.6761 | 2.1995 |
| 26 |  |  |  |  |  |  |  |  | 2.4994 |
| 27 |  |  |  |  |  |  |  |  |  |

Fig. 90. Pairwise distamce matrix calculated from tramsition/transversiom ratios for the combined ITS1 amd ITS2 sequence data sets ( 557 mucleotides). Gap sites and missing information were removed from the subset data. Gamma distamces were used with the Kimmura 2 -parameter model ( $a=1.0$ ). See Fig. 88. for am explamation of the taxa mumbers. Comtimued overleaf.

Fig. 90.comtimued

| T®Xal | 28 | 29 | 30 |
| :---: | :---: | :---: | ---: |
| 1 | 2.3593 | 1.5735 | 1.3884 |
| 2 | 1.7048 | 1.4813 | 1.4660 |
| 3 | 2.8642 | 1.2835 | 1.8800 |
| 4 | 2.1096 | 0.5865 | 1.2677 |
| 5 | 2.6733 | 1.1027 | 1.7479 |
| 6 | 1.8593 | 1.6897 | 1.2677 |
| 7 | 1.2855 | 1.1882 | 1.4213 |
| 8 | 1.6657 | 1.3808 | 1.0811 |
| 9 | 2.4900 | 0.9277 | 1.3808 |
| 10 | 2.0414 | 1.2617 | 1.2265 |
| 11 | 2.3952 | 1.3286 | 1.3652 |
| 12 | 1.3449 | 1.1947 | 1.2878 |
| 13 | 2.1362 | 0.8339 | 1.7708 |
| 14 | 2.2638 | 0.9803 | 1.6148 |
| 15 | 2.0122 | 1.2158 | 1.7048 |
| 16 | 2.3116 | 1.3808 | 1.2164 |
| 17 | 3.7703 | 1.8501 | 1.5993 |
| 18 | 2.3025 | 1.2164 | 1.6621 |
| 19 | 1.9561 | 1.4813 | 1.3884 |
| 20 | 1.7832 | 2.1911 | 1.4387 |
| 21 | 1.9632 | 0.4735 | 1.3432 |
| 22 | 1.6736 | 1.1182 | 0.7339 |
| 23 | 1.6923 | 1.3461 | 1.2835 |
| 24 | 1.9384 | 5.8946 | 1.4841 |
| 25 | 1.7516 | 3.9237 | 0.9237 |
| 26 | 2.0122 | 2.5597 | 1.1461 |
| 27 | 8.1538 | 2.5597 | 1.3286 |
| 28 |  | 1.6124 | 1.2070 |
| 29 |  |  | 1.2070 |
| 30 |  |  |  |

### 7.3.6.2 Molecular Plinylogemetic Amalysis

Studies by Baldwin et al. (1995) have shown that there is considerable complimentarity between the ITS1 and ITS2 regions and that better (more robust) resolutions are obtained when both data sets are combined. The use of each individual data set may be justified under certain conditions where there is a lack of resolution in some branches of a combined tree.

## 1. Neigllbounc-Jaimimg Methods

The use of methods which cluster taxa that are most similar has a strong intuitive appeal but such methods cannot join two taxa unless at least one pairwise distance links them. For this reason, missing data can force taxa out of their natural groups. The neighbour-joining method (Saitou \& Nei, 1987) is a distance method which does not require the data to be ultrametric and does not assume equal amounts of divergence in all lineages (Swofford et al., 1996). It constructs a single tree but there is no criterion of optimality written in to the algorithm. In general the branch length estimates from this method do not satisfy the minimum evolution (Rzhetsky \& Nei, 1992) criterion (ME). Swofford, et al.(1996) suggest that the neighbour-joining method should be used to obtain a starting tree but not for the choice of the final tree. Fig. 91 shows a phylogram produced by the program TREEVIEW (Page, 1996) of a bootstrapped neighbour-joining tree (Saitou \& Nei, 1987) using the combined ITS1 and ITS2 data sets. Neighbor-joining methods are claimed to yield more accurate trees (in the sense of being closer to the true phylogenetic tree) than either UPGMA or parsimony (Rohlf, 1992). The algorithm used to find NJ trees is similar to that of the distance Wagner procedure (Farris, 1972) but trees are constructed by linking two OTUs that are closest mutual neighbors whereas the distance Wagner algorithm differs in the definition of "closest" and in the way the distance between a new node and the existing nodes is computed (see Studier \& Keppler, 1988).

The input file was produced by CLUSTALW with gaps and missing data excluded. The data was corrected for multiple substitutions and 2000 replicates were used for the bootstrap analysis. The outgroup is Nicotiana rustica (Nicr). The cluster of taxa which comprise the Platycodoneae s.s. has a bootstrap value of $92.4 \%$ which indicates very strong support. Within this cluster there is strong support ( $76.3 \%$ ) for two major subclusters which are
coincident with the division of the Platycodoneae s.s. into colpate ie. Codonopsis (Codl), Leptocodon (Lepg), Obconicapsula (Obcd) and Cyanathus (Cyasp) and colporate ie. Canarina (Canc) and Platycodon (Plag) taxa. However the separation of minor clusters within the colpate taxa is poorly supported ( $43.9 \%$ ). The strongest support for minor clusters is obtained for those comprising Cyananthus and Obconicapsula (91.0 \%), Codonopsis and Leptocodon ( $84.5 \%$ ), Canarina and Platycodon (69.1 \%). The separation of the remaining taxa from Craterocapsa (Crac) is strongly supported by a bootstrap value of $92.4 \%$ whereas the separation of Jasione (Jasc) is supported slightly less at $71.1 \%$. The remaining taxa comprise the Campanuleae s.s. and these divide into two major subclusters. This division is very weakly supported at $37.5 \%$ as is the division of the larger of the two subclusters ( $39.8 \%$ ). However the association of Musschia (Musa) with Gadellia (Gadl) within this latter subcluster is very strongly supported by a bootstrap value of $93.6 \%$. The two species of Legousia (Legf \& Legs) plus Campanulastrum (Cama) diverge from the other taxa of this subcluster and are very strongly supported (98.9\%). Other minor clusters within the larger subcluster which receive strong support are Adenophora (Aded) with Hanabusaya (Hana) (99.0 \%), Phyteuma (Phys) with Physoplexis (Phyc) (92.1 \%) and the latter two taxa much more weakly with Petromarula (Petp) (54.3 \%). Within the smaller subcluster the strongest support ( $92.7 \%$ ) is for the separation of Azorina (Azov) from the remainder of the taxa. The separation of Roucela (Roue) from the remaining taxa is supported by a bootstrap value of $62.8 \%$. The remainder split into minor clusters with Michauxia (Mict) showing great divergence (branch length) and bootstrap support of 88.6 \% , while Campanula barbata (Camb) and Diosphaera (Dior) have a support value of $81.9 \%$. Collectively, these three taxa separate from the remaining Campanuleae with a support value of $67 \%$.

A second neighbour-joining tree (Fig.92) was produced by the same method but with gaps and missing data included. The overall topology is very similar to the first tree but with differences principally in branch length. Bootstrap values of $100 \%$ are given for the separation of Craterocapsa, for Musschia with Gadellia, for Adenophora with Hanabusaya, for the separation of Legousia and Campanulastrum, and for the separation of Azorina. The topology of the Platycodoneae branch is slightly different, with Cyananthus branching off
from a minor cluster formed by the remaining colpate genera. Support for Codonopsis with Leptocodon is increased ( 94.7 \%) but support for Platycodon with Canarina is decreased (67.6\%). Support for the early separation of Jasione is increased to $99.6 \%$. Musschia and Gadellia branch off together before the two main subclusters of the Campanuleae instead of being included with them. This has a support value of $55.4 \%$ which is weak Support for the association of Phyteuma with Physoplexis is weakened to $64.1 \%$ while the collective grouping which includes Petromarula has increased support (97.9\%). Support for the separation of Roucela has dropped to $64.1 \%$ while Campanula lanata (Caml) and Campanula punctata (Campu) separate out from the residue of taxa with support values of $71.3 \%$ and $52.8 \%$ respectively.

The inclusion of gaps and missing data can quite profoundly alter the topology of the tree and branch lengths. On the one hand an increase in bootstrap support values suggests that the extra data is probably accurate while on the other hand a decrease in bootstrap values suggests that such data merely increases "noise". Unfortunately there is no easy way to discriminate between good and bad data without empirical approaches. Leaving out the gaps may have the effect of throwing away valuable data. This situation can be somewhat alleviated by the use of the pairwise-deletion option which can be implemented on the MEGA program and by the parsimony methods of the PAUP program (see Section. below).

Figs.93-95 show three bootstrapped neighbour-joining trees produced by the program MEGA using a combination of different parameters not available with the tree-building program of CLUSTALW. All use the gamma distances with the K2P model (gamma value $=$ 1.0 ) and with either complete deletion or pairwise deletion. Pairwise distances based on transversions only were also included in these analyses and 2000 replicates were used for bootstrapping. With the complete deletion option using transitions and transversions (Fig.93) the greatest support ( $98 \%$ ) was obtained for the separation of Campanulastrum and Legousia from the remaining genera within the larger subcluster of the Campanuleae s.s. A very high value of $97 \%$ was obtained for Adenophora with Hanabusaya while a slightly lower value of $91 \%$ supported the basal separation of Azorina from the remainder of the smaller subcluster of the Campanuleae. The minor clusters formed by Musschia and

Gadellia and Physoplexis with Phyteuma had support values of $89 \%$. Support of $92 \%$ was obtained for Obconicapsula with Cyananthus and for the major divergence of Craterocapsa from the Campanuleae s.s. The topology of the Platycodoneae is identical to that obtained with the CLUSTALW tree using the complete exclusion option but the bootstrap values are all slightly lower. At the higher levels the topology of the CLUSTALW and MEGA trees are very similar. Only the minor clusters differ to any extent. Musschia and Gadellia are clearly with the larger subgroup of the Campanuleae but branch off early. In the MEGA tree, the smaller subcluster has less resolution among taxa represented by Campanula lanata, $C$. punctata, C. thyrsoides and C. petraea.

With the pairwise deletion option and with transitions and transversions (Fig.94) support for a number of groupings has increased to $100 \%$. These include the early separation of Craterocapsa from the Campanuleae s.s. and the separation of Gadellia and Musschia from the remainder of the Campanuleae. Jasione is nested between these two clusters although its position is only weakly supported ( $45 \%$ ). Adenophora with Hanabusaya and the division of the larger subgroup of the Campanuleae have $100 \%$ support while Azorina from the smaller Campanuleae subgroup and the trichotomy formed by Physoplexis, Petromarula and Phyteuma have support of $99 \%$ and $98 \%$ respectively. The topology of this tree differs considerably. Canarina branches off early from the Platycodoneae and is no longer in close association with Platycodon, while Cyananthus is not so closely associated with Obconicapsula. However, within the Platycodoneae, the only strongly supported group is that formed by Codonopsis and Leptocodon (82\%). Within the larger Campanuleae subgroup, Campanula pyramidalis clusters with Campanula persicifolia but without much support ( $40 \%$ ).

Finally, with the pairwise-deletion option but using transversion data only (Fig.95) the Platycodoneae again form a single cluster with moderate support for major branching at 72 \%. Canarina rejoins Platycodon, albeit weakly at $54 \%$ and Obconicapsula separates from the remaining taxa with $89 \%$ support. Support values for the remaining minor clusters are only weakly supported. Craterocapsa again consistently separates early with high support
of $86 \%$ followed by Musschia and Gadellia at $93 \%$. Collectively the two latter taxa have a support value of $98 \%$. Jasione again is nested within the Campanuleae proper but with only 51 \% support. Azorina branches early within the smaller Campanuleae subcluster ( $99 \%$ ) and the major split within the larger subcluster has $95 \%$ support. There are a few minor surprises within the subclusters although none is very strongly supported. Petromarula associates closely with Physoplexis ( $64 \%$ ) and this cluster together with Phyteuma, Legousia and Campanulastrum are largely unresolved.

The final strategy with neighbour-joining trees was to obtain pairwise distances from MEGA using gamma and the K2P model, pairwise deletion and transversion data only, and use these with the program BIONJ (Gascuel, 1997). This program is a modification of the basic NJ algorithm and takes into account the fact that high evolutionary distances present a higher variance than do short distances. It also uses a simple model of the sampling noise of evolutionary distances as well as coevolutionary distances. For greater details of this new algorithm, see Gascuel, 1997. Figs. 96-98 show the BIONJ trees obtained using pair-wise deletion and the Kimura-2-parameter model with gamma distances. The bootstrapping option is not available in the BIONJ program so these phylograms should be interpreted for their topology and relative branch lengths only. In Fig. 96 with the complete-deletion option for both transitions and transversions the topology of the tree is very similar to the standard NJ tree obtained from MEGA (Fig.93). The major differences occur within the two large subclusters of the Campanuleae. In the BIONJ tree Adenophora and Hanabusaya branch off basally from the remaining taxa of the subcluster whereas in the NJ tree they are nested within the subcluster. There are also several other minor rearrangements of the taxa, eg. Campanula persicifolia joins a minor subcluster with Campanula pyramidalis. In the other large subcluster of the Campanuleae, the taxa are more resolved in comparison with the NJ tree. In Fig. 97 with the pairwise-deletion option for transitions and transversions the topology of the BIONJ tree differs more strikingly from the standard NJ tree obtained from MEGA (Fig.94). Cyananthus clusters with Obconicapsula while Platycodon branches off independently before the remainder of the Platycodoneae. Jasione also branches off from the rest of the Campanuleae and before the minor subcluster formed by Musschia and Gadellia. Hanabusaya and Adenophora again branch off early from the remainder of the larger
subclusters while Legousia falcata also branches off independently and basally to the remaining taxa. In the other large subcluster Azorina vidalii, Roucela erinus and the remaining group of taxa collectively form an unresolved cluster. Finally, Fig. 98 shows the pairwise-deletion option with transversions only. In the BIONJ tree Obconicapsula again links with Cyananthus. Craterocapsa again branches off early but Musschia and Gadellia again branch off next before Jasione. Hanabusaya and Adenophora branch off early and are basal to all the remaining taxa of the larger major subcluster of the Campanuleae. Within this subcluster the two species of Legousia unite to form a minor subcluster while all the other taxa display greater resolution in comparison with standard NJ tree from MEGA (Fig. 95). The other large subcluster shows only minor rearrangements.


Fig.91. Bootstrapped meighbour-joimimg phylogram of the aligmed ITSI amd ITS2 combime sequemces for 29 taxa of the Campamulaceae amd the outgroup Nicotiana rustica fromm thr program CLUSTALW, ver. 1.t, amd imported imto the program TREEVIEW. Correction for multiple substitutioms were used amd gaps amd missimg data were imelunded. 200 bootstrap replicates were used. Bootstrap values shown are the actual replicate mumben rather tham percemtages.


Fig.D2. BBootstrapped meiglnbour-joimimg phylogranm of othe aligmed ITS1 amalit 2 combimed sequences for 29 taxa of the Campamonaceæe amol the ontyroup Nicotiana restica from the programn $\mathbb{C L U S T A L W}$, ver. 1.6, amd imported imid the program TREIEVIEW. Correctioms for multiple substitontioms were used amd gaps amd missimg imformatiom were exclunded. 2000 bootstrap replicates were used. Bootstrap values shown are the actomall replicate numbers rather tham percentages.


Fig. 93 . Bootstrapped meighlowar-jimimimg phylogram of the aligmed ITS1 amd ITS2 combimed sequences for 29 taxa of the Campamulaceac amd the outgroup Nicotiana rustica from the program $\mathbb{M I E G A}$, ver.1.02. Gamma distamces with the Kimaura-2-parameter modell were calculated for tramsversioms amd tramsitioms using the complete deletiom optiom. 2000 bootstrap replicates were used.


Scale: each - is approximately equal to the distance of 0.010448

Fig.94. Brootstrapped meightoonr-joimimg phylogram of the aligmed ITSI amd ITS 2 combimed sequences for 29 taxa of the Campamulaceac and the outgroup Nicotionar rustica from the program $\mathbb{M E G A}$, ver. 1.02 . Gamma distamees with the $\mathbb{K} i m m a n-2$-parameter modlel were calculated for tramsversioms amd tramsitioms using the ppairwise-deletion opption. 2000 bootstrap replicates were used.


Scale: each - is approximately equal to the distance of 0.00332

Fig.95. Bootstrapped meighbrour-joiming phylogramn of the aligmed ITSI amol ITS2 combimed sequences for 29 taxa of the $\mathbb{C}$ muppmulaceax amd the outgroup Nicotiana rustica fromm the program MIEGA, ver. 1.02. Gamman distamces with the Kimura-2-parameter model were calculated for tramsversioms omly usimg the pairwise deletion optiom. 2000 bootstrap replicates were used.


Fig.96. Neighbour-joiming phyllogramn of the aligmed ITS1 amd ITS2 commbimed sequemces for 29 taxa of the Campamulaceae amd the oungroup Nicotiona rustica from the program $\mathbb{B I O N J}$. Ganmma distamces witlo the Kimmura-2-parameter model were calculated for transitioms amd tramsversioms using the complete-deletiom option.


Fig.97. Neighbour-joimimg playlogram of the aligmed ITSI amoll ITS2 combined sequemces for 29) taxa of the Campamulaceax amal the outgroup Nicotiana reastica from the programn BIONJ. Gamman distamces witlh the Kimmra-2-parameter modlel were callculated for tramsitioms amd tramsversioms usimg the pairwise-deletiom option.


Fig.98. Neiglmbour-joimimg plnylligramn of the aligmed ITS1 amdl ITS2 combimedl sequemees for 29 taxa of the Cæmpamolaceae amd the oungroup Nicotianea restica fromm the progranm BBIONJ. Gamama distamces with the Kimmura-2-parameter moodel were calleulatedl for tramsversioms omly usimg the pairwise-deletiom option.

## 2. Parsimamy methods

Parsimony is used for judging the phylogenetic tree(s) obtained and for reconstructing the history of character change. Parsimony methods do not require an explicit evolutionary model of nucleotide substitution. They assume independence of characters and allow for independent models for each character but implicit in parsimony methods are assumptions about the history of character change. This is both its strength and weakness. If a certain group is very well known it is likely that correct assumptions will be made about characters and that accurate phylogenies will be recovered. However, as stated by Maddison \& Maddison (1993), the models of evolution investigated to date are overly simplistic and unrealistic and there are certain situations where parsimony as a methodological principle can be positively misleading (Felsenstein, 1978). Parsimony methods are routinely favoured by many systematists because of the individual assessment of each character and also because it can produce a number of conflicting hypothesis which, in itself, can have the benefit of actually aiding the final choice of phylogenetic tree. This is particularly the case where certain classes of characters are statistically highly inconsistent across a particular range of taxa (Maddison \& Maddison, 1993). For these reasons, parsimony methods were considered to be an alternative and valid approach to the reconstruction of Campanulaceae phylogeny for both morphological and molecular characters.

The aligned sequences for the ITS1 and ITS2 regions obtained from CLUSTALW, ver. 1.6 were imported into the program MacCLADE (Maddison \& Maddison, 1993). Basic statistical characters of the aligned sequences were calculated and are shown in Table 32. The data matrix was then imported into PAUP, ver. 3.1 (Swofford, 1993) and a search for the most parsimonious tree was initiated. The basic strategy for choice of search parameters was similar to that used for the morphological characters and for the first run 315 informative characters were used. Characters were all given equal weight and were unordered. An heuristic search algorithm was chosen and the "keep minimal trees" and "collapse zero-length branches" were invoked. The starting trees (Start Tree Length = 1201; $\mathrm{CI}=0.467 ; \mathrm{RI}=0.575$ ) for branch-swapping was imported from MacCLADE. This was subjected to 1000 random-edition replicates with no swapping, followed by TBR (Tree bisection-reconnection) swapping on the trees obtained. The MULPARS and "steepest
descent" options were selected. Four trees were obtained by these methods and consensus trees (Strict, Semistrict and $50 \%$ Majority-Rule) were computed (Figs.). The consensus indices are shown below in Table 32.

Table 32. Consensus indices for consensus trees obtained from four most-parsimonious trees from the combined ITS1 and ITS2 data sets of the the Campanulaceae. 315 informative characters were used

| CONSENSUS TREE INDEX | STRICT | SEMISTRICT | MAJ.-RULE |
| :---: | :---: | :---: | :---: |
| Component Information | 18 | 18 | 26 |
| (consensus fork) | (norm. $=0.643$ ) | (norm. $=0.643$ ) | (norm. $=0.929$ ) |
| Nelson-Platnick term information | 103 | 103 | 152 |
| Nelson-Platnick total information | 121 | 121 | 178 |
| Mickevich's consensus informat. | 0.290 | 0.290 | 0.462 |
| Colless weighted consensus fork (proportion max, information) | 0.279 | 0.279 | 0.410 |
| Sehuh-Farris levels sum | $833$ | $833$ | $1154$ |
| Rohifs CI (1) | $0.526$ | $0.526$ | $0.800$ |
| Rohifs - ln CI (2) | 73.786 | 73.786 | 86.390 |
| C1 (2) | $9.02 \mathrm{e}-33$ | $9.02 \mathrm{e}-33$ | 3.03e-38 |

A bootstrap analysis was then done on the four most-parsimonious trees using the heuristic algorithm of PAUP, simple addition-sequence, TBR swapping, COLLAPSE, MULPARS and STEEPEST in effect, and 1000 bootstrap replicates. The bootstrap consensus tree is shown in Fig. 99.

Very high support values ( $100 \%$ ) were found for the basal clade formed by the outgroup Nicotiana rustica, for the clades formed by Platycodon and the remainder of the Platycodoneae, and within that latter group, the clade formed by the clade minus Platycodon (70 \%), for Codonopsis and Leptocodon (100 \%) and for Cyananthus with Obconicapsula (93 \%). The sequential separation of Craterocapsa and Jasione as basal taxa to the remainder of the Campanuleae received $100 \%$ support as did the subclusters formed by Musschia with Gadellia and Adenophora with Hanabusaya. The actual separation of Musschia and Gadellia jointly from the remainder of the Campanuleae had $88 \%$ support while the separation of the Campanuleae into two major blocks of taxa had $82 \%$ support. The two major blocks of taxa were more poorly supported and lacked complete resolution
although Adenophora with Hanabusaya and the minor clade formed by Petromarula, Physoplexis and Phyteuma ( $89 \%$ ) had strong support. The separation of Legousia speculumveneris from the other taxa within one of the blocks and from Legousia falcata was very strongly supported (99 \%). Legousia falcata formed a clade with Campanulastrum americanum although this was not strongly supported. The other block had a support value of $92 \%$ but was largely unresolved except for the weak support for Campanula barbata with Diosphaera rumelianum and Azorina vidalii with Roucela erinus. The Strict and Semistrict Consensus trees were identical. Only the Semistrict is shown in Fig.100. Strict Consensus and 50 \% Majority-Rule Consensus trees both show similar topology. The Platycodoneae in both are isolated as a monophyletic group and in both trees have identical branch topology (with $100 \%$ for all minor clades with the Majority-Rule tree). The main block of the Campanuleae is slightly less resolved because of the minor clade formed by Musschia and Gadellia, and by Jasione and Craterocapsa. In the Majority-Rule tree Craterocapsa (57 \%) actually separates off as basal to the remainder of the Campanuleae. With all the consensus trees there is a consistent formation of two major clades of taxa within the Campanuleae. Michauxia tchihatchewii is consistently basal within one of the clades while Azorina only reveals this basal tendency in the Majority-Rule tree. This is also seen with Legousia speculum-veneris in the other block of taxa. Although there is lack of resolution in both of these blocks, certain minor clades appear to be consistent eg. Adenophora with Hanabusaya, Petromarula with Physoplexis and Phyteuma, and Campanula persicifolia with Campanula pyramidalis.

The MacCLADE data matrix was then recoded to include informative gaps following the methods of Bruns et al. (1992) and a second search was initiated using identical parameters as the first search but with 397 informative characters (Start Tree Length $=2057 ; \mathrm{CI}=0.47$; $\mathrm{RI}=0.56 ; \mathrm{RC}=0.26$ ). A single most-parsimonious tree was found (Fig.101) with a Length $=2050(\mathrm{CI}=0.467 ; \mathrm{HI}=0.535 ; \mathrm{RI}=0.559 ; \mathrm{RC}=0.261)$. The skewness index or $g 1$ statistic was calculated to assess the amount of phylogenetic signal in the data set (Hillis \& Huelsenbeck, 1992). This was obtained by invoking the RANDOM trees option of PAUP and generating 10000 random strees. The value found was -0.835883 which is indicative of very significant skewness. This was confirmed by the histogram which was simultaneously
produced by the program (not shown). Thus the data sets do carry a strong phylogenetic signal. The single most-parsimonious tree was then used in a bootstrap analysis using 1000 replicates. Fig. 101 shows the bootstrap values superimposed on the single phylogram obtained for ITS1 and ITS2 using the modified data matrix.

For additional corroboration of support for the groups which consistently appear to be monophyletic in all the above analyses, the combined ITS1 and ITS2 aligned sequences matrix was subjected to a parsimony jack-knife analysis (Farris, et al., 1996) using the program JAC (Farris, 1995). This method is an independent-removal jack-knife in which each replicate is formed by deleting characters randomly and independently from the original matrix. 10000 replicates were used for the analysis and the default cutoff level of 50 $\%$ for the jack-knife frequency $G$ was selected. The results are shown in Fig.102. The jackknife tree was reconstructed by the TREEVIEW program in order to improve clarity. The $G$ values are shown on the most strongly supported branches. Although there is much lack of resolution several groups of taxa appear to be well supported and the overall topology is similar to that obtained by the parsimony program of PAUP. The Platycodoneae form a monophyletic group with $G=0.8129$ and which is basal to all other taxa, although subdivision of this clade lacks resolution. The minor clades formed by Codonopsis and Leptocodon ( $G=0.9074$ ), Cyananthus and Obconicapsula $(G=0.6872)$ and Canarina and Platycodon ( $G=0.7099$ ) all have high support values. The major block formed by the remaining taxa is unresolved but does show a familiar pattern with Craterocapsa and Jasione branching independently and the clade formed by Musschia and Gadellia ( $G=$ 0.9984 ). The residues of this major clade are the two major blocks of the Campanuleae which completely lack resolution in the smaller of the two. The larger block has two minor clades. One is formed by Petromarula with Physoplexis and Phyteuma ( $G=0.9553$ ) and the other is formed by Hanabusaya with Adenophora $(G=0.9986)$.


Fig.99. 50\% majority-rule bootstrap comsemsus tree obtaimed for the aligmed ITSI amc ITS2 combimed sequences for 29 tass of the Cammpamulaceae and the outgroup Nicotiant rustica. 1000 lbootstrap replicates amd 315 imformative sites were used.

Majority rule


Semistrict


Fig. $100.50 \%$ majority-rule and semistrict comsemsus trees from 4 most-parsimomious trees foumd for the aligned $\mathbb{T T S} \mathbb{1}$ amd $\mathbb{T}$ S2 combimed sequemces. 29 taxa of the Campamonlaceas and the outgroup Nicotianea rustica were sampled using 315 imformative sites.


Fig.101. 50\% majority-rulle bootstrap comsemsus tree obtaimed for the aligned ITSI amd ITS2 combimed sequences for 29, taxa of the Campamulaceac amel the ountgroup Nicotianos rustica. 1000 bootstrap replicates and 397 informative sites were used.


Fig.102. Most parsimomious jacklkmife tree foumd for the aligmed $\mathbb{T T S 1}$ amd ITS2 combimed sequences of 29 taxa of the Campamulaceac amd the outgroup Nicotiana reastica usimg the progran JAC. Jackkmife frequemcies > $50 \%(G)$ are shown alomg the most-supprorted bramehes. 10000 replicates amal 557 sites were used.

## 3. Maximumn-likelihood methods

The third and final method used in this study for evaluating the sequence data was Maximum-likelihood method. This method often gives results which are least affected by sampling errors and is relatively robust to assumptions about sequence evolution. Maximum -likelihood methods tend to outperform parsimony methods when simulated over a range of sequence-evolution models (Hasegawa $\&$ Fujiwara, 1993). The essence of the method is that it evaluates hypotheses about evolutionary history in terms of the probability that a proposed model of evolutionary history and of the hypothesised history would give rise to the observed data. (Swofford, et al., 1996).

The aligned sequences of 30 taxa and 557 characters (sites) for the combined ITS1 and ITS2 data sets were imported into the program DNAML of the PHYLIP package, ver. 3.5 (Felsenstein, 1993). The transition/transversion ratio was selected at 1.7000 and empirical base frequences were used $(\mathrm{A}=0.21297 ; \mathrm{C}=0.30317 ; \mathrm{G}=0.28533 ; \mathrm{T}=0.19854$ ). "One category of substitution rates" was selected but the "jumble" option for input order and the "global rearrangements" option were not selected due to computing costs. The likelihood for each nucleotide site was calculated separately under the homogeneous Markov model which assumes that the site evolves independently, that the probability of change at a given site does not depend on the history of the site and that the substitution probabilities do not change in different parts of the tree. The combined values for each likelihood is summed to give a total likelihood value which is the probability that the tree and the model are congruent at all sites. In practice, the log of the likelihood is used and the probabilities are accumulated as the sum of the logs of the single-site likelihoods. Fig. 103 shows the likelihood values and confidence limits obtained, while Fig. 104 shows the Maximumlikelihood tree. The overall topology is very similar to the trees obtained by the other two methods but with one or two striking exceptions. Gadellia and Musschia are firmly nested with one of the larger subgroups of the Campanuleae and most closely linked to Diosphaera rumelianum. Jasione crispa forms a cluster with Craterocapsa congesta which is both independent of and basal to all the Campanuleae. Within the other large subcluster of the Campanuleae Adenophora and Hanabusaya are joined to Campanula pyramidalis as a basal group to the remaining taxa in this subcluster. Apart from minor topological rearrangements,
the tree is remarkably congruent with NJ trees and parsimony trees. The Platycodoneae again form a consistently isolated group.

Examined 1802 trees

| Between | And | Length | Approx. Con | ce Limita |
| :---: | :---: | :---: | :---: | :---: |
| 28 | 26 | 0.07673 | 10.03220. | $0.12163)$ |
| 26 | 25 | 0.02852 | 0.00193, | $0.05503)$ |
| 25 | Plag | 0.08332 | 0.04915 , | $0.11785)$ |
| 25 | Canc | 0.07184 | ( 0.04079, | $0.10326)$ |
| 26 | 24 | 0.05788 | 0.02571 , | $0.08996)$ |
| 24 | 27 | 0.04765 | 0.01901 , | $0.07651)$ |
| 27 | Obcd | 0.06474 | 0.03435 , | $0.09517)$ |
| 27 | Cyasp | 0.16730 | 0.12097 , | $0.21458)$ |
| 24 | 23 | 0.03563 | 0.01124, | $0.06012)$ |
| 23 | Lepg | 0.08952 | 0.05662 , | $0.12251)$ |
| 23 | Codl | 0.04648 | 0.02165 , | $0.07174)$ |
| 28 | 21 | 0.19731 | 0.13976 , | $0.25588)$ |
| 21 | 22 | 0.03407 | 0.00689 , | 0.06139) |
| 22 | Crac | 0.08238 | 0.04929 , | 0.11581) |
| 22 | Jasc | 0.11513 | ( 0.07685, | 0.15341) |
| 21 | 20 | 0.02938 | ( 0.00287, | 0.05586 ) |
| 20 | 15 | 0.02985 | ( 0.01029, | 0.04941) |
| 15 | Azov | 0.06833 | ( 0.04256, | 0.09460 ) |
| 15 | 16 | 0.01212 | $($ zero, | 0.02520 ) |
| 16 | Mict | 0.07117 | ( 0.04466, | 0.09809 ) |
| 16 | 8 | 0.03597 | ( 0.01665, | $0.05544)$ |
| 8 | 7 | 0.00925 | ( zero, | 0.02180 ) |
| 7 | 19 | 0.00918 | $($ zero, | $0.02072)$ |
| 19 | Camt | 0.04505 | ( 0.02480, | 0.06552 ) |
| 19 | 12 | 0.01468 | ( 0.00188, | 0.02743 ) |
| 12 | Campu | 0.02498 | ( 0.00938, | 0.04069 ) |
| 12 | Campet | 0.01745 | ( 0.00406, | 0.03085 ) |
| 7 | 3 | 0.03731 | ( 0.01818, | 0.05686 ) |
| 3 | 2 | 0.05945 | ( 0.03407, | 0.08505 ) |
| 2 | Dior | 0.01882 | ( 0.00211. | 0.03555 ) |
| 2 | 13 | 0.10314 | ( 0.07049, | 0.13701) |
| 13 | Gadl | 0.04182 | ( 0.01944, | $0.06443)$ |
| 13 | Musa | 0.11519 | ( 0.07958, | $0.15081)$ |
| 3 | 11 | 0.02107 | ( 0.00590, | $0.03644)$ |
| 11 | Roue | 0.04836 | 0.02668 , | 0.07029 ) |
| 11 | Camb | 0.03631 | 0.01772 , | 0.05490 ) |
| 8 | Caml | 0.03933 | ( 0.02026, | 0.05840 ) |
| 20 | 1 | 0.05149 | ( 0.02751, | $0.07562)$ |
| 1 | 17 | 0.01022 | zero, | $0.02430)$ |
| 17 | 9 | 0.04787 | 0.02550 , | 0.07043 ) |
| 9 | Aded | 0.01403 | 0.00258 , | 0.02547) |
| 9 | Hana | 0.00753 | zero, | $0.01641)$ |
| 17 | Campy | 0.14658 | ( 0.10745, | $0.18675)$ |
| 1 | 5 | 0.01511 | ( 0.00020, | $0.03003)$ |
| 5 | 4 | 0.01810 | ( 0.00258, | 0.03370 ) |
| 4 | 18 | 0.02203 | ( 0.00659, | 0.03769 ) |
| 18 | Legs | 0.08305 | 0.05390 , | $0.11212)$ |
| 18 | 14 | 0.04461 | ( 0.02236, | $0.06687)$ |
| 14 | Camper | 0.08532 | 0.05660 , | $0.11396)$ |
| 14 | Cama | 0.02919 | ( 0.01121, | 0.04724 ) |
| 4 | Legf | 0.04088 | ( 0.02016. | $0.06154)$ |
| 5 | 6 | 0.04154 | ( 0.01997, | $0.06308)$ |
| 6 | Phys | 0.02358 | ( 0.00699, | $0.04021)$ |
| 6 | 10 | 0.04769 | ( 0.02561, | 0.06982 ) |
| 10 | Phyc | 0.03484 | ( 0.01606, | $0.05397)$ |
| 10 | Petp | 0.05697 | ( 0.03351, | $0.08086)$ |
| 28 | Nicr | 0.33594 | ( 0.25850, | $0.41606)$ |

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* = significantly positive, P < 0.05
#म = significantly positive, P < 0.01
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Fig. 103 Maximum-likelihood values and confidence limits for the aligned ITSI and ITS 2 combined sequences of 29 taxa of the Campanulaceae and the outgroup Nicotiana rustica from the program $\mathbb{D} N A M L$. 557 sites were examined. Numbers refer to internal nodes.


Fig. 104. Maxjmunm-likelihood phylogram for the aligmed ITS1 amd ITS2 combimed sequences of 29 taxa of the Campamulaceae amd the outgroup Nicotiana rustica obtaimed by the $\mathbb{P H Y M L I P}$ program $\mathbb{D N A M I L} 557$ sites were used. The mumbers on the tree are the modes for which the maximum-likelihoods are calculated. See Fig. 103 opposite.
"Faced with the excessive development of rationality one must return to the nameless simplicity (nonconceptual), to the condition in which one lets Tao take its harmless course, without attracting names to it." Lao Tzu
"The Phenomenal World"

### 8.11 1 Discussimm

The phenetic, cladistic and molecular analyses have to be evaluated jointly in order to ascertain areas of congruence before any firm conclusions and any phylogenetic hypothesis can be made. As far as the position of the Campanulaceae is concerned the phenetic analysis of the Asterales based on the data matrix of Gustaffson \& Bremer (1995) and the Campanulales subset supports the inclusion of the Campanulaceae, Cyphocarpaceae, Lobeliaceae, Cyphiaceae and Nemacladaceae within a single group. This was consistent with UPGMA, Single-linkage and Complete-linkage methods and in all three the Campanulaceae was basal to the other four families. The Cyphocarpaceae was consistently most close to the Lobeliaceae while the Cyphiaceae was consistently most close to the Nemacladaceae. This is slightly contradicted by the parsimony analysis of Gustaffson \& Bremer which showed the relationship of the Nemacladaceae and Cyphiaceae as either unresolved or the Cyphiaceae as a sister group of the clade formed by the Lobeliaceae and Cyphocarpaceae. The UPGMA analysis found that the next most similar cluster was that formed by the Menyanthaceae, Goodeniaceae, Asteraceae, Calyceraceae and Brunoniaceae whereas the cladistic analysis of Gustaffson \& Bremer (1995) found the sister group of the Campanulaceae and related families to comprise the Pentaphragmataceae, Sphenocleaceae, Donatiaceae and Stylidiaceae. This result differed slightly for the Single-linkage method which showed the Menyanthaceae branching off basally to the cluster formed by Asteraceae, Goodeniaceae, etc. and strikingly for the Complete-linkage method which was more similar to the results obtained by Gustaffson \& Bremer (1995). Strict Consensus trees of these clustering methods showed that the Asteraceae/Goodeniaceae cluster and the Campanulaceae/Lobeliaceae cluster form a grand single cluster with the UPGMA + Singlelinkage consensus. With the UPGMA Complete-linkage consensus there is little resolution except for the minor cluster formed by the Cyphocarpaceae and the Lobeliaceae. The

UPGMA analysis of the Campanulales subset is interesting in that the cluster formed by the Campanulaceae and most closely-related families forms the next largest cluster with the Pentaphragmataceae, Sphenocleaceae, Donatiaceae and Stylidiaceae. It therefore comes closest to the analysis by the Complete-linkage method.

These results partially support the conclusions of Cosner et al. (1994) which place the Lobeliaceae as the sister group of the Campanulaceae and the Cyphocarpaceae and Cyphiaceae branching off sequentially and earlier as individual monophyletic clades. Also, these results do not support the inclusion of the Nemacladaceae as the immediate sister group of the Campanulaceae s.s. It does however support the conclusions of Lammers 1992 that the Campanulaceae and Lobeliaceae should be accorded family rank. Whether the Cyphocarpaceae, Cyphiaceae and Nemacladaceae should be treated as subfamilies of the Lobeliaceae or given family status must await further studies. The phylogenetic position of these families within the Asterales as a whole still remains a contentious issue.

The relationships of the genera within the Campanulaceae are more difficult problems to resolve. Sequence data from the $r b c \mathrm{~L}$ gene of chloroplast DNA (Cosner, Jansen $\&$ Lammers, 1994) has indicated that within Campanulaceae there are two major clades, one formed by Cyananthus/Codonopsis and the other by Campanula/Trachelium but the sample sizes are small and taxa examined very few. The following discussion is structured around the traditional division of the family into three tribes. Firstly the genera of the Platycodoneae are discussed, followed by the Wahlenbergeae and then the Campanuleae.

### 8.1.1.The Platycodmeate

The UPGMA phenetic analysis of the Flowers \& Fruits data set (Flowers.DAT) shows that the colpate and colporate genera traditionally associated within the Platycodoneae (ie. Platycodon, Codonopsis, etc.) do indeed cluster most closely with one another and that this group collectively clusters with "wahlenbergioid" genera such as Nesocodon, Heterochaenia, Roella, Craterocapsa and Berenice, and with the "campanuloid" genus Azorina. Within the "platycodonoid" clusters, the subclusters do not appear to be too deviant from traditional arrangements, eg. Campanumoea and Cyclocodon are closest and cluster
with Canarina. Codonopsis clusters with "Himalcodon" (Obconicapsula). There are some minor clusters which appear to contradict traditional arrangements, eg. Leptocodon with Cyananthus and Echinocodon with Pseudocodonopsis. This result is confirmed by the Complete-linkage method which also clusters the "wahlenbergioids" and "campanuloids" in a single more aggregate cluster. With the Single-linkage method this topology breaks down and, although the homogeneity of the "platycodonoids" is maintained, the group is thrown into more obscure relationships with a larger number of "wahlenbergioid" and "campanuloid" genera. Strict Consensus of the UPGMA and Complete-linkage only reveals the strong similarity between Codonopsis and Ostrowskia, and between Canarina and "Himalcodon" (Obconicapsula) among the "platycodonoids". The phenetic data subset for the Platycodoneae does not substantially reveal any new topology, although the clustering of the outgroup Lobelia with Cyananthus and Leptocodon in intriguing. This suggests that floral and fruit morphology within the "platycodonoids" is relatively conservative.

The Strict Consensus of 2 tied trees from the UPGMA phenetic analysis for the pollen data set (CampPal.DAT) has shown clearly that the colpate and colporate "platycodonoid" genera do stand apart from all other porate campanulaceous genera. However the topology of this tree does not group these genera into a single homogeneous cluster. Cyananthus with Echinocodon and Leptocodon, and Pseudocodonopsis with the outgroup Lobelia branch off basally as the first cluster. This is then followed by Platycodon with Codonopsis, and finally with Canarina on its own. This topology is repeated with the Complete-linkage method. However, with the Single-linkage methods the homogeneity of the "platycodonoids" breaks down, the genera are dispersed throughout the Campanulaceae and link with disparate "wahlenbergioid" or "campanuloid" genera. Strict Consensus trees merely emphasise the strong similarity of Cyananthus with Echinocodon and Leptocodon (UPGMA + Singlelinkage) or even produce very odd results such as Ostrowskia with Peracarpa (UPGMA + Complete-linkage). The pollen data subset for the Platycodoneae reveals two major clusters, one of which essentially groups the colporate genera but also includes Leptocodon and Ostrowskia, plus the outgroup Nesocodon. The other cluster includes the colpate genera Codonopsis, Cyananthus, Echinocodon and the outgroup Lobelia. Pollen morphology within the "platycodonoids" is therefore less conservative than flower or fruit morphology.

The UPGMA phenetic analysis for the seeds data set (Campseed.DAT) reveals a depressingly confusing picture, although the samples used in the analysis are admittedly very biased towards the Campanuleae. The "platycodonoids" do not cluster with each other, except in the case of Leptocodon with Platycodon which then breaks down in the Strict Consensus trees. The seeds data subset for the four "platycodonoid" genera reveals a dichotomy. Platycodon clusters with Leptocodon while Codonopsis clusters with Cyananthus and to the outgroups, Nesocodon and Roella. It is clear that seed characters are poor at showing similarity relations which are congruent with those from flower and fruit characters or with traditional arrangements. This strongly suggests that seeds are highly adaptive and are under intense selection pressure, a conclusion which is supported by the frequent observations that two or more closely related species within the Campanulaceae often possess radically different seed morphologies.

The baseline cladistic analysis using parsimony for the Flowers \& Fruits data set and rooted through the hypothetical "HYPOTH. EUDICOT" showed that the "platycodonoid" genera were mostly basal to all other campanulaceous genera but there were anomalies such as the grouping of Cyananthus and Leptocodon with Musschia. The basal genera did not form a single monophyletic clade but instead branched off sequentially as minor clades of 2-3 genera or as monotypic clades. Perhaps most surprising was the basal position of colporate genera such as Canarina, Campanumoea and Cyclocodon and the clade formed by Ostrowskia and Platycodon. Several of these anomalies, especially the grouping of Leptocodon and Cyananthus elsewhere in the tree is probably the result of homoplasy within the data matrix. The baseline cladogram for the pollen data reveals a more traditional arrangement and one that is more congruent with the phenetic analysis. Here, Cyananthus is basal and Canarina forms a monophyletic clade with Codonopsis. Campanumoea does not come close to Codonopsis, an arrangement which is probably decidedly anomalous. The baseline cladogram for the seeds data set is utterly confusing and little sense can be made of the associations of the "platycodonoids" with the other campanulaceous genera. The consensus trees of the baseline cladograms for the Platycodoneae subset show the colporate genera, Canarina, Campanumoea and Cyclocodon to be basal to the rest with Codonopsis
and Himalcodon (Obconicapsula) as the next derived genera. Cyananthus consistenly forms a monophyletic clade with Leptocodon, whereas Pseudocodonopsis is often more closely associated with Platycodon. A bootstrap consensus tree gave very little support for any of the clades. The greatest support (70\%) was found for the clades formed by Node 2 , ie. Codonopsis as a sister group to Ostrowskia which in turn is a sister group to Cyananthus with Leptocodon, Echinocodon with Pseudocodonopsis and Platycodon. A Strict Consensus tree of the pollen data for the Platycodoneae shows Cyananthus as the basal taxon and Canarina with Codonopsis forming a monophyletic group. Most interesting is the monophyletic group formed by the outgroup Musschia and Platycodon, an association which can be found in the classification of Schönland (1889). The Consensus trees for the seeds data of the Platycodoneae generally showed some support for a monophyletic group formed by Codonopsis and Cyananthus but the Strict Consensus showed the Platycodoneae as an unresolved group which also included the outgroup Nesocodon. A bootstrap consensus tree for the Platycodoneae gave a bootstrap value of $100 \%$ for a monophyletic group formed by Platycodon and Leptocodon. The combined cladistic analysis for the three data sets had 49 taxa and 76 informative characters.

The combined ITS1 and ITS2 molecular data sets for 29 taxa of the Campanulaceae plus the outgroup Nicotiana rustica was analysed using Neighbour-joining, Parsimony and Maximum-likelihood methods. Trees were constructed using a variety of parameters and bootstrap and jackknife values obtained in addition to consistency and consensus indices and other measures of confidence. In all of the methods used the Platycodoneae emerged as a relatively homogeneous and isolated group which is basal to and forms a sister group with all other campanulaceous taxa. In the Neighbour-joining trees the inclusion of gaps and missing data caused Cyananthus to branch off basally to the other taxa in one of the subclusters wheareas when such sites were excluded Cyananthus clustered with Obconicapsula. Canarina and Platycodon consistently formed a cluster independently of the other taxa, while Codonopsis and Leptocodon consistently clustered together. When the Gamma distances with the Kimura-2-parameter model and pairwise-deletion option chosen for transitions and transversions, the homogeneity of the Platycodoneae broke down.

Canarina then branched off basally, the majority of the "platycodonoid" genera then formed a single cluster which was followed by the independent branching off of Platycodon.

This topology was not supported by bootstrap analyses and probably is an artifact of transition bias in the data. These results were confirmed by the parsimony analyses and to a lesser extent by the jackknife analyses. The latter gave an unresolved cluster of three subclusters with high $G$ values for Codonopsis and Leptocodon and moderate values for Cyananthus with Obconicapsula, and Canarina with Platycodon. Finally, this topology for the Platycodoneae was confirmed by the Maximum-likelihood analysis. It would appear that transversion data alone produce tree topologies which are more congruent with the topologies obtained from the other methods of analysis than with a combination of transitions and transversions. This is true also for pairwise-deletion, as opposed to complete inclusion or complete exclusion, of sites containing missing data or gaps.

### 8.1.2. The Walllembergeae

The UPGMA phenetic analysis of the flowers and fruits data set for the Campanulaceae (Flowers.DAT) produced a phenogram with three major clusters or blocks of taxa. One of these major clusters mainly comprised the Platycodoneae as discussed above but it also included Berenice, Nesocodon, Heterochaenia, Roella and Craterocapsa (as well as Azorina of the Campanuleae) from the Wahlenbergeae. The remainder of the Wahlenbergeae were divided among the other two major clusters, eg. Cephalostigma with Wahlenbergia in one block with the rest of the South African taxa in the other. The latter formed subclusters as follows: Rhigiophyllum with Siphocodon, then with Microcodon, Treichelia and Theilera; Gunillaea with Namacodon, then with Prismatocarpus and Githopsis, Legousia and Brachycodon (latter 3 taxa in the Campanuleae); Merciera with Trachelium, Feeria and Diosphaera (latter 3 taxa in the Campanuleae). The Complete-linkage method brings these taxa into a single subcluster and also emphasises the isolation of the Platycodoneae but it also confounds the topology found for the UPGMA analysis (eg. Muehlbergella clusters with Prismatocarpus and Merciera with Peracarpa, etc.). The Single-linkage method obscures even further any meaningful groupings of the taxa whereas a Strict Consensus for the UPGMA + Complete-linkage merely confirmed the great similarity between

Heterochaenia and Roella. It also produced some odd groupings such as Asyneuma with Wahlenbergia or Adenophora with Cephalostigma. The UPGMA phenetic analysis of the flowers and fruits data subset for the Wahlenbergeae (Flowers.DAT) produced a phenogram with two major clusters, each of which had several minor clusters. The first major cluster contained the outgroups Legousia, Githopsis, Jasione and Lobelia, while the second major cluster contained the outgroups Musschia and Feeria. Thus, from flower and fruit data, the integrity of the Wahlenbergeae and the Campanuleae as discrete entities breaks down. The genera of the Wahlenbergeae would appear to have affinities with several other groups within the Campanuleae or, more distantly, with the Platycodoneae.

The UPGMA phenetic analysis of the pollen data set (CampPal.DAT) for the Campanulaceae clustered all the porate genera into one major cluster. Within this cluster there was considerable lack of resolution and some unexpected groupings. For example, Phyteuma (in the Campanuleae) clustered with Roella and collectively both of these taxa clustered with Wahlenbergia. Prismatocarpus clustered with Hanabusaya (in the Campanuleae) and collectively both of these taxa clustered with Jasione. Namacodon clustered with Musschia, while the similarity relations of Gunnillaea, Heterochaenia, and Nesocodon were unresolved. The topology of the trees became more resolved in the Strict Consensus of 2 tied trees using the Single-linkage method but the actual clusters produced remained problematical. For example, Wahlenbergia clusters with Legousia, Prismatocarpus with Githopsis, Edraianthus with Namacodon, Roella with Phyteuma, Gunnillaea with Nesocodon and Heterochaenia with Musschia. The Strict Consensus of 2 tied trees using the Complete-linkage method confuses the picture even further. Here we see Prismatocarpus with Trachelium, Gunillaea with Michauxia, Nesocodon with Homocodon, and Musschia with Namacodon. The UPGMA phenetic analysis of the pollen data subset for the Wahlenbergeae (CampPal.DAT) clustered Prismatocarpus with the outgroup Trachelium, Wahlen-bergia with the outgroups Legousia and Githopsis, Heterochaenia with Roella, Gunillaea with Namacodon, and Musschia with Nesocodon. Although the subset data (which included at least 8 outgroups) produced results which appear to be more congruent with the other methods of analysis, the conclusion is inescapable that a phenetic analysis of pollen morphology alone fails to reveal the true relations of the taxa.

The UPGMA phenetic analysis of the seeds data set for the Campanulaceae (CampSeed.DAT) yielded very confusing results. Apart from the clusters which comprised Edraianthus with Roella, and both these genera collectively with Craterocapsa, very little sense can be made of the topology obtained. This is also the case for the Single-linkage and Complete-linkage methods and the Strict Consensus trees obtained from several permutations of methods. The UPGMA phenetic analysis of the seeds data subset for the Wahlenbergeae yielded more interesting results. Nesocodon formed a minor cluster with "Fernandeziocodon" ( = Wahlenbergia fernandeziana and allies) and collectively both taxa clustered with Musschia. The outgroup Edraianthus again clustered with Roella and Craterocapsa, while Wahlenbergia clustered with the outgroup Jasione.

The baseline cladistic analysis using parsimony for the Flowers \& Fruits data set for the Campanulaceae and rooted through the hypothetical "HYPOTH. EUDICOT" showed that the Wahlenbergeae are widely dispersed over the cladogram with Nesocodon and Heterochaenia as the most basal taxa. Roella forms a monophyletic group with Githopsis and Craterocapsa, and at a higher level with Edraianthus and Petkovia. Treichelia and Merciera form a monophyletic group with Diosphaera and Peracarpa. Rhigiophyllum and Siphocodon form a monophyletic group with Microcodon whereas Theilera branches off with Feeria, Jasione, Trachelium, etc. Basal to these clades is a monophyletic group formed by Berenice, Cephalostigma and Wahlenbergia. Namacodon and Gunillaea form a monophyletic group which forms the sister group of a clade formed by Prismatocarpus, Legousia and Brachycodon. These latter taxa are therefore on a larger clade which is quite isolated from the other "wahlenbergioid" taxa.

The Strict Consensus tree obtained from the baseline cladistic analysis using parsimony for the Flowers \& Fruits data subset for the Wahlenbergeae again showed Nesocodon and Heterochaenia to be basal, followed by a major dichotomy comprising two relatively symmetrical large blocks of taxa. In the smaller of these two clades, Craterocapsa is basal followed by Roella and then by the outgroup Edraianthus. This is then followed by Treichelia and Prismatocarpus, the clades formed by the outgroups Githopsis and Legousia, and by Gunillaea and Namacodon. The larger clade has the monophyletic group formed by

Berenice, Cephalostigma and Wahlenbergia as basal followed by the clade formed by Microcodon, Rhigiophyllum and Siphocodon. The sister group of this latter clade is not fully resolved but comprises Theilera, Merciera and the outgroups Feeria, Jasione, Musschia and Trachelium.

The Strict Consensus tree obtained from the baseline cladistic analysis using parsimony for the pollen data subset for the Wahlenbergeae was considerably unresolved. There was, however, a minor clade comprising Heterochaenia, Nesocodon, Prismatocarpus, Roella and the outgroup Musschia. The sister group of this clade was Wahlenbergia. The baseline cladistic analysis for the seeds data set for the Campanulaceae and the Strict Consensus tree from the subset for the Wahlenbergeae yielded only a few interesting groups. The W.angustiflora group ("Helenacodon") and Craterocapsa with Roella formed an unresolved clade with the rest of the taxa. Musschia was a sister group to a monophyletic group comprising Nesocodon, Wahlenbergia, the W. berteroi group ("Fenandeziana") and the outgroups Jasione, Githopsis, Azorina, Edraianthus, Trachelium and Legousia.

Since only one genus was available for molecular analysis discussion of the results is relatively straightforward. However, some degree of caution should be observed with such a low sample. This is particularly poignant if one considers the problematic position of genera such as Jasione or even Legousia or Musschia which, for the purposes of this discussion are included in the Campanuleae. In almost all of the trees found by Neighbour-joining, Parsimony and Maximum-likelihood methods Craterocapsa branched off basally after the colpate and colporate taxa to form a monophyletic group on its own. In the Parsimony analysis it formed part of an unresolved clade with the remainder of the porate taxa when subjected to a Semistrict Consensus using 315 informative sites, and with the Parsimony Jackknife analysis. In the Maximum-likelihood analysis it formed a monophyletic group with Jasione, using 557 sites.

### 8.1.3. The Campamulleae

The UPGMA phenetic analysis of the flowers and fruits data set for the Campanulaceae (Flowers.DAT) produced a phenogram which, with the exception of Azorina, divides the

Campanuleae over two major subclusters. These are subsequently divided, more or less symmetrically into numerous minor clusters. Some of the clustering appears congruent with traditional arrangements, eg. Asyneuma with Cylindrocarpa, Campanulastrum with Triodanis, Petromarula with Phyteuma and Physoplexis, Gadellia with Rapunculus, Campanula with Hanabusaya and Symphyandra, Edraianthus with Petkovia, Heterocodon with Homocodon and Peracarpa, Brachycodon with Legousia and Githopsis, and Feeria with Trachelium and Diosphaera. There are some rather odd clusters such as Musschia with Lobelia and Adenophora with Wahlenbergia. The UPGMA phenetic analysis of the flowers and fruits data subset for the Campanuleae (Flowers.DAT) produced a phenogram which has two large subclusters of taxa and which is essentially similar to the full data set. The UPGMA phenetic analysis of the pollen data set (CampPal.DAT) gave a Strict Consensus tree with considerable lack of resolution. It had some rather odd clusters, eg. Musschia with Namacodon. A Strict Consensus of 2 tied trees for the pollen data subset for the Campanuleae was considerably unresolved. There were some clusters, eg. Adenophora with Asyneuma, Campanulastrum with Rapunculus, Edraianthus with Legousia and Githopsis, and Hanabusaya with Jasione and "Isophylla" (eg. C.garganica group). The UPGMA phenetic analysis for the seeds data set (CampSeed.DAT) for the Campanulaceae was again difficult to interpret. Some clusters were found which have a degree of congruence with traditional arrangements, eg. Rapunculus with Melanocalyx and Legousia, Symphyandra with C.formanekiana, Megalocodon, and Rupestres with Tulipella, Quinqueloculares, C.sartorii, Otocalyx and Symphyandra. The seeds data subset for the Campanuleae gave similar results to the full data set.

The baseline cladistic analysis using parsimony for the Flowers \& Fruits data set for the Campanulaceae and rooted through the hypothetical "HYPOTH. EUDICOT" showed that Azorina is basal to and the sister group of all the remaining taxa which also includes the majority of the Wahlenbergeae. Adenophora branches off next followed by a monophyletic group formed by Symphyandra and Hanabusaya. Many of the clades are not unexpected, eg. Legousia and Brachycodon, Asyneuma and Phyteuma, or Campanula s.s. with Michauxia, Sicyocodon and Zeugandra, etc., while others suggest possible relationships, eg. Popoviocodonia with Triodanis. Much of the parsimony analysis for the pollen data subset
yielded largely unresolved cladograms although some plausible minor clades were found, eg. Asyneuma with Phyteuma and Heterochaenia with Musschia, Nesocodon and Roella. The parsimony analysis of the seeds data subset for the Campanuleae also yielded a few plausible groupings, eg. Quinqueloculares with Tulipella, Symphyandra hoffmannii with Otocalyx and Symphyandriformes with C.formanekiana and Megalocodon.

The bootstrapped Neighbour-joining analysis of the molecular data with gaps and missing information included yielded a topology which divides the Campanuleae into two major blocks with Jasione as the basal cluster followed by the independent cluster of Musschia with Gadellia. The larger of the two major clusters is unevenly divided into two subclusters, the smaller of the two comprising Legousia falcata as basal to the minor cluster formed by Campanulastrum and Legousia speculum-veneris. The other subcluster has Adenophora and Hanabusaya as a basal cluster followed sequentially by the independent branching off of Campanula pyramidalis ("Isophylla"), Campanula persicifolia, and the minor cluster formed by Petromarula, Physoplexis and Phyteuma. The smaller of the two major clusters has Azorina as the basal taxon, followed sequentially by the independent branching of Roucela, Campanula lanata, Campanula punctata and a subcluster which is divided into several minor clusters. One of these is formed by Campanula thyrsoides with Campanula petraea while the other is formed by Michauxia clustering with Campanula barbata and Diosphaera. When the gaps and missing information are excluded Jasione remains the basal taxon but the cluster formed by Musschia and Gadellia is joined to the larger of the two major blocks of taxa. There are also minor rearrangements in the topology of the smaller block of taxa, eg. Campanula lanata clusters with Campanula thyrsoides. Using the Gamma distances with the Kimura-2-parameter model for transversions and transitions and with the complete deletion option a similar topology was obtained apart from minor rearrangements of some taxa. With the pairwise-deletion option the cluster formed by Musschia and Gadellia was the most basal grouping, followed by Jasione and then the two large blocks of taxa. The larger block had a more altered topology. Adenophora and Hanabusaya clustered with Campanula pyramidalis and Campanula persicifolia while the relationships of the remaining taxa were more unresolved. When the analysis was then made using transversion data only Musschia and Gadellia still remained basal followed by Jasione but the resolution
of the two major blocks of taxa improved. This topology improved even further when an analysis using the same parameter was run with the BIONJ program. Both species of Legousia then clustered, followed by Campanulastrum which was basal to the group formed by Phyteuma, Physoplexis and Petromarula. Hanabusaya and Adenophora were basal to this block followed by Campanula persicifolia with Campanula pyramidalis. Azorina was basal to all the remaining taxa in the other block.

The parsimony analysis of the molecular data using 315 sites again placed Jasione as the basal clade followed by the clade formed by Musschia and Gadellia. The remaining taxa again formed two major clades but with considerable lack of resolution. The larger of the two clades had Legousia speculum-veneris as the sister group of the remaining taxa. Of these, minor clades were formed by Adenophora with Hanabusaya, Petromarula with Physoplexis and Phyteuma, and Campanulastrum with Legousia falcata. In the smaller of the two major clades the only resolution was formed by the clades Campanula barbata with Diosphaera, and Roucela with Azorina. When sites with informative gaps were used (ie. 397 sites) the topology of both major clades changed considerably. In the larger of the two clades, Legousia speculum-veneris was then the basal clade and sister group of the rest, while in the smaller clade Michauxia was the basal taxon. There were also rearrangements in the topology of the minor clades. The Jackknife Parsimony analysis showed no resolution for the smaller of the two clades and little resolution for the larger. However the minor clades formed by Petromarula, Physoplexis and Phyteuma, and by Hanabusaya and Adenophora had $G$ values of 0.9553 and 0.9986 respectively. The small clade formed by Musschia and Gadellia had a $G$ value of 0.9984 .

The Maximum-likelihood analysis yielded a topology which was strikingly different from both Neighbour-joining and Parsimony methods. Jasione clustered with Craterocapsa forming a group basal to all remaining taxa which were again divided into two major blocks. Gadellia and Musschia form a clade which is nested within the block which has Azorina as the basal taxon and which has Diosphaera as the sister group. The other major clade has a major dichotomy with Campanula pyramidalis, Adenophora and Hanabusaya in one clade and the "legousioid/phyteumoid" taxa in the other.

### 8.2 Comelusioms

Much of this study has been an exercise in data exploration and, although the results obtained in this study could be optimised and analysed further, satisfies one of its principal aims. From the disparity of results obtained from phenetic, cladistic and molecular approaches using different data sets or subsets it is strikingly clear that there is no single method of analysis which will produce a demonstrably optimal phylogenetic reconstruction of the Campanulaceae. There can be no single-character taxonomy of the Campanulaceae and this illustrates how ludicrous it is to present a molecular hypothesis alone as the nearest approximation to the true phylogeny. It is also evident that the implementation of a phylogenetic nomenclatural system to replace the Linnaean binomial system would be disasterous for botany.

Phenetic analysis has not proved to be be superior to cladistic analysis in this study and in several instances has produced very erroneous results (eg. with pollen and seed data). Combining these data sets in a phenetic analysis may have produced better results but the level of incongruence between them and the flower data set was so high that combining the data set was discounted. Where the scoring of the data is highly accurate and there are few missing data the phenetic approach may yield accurate results, but there is still the problem of homoplasy. In the Campanulaceae this would appear to be considerable, especially with respect to flower and seed morphology. In a cladistic approach using parsimony with certain evolutionary assumptions, the topologies produced by the different data sets are more congruent and therefore the combination approach was tried and produced reasonable results. The use of the ITS region in a molecular analysis, although not without problems such as those of multiple alignment, has produced results which have proved to be remarkably congruent with Neighbour-joining, Parsimony, and Maximum-likelihood methods. This is due most likely to the high phylogenetic signal from the data set but there may also be a trade-off in the accuracy of the results due to alignment problems and the models of nucleotide substitution used. With ITS being used at the generic level it is rather unlikely that inaccuracies will arise due to sampling problems. This may not be so when the ITS region is used at the species or population level. Of the three methods, Parsimony and
the modified BIONJ Neighbour-joining methods give the most congruent results. The assumptions of the model used in Maximum-likelihood may have to be tested empirically before the results compare favourably with the other methods. At present, with the DNAML program of the PHYLIP package this is very costly in computing terms. As a method of choice for large data sets maximum-likelihood in not attractive. The Neighbour-joining method has the disadvantage that it only produces a single tree which is not guaranteed to be optimal, although for molecular data the practicality of this method and the relative accuracy of the results should ensure that it is used in conjunction with parsimony methods. At present the use of heuristic algorithms with parsimony analyses does theoretically limit the accuracy of the results. However, with judicious use and with the comparison of results with other methods such as Neighbour-joining these problems should be minimalised.

Personal experience of the subject matter still has a strong influence on the plausibility of the results. However, in terms of providing as extensive an exploration of the available data as possible, a multiple or eclectic approach is superior to a one-dimensional intuitional approach or even an approach using just one or two of these methods. The trade-off, of course, is one of time and cost. The combination of an eclectic approach and intuitive evaluation of the results would seem the most logical way to progress with systematics. Without advanced techniques of analysis, no progress in the reconstruction of phylogeny in the Campanulaceae can be made but in so doing we are in danger of dismissing altogether the value of intuitive thought in synthesising the disparate facets of our knowledge. This ability to comprehend total structure rather than the analysis of detail is what Ehrenzweig (1970) called "syncretistic vision" in "The Hiddem Order of Art". His comment (p.21) states:

[^1]The strong subjective input in both the analytic and synthetic aspects of phylogenetic reconstruction and classification would suggest that systematics is still very far from being an objective, repeatable science.
"It is highly likely, in fact, that virtually every phylogenetic tree found in the literature is wrong in one way or another."

MI. J. IDonoghue \& $\mathbb{D} . \mathbb{D}$. Ackerly, 1997<br>"Plant Life Histories"

For the reconstruction of phylogeny consideration must be given to all the relevant results and reconciliation of conflicting data obtained. Ideally, the pursuit of maximum congruence between the multiple data sets is the major goal. There are several schools of thought as to the handling of multiple data sets and a discussion is given above in section 4.2.1. The conclusions must be reconciled with biogeographic hypotheses and with other independent data sets. For this reason the phylogenetic hypothesis of the Campanulaceae presented here and based on the data analyses performed in this study was compared with the distribution of chromosome numbers and area cladograms in Fig.107.

No single extant genus can be regarded as ancestral to the others. Some have retained more primitive characters than others but that, in itself, doesn't qualify a particular genus for the status of ancestor. For example, Cyananthus with its superior 5-loculed ovary and low chromosome base number has been considered by many authors as the archetype. However it also displays many "advanced" features associated with adaptation to high altitudes in the alpine regions of the Himalayas and S.W.China.

It is likely that the ancestral campanuloids evolved in a fragmenting eastern Gondwanaland, probably sometime in the early Tertiary period. Some of these early progenitors of the Campanulaceae, as exemplified by putative direct descendants such as the genus Canarina, had already advanced from a primitive colpate condition of the pollen to a colporate condition. The colporate lineages are represented in Africa only by Canarina which has a relict distribution between tropical East Africa and Macaronesia. From southeast Asia to New Guinea they are represented by the genus Campanumoea s.l. (includes Cyclocodon) and in east Asia by Platycodon. The colpate genera (such as Codonopsis and Cyananthus) are now entirely confined to the Himalayan region, east and southeast Asia and all have valvate capsules except for Ostrowskia which has unique vertical medial slits (see Fig. 105).

However, it is likely that the capsule evolved from colpate taxa which possessed berries which are now only to be found in the two colporate taxa mentioned above.

The nectar dome concealing the nectary region had already appeared in the colpate taxa (eg. in Pseudocodonopsis) and this feature probably evolved only once in the family as a whole. From the colporate group the porate lineages probably evolved. The most primitive porate taxa appear to be the genus Nesocodon from Mauritius and Heterochaenia and Berenice from Réunion, all of which have a close alliance with the genus Wahlenbergia s.l. (including Cephalostigma). From this ancestral wahlenbergioid stock the family rapidly spread over much of the southern hemisphere. Probably the most primitive extant members of the genus Wahlenbergia s.l. are those found in the Juan Fernandez Islands, St. Helena, New Guinea and New Zealand, together with certain lineages of the genus in continental Africa and the Andes of South America.

There appears to have been several parallel lineages of capsule evolution in the wahlenbergioids of southern Africa and in the campanuloids of Eurasia (see Fig. 105). Within southern Africa primitive valvate stock gave rise to chaliced taxa such as Craterocapsa and those with apical pores such as Roella. Indehiscent taxa include genera such as Mericiera and Gunillaea, while those with laterally splitting prismatic capsules include genera such as Prismatocarpus and Namacodon. This was probably related in some measure to changing climatic conditions in southern Africa as well as the general trend within the Campanulaceae of increasing fusion of the hypanthium to the ovary wall to produce an inferior ovary. This may have been in response to predation of the flower-bud. Radiation of different floral morphologies due to pollinator selection pressure and ecological conditions such as fire-tolerance have probably been of profound importance in the subsequent evolution of Campanulaceae within southern Africa. Other taxa have evolved aggregated inflorescences and tubular flowers, often accompanied by floral modifications such as epipetaly. This radiation of the Campanulaceae within Africa must surely have been more widespread than the present-day distribution and given rise in the north to another massive wave of campanuloid evolution which spread eventually into Eurasia and North America. Jasione occupies a somewhat intermediate position between true wahlenbergioids
and campanuloids and does not appear to have any close extant relatives. If Feeria is correctly placed within the campanuloids then it is the only genus within that group which possesses a valvate capsule. It may be the most primitive genus of the true campanuloids although there are other contenders such as Legousia, Musschia and Trachelium. These basal genera are today to be found in the Mediterranean Basin and Macaronesia and it is from this ancient campanuloid stock that the rapunculoid group exemplified by Rapunculus, Gadellia, and the "isophylloid" group arose.

The morphology of the capsule is almost as diverse in the campanuloids as in the wahlenbergioids. The valvate capsule of Feeria probably represents a plesiomorphy while the unique horizontal fissures of Musschia are clearly apomorphic. The bulk of campanuloid taxa have a dehiscent capsule. In Legousia this, in no small measure, recalls the splitting capsule of Prismatocarpus, while in other taxa such as Roucela and Trachelium the capsule can be disk-like or globular respectively. There are taxa such as the "isophylla" group in which the breakdown of the capsule wall is irregular while in others such as Rapunculus and Campanula s.str. the breakdown occurs in definite regions of the capsule wall (either apical or basal pores respectively). Several lineages of the genus Campanula str. have indehiscent capsules and this may be correlated with isolation on islands or mountain tops. Other genera such as Edraianthus and Petkovia have irregular breakdown of the capsule apex and this also may be correlated either with montane isolation or the aggregation of flowers into inflorescences. There can be little doubt that much of the subsequent evolution of the campanuloids is linked to the alpine orogenic processes of the Tertiary Period in Eurasia and North Africa. There appears to be two major groupings of campanuloids in Eurasia. Genera such as Azorina, Roucela and Adenophora are likely to be the most ancient, leading to the bulk of taxa which have usually been incorporated within the genus Campanula. It was the "legousioid/rapunculoid" lineage which spread westward into North America with the "adenophoroids" possibly entering that continent from eastern Asia. Four genera of Campanulaceae are native to North America but very little is known about them. It seems likely that these taxa have subsequently evolved independently of taxa in the Old World (Morin, 1983). Campanulaceae in North America are probably not monophyletic and, as McVaugh (1945) pointed out, "the relationship between genera... is probably not to be thought of as a
simple linear one, but as a series of links between groups of species" (Morin, 1983). The distribution of Githopsis is very closely associated with sclerophyllous vegetation and its history probably parallels the history of the Madro-Tertiary Geoflora (Morin, 1983). This vegetation had assumed dominance in southern California by the Miocene and is reported from the west Sierran slope by late Miocene. It became dominant in west-central California by the Middle Pliocene (Raven \& Axelrod, 1978). Morin (1983) has given a detailed scenario for the evolution of extant species of the genus Githopsis and suggests that ancestral diploid Githopsis pulchella could have migrated to southern California or the central Sierra Nevada range in late Pliocene. At some point the tetraploid taxa evolved both in the Coast Ranges and in the Sierra Nevada. As the climate became warmer and drier towards the end of the Pleistocene, the tetraploid taxa began to spread further north. Colonization of Oregon and Washington by G. specularioides was probably a post-Pleistocene event (Morin, 1983).

There is no evidence for evolutionary processes acting above the level of the individual or population, nor is there any evidence of macromutational processes in the sense of Goldschmidt's "hopeful-monster" (Goldschmidt, 1940). The most parsimonious process is probably for a genus to evolve from a single progenitor population but it may well be that a mosaic of sibling species (sensu Mayr, 1942) undergoes a homogenisation process due to parallel selective pressure and that the essential characters of the genus derive from more than a single population. Those genera which are most divergent are mostly isolated on islands (eg. Musschia, Azorina, Petromarula, Heterochaenia, Nesocodon, etc.), or mountains (eg. Physoplexis, Ostrowskia, Feeria, Muehlbergella, Craterocapsa, etc.). Taxa which have a more continental distribution, whether it be Eurasia, North America or southern Africa tend to resemble one another more, even though the taxa of each continent are equally isolated from one another. This would suggest that for the Campanulaceae strong disruptional selection on founding populations has played an important role in the evolution of island endemics in much the same way as it is believed to have done for numerous other angiosperm families. In contrast, continental taxa seem more constrained by the available niches and have fewer opportunities available to them for evolutionary radiation. They display a mosaic of parallel vegetative parameters which fall within a limited range of types, of which the herbacious perennial or biennial is the dominant form over much of Eurasia and

North America. The shrubby life-form is dominant in southern Africa but this is surprisingly absent from the Mediterranean regions of Eurasia. In addition, the phenomena of ontogenetic contingency and the Baldwin Effect have probably given the Campanulaceae considerable evolutionary amplitude. In general, however, the Campanulaceae do not dominate any particular niche and appear to be largely outcompeted by other angiosperm families wherever they occur. They do appear to have competitive advantages as chasmophytes and on dry limestone cliffs in general, probably because of their developmental plasticity, storage caudices and fine ramifying root systems. Many taxa therefore appear to be relicts within their ranges and occupy tiny geographical areas which only exacerbates efforts to conserve them. They have not invaded tropical forests to any extent and the few taxa found there are climbers and confined to more open areas of high mountains (eg. Canarina). Such taxa are therefore most likely to be closer to the original ancestors of the family (see Plate 1.). The Campanulaceae have an equally diverse mosaic of floral types but again this is but a variation of the highly-conserved insect-pollination "bauplan".

The great diversity of species numbers within the major lineages of the Campanulaceae, not only on the mountain chains of Eurasia, but also on a much smaller scale in the fynbos regions of South Africa and on numerous continental and oceanic islands certainly suggests that the evolutionary rates of these lineages vary dramatically. This is in accord with the punctuated-equilibrium hypothesis of Gould and Eldredge (1977). The differences between taxa have also been accentuated by extinctions, particularly in the Mediterranean areas, central Asia, Africa and perhaps also in North America.

## PLATYCODDONEAE


CAMIPANULEAE

$\mathbb{C}$ limilice/Apicall Pere ©r Rupture (Roella, Crbserocapsa)


Horizomtal Fissures (Musschia)


Lateral Basal Pore
(Campanula, Roscela, Trachelium, Azorina, etc.)

Indehiscemt or Apical $\mathbb{R}$ unpturre (Edraianthus, Campamula, Pethovia)

Fig. 105 . Diagram showimg the thypothetical evalution of the capsule from am imdehiscemt frunit in the Camppamilaceae. The arrows suggest possible morplnalagical uramsiormantiom omly and da mat mecessarilly imdicate phylngemetic relatiomships amomg the mamed examples.
"Things can be named and from which concepts can be formed. If the names that can be named are correctly chosen, they somehow come close to existence - even if only as "guests of reality", not as reality's master. They can serve in some way to create order, to pass on tradition and thus preserve the continuity of human activity."

Lao Tzu
"The Phenomenal World"
"Is it really a paramount consideration that Wahlenbergia and Lightfootia be kept up as distinct genera or
not? No doubt, with the taxonomist who worries about formal dispositions the question is all important.
On the other hand, formal dispositions are by far not an end to the question of what nature has performed,
and still is performing, over space, in time, by form."
Léon Croizat, 1962
"Space, Time, Form: The Biological Synthesis"

Before an attempt is made to formalise a taxonomic system, it is necessary to understand the phylogenetic relations between the genera, the tribes and at the infrageneric level between subgenera and sections. All factors have to be evaluated carefully when a classification is being constructed and such information incorporated into the system via the nomenclatural process. A lack of correspondence between patterns resulting from different causal processes, and the gradual nature of breeding discontinuities in plants cannot be waved aside casually (Brandon \& Mishler, 1996). Monophyletic groups (in the traditional sense) can exist at all levels of inclusiveness so a ranking criterion is needed to delimit the genera. No universal ranking criterion can be found because there is a diversity of causal agents directing evolution in different lineages. Genera are aggregate units, not units of selection per se, and in the absence of known causal agents, most commonly it is the distribution of characters which allows us to rank monophyletic groups. The phylogenetic concept in its traditional sense, with its pluralistic ranking criteria, may therefore be superior than morphological discontinuity alone and is accordance with the Darwinian view that evolution is descent with modification.

At present in the Campanulaceae there is much confusion regarding generic limits, inter- and intrageneric relationships etc. Many Russian authors follow the system of Fedorov, but with modifications based on recent research in the former Soviet Union whereas Western botanists generally adopt the system used in Flora Europaea, which is incompletely based on Fedorov and does not include all his sections and subsections of Campanula. A proper
understanding of the complexity of the genus Campanula is impossible with the limited coverage of Flora Europaea which is also badly out of date and in need of revision. The system used in Flora of Turkey (Davis, 1978, 1988), is essentially a refinement of Fedorov's system by Damboldt and (in part) by Phitos. The degree of inconsistency can be seen by comparing the extreme splitting approach of Russian and Chinese authors with the extreme lumping at the generic level by Damboldt and Phitos. Yet, within the Aegean flora, in groups such as that of the Campanula rupestris Sm . complex, we see extreme splitting by Phitos. There is also inconsistency with regard to the recognition of monotypic genera, eg. Davis (1950), showed no hesitation in recognising the monotypic Zeugandra but submerged genera which are distinct in a "de Candollean sense" such as Diosphaera Buser, to the inreasingly large, unwieldy genus Campanula. There is therefore a great instability and burdening of the nomenclature attributable mainly to the lack of consensus as to generic limits, which is ultimately the result of inconsistency in the application of, or complete lack of, a sound philosophical concept of the genus. This is, without a doubt, at least partially attributable to the fact that there is non-equivalency of genera within the angiosperms as a whole (Antonov, 1988). There is simply no single generic model or objective criteria which can be applied to any single plant family and this immediately imposes limitation on a nomenclatural system for the provision of recoverable phylogenetic information. The problem of generic and specific circumscription is not confined to Eurasian taxa. The studies of Morin (1980-1983), Morin \& Shetler (1981) and McVaugh (1941-1948) have shown that further studies of North American taxa are needed in order to clarify the relationships of species and genera within the North American continent and also with other taxa worldwide, especially Eurasia. In Africa, the studies of Thulin, and Hilliard \& Burtt q.v. have shown that generic limits there are by no means finally established.

Not all botanists who engage in systematic work are familiar with all of the techniques which have been either outlined or used in this study. The conclusion must be drawn that it is becoming increasingly desirable to use a combined eclectic/intuitive approach. This means that it is more imperative for botanists with different skills to cooperate in joint systematic research programmes.

Having a set of rules such as McVaugh's Principles certainly is desirable and morphological criteria should have primacy. The historic purpose and utility of classification are destroyed if a more or less absolute morphological criterion is not upheld and a host of cryptic species is created on purely experimental or other biological grounds (Shetler, 1982). Discontinuity of variation enables us to have a workable classification. This is less of a problem with genera which are generally recognised by a suite of characters most of which are morphological but often include cytological and ecological characters as well. Species taxa in theory should meet the criterion of spatial localization (Brandon $\&$ Mishler, 1996) but this cannot easily be applied to genera. Nor can genera be defined on the basis of reproductive criteria although many genera are interfertile. The ease with which different genera may hybridise may be used as a measure of the genealogical distance between them but for the Campanulaceae there have been few recorded instances of intergeneric or wide crossing. Hanabusaya may be an exception since it appears to be a cross between Adenophora and Campanula but at present this is merely speculative. Most of the hybrids recorded for the family have been between sections of the genus Campanula. It is implicit in our understanding of evolving genera that differences will usually be observed within the genotype. Therefore, in the construction of a classification, it is inevitable that paraphyletic taxa will be created if we are to give due recognition to the processes of evolution.
"Some day the 'nomenclatural noise' generated by intellectuals must be muted by the overwhelming magnitude of the data assembled. The phyletic-numerical treatment of these data, combined with the imerplay of practitioner and user, will ultimately permit a relatively stable nomenclature."

## B. L. Turner, 1985

## 10. 1 A New Higher Classificatiom of the Campmoulaceae based om the imtegratiom of plhemetic amd plhylogemetic data.

The following arrangement expresses the phylogenetic hypothesis outlined above and will be fully written-up elsewhere. The suggested names for the higher taxa are provisional. The division of the family into two major tribes rather than subfamilies expresses the uniformity that exists throughout the family but is sufficient to emphasise the ancient split of the family into two major lineages. The tribe Platycodoneae is characterised largely by the possession of a broad hypanthium and colpate or colporate pollen. The subdivision of the tribe into seven subtribes expresses the evolutionary distance that separates many of the taxa. The Canarininae and Campanumoeinae are mostly tropical to subtropical scrambling vines or twiners and possess colporate pollen and berries. They are geographically distinct from each other, the sole genus Canarina of the Canariinae occupying parts of tropical East Africa and the Canary Islands, while Campanumoea and Cyclocodon of the Campanumoeinae are distributed from S.E.Asia to New Guinea. The Platycodoninae contains the sole genus Platycodon which possesses colporate pollen but is a herbaceous herb whose open stellate flowers, nectar dome and bulging hypanthium connect it to the colpate genera Pseudocodonopsis and Obconicapsula of the Codonopsiinae. Both subtribes Ostrowskiinae and Echinocodoninae are placed provisionally. Ostrowskia is a tall herb from the mountains of Asia and, although its pollen is colpate, it has a unique capsular dehiscence. Echinocodon occupies a tiny range in central China and is characterised by highly variable and reduced vegetative parts. The Cyananthinae contains the single genus Cyananthus which is characterised by valvate dehiscence, colpate pollen and a fully superior ovary. It is a highly specialised plant genus of the high Himalayan and Chinese mountains. The residue of
genera such as Codonopsis and Leptocodon, although quite diverse, are comfortably accomodated within the single subtribe Codonopsiinae.

The tribe Campanuleae contains all the other genera and is altogether a much larger grouping than the Platycodoneae. It is characterised by porate pollen, a narrower hypanthium, inferior ovary and diverse modes of capsular dehiscence. Probably this group is in a more active stage of evolution than the Platycodoneae and the evolutionary distances between the taxa cannot be so easily expressed by a binomial system. It accomodates the two major subtribes, the Campanulinae and the Wahlenberginae but it also includes taxa which have been given subtribal status because of the difficulty in placing them in any one group. These include Jasione in the subtribe Jasioneinae which is a provisional arrangement and the two distinct Macaronesian taxa, Musschia and Azorina in the subtribes Musschiinae and Azorinae respectively. Other taxa are also given provisional placement in certain subfamilies, eg. Peracarpa in the Campanulinae. Many taxa which were formerly included in the genus Campanula consistently separate in the topologies derived from the different analyses. There is sufficient congruence to justify the recognition of genera such as Brachycodon, Rapunculus, Campanulastrum, etc. and to include them in more logical collective categories such as the subtribe. Other genera have diverged within a single lineage to warrant separate recognition, eg. Azorina and Michauxia. This is not only more logical but also more satisfactory from a phylogenetic point of view. The following arrangement (see also Figs. ) of the genera, subtribes and tribes of the Campanulaceae is the classification recommended by this study:


Table 33. A new classification of the Campanulaceae to the subtribal level inferred from phenotypic and molecular (ITS) data.


Fig.106. Hypothetical phylogenetic tree showing a new arrangement of the Campanulaceae to the generic level. The two tribes are the PLATYCODONEAE and the CAMPANULEAE. The thirteen subtribes are indicated by the ending "inae".


Fig.107. Hypothetical phylogenetic tree showing a new arrangement of the Campanulaceae to the subtribal level. Superimposed on this diagram are the haploid numbers of the genera each subtribe contains, plus the geographical areas of each subtribe.

The relationships of the genera within the two tribes have not been fully established. This is particularly true for the Campanulinae of Eurasia and North America and for the Wahlenberginae of southern Africa. These are areas where research priorities should be focused. The ITS region has proved to be an effective source of data for phylogenetic reconstruction and should be explored further among different levels of the taxonomic hierarchy and contrasted with data from genes such as $r b c \mathrm{~L}$ and $t r n \mathrm{~L}$. The 5.8 S subregion may yet yield valuable phylogenetic data for an understanding of relationships among the higher taxa (Hershkovitz \& Lewis, 1996) particularly the relations between the Campanulaceae and other families of the Campanulales. This is also true for the studies on the highly rearranged chloroplast genome of the Campanulaceae pioneered by the late M.E. Cosner, and by R. K. Jansen and his colleagues (Cosner et al., 1997). Cytological research is another area that may yield surprising results, as shown by the work of Stace \& James (1996). In addition, the variation at and below the species for most taxa is unknown and this too is an area of research which would repay greater effort, especially from molecular systematists. It is increasingly imperative that we know the boundaries of taxa if we are to make conservation efforts worthwhile. All the taxa of the Campanulaceae provide an intellectual challenge to the student of evolution, but perhaps not so pressing as the challenge to conserve many rare and endangered species such as those of St. Helena (2 species already extinct, 1 virtually extinct and 1 severely threatened), Juan Fernandez Islands ( 1 species extinct in the wild, 3 others threatened), Madeira ( 1 species severely threatened), Reunion ( 1 species virtually extinct, 3 species severely threatened) and Mauritius ( 1 species severely threatened). Conservation in these islands is urgent if many unique taxa in the Campanulaceae are to be saved from extinction through habitat destruction and mismanagement. One only has to consider the fate of many of the Hawaiian species of lobelias to realise how precarious the existence of these unique island forms are. Continental species of Campanulaceae are also severely threatened, the two greatest areas for concern are the Fynbos of the western Cape region of South Africa and the dry overgrazed mountain ranges of the eastern Mediterranean and south-central Asia. Already one unique species,

Campanula oligosperma Damboldt, from Anatolia is reported as extinct (Greuter, 1995; Ekim et al, 1989).

## The Begimmimg

"I have returned to my beginning. I realize that, if through science I can seize phenomena and enumerate them, If cannot for all that apprehend the world. Were I to trace its entire relief with my finger, I should not know any more."

Albert Camus, 1955<br>"The Myth of Sisyphus"

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## 12. $A P P P E N D I C E S$

$12.1 \mathbb{D}$ ata Sets
Table $\mathbb{1}$. Mimimum spammimg tree for Asterales data set (G\&B. $\mathbb{D} A T$ )

| i | j | Iemgtth |
| :---: | :---: | :---: |
| 1. Aquifo | 3. Brunia | 0.218650 |
| 3. Brunia | 2.Aralia | 0.230280 |
| 3. Brunia | $8 . V i b u r n$ | 0.191310 |
| 8.Viburn | 5.Grisel | 0.248600 |
| 8.Viburn | 7. Sambuc | 0.236360 |
| 5.Grisel | 10.Donat | 0.153390 |
| 10. Donat | 14.Styli | 0.185740 |
| 14. Styli | 13. Sphen | 0.126950 |
| 2.Aralia | 6. Pittos | 0.125150 |
| 10. Donat | 4.Escall | 0.107050 |
| 4.Escall | 9.Argoph | 0.161700 |
| 9.Argoph | 12. Penta | 0.081740 |
| 12. Penta | 19. Cyphi | 0.081500 |
| 19. Cyphi | 23.Nemac | 0.291870 |
| 19. Cyphi | 20. Cypho | 0.273470 |
| 20. Cypho | 22. Lobel | 0.288290 |
| 22. Lobel | 18. Campa | 0.217760 |
| 23. Nemac | 21. Goode | 0.211980 |
| 21. Goode | 16. Bruno | 0.261530 |
| 16. Bruno | 17. Calyc | 0.305070 |
| 16. Bruno | 15.Aster | 0.286410 |
| 21. Goode | 11. Menya | 0.104640 |

Talble 2. Mimimonm spanmimg tree for Asterales data sulbset ( $\mathbb{G} \& \mathbb{B}$. $\mathbb{D} A \mathbb{T}$ ): Campamulales s.l. amd punarive "curtgroups".

| $\dot{1}$ | $\dot{j}$ | lemgth |
| :--- | :---: | :---: |
| 10. Donat | 14.Styli | 0.231400 |
| 10. Donat | 13.Sphen | 0.209760 |
| 10. Donat | 12. Penta | 0.109340 |
| 13. Sphen | 11. Menya | 0.083420 |
| 11. Menya | 15. Aster | 0.111350 |
| 15. Aster | 16. Bruno | 0.228980 |
| 16. Bruno | 17. Calyc | 0.210120 |
| 16. Bruno | 21. Goode | 0.131910 |
| 21. Goode | 23. Nemac | 0.053260 |
| 23. Nemac | 19. Cyphi | 0.140450 |
| 19. Cyphi | 20. Cypho | 0.142560 |
| 20. Cypho | 22. Lobel | 0.151580 |
| 22. Lobel | 18. Campa | 0.093860 |
|  |  |  |

Table 3. Minimumn spammimg tree for Flowers \& Frunit data set (Flowers. $\mathbb{D} A T$ )

| i | J | lemgth |  |
| :---: | :---: | :---: | :---: |
| 1. Adenop | 4.Azorin | 0.077050 |  |
| 4.Azorin | 10.Canar | 0.149100 |  |
| 10.Canar | 16. Cyclo | 0.375730 |  |
| 16. Cyclo | 9. Campan | 0.478890 |  |
| 16. Cyclo | 28. "Hima | 0.346470 |  |
| 16. Cyclo | 12. Codon | 0.345010 |  |
| 9. Campan | 47.Platy | 0.312000 |  |
| 16. Cyclo | $41.0 s t r o$ | 0.269540 |  |
| 12. Codon | 33.Lepto | 0.185330 |  |
| 33. Lepto | 15. Cyana | 0.216600 |  |
| 28."Hima | 40.Nesoc | 0.171800 |  |
| 40.Nesoc | 26.Heter | 0.160090 |  |
| 28."Hima | 50.Pseud | 0.150060 |  |
| 33. Lepto | 34.Merci | 0.136610 |  |
| 34.Merci | 21.Feeri | 0.137830 |  |
| 21.Feeri | 60.Trach | 0.205690 |  |
| 28. "Hima | 53.Roell | 0.135650 |  |
| 53. Roell | 13. Crate | 0.143920 |  |
| 60. Trach | 18. Diosp | 0.130850 |  |
| 15. Cyana | 19.Echin | 0.130800 |  |
| 4.Azorin | 5.Bereni | 0.122280 |  |
| 15. Cyana | $31 . J$ Jasio | 0.106950 |  |
| 31.Jasio | 45. Phyte | 0.105560 |  |
| 45. Phyte | 46. Physo | 0.262390 |  |
| 45. Phyte | 8. Campan | 0.176580 |  |
| 45. Phyte | 3. Asyneu | 0.173360 |  |
| 8. Campan | 62. Triod | 0.170680 |  |
| 3.Asyneu | 17. Cylin | 0.160200 |  |
| 62. Triod | 55.Sergi | 0.157660 |  |
| 17. Cylin | 39. Namac | 0.141680 |  |
| 39. Namac | 24.Gunil | 0.167150 |  |
| 3 . Asyneu | 48. Popov | 0.140300 |  |
| 45. Phyte | 44. Petro | 0.139100 |  |
| 17.Cylin | 32. Legou | 0.134610 |  |
| $32 . L$ Legou | 6. Brachy | 0.166330 |  |
| 3 . Asyneu | 11. Cepha | 0.119830 |  |
| 39.Namac | 49. Prism | 0.119200 | ; |
| 24.Gunil | 23. Githo | 0.107250 |  |
| 11. Cepha | 63. Wahle | 0.103920 |  |
| 62.Triod | 51. Rapun | 0.103010 |  |
| 51.Rapun | 22. Gadel | 0.098060 |  |
| 34.Merci | 52.Rhigi | 0.098020 |  |
| 52.Rhigi | 57. Sipho | 0.207000 |  |
| 52.Rhigi | 61. Treic | 0.134670 |  |
| 52.Rhigi | 36.Micro | 0.121530 |  |
| Continued overleaf |  |  |  |

Table 3. continued

| 52.Rhigi | 42. Perac | 0.112430 |
| :---: | :---: | :---: |
| 42. Perac | 29. Homoc | 0.118970 |
| 29. Homoc | 27. Heter | 0.135820 |
| 52.Rhigi | 59.Theil | 0.099700 |
| 8. Campan | 65.Lobel | 0.094320 |
| 33. Lepto | 38.Mussc | 0.091340 |
| 3.Asyneu | 30.. 1 Isop | 0.090180 |
| 53.Roell | 20.Edrai | 0.087350 |
| 20.Edrai | 43. Petko | 0.145800 |
| 43. Petko | 25. Hanab | 0.142670 |
| 25.Hanab | 58. Symph | 0.166690 |
| 58. Symph | 7. Campan | 0.140690 |
| 20.Edrai | 14. Crypt | 0.133910 |
| 25. Hanab | 64. Zeuga | 0.120970 |
| 64. Zeuga | 56. Sicyo | 0.138570 |
| 14. Crypt | 37. Muehl | 0.116010 |
| 64. Zeuga | 35.Micha | 0.109520 |
| 58. Symph | 2. Astroc | 0.097140 |
| 25. Hanab | 54.Rouce | 0.08979 |

Tabble 4. Minnimum spamming tree for Flowers \& Fronits dâa sulbset (Flowers. DDAT): Campamunleae amd purative "outgroups".

| i | j | lengeth |
| :---: | :---: | :---: |
| 1. Adenop | 4.Azorin | 0.097050 |
| 4.Azorin | 15. Hanab | 0.096720 |
| 15.Hanab | 35.Symph | 0.144540 |
| 15. Hanab | 25. Petko | 0.129470 |
| 25. Petko | 11. Edrai | 0.140450 |
| 11. Edrai | 8. Crypto | 0.119280 |
| 35. Symph | 6. Campan | 0.114350 |
| 8. Crypto | 22.Muehl | 0.107520 |
| 15.Hanab | 38. Zeuga | 0.099180 |
| 38. Zeuga | 34.Sicyo | 0.116930 |
| 34. Sicyo | 21. Micha | 0.076690 |
| 22. Muehl | 17. Homoc | 0.067580 |
| 17. Homoc | 16. Heter | 0.118250 |
| 17. Homoc | 24. Perac | 0.115470 |
| 16. Heter | 5. Brachy | 0.077500 |
| 5. Brachy | 20.Legou | 0.155750 |
| 20.Legou | 9. Cylind | 0.115070 |
| 9.Cylind | 3. Asyneu | 0.115150 |
| 3. Asyneu | 27. Phyte | 0.111520 |
| 27. Phyte | 28. Physo | 0.199640 |
| 27. Phyte | 7. Campan | 0.110990 |
| 7. Campan | 37. Triod | 0.107620 |
| 37.Triod | 33.Sergi | 0.102490 |
| 5. Brachy | 14. Githo | 0.097880 |
| 14. Githo | 30. Prism | 0.107650 |
| 30.Prism | 12.Feeri | 0.106870 |
| 12.Feeri | 36.Trach | 0.215480 |
| 36.Trach | 10. Diosp | 0.124550 |
| 27. Phyte | 26. Petro | 0.089580 |
| 33.Sergi | 29. Popov | 0.087090 |
| 36. Trach | 23. Mussc | 0.084920 |
| 12.Feeri | 19.Jasio | 0.081320 |
| 37.Triod | 31. Rapun | 0.080480 |
| 31.Rapun | 13. Gadel | 0.092080 |
| 15. Hanab | 32.Rouce | 0.064150 |
| 35. Symph | 2.Astroc | 0.062680 |
| 3.Asyneu | 18."Isop | 0.045320 |

Table 5. Mimimum spamming tree for Flowers \& Fruits data suloset (Flowers. $\mathbb{D} A \mathbb{A}$ ): Platycodomeac amd putative "ountgroups".

| i | $j$ | lemgth |
| :--- | :---: | :---: |
| 1.Campan | 5.Cycloc | 0.160180 |
| 5. Cycloc | 2.Canari | 0.102470 |
| 5. Cycloc | 3. Codono | 0.054220 |
| 3. Codono | 7. "Himal | 0.063460 |
| 1.Campan | 10.Platy | 0.049500 |
| 10.Platy | 9.Ostrow | 0.054360 |
| 10.Platy | 11.Pseud | 0.023970 |
| 11.Pseud | 6.Echino | 0.073760 |
| 6.Echino | 12. Lobel | 0.071960 |
| 12.Lobel | 4.Cyanan | 0.072710 |
| 4.Cyanan | 8.Leptoc | 0.104910 |
|  |  |  |

Table đ. Mimimum spammimg tree for Flowers \& Fronits data subset (Flowers. $\mathbb{D} A \mathbb{A}$ ): Walhlembergear and putarive "outgroups".

| $\dot{1}$ | J | Iemgth |
| :---: | :---: | :---: |
| 1.Bereni | 2.Cephal | 0.083810 |
| 2. Cephal | 21.Wahle | 0.085100 |
| 21. Wahle | 17. Roell | 0.063500 |
| 17. Roell | 3. Crater | 0.138600 |
| 17.Roell | 14.Nesoc | 0.137020 |
| 14. Nesoc | 7.Hetero | 0.159310 |
| 7. Hetero | 12.Mussc | 0.045950 |
| 2. Cephal | 6.Gunill | 0.036270 |
| 6.Gunill | 13. Namac | 0.140560 |
| 13. Namac | 15. Prism | 0.092080 |
| 6.Gunill | 5.Githop | 0.079040 |
| 5.Githop | 9.Legous | 0.079230 |
| 9.Legous | 8.Jasion | 0.049220 |
| 8.Jasion | 22. Lobel | 0.047940 |
| 15. Prism | 4.Feeri | 0.041440 |
| 4.Feeria | 10.Merci | 0.093510 |
| 10.Merci | 16.Rhigi | 0.050540 |
| 16.Rhigi | 18.Sipho | 0.148980 |
| 16.Rhigi | 20.Treic | 0.082490 |
| 16.Rhigi | 11. Micro | 0.070650 |
| 11.Micro | 19.Theil | 0.059290 |

Table 7. Mimimumn spammimg tree for the Pallem data set (CamplPaldidet ).

| i | j | nemgth |
| :---: | :---: | :---: |
| 1.Adenop | 3. Campan | 0.198460 |
| 3 . Campan | 2. Asyneu | 0.237600 |
| 3 . Campan | 32.Rapun | 0.209540 |
| 2 . Asyneu | 37.Wahle | 0.141720 |
| 37. Wahle | 19.Legou | 0.124650 |
| 19.Legou | 12.Githo | 0.123900 |
| 12.Githo | 4. Campan | 0.159690 |
| 32. Rapun | 30.Prism | 0.120510 |
| 4. Campan | 8. Cyanan | 0.116960 |
| 8. Cyanan | 20.Lepto | 0.565880 |
| 20.Lepto | 7. Codono | 0.650240 |
| 7. Codono | 9.Echino | 0.480010 |
| 9.Echino | 31. Pseud | 0.605560 |
| 9.Echino | 38.Lobel | 0.441270 |
| 38.Lobel | 6. Canari | 0.393130 |
| 6.Canari | 29.Platy | 0.586460 |
| 29.Platy | 5. Campan | 0.558490 |
| 20.Lepto | 25.Ostro | 0.286660 |
| 25.Ostro | 28. Physo | 0.175740 |
| 28. Physo | 26. Perac | 0.187380 |
| 26.Perac | 16. Homoc | 0.203210 |
| 30. Prism | 17."Isop" | 0.111670 |
| 17."Isop | 10.Edrai | 0.159300 |
| 17."Isop | 18.Jasio | 0.140480 |
| 17."Isop | 21. Micha | 0.140330 |
| 21. Micha | 14. Hanab | 0.188890 |
| 21. Micha | 24.Nesoc | 0.124550 |
| 24.Nesoc | 22.Mussc | 0.172460 |
| 24.Nesoc | 11. Gadel | 0.152230 |
| 11. Gadel | 35.Symph | 0.183040 |
| 35. Symph | 34.Rouce | 0.183040 |
| 35. Symph | 15.Heter | 0.179050 |
| 11. Gadel | 36.Trach | 0.157010 |
| 22.Mussc | 23. Namac | 0.142450 |
| 23. Namac | 13. Gunil | 0.214480 |
| 36.Trach | 27. Phyte | 0.123390 |
| 35. Symph | 33.Roell | 0.101730 |

Table 8. Mimimum spammimg tree for the $\mathbb{P}$ ©llem data sulbset (CampPal. $D$ AT): Campamuleae andlputative "outgroupss".

| i | j | lengeth |
| :---: | :---: | :---: |
| 1. Adenop | 3. Campan | 0.255760 |
| 3. Campan | 2 . Asyneu | 0.269550 |
| 3. Campan | 32.Rapun | 0.262680 |
| 3. Campan | 12.Githo | 0.121760 |
| 12. Githo | 4. Campan | 0.195940 |
| 12. Githo | 19. Legou | 0.098340 |
| 4. Campan | 16. Homoc | 0.088370 |
| 16. Homoc | 26. Perac | 0.279860 |
| 26. Perac | 28. Physo | 0.278950 |
| 1. Adenop | 18.Jasio | 0.082440 |
| 18.Jasio | 17."Isop" | 0.138170 |
| 17."Isop | 10.Edrai | 0.183860 |
| 17. ${ }^{\text {I }}$ Isop | 21. Micha | 0.160090 |
| 21. Micha | 14.Hanab | 0.243380 |
| 14. Hanab | 36.Trach | 0.089740 |
| 36. Trach | 11. Gadel | 0.165200 |
| 11. Gadel | 35. Symph | 0.224100 |
| 35. Symph | 34.Rouce | 0.224100 |
| 11. Gadel | 22. Mussc | 0.121430 |
| 36. Trach | 27. Phyte | 0.080030 |

Table 9. Mimimum spammimg tree for the Pollem data sulbset (Camp Pal. DAT): Walnlembergeae amd putative "outgroups".


Tanble 10. Mimimunm spamming tree for the Seed data set (CampSeed. $\mathbb{D}$. $\mathbb{T}$ ).

| i | j | lemgth |
| :---: | :---: | :---: |
| 1.Adenop | 51. Wahle | 0.249210 |
| 51. Wahle | 41. Rapun | 0.212620 |
| 41. Rapun | 42.Melan | 0.358630 |
| 41.Rapun | 31.Legou | 0.316330 |
| 42. Melan | 12."Oreo | 0.273440 |
| 12."Oreo | 24.Cylin | 0.284180 |
| 42. Melan | 32. Lepto | 0.247450 |
| 32. Lepto | 40.Platy | 0.417220 |
| 12."Oreo | 44.Rouce | 0.212650 |
| 24. Cylin | 2 . Asyneu | 0.202570 |
| 32. Lepto | 46.5 Sergi | 0.198690 |
| 46.Sergi | 28. Githo | 0.254920 |
| 28. Githo | 21. Codon | 0.261220 |
| 21. Codon | 53."Fern | 0.233740 |
| 21. Codon | 29.Isoph | 0.195260 |
| 29.Isoph | 52."Hele | 0.410790 |
| 52."Hele | 16.C.lin | 0.498720 |
| 52."Hele | 35. Nesoc | 0.436790 |
| 52."Hele | 45.Roell | 0.360610 |
| 45.Roell | 26.Edrai | 0.574680 |
| 45.Roell | 22.Crate | 0.416090 |
| 16.C.lin | 34.Mussc | 0.307710 |
| 35.Nesoc | 37. Petko | 0.283670 |
| 37. Petko | 6."Ibero | 0.688620 |
| 16.C.lin | 14.Megal | 0.210390 |
| 14.Megal | 8. Symphy | 0.378540 |
| 8. Symphy | 13.C.for | 0.385940 |
| 8. Symphy | 38. Petro | 0.363460 |
| 38. Petro | 49.Symph | 0.369390 |
| 38. Petro | 20. Codon | 0.237370 |
| 20. Codon | 50.Trach | 0.250170 |
| 50. Trach | 25.Diosp | 0.253990 |
| 13.C.for | 17. Spinu | 0.236810 |
| 17.Spinu | 27.Gadel | 0.213350 |
| 25. Diosp | 9. Involu | 0.210810 |
| 46. Sergi | 3.Azorin | 0.192450 |
| 2. Asyneu | 39. Phyte | 0.189140 |
| 39. Phyte | 5. Campan | 0.590110 |
| 50. Trach | 4.Brachy | 0.188320 |
| 4. Brachy | 15.C.lan | 0.233520 |
| 53."Fern | 43.Ptero | 0.187710 |
| 17. Spinu | 18.Tulip | 0.180270 |
| 18.Tulip | 10. Rupes | 0.227390 |
| 10.Rupes | 11. Quing | 0.208060 |
| 11. Quing | 48.Otoca | 0.215680 |

Continued overleaf

Table 10. continued

| 48.Otoca | 19.C.sar | 0.257290 |
| :--- | :---: | :---: |
| 48.Otoca | 47.Symph | 0.219300 |
| 52. "Hele | 23. Cyana | 0.174430 |
| 23. Cyana | 36. Perac | 0.341680 |
| 36. Perac | 33.Micha | 0.207900 |
| 36. Perac | 7.Scapif | 0.190520 |
| 36. Perac | 30.Jasio | 0.172240 |

Table 11. Mimimumm spammimg tree for the Seed data sulbset (CampSeed.DAT): Campamuleae amd putative "هutgroups".

| i | j | lemgth |
| :---: | :---: | :---: |
| 1. Adenop | 25. Diosp | 0.126740 |
| 25. Diosp | 50.Trach | 0.219490 |
| 50. Trach | 20. Codon | 0.212620 |
| 20. Codon | 38. Petro | 0.198640 |
| 38. Petro | 49. Symph | 0.332530 |
| 38. Petro | 8. Symphy | 0.326940 |
| 8. Symphy | 13.C.for | 0.349230 |
| 8. Symphy | 14.Megal | 0.346850 |
| 14.Megal | 16.C.lin | 0.224700 |
| 16.C.lin | 34. Mussc | 0.344270 |
| 16.C.lin | 29.1soph | 0.263080 |
| 29.Isoph | 37. Petko | 0.287390 |
| 37. Petko | 6."Ibero | 0.727270 |
| 29.Isoph | 18.Tulip | 0.204560 |
| 18.Tulip | 10.Rupes | 0.220780 |
| 13.C.for | 17. Spinu | 0.202440 |
| 10.Rupes | 11. Quinq | 0.195650 |
| 11. Quinq | 48. Otoca | 0.196910 |
| 48. Otoca | 19.C.sar | 0.231680 |
| 17.Spinu | 27. Gadel | 0.195190 |
| 48.Otoca | 47. Symph | 0.191190 |
| 25.Diosp | 9.Involu | 0.181210 |
| 37. Petko | 26.Edrai | 0.171070 |
| 50. Trach | 4. Brachy | 0.166450 |
| 4.Brachy | 15.C.lan | 0.217450 |
| 20. Codon | 46.Sergi | 0.143200 |
| 46. Sergi | 28. Githo | 0.261830 |
| 46.Sergi | 3.Azorin | 0.191880 |
| 46.Sergi | 42.Melan | 0.163480 |
| 42.Melan | 41.Rapun | 0.358400 |
| 41.Rapun | 31.Legou | 0.312290 |
| 42. Melan | 12."Oreo | 0.262340 |
| 12. "Oreo | 24.Cylin | 0.267930 |
| 12."Oreo | 44.Rouce | 0.196330 |
| 24.Cylin | 2. Asyneu | 0.188750 |
| 2. Asyneu | 5. Campan | 0.177600 |
| 5. Campan | 39. Phyte | 0.582010 |
| 44. Rouce | 7.Scapif | 0.157380 |
| 7.Scapif | 36. Perac | 0.199460 |
| 36. Perac | 33. Micha | 0.210020 |
| 36. Perac | 30.Jasio | 0.182320 |
| 41.Rapun | 43. Ptero | 0.131450 |

Table 12 . Mimimum spamming tree for the Seed data sulbset (CampSeed. $\mathbb{C D} A T$ ): Platycodlomeae amd purarive "oungroups".

| $\dot{\mathrm{i}}$ | $\dot{\mathrm{j}}$ | lemgtth |
| :--- | :--- | ---: |
| 21. Codon | 23. Cyana | 0.020930 |
| 21. Codon | 35. Nesoc | 0.020330 |
| 35. Nesoc | 45. Roell | -0.005220 |
| 23. Cyana | 32. Lepto | -0.069250 |
| 32. Lepto | 40. Platy | 0.228580 |

Tablle 13. Mimimum spamming tree for the Seed data sulbset (CampSeedldiAT); Walllembergeae and putarive ${ }^{66}$ outgroupss".

| i | j | lemgth |
| :---: | :---: | :---: |
| 3.Azorin | 28. Githo | 0.207660 |
| 28.Githo | 53. F Fern | 0.106610 |
| 28.Githo | 34. Mussc | 0.075190 |
| 3.Azorin | 50. Trach | 0.064150 |
| 50. Trach | 31.Legou | 0.140160 |
| 31.Legou | 51. Wahle | 0.083930 |
| 51. Wahle | 30.Jasio | 0.154890 |
| 34.Mussc | 52."Hele | 0.047820 |
| 52."Hele | 35.Nesoc | 0.313490 |
| 52."Hele | 45.Roell | 0.133330 |
| 45.Roell | 26. Edrai | 0.356830 |
| 45.Roell | 22. Crate | 0.222970 |

12.1.1.1 $\mathbb{G} \& \mathbb{B} . \mathbb{D D A T}$ (Asterales)...Gustaffism \& Bremer's $\mathbb{D}$ Data (IDelita Data Fille fior Pamkey, SC3)
*ITEM $\mathbb{D E S C R I P T I D N S}$
\#1.Aquaifoliaceae/
$\mathbb{1}, 22, \mathbb{1} 3, \mathbb{U} \mathbb{4}, 25, \mathbb{1} 6, \mathbb{1} 7, \mathbb{1} 8,2 \mathbb{2}, \mathbb{V} \mathbb{1 0}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 2,2 \mathbb{1}, \mathbb{1} \mathbb{1} 4, \mathbb{1} \mathbb{5}, \mathbb{V} \mathbb{1}(6, \mathbb{V} \mathbb{1} 7, \mathbb{1}$ $\mathbb{1 8}, \mathbb{1} \mathbb{1 9}, \mathbb{U} 2 \mathbb{C}, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22,223, \mathbb{1} 24, \mathbb{1} 25,126,127,228,129,230, \mathbb{U} 31,132, \mathbb{1}$ $33, \mathbb{V} 34, \mathbb{V} 35,136, \mathbb{1} 37, \mathbb{1} 38,339, \mathbb{1} 40, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{U} 44, \mathbb{U} 45, \mathbb{U} 46, \mathbb{U}$
\#2.Aralizaceae/
$\mathbb{1}, 2 \mathbb{2}, \mathbb{1} 3, \mathbb{1} \varangle, 25, \mathbb{1} 6, \mathbb{1} 7,28, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{V} \mathbb{1}, \mathbb{V} \mathbb{1} 3, \mathbb{1} \mathbb{1} 4, \mathbb{1} \mathbb{1 5}, \mathbb{V} \mathbb{1} 6, \mathbb{V} \mathbb{1} 7, \mathbb{1}$
$\mathbb{1 8}, \mathbb{1} 19, \mathbb{U} 20, \mathbb{U} 21, \mathbb{1} 22, \mathbb{1} 23, \mathbb{1} 24, \mathbb{1} 25, \mathbb{1} 2(\mathbb{T}, \mathbb{V} 27, \mathbb{V} 28, \mathbb{V} 29,130, \mathbb{U} 31, \mathbb{1} 32,2$
$33, \mathbb{V} 34, \mathbb{V} 35,136,1137,1138,339, \mathbb{V} 40, \mathbb{V} 41,242,243,244,245, \mathbb{V} 46, \mathbb{V}$
\#3.Brumiaceae/
 $\mathbb{1 8}, \mathbb{1} 19, \mathbb{U} 20, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23, \mathbb{V} 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27, \mathbb{U} 28, \mathbb{U} 29, \mathbb{1} 30, \mathbb{U} 31, \mathbb{V} 32, \mathbb{V}$ $33,2 / 314, \mathbb{1} 35,136,137, \mathbb{1} 38,339, \mathbb{V} 40, \mathbb{U} 41,242, \mathbb{U} 43, \mathbb{U} 44, \mathbb{U} 45, \mathbb{U} 46, \mathbb{U}$
\# a. Escallamiaceae/ $^{\text {a }}$

$\mathbb{1 8}, \mathbb{1} \mathbb{1 9}, \mathbb{U} 20, \mathbb{U} 21, \mathbb{1} 22, \mathbb{V} 23, \mathbb{V} 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27, \mathbb{1} 28, \mathbb{U} 29, \mathbb{1} 30, \mathbb{U} 31, \mathbb{1} 32, \mathbb{V}$
$33, \mathbb{V} 34, \mathbb{V} 35, \mathbb{1} 36, \mathbb{1} 37,1138, \mathbb{1} 39,140,241, \mathbb{U} 42,243, \mathbb{U} 44, \mathbb{U} 45, \mathbb{U} 46, \mathbb{U}$
\#5. Griselimiaceae/
$\mathbb{1}, \mathbb{1} 2, \mathbb{U} 3, \mathbb{1} 4, \mathbb{1} 5, \mathbb{1} 6,27, \mathbb{1} 8, \mathbb{1} 9,2 \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} 12, \mathbb{1} 13, \mathbb{1} \mathbb{1} 4, \mathbb{1} 15, \mathbb{1} 16, \mathbb{1}$ $\mathbb{1 7 , \mathbb { 1 }} \mathbb{1 8}, \mathbb{1} \mathbb{1} 9, \mathbb{U} 20, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23, \mathbb{1} 24,325, \mathbb{1} 26, \mathbb{1} 27, \mathbb{U} 28, \mathbb{U} 29, \mathbb{1} 30, \mathbb{U}$ $3 \mathbb{1}, \mathbb{1} 32,233,234, \mathbb{V} 35, \mathbb{1} 36, \mathbb{1} 37, \mathbb{1} 38,339,240, \mathbb{U} \mathbb{1}, \mathbb{U} 42, \mathbb{U} 43, \mathbb{U} 44, \mathbb{U}$
$45, \mathbb{U} 46, \mathbb{U}$
\#t. Pittosporaceae/
$\mathbb{1}, 2 \mathrm{Z}, \mathbb{1} 3, \mathbb{1} 4,25,26, \mathbb{1} 7, \mathbb{V} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 2, \mathbb{1} 13, \mathbb{1} \mathbb{1}, \mathbb{1} 15, \mathbb{1} \mathbb{1 6}, \mathbb{V} \mathbb{1 7 , \mathbb { 1 }}$ $\mathbb{1 8}, \mathbb{V} \mathbb{1} 9, \mathbb{1} 20,121, \mathbb{1} 22, \mathbb{V} 23, V 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27, \mathbb{V} 28, \mathbb{V} 29, \mathbb{1} 30, \mathbb{U} 31, \mathbb{1} 32, \mathbb{1}$ $33, \mathbb{V} 34,235,1136,137,138,2$
$39, \mathbb{1} 40,241, \mathbb{1} 42,243, \mathbb{U} 44, \mathbb{U} 45, \mathbb{1} 46,2$
\#7.Samburcaceael
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} \mathbb{4}, \mathbb{1} 5,2 \mathbb{2}, 27,28, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{2}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 4, \mathbb{1} \mathbb{1 5}, \mathbb{V} \mathbb{1} 6,2 \mathbb{1}, \mathbb{1}$ $\mathbb{1 8}, \mathbb{1} 19, \mathbb{U} 2 \mathbb{0}, \mathbb{U} 21, \mathbb{1} 22,223,1124,225,126,127, \mathbb{U} 28,229,230,1131, \mathbb{1}$
$32,233, \mathbb{1} / 234,235,136,1137,138,339,140,241, \mathbb{U} 42, \mathbb{1} 43, \mathbb{U} 44, \mathbb{U}$
45,1 4.6,2
\#8. Viburmaceae/
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1} 5, \mathbb{1}(\mathbb{T}, \mathbb{V} 7, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} 10, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{V} \mathbb{1 3}, \mathbb{1} \mathbb{1} 4, \mathbb{1} 15, \mathbb{1} \mathbb{1}, 2$
$\mathbb{1 7}, \mathbb{1} \mathbb{1 8}, \mathbb{1} \mathbb{1 9}, \mathbb{U} 20, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23, \mathbb{1} 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27, \mathbb{U} 28,2 \mathbf{2 9}, 230, \mathbb{1}$
$31,1132,233,234,235,1136,1137,138,339,240,141, \mathbb{U} 42,143, \mathbb{U} 44, \mathbb{U}$ $45,1146,2$
\#Ф.Argophyyllaceae/

$18, \mathbb{1} 19, \mathbb{U} 20, \mathbb{U} 21, \mathbb{1} 22, \mathbb{1} 23,124,125,126,1127, \mathbb{U} 28, \mathbb{U} 29, \mathbb{1} 30, \mathbb{U} 31,1132,2$
$33, \mathbb{V} 34,235, \mathbb{1} 36, \mathbb{1} 37, \mathbb{1} 38, \mathbb{1} 39, \mathbb{1} 40, \mathbb{U} 41, \mathbb{U} 42, \mathbb{U} 43, \mathbb{U} 44, \mathbb{U} 45, \mathbb{U} 46, \mathbb{U}$
\#1D. Domariaceac/
$\mathbb{1}, \mathbb{U} 2,2 \mathbb{Z}, \mathbb{1} \mathbb{4}, \mathbb{U} 5, \mathbb{1} 6, \mathbb{U} 7, \mathbb{U} 8,2 \mathbb{2}, \mathbb{U} \mathbb{1 0}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 2, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 4, \mathbb{1} 15, \mathbb{1} 16, \mathbb{1}$ $\mathbb{1 7}, \mathbb{1} 18, \mathbb{1} \mathbb{1} 9, \mathbb{U} 2 \mathbb{1}, \mathbb{U} 2 \mathbb{1}, 222, \mathbb{1} 23, \mathbb{1} 24,225, \mathbb{1} 26, \mathbb{1} 27, \mathbb{U} 28, \mathbb{U} 29,130, \mathbb{U}$
 $\triangle 4, \mathbb{1} 4 \cdot 5, \mathbb{U} 46, \mathbb{U}$

## \#11.Memyanthaceae/

$\mathbb{1}, \mathbb{1} 2,23, \mathbb{1} 4, \mathbb{1} 5,2 \mathbb{6}, \mathbb{U} 7, \mathbb{U} 8, \mathbb{1} 9,2 \mathbb{1 0}, 2 \mathbb{1}, \mathbb{1} \mathbb{1 2 ,} \mathbb{1} \mathbb{1} 3, \mathbb{1} \mathbb{1} 4, \mathbb{1} \mathbb{1}, \mathbb{V} \mathbb{1} 6,2 \mathbb{1} 7,2$ $18,2 \mathbb{1 9}, 220,221, \mathbb{1} 23,124,1125,126,127,228,229,130,131, \mathbb{V} 32, \mathbb{V} 33,3$ $34,235,1136,1137,138,239,140,241,242,143,244,245,146,2$
\#12.Pemtaphragmatacear/
$\mathbb{1}, \mathbb{U} \mathbf{2}, \mathbb{U} 3, \mathbb{U} \mathbb{4}, \mathbb{1} 5, \mathbb{1} 6,27, \mathbb{1} 8, \mathbb{U} 9, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 1, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4, \mathbb{1} \mathbb{1} 5,2 \mathbb{1} 6, \mathbb{V} \mathbb{1} 7,2$ $18,2 \mathbb{1 9}, \mathbb{1} 20,121,122,223,124,125,126,127,128,129,1130,1131,1$ $32,233,2 / 334,235,136,137,138,139,1140,241,142,143,144,2$ $45,246,11$
\#13.Splnemocleaceae/
$\mathbb{1}, \mathbb{U} 2, \mathbb{U} 3, \mathbb{1} \mathbb{4}, \mathbb{1} 5,2 \mathfrak{6}, \mathbb{U} 7, \mathbb{U} 8, \mathbb{U} \mathbb{9}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 2, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 4, \mathbb{1} 15, \mathbb{1} 16,2$
$\mathbb{1} 7, \mathbb{1} \mathbb{1 8}, \mathbb{1} \mathbb{1} \mathbb{D}, \mathbb{U} 2 \mathbb{D}, \mathbb{U} 21, \mathbb{1} 22, \mathbb{1} 23, \mathbb{1} 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27, \mathbb{1} 28,229, \mathbb{1} 30, \mathbb{1}$ $31, \mathbb{1} 32,233,334,235,136,137,138,139,140,241,1142,113,144,1$ $45,146,1$

## \#14.Stylidliaceae/

 $18, \mathbb{1} 19, \mathbb{U} 20, \mathbb{U} 21,222, \mathbb{U} 23,224,225,126,127,128, \mathbb{V} 29,1130, \mathbb{U} 31,232,2$ $33,334,235,1136,1137,1138,139,140,241, \mathbb{1} 42, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,246,1$

## \#15.Asteraceae/

 $18,2 \mathbb{1 9}, 220,2 \operatorname{21}, \mathbb{1} 22,223, \mathbb{V} 24,125,226,2 / 327,228,229,130,231,2$ $32,233,334,235,136,137,238,439,240,241,1142, V 43,244,245,1$ 46,2
\#16. Branomiaceae/
 $\mathbb{1 7}, \mathbb{1} \mathbb{1 8}, \mathbb{U} 19,220, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22,223,224,125,226,327, \mathbb{U} 28, \mathbb{1} 29,1130,2$ $31,232,133,334,235,236,237,238,439,240,241,142, \mathbb{U} 43,244,2$ $45, \mathbb{U} 46, \mathbb{U}$
\#17.Callyceraceae/
 $17, \mathbb{1} 18,219,220,221,122,223,224,125,226,327, \mathbb{U} 28,129,1130,2$ $31,232,233,334,235,116,137,238,339,240,241,142,143,244,2$ $45, \mathbb{U} \triangle \mathbb{G}, \mathbb{U}$

## \#18.C风mpamulaceac/

 $\mathbb{1 8}, \mathbb{V} 19, \mathbb{1} 20,121,122,223,224, \mathbb{1} 25, V 26,327, \mathbb{1} 28, V 29,1130,131,232, V$ $33, \mathbb{V} 34,235,116,237,238,1139, \mathbb{1} 40,241, \mathbb{1} 42, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,246, \mathbb{1}$
\#19. Cyplhiaceae/
 $17,118,2 \mathbb{1} 9,1120,121,122,223,224,1125, \mathbb{1} 26,327, \mathbb{U} 28, \mathbb{U} 29, \mathbb{1} 30, \mathbb{U}$ $3 \mathbb{1}, \mathbb{1} 32,233,334,235, \mathbb{1} 36,237, \mathbb{1} 38,139, \mathbb{1} 40, \mathbb{U} 4 \mathbb{1}, \mathbb{U} 42, \mathbb{U} 43, \mathbb{U} 44, \mathbb{U}$ $45, \mathbb{U} 4,6, \mathbb{U}$
\#20.Cyplnocarpaceae/

$\mathbb{1 7 , \mathbb { 1 }} \mathbb{1 8}, \mathbb{1} \mathbb{1 9}, \mathbb{U} 20, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22,223,224, \mathbb{1} 25, \mathbb{1} 26,327, \mathbb{U} 28, \mathbb{U} 29,230, \mathbb{1}$
$31, \mathbb{1} 32,233,334,235, \mathbb{1} 36,237,238,139,140, \mathbb{U} 41, \mathbb{U} 42, \mathbb{U} 43, \mathbb{U} 44, \mathbb{U}$
$45, \mathbb{U} 4 \mathbb{G}, \mathbb{U}$
\#21.Goodemiaceae/

$17,2 \mathbb{1 8}, 2 \mathbb{1 9}, 220,221,122,223,224,125, V 26,327,228,1129,1130,2$
$3 \mathbb{1}, \mathbb{V} 32, \mathbb{V} 33,334,235,236,237,238, \mathbb{1} 39, \mathbb{V} 40,241,242,143,244,2$
$4.5,24.6,1$
\#22.Lobeliaceae/
 $\mathbb{1 7 , 1 1} \mathbb{1}, \mathbb{1} \mathbb{1} 9, \mathbb{U} 20, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22,223,224, \mathbb{1} 25,226,227, \mathbb{1} 28, V 29,230, \mathbb{1}$ $31, \mathbb{1} 32, \mathbb{V} 33,334,235,1136,237,238,1139,140,241, \mathbb{1} 42, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1}$ $45,246,11$
\#23.Nemacladaceae/
 $17, \mathbb{1} 18, \mathbb{1} \mathbb{1 9}, \mathbb{U} 20, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22,223,224, \mathbb{1} 25, \mathbb{1} 26,327, \mathbb{U} 28, \mathbb{U} 29, \mathbb{1} 30, \mathbb{1}$ $31,232,233,334,235, \mathbb{1} 36,237,238, \mathbb{1} 39, \mathbb{1} 40, \mathbb{U} 41, \mathbb{U} 42, \mathbb{U} 43, \mathbb{U} 44, \mathbb{U}$ $45, \mathbb{U} 4, \mathbb{U}, \mathbb{U}$

* $\mathbb{E N} \mathbb{D}$
12.1.1.2 G\&BSUB.DAT (Asterales)...Campamulales data sulbset (DDelta data fille for Pamkey, SC3)
*ITEMI IDESCRIPTIONS
\#1D.IDomatiaceae/
 $17, \mathbb{1} 18, \mathbb{1} 19, \mathbb{U} 20, \mathbb{U} 2 \mathbb{1}, 222, \mathbb{1} 23,124,225, \mathbb{1} 26,1127, \mathbb{U} 28, \mathbb{U} 29,1130, \mathbb{U}$ $31,132,233,2 / 334, \mathbb{1} 35,136,137,138,139,1140,241,242,143,1$ $44, \mathbb{1} \mathbb{4}, \mathbb{U} \mathbb{U} \mathbf{4}, \mathbb{U}$
\#11.Memyamthaceae/

 $34,235, \mathbb{1} 36,1137, \mathbb{1} 38,239, \mathbb{1} 40,241,242, \mathbb{1} 43,244,24.5,146,2$
\#12.Pemtaphragnmataceac/
 $18,2 \mathbb{1 9}, \mathbb{1} 20,1121, \mathbb{1} 22,223, \mathbb{1} 24, \mathbb{1} 25, \mathbb{1} 26,127,128,129,130, \mathbb{1} 31, \mathbb{1}$ $32,233,2 / 3 \quad 34,235,136,137,138,139,140,241,1142,143,144,2$ $45,246,1$
\#13.Sphemocleaceae/
 $\mathbb{1 7}, \mathbb{1} \mathbb{1} 8, \mathbb{1} \mathbb{1} 9, \mathbb{U} 2 \mathbb{1}, \mathbb{U} 2 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23, \mathbb{1} 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27, \mathbb{1} 28,229, \mathbb{1} 30, \mathbb{1}$ $3 \mathbb{1}, \mathbb{1} 32,233,334,235, \mathbb{1} 36, \mathbb{1} 37, \mathbb{1} 38,139, \mathbb{1} 40,241, \mathbb{1} 42, \mathbb{1} 43,1144, \mathbb{1}$ $45,146,11$
\#14.Stylidiaxceae/
$\mathbb{1}, \mathbb{1} 2,2 \mathbb{3}, \mathbb{1} \mathbb{4}, \mathbb{U} 5,2 \mathbb{2}, 27, \mathbb{1} 8,2 \mathbb{2}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 2, \mathbb{1} \mathbb{1}, \mathbb{V} \mathbb{1} 4, \mathbb{1} 15, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1}$
$\mathbb{1 8}, \mathbb{1} \mathbb{1} 9, \mathbb{U} 2 \mathbb{C}, \mathbb{U} 21,222, \mathbb{U} 23,224,225, \mathbb{1} 2 \sigma, 127, \mathbb{1} 28, \mathbb{V} 29,1130, \mathbb{U} 31,232,2$
$33,334,235,116,137, \mathbb{1} 38, \mathbb{1} 39,140,241,142, \mathbb{1} 43, \mathbb{1} 44,145,246,11$
\#15.Asteraceae/
 $18,219,220,221,122,223, V 24,125,226,2 / 327,228,229,1130,231,2$ $32,233,334,235,136,137,238,439,240,241,142, V 43,244,245,1$ 46,2
\#16. Brommomiaceac/
 $17, \mathbb{1} 18, \mathbb{U} 19,22 \mathbb{2}, \mathbb{U} 21, \mathbb{1} 22,223,224,125,226,327, \mathbb{U} 28, \mathbb{1} 29,130,2$ $31,232,1133,334,235,236,237,238,439,240,241,142, \mathbb{U} 43,244,2$ $45, \mathbb{U} 46, \mathbb{U}$
\#17. Callyceraceae/
 $17,118,219,220,221,122,223,224,1125,226,327, \mathbb{U} 28,1129,1130,2$ $31,232,233,334,235,136,137,238,339,240,241,1142,113,244,2$ $45, \mathbb{U} 46, \mathbb{U}$

```
#18.Campamulaceae/
```



```
18,V 19,1 20,1 21, 1 22,2 23,2 24,1125,V 26,3 27,1 28,V 29,1 30,1 31,2 32,V
```



```
#19.Cyplniaceae/
1,2 2,2 3,2 &,U S,U 6,U 7,U 8,U \,U 10,2 11, \mathbb{12,\mathbb{1}3,3 14,2 15,2 16,2}
17,1 18,2 19, 11 20,1 21, 1 22,2 23,2 24,1 25,1 26,3 27,U 28,U 29,1 30, U
```



```
4.5,U 4|,U
#20.Cyphocærpaceae/
```




```
31,\mathbb{1 32,2 33,3 34,2 35,1 36,2 37,2 38,\mathbb{1 39,1140,U 41,U 42,U 43,U 44,U}}\mathbf{|}|
45,U 4 4\sigma,U
#21.Goodemiaceac/
```



```
17,2 18,2 19,2 20,2 21,1 22,2 23,2 24,1 25,V 26,3 27,2 28,1 29,1 30,2
31,V 32,V 33,3 34,2 35,2 36,2 37,2 38,11 39,V 40,2 41,2 42,1 43,2 44,2
45,2 46,1
#22.L.lbeliaceae/
1,2 2,2 3,2 4,\mathbb{1 5,2 6,2 7,2 8,2 9, 110,2 11, 112,1113,3 14,1/2 15,2 16,2}
17,1 18,\mathbb{119,U 2\mathbb{O},\mathbb{U}2\mathbb{1,}\mathbb{1}22,2 23,2 24,1 25,2 26,2 27,1 28,V 29,2 30,1}
31,\mathbb{1 32,V 33,3 34,2 35,1 36,2 37,2 38,1 39,1 40,2 41, 1 42, 143,144,1}
4.5,2 4.6,11
#23.Nemnacladmceae/
```



```
17,\mathbb{1}18,\mathbb{1}19,\mathbb{U}20,\mathbb{U}21,\mathbb{1}22,2 23,2 24,\mathbb{1 25,1}26,3 27,U 28,U 29,11 30,\mathbb{I}
31,2 32,2 33,3 34,2 35,1 36,2 37,2 38,1 39,1 40, U 41,U 42,U 43,U 44,U
45,U 46,U
*END
```

12.1.1.3 FILOWIERS.IDAT (Flowers \& Fruits)... Flowers \& Fruits data set (Delta data fille for Pamkey, SC3)

## *TTEM IDESCRIPTIONS

```
#1.Adlem@plnora < Fischo>/
```



```
19,2 20,2 21, 122,1123,3 24,1125,1126,2/3 27,3 28,1 29,1/2/3 30,1131,3
32,2 33,1 34,3 35,1 36,2 37, 1 38,3 39,1 41,242,143, 144,1/245,3
47,5 48,3
```

\#2.Astrocodicn < $\mathbb{F e d}$.>1
$\mathbb{1}, \mathbb{1} / 2 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25,2 \mathbb{2}, 27,2 / 5 \mathbb{8}, \mathbb{1} 9,2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1 5}, \mathbb{1} 16, \mathbb{1}$
$17,219,320,221, \mathbb{1} 22, \mathbb{U} 23,324,125,126,227,128,129,230, \mathbb{1} 31,332,1$
$33, \mathbb{1} 34,335,136,237,138,339,141,242, \mathbb{1} 43, \mathbb{1} 44,145,347,548,3$
\#3.Asymeurma < Grisebb. \& Schemk $\mathrm{c}_{0}>1$

$17,219,2 / 320,221,122,123,324,1 / 225,126,2 / 327,228,1129,2 / 330,1 / 2$
$31,332,1 / 233,134,335,116,237,118,339,141,242,1 / 243,1 / 244,1 / 2 / 3$
$45,347,548,1 / 2$
\# d.A. $_{\text {ancrima }}<$ Feer>/
$\mathbb{1}, 22, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1} 5,26, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1 5}, \mathbb{1} \mathbb{1 6 ,} \mathbb{1} 17,2 \mathbb{1 9}, \mathbb{1}$
$20,121, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27,328, \mathbb{1} 29, \mathbb{1} 30, \mathbb{1} 31,132, \mathbb{1} 33,1134,3$
$35,136,237,138,339,141,242, \mathbb{1} 43,144,1145,347,548,3$
\#5. IBeremice <Tunl.>1
$\mathbb{1}, 2 \mathbb{2}, \mathbb{1} 3, \mathbb{1} \mathbb{4}, 25,26,27,5 \mathbb{S}, \mathbb{1} 9,3 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{2} 3, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$
$19, \mathbb{1} 20,12 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27,228, \mathbb{1} 29, \mathbb{1} 30,131,132,133,1$
$34,335,1136,237,138,339,141,242,143,144,145,146,149,2$
\#6.Brachyycodom <Fed.>1

$\mathbb{1 7 , 2} \mathbb{1 9}, \mathbb{1} 2 \mathbb{1}, \mathbb{1} 21, \mathbb{1} 22, \mathbb{U} 23,324, \mathbb{1} 25, \mathbb{1} 26,327, \mathbb{1} 28, \mathbb{1} 29,130, \mathbb{1} 31,332, \mathbb{1}$
$33, \mathbb{1} 34,335,136,237, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43,244, \mathbb{1} 45,347,548, \mathbb{1}$
\#7.Campamula < LL.: essemtially Sect.Medium $>$ /

$\mathbb{1 4}, 2 \mathbb{1 5}, \mathbb{1} 16,117,2 \mathbb{1} 9,320,221,1 / 2 / 422,1 / 223,324, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} / 2 / 327,2$
$28,129,1 / 230,131,2 / 332,133,134,2 / 335,1136,237,1138,339,1 / 2 / 3$
$40,1 / 241,242,143,144,1 / 245,2 / 347,548,350,1 / 2$
\#8. Caumpamußastrunm <Smali: $\mathbb{C}$.americama>/
$\mathbb{1}, 32, \mathbb{1} 3, \mathbb{1} 4,25,26,27,58, \mathbb{1} 9,2 \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} 16, \mathbb{1} 17,2$
$19,320,2$ 21, $1122,223,324,235,126,327,228,129,330,231,332,233,1$
$34,335,116,237,138,339,141,242,143,244,145,347,548,1$

```
#9.Campamammeea <BRumme>/
```



```
20,1 21,1 22,U 23,2 24,1 25,1 26,1 27,3 28,1 29,2 30,1 31,1 32,1 33,1 34,2
35,1136,2 37,1138,2/4 39,1141,1 42,\mathbb{1}
#10.Camarima<ll.>/
```




```
33,\mathbb{1 34,3 35,1 36,2 37,1 38,3 39, 1 41, 142, 1}
#11.Ceplnalostigmma/
```



```
19,2 20,1/2 21,1 22,1 23,3 24,1 25,1 26,2/3 27,2 28,1 29,2 30,1/2 31,4 32,1
33,1 34,2 35,1 36,2 37,1/2 38,3 39,1 41,2 42,1 43,1/2 44,1/2 4.5,1 46,1
49,2/3
#12.Codomopsis<Walll>/
```





```
4.5,1146,1 49,2
#13.Craterocapsa<MHi#liard & B.L. \mathbb{Burft>/}
1,1/2/4 2,113,1 4,2 5,2 6,1/2 7,2/4/5/6 8,1 9,1/2 10,\mathbb{111, 1/2 12,\mathbb{113,2 14,2}}\mathbf{2}=1
15,\mathbb{1}16,\mathbb{1}17,2\mathbb{19,}\mathbb{1}20,\mathbb{1}/2,2\mathbb{1},\mathbb{1}22,\mathbb{1}23,324,\mathbb{1}25,\mathbb{1}26,227,2 28,\mathbb{1}29,130,\mathbb{1}
```



```
#114.Cryptocodom <Fedl.>/
```



```
19,3 20,2 21,1 22,\mathbb{1 23,3 24,1 25,1 26,2 27,2 28,1129,1130,11 31,2 32,1133,1}
34,3 35,1 36,2 37,1 38,3 39,2 40,1 41,2 42,1 43,1 44,1 45,3 47,5 48,2
#15.Cyamamthus <W,Wall. ex Bemth.>1
```





```
#16.Cyclocodom/
```




```
35,1 36,2 37,1 38,1/2/4 39,1 41,1 42,1
#17.Cylimdrocarpa <Regel>/
```



```
19,3 20,2 21, 11 22,1 23,3 24,1 25,1 26,3 27,2 28,1 29,1130,1 31,3 32,1 33,1
34,3 35,1136,2 37,1 38,3 39, 1 4 1,242,1 43,344,345,347,548,\mathbb{1}
```

```
#18.Diosplnaera <Buser>/
```




```
31,3/5 32,\mathbb{1 33,1 34,3 35,1 36,2 37,2 38,3 39,1141,2 42,1 43,1 44,1/2}
45,347,5 48,3
#19.Eclnim@cod@m <\mathbb{D.Y. Homg>/}
```





```
#20.Edlraiamthus <(A.DDC.) DDC.>1
```



```
19,3 20,2 21,1 22,1123,3 24,1/2 25,1 26,1/2 27,2 28,1 29,1 30,1 31,2 32,1
33,1 34,3 35,1 36,2 37,1 38,3 39,1/2 40,1 41,2 42,1 43,1 44,1 45,1 46,3
#21.|Peerim <Buser>/
```



```
19,\mathbb{1 20,1 2\mathbb{1,}122,123,3 24,1 25,1 26,3 27,2 28,1 29,3 30,1 31,3 32,11 33,1}
34,3 35,1 36,4 37,1 38,3 39, 1 41,2 42, 143,1 44, 2 4.5,1 46,1 49,2
#22.Gadellia| <Sclhullkima>/
```



```
19,2 20,2 21, 1 22,2 23,3 24,1 25,1 26,2 27,2 28,1129,1 30,1 31,3 32,11 33,1
34,3 35,1136,2 37,1138,3 39, 1 & 1,2 42,143,\mathbb{144,}\mathbb{1 45,3 47,5 48,1/2}
#23.Githoppsis <Noutt.>1
```




```
33,1 34,3 35,11 36,2 37,1 38,3 39,1 41,2 42,1 43,2 44, 1/2 4.5,1/2 46,3
50,11/2
#24.Gummillamea <Tlnulim>1
1,2 2,1 3,\mathbb{14,2 5,2 6,18,19,2 10, 111,2 12,113,2 14,2 15,1116,1 17,2 19,2}
20,1/2 21,1 22,1 23,3 24,1 25,1 26,3 27,2 28,1 29,1 30,1 31,3 32,1 33,1/2
34,3 35,11 36,2 37,11 38,3 39,1 41,2 42,2 43,2/3 44,1/2 45,2 50,1
#25.Hamalbunsaya <Nalkai>/
```



```
19,3 20,2 21,4 22, 123,3 24,1 25,1 26,2 27,2 28,1 29,1130,1 31,2 32,1133,1
34,3 35,1 36,2 37,\mathbb{1 38,3 39,11 4,1,2 42, 1 43,144,1 45,3 47,5 48,3}
#26.Heterochaemia <A. DDC.>/
```



```
17,2 19,1 20,1 21,1 22,\mathbb{1 23,3 24,1125,1 2\sigma,2 27,3 28,1 29,1/2 30,11 31,2 32,1}
```


\#27. Heteracodom < Nuntt.>1
 $19,120,221,1122,123,324,125,126,227,228,1129,1130,131,332,1133,1$ $34,335,1136,237, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43,144,145,347,548,3$


$20, \mathbb{1} 21, \mathbb{1} 22,123, \mathbb{1} 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27,328, \mathbb{1} 29,1130,1131,132,1133,1134,2$
$35,136,237,138,239, \mathbb{1} 41,242, \mathbb{1} 43,144,145,1146,1149,2$
\#29. Hiomnocodom < $\mathbb{D}$.Y. $H$ Homg>1

$\mathbb{1 7 , 2} 19,1$ 20,2 21, $\mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,227,228, \mathbb{1} 29,130,1131,3$
$32, \mathbb{1} 33,1134,335, \mathbb{1} 36,237,138,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,347,5$ 48,3
\#30. ${ }^{\text {"II }}$ s $\quad$ pphylla"/
$\mathbb{1}, \mathbb{1} / 2 / 32, \mathbb{1} 3,1 \mathbb{1}, 25,2(6,1 / 27,2 / 4 / 5 / 88, \mathbb{1} 19,1 / 2 \mathbb{1 0}, \mathbb{1} 11,212,113,2 \mathbb{1} 4,2$ $15,116,117,219,320,221,122,1123,324,1 / 225,126,227,228,1$ $29,1 / 2 / 330,1 / 231,3 / 432,1 / 233,134,335,136,237,1138,339,1$ $41,242,143,1 / 244,145,347,548,2$
\#31.Jasiome < $\mathbb{L}_{0}>$ /
 $19, \mathbb{1} 20, \mathbb{1} 21,322, \mathbb{1} 23,324,225, \mathbb{1} 26,227, \mathbb{1} 28, \mathbb{1} 29,330, \mathbb{1} 31,332,233, \mathbb{1}$ $34,335, \mathbb{1} 36,237,238,339,141,242, \mathbb{1} 43, \mathbb{1} 44,245, \mathbb{1} 46,1149,3$

## \#32.Leg@usiam < $\mathbb{D}$ uram@le>/

 $17,2 \mathbb{1 9}, \mathbb{1} 20,121, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,327, \mathbb{1} 28, \mathbb{1} 29,130,131,332, \mathbb{1}$ $33,1144,335,136,237,1138,339,141,242,143,344,2 / 345,347,548,1$
\#33.Leptocodlon < (H1OOk. $\mathbb{I}_{0}$ ) Lem. $>1$
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1} 5, \mathbb{1} 6,27,3 / 48, \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} \mathbb{1} 6, \mathbb{1}$ $17,2 \mathbb{1 9}, \mathbb{1} 20,12 \mathbb{1}, \mathbb{1} 22,223, \mathbb{1} 24,125,126,227,328,129,330,131,4$ $32,233,1134,335,136,137,138,339,141,242, \mathbb{1} 43,144,1145,146,1$ 49,2
\#34.Mercieral $<\mathbb{A} . \mathbb{D} C$. $>1$
 $17,2 \mathbb{1} 9,120,221, \mathbb{1} 22,123,324,125,126,227,228,129,330,1131,432,1$ $33, \mathbb{1} 34,335,1136,437,238,339,1141,242,143,144,245,250,1$
\#35.Michauxxia < $\mathbb{L}^{9}$ Her.>/
$\mathbb{1}, 2 / 32, \mathbb{1} 3, \mathbb{1} 4,25,26,27,58, \mathbb{1} 9,2 / 3 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} 16, \mathbb{1}$ $17,2 \mathbb{1 9}, 320,221,122,1123,324,1125,1126,127,228,129,2 / 330,1131,1 / 2$ $32,133,1134,335,136,237,138,339,340,241,242,143,144,145,3$ $47,548,3$

```
#36.Micracodlom<A.IDC.>/
```



```
17,2 18,\mathbb{119, 1 20, 1 21, 1 22, 1 23,3 24,1 25,1 26,2 27,2 28,1129,1 30,1 31,3}
32,1133,11 34,2/3 35,1 36,2 37,1 38,2/3 39,1 41,2 42,14 43,144,1 4.5,1 46,1
49,11
#37.Muehnlbergellam <Feer>/
```




```
33,1 34,3 35,1 36,2 37,\mathbb{1 38,3 39,2 40,1 41,242,1143,1144,1145,3 47,6}
#38.Munsschim <IDummort.>/
```



```
19,1 20,1 21,1 22,1 23,3 24,1125,1 26,2 27,2/3 28,1129,3 30,1 31,2 32,2 33,1
34,3 35,1 36,2 37,11 38,3 39,1 41,2 42,1 43,2 44,1 45,34.7,4
#39.Nammacodom<Tlumlim>/
```



```
19,2 20,2 21,1122,1 23,3 24,1 25,2 26,3 27,2 28,1 29,1 30,1 31,3 32,1 33,1
34,3 35,1 36,2 37, 1 38,3 39,1 41,2 42,2 43,3 44,2 4.5,3 4,7,2
#{0.Nesocodlom<Thnonlim>/
```





```
#&1.0strowskkia <Regel>/
```




```
33,1 34,3 35,1 36,2 37,1 38,2 39,1 41,2 42,143,1 44,2 45,3 47,3
#&2.Peracarpm<|Hooksif.& Thomms.>/
```




```
34,3 35,1 36,3 37,2 38,3 39,1 41,2 42,1 43,144,2 45,2/3 47,5 48,3 50,11
\#\&3.Petkovia/
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20,2 2\mathbb{1,122,1 23,3 24,1 25,1 26,2 27,2 28,1 29,1 30,1 31,2 32,1133,1 34,3}
35,1 36,2 37,1 38,3 39,3 40,1 4 1,2 42,1 43,1 44,1 45,1 46,3
#\4.PPetrommarula <Vent. ex Hedw. \mathbb{T.>1}
```



```
19,3 20,1121,1 22,1123,3 24,2 25,1 26,2 27,2 28,1 29,1 30,1 31,7 32,2 33,1
34,3 35,1136,2 37,1 38,3 39,1 4 1,2 42,1 43,1 44,1 45,3 47,5 48,2
```


$\mathbb{1}, 3 / 7 \operatorname{2,} \mathbb{1} 3, \mathbb{1} 4,25,26,27,5 / 78, \mathbb{1} 9,3 \mathbb{1}, 3 \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1}, 2 \mathbb{1 5}, \mathbb{1} 16, \mathbb{1}$
$17,219,320,2$ 21, $122,123,324,225,126,227,228,1129,330,231,332,2$ $33, \mathbb{1} 34,335,116,237, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,347,548,1 / 2$
\# $\backslash$ 6. PIhysopllexis <(Emdll.) Schnur>/
$\mathbb{1}, \mathbb{1}, \mathbb{1} 3, \mathbb{1} 4,25,2 \quad 6,27,7 \mathbb{8}, \mathbb{1} 9,3 \mathbb{1}, 4 \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1 3}, 2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 7,2$ $19,320,2$ 21, $122,123,324,225,126,227,228,129,330,231,332,233,1$ $34,335, \mathbb{1} 36,237, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43,144,145,347,548,2$
\# 4 7.Platycodom <A.IDC.>1
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} \mathbb{4}, 25, \mathbb{1}(6,27,5 \mathbb{8}, \mathbb{1} 9,2 \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1 2}, \mathbb{1} \mathbb{1 3}, 2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$
$\mathbb{1 9}, 220,221,122, \mathbb{1} 23,224, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27,328,129,230,131,1132,233,1$
$34,235,1136,237,1138,239,141,242,143,144,245,146,149,1$
\# $\AA 8$. Papoviocodamia < $\mathbb{F e d} .>1$
$1,22, \mathbb{1} 3, \mathbb{1} 4,25,26,27,58, \mathbb{1} 9,3 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} \mathbb{1 6 , \mathbb { 1 }} \mathbf{1 7 , 2}$ $119,320,22 \mathbb{1}, 122, \mathbb{1} 23,324,125,126,227,228,129,330,131,332,133,1$ $34,335,1136,237,138,339,141,242,143,244,245,347,548,1$
\# 19. Prismatocarpus $<\mathbb{L} \cdot \mathbb{H e r} .>1$
$\mathbb{1}, \mathbb{1} / 2 / 52, \mathbb{1} 3, \mathbb{1} 4,25,2(6, \mathbb{1} / 27,2 / 3 / 48, \mathbb{1} 9, \mathbb{1} / 2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1}, 2 \mathbb{1}, \mathbb{1}$ $116,117,2 \mathbb{1}, 1 / 220,221,122,123,324,125, \mathbb{1} 26,327,228,1129,1 / 330, \mathbb{1}$ $31,332,133,1144,335,136,237,138,339,141,242, \mathbb{1} 43,344,245,3$ 47,1
\#50. Pseudlocodomopsis <Kikmarav>/
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25, \mathbb{1} 6,27,58, \mathbb{1} 9,2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$
 $34,335, \mathbb{1} 36,237,138,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45, \mathbb{1} 46,149,2$
\#51. Rapunncullus s.s.<(Fourrr.) A.L. Klharadze>/

$15, \mathbb{1} 16, \mathbb{1} 17,2 \mathbb{1} 9,320,221, \mathbb{1} 22, \mathbb{1} 23,324,1 / 225,126,227,228,1$
$29, \mathbb{1} 30, \mathbb{1} 31,332, \mathbb{1} 33, \mathbb{1} 34,335, \mathbb{1} 36,237, \mathbb{1} 38,339,1141,242,1$
$43,144,115,2 / 347,548,1 / 250,1 / 2$
\#52. R1higiopphyllonm <Hioclnst.>1
 $18,219, \mathbb{1} 20,1121,122,123,324,125,126,227,228,1129,330,1131,332,1$ $33,134,335,116,337,238,339,141,242,143,144,145,11646$
\#53. Roella <ll.>1
 $19,220,221,1122,123,324,1125,126,1 / 227,328,1129,1130,1131,232,1 / 2$ $33, \mathbb{1} / 234,335,136,237,1138,239, \mathbb{1} 41,242,113,1144,145,146,2$
\#S4. Roucela < Dionm.>1
$\mathbb{1}, 2 / 52, \mathbb{1} 3, \mathbb{1} 4,25,2 \mathbb{6}, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1 5}, \mathbb{1} 16, \mathbb{1} 17,2$ $119,320,2$ 21, $122, \mathbb{1} 23,324,125,126,227,228,129,1130,1131,332,1$ $33,134,335,116,237, \mathbb{1} 38,339,141,242,143,144, \mathbb{1} 45,347,548,3$
\#5s. Sergia < $\mathbb{F e d} .>1$
 $17,2119,320,221,122,123,324,125,126,227,228,129,230,1131,3$ $32,233,1134,335,136,237,138,339,1411,242,143,144,245,347,5$ 48,2
\#56.Sicyacodon <(Feer) J. Damloolditl
$1, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25,26,27, \mathbb{1} 8, \mathbb{1}, \mathbb{1} \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1 2}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} 16, \mathbb{1} 17,2$
$\mathbb{1 9}, 320,22 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228,129,330,1131,232,1133,1$
$34,335,116,237,138,339,340,241,242, \mathbb{1} 43, \mathbb{1} 44,145,347,548,3$
\#57.Siplhocodom <Turez. $>1$
$\mathbb{1}, 2 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25,2 \pi, 27,48, \mathbb{1} 9,1 / 2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6,2 \mathbb{1} 7,2$ $18,2 \mathbb{1}, \mathbb{1} 20, \mathbb{1} 21, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228,129,230, \mathbb{1} 31,332, \mathbb{1}$ $33,134,335,1136,237,238,339,141,242,143,144,145,146,2$
\#58.Symphyyamdral <A.DC. $>1$

$\mathbb{1 6 , 1 1 7 , 2 \mathbb { 1 9 } , 3 2 0 , 2 2 1 , 4 2 2 , \mathbb { 1 } 2 3 , 3 2 4 , \mathbb { 1 } 2 5 , \mathbb { 1 } 2 6 , 2 2 7 , 2 2 8 , 1 2 9 , 1 / 2 3 0 , 1 1 3 1 , 2}$
$32, \mathbb{1} 33,134,335,136,237,138,339,1 / 2 / 340,141,242,143,144,145,3$ $47,548,3$
\#59.Theilera <E. 1 Phinillips>/
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25,26,27,48, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} \mathbb{1}, \mathbb{1} 17,2$ $\mathbb{1 9}, \mathbb{1} 20,221, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25,126,227,228, \mathbb{1} 29,330,1131,332,133,1$ $34,335, \mathbb{1} 36,237,138,339, \mathbb{1} 41,242, \mathbb{1} 43,144, \mathbb{1} 45,146,149,2$
\#GV.Trachnelium $<\mathbb{L} .>1$
$\mathbb{1}, 52, \mathbb{1} 3, \mathbb{1} 4,25,2 \mathbb{6}, 27,38, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} \mathbb{1 3}, 2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$ $19, \mathbb{1} 20, \mathbb{1} 21, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,327,228, \mathbb{1} 29,330, \mathbb{1} 31,532,233, \mathbb{1}$ $34,335,1136,237,138,339,141,242, \mathbb{1} 43,144,245,347,548,3$
\#®1.Treichelia< $<\mathbb{V}$ atke>/
$\mathbb{1}, 42, \mathbb{1} 3, \mathbb{1} 4,25,26,27,48, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1 2}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$ $\mathbb{1 9}, 220,221, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,227,228,129,130,131,332,133, \mathbb{1}$ $34,335,136,237,238,339,1411,242,143,244,1145,347,7$
\#62. Triodlamis $<\mathbb{R}$ afi. $>1$
$\mathbb{1}, 32, \mathbb{1} 3, \mathbb{1} 4,25,2 \mathbb{6}, \mathbb{1} / 27,58, \mathbb{1} 9,2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2,2 \mathbb{1} 3, \mathbb{U} \mathbb{1} 4,2 \mathbb{1 5}, \mathbb{1} \mathbb{1} 6, \mathbb{1}$ $17,2 \mathbb{1 9}, 320,221,1222,233,324,125,126,227,228,129,230,131,3$ $32,133,1144,335,236,237,1138,339,141,242,143,244,245,347,5$ 48,2
\#63.WaInlembergia <Schrad. ex $\mathbb{R}$ outh>/



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27,2 28,1129,1/2/3 30,11 31,1/3/5 32,1/2 33,1/2 34,2/3 35,1 36,2 37,1
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#G4.Zemgamalra < PP.HH. DDavis>/
```




```
34,3 35,1 36,2 37,1 38,3 39,3 40,2 41,242,1 43,1 44,1145,3 4,7,548,3
#65.L.\mp@code{belia <L.}>/
1,1/2/3 2,2 3,2 \,2 5,2 6,2 7,9 8,\mathbb{1 m,2 10, 111,2 12, 113,2 14,2 15,2 16,1}
17,2 19,1 20,1 21,4 22,1 23,1/2 24,1 25,1 26,3 27,2 28,1 29,3 30,2 31,3
32,1/2 33,1 34,3 35,1 36,2 37,1 38,3 39,1 41,1/2 42,1 43,1/2 44,1 45,1
46,144,3
* END
```

12.1.1.4 FLOWERSC.DAT (Flowers \& Fruits)...Cammpamuleae data subset (Delita data finle for Pamkey, SC3)

## *ITEM DESCRIPTIONS

$$
\begin{aligned}
& \text { \#1. Adlemophora < Fisclh. }>1 \\
& \mathbb{1}, 2 \mathbb{2}, \mathbb{1}, \mathbb{1} \mathbb{4}, \mathbb{1} 5,2 \mathbb{2}, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1 0}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 4,2 \mathbb{2}, \mathbb{1} 16, \mathbb{1} 17,2 \\
& 19,220,221,122,1123,324,125,126,2 / 327,328,129,1 / 2 / 330,1131,3 \\
& 32,233,134,335,136,237,138,339,141,242,143,144,1 / 245,3 \\
& \text { 47,5 48,3 }
\end{aligned}
$$

\#2. Astrocealom < $\operatorname{Fed} .>1$
 $17,219,320,221, \mathbb{1} 22, \mathbb{U} 23,324, \mathbb{1} 25,126,227,128,1 \operatorname{lig}, 230,131,332, \mathbb{1}$ $33, \mathbb{1} 34,335,116,237, \mathbb{1} 38,339,141,242,143,144,145,347,548,3$
\#3.Asymewmm <Griselb. \& Schemks.>1
$1,2 / 32,113,14,25,26,27,58,19,310,211,212,113,214,215,116,1$ $17,219,2 / 320,2211,1122,123,324,1 / 225,12 \pi, 2 / 327,228,129,2 / 330,1 / 2$ $31,332,1 / 233,134,335,136,237,1138,339,141,242,1 / 243,1 / 244,1 / 2 / 3$ $45,347,548,1 / 2$
\#d.Azorima < Feer>/
$\mathbb{1}, 22, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1} 5,2 \mathbb{2}, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2 \mathbb{1}, \mathbb{1}$ $20,1121,122,123,324,125,1126,127,328,129,130,131,1132,133,1134,3$ $35,136,237,138,339,141,242,143,144,145,347,548,3$
\#S. Brachycodom <Fed.>1
 $\mathbb{1 7}, 2 \mathbb{1} 9, \mathbb{1} 2 \mathbb{1}, \mathbb{1} 21, \mathbb{1} 22, \mathbb{U} 23,324, \mathbb{1} 25, \mathbb{1} 26,327, \mathbb{1} 28,129,130,131,332,1$ $33,134,3$ 35,1 $16,237,1138,3$ 39, $141,242,143,244,145,347,548,1$
\#б. Camppamula <LL.: essemciallly Sect.Medinum>/
$1, \mathbb{1} / 2 / 3 / 48, \mathbb{1} 3,14,1 / 25,26,1 / 27,1 / 2 / 4 / 68,19,1 / 210,1111,212,1 / 213,2$
$\mathbb{1 4}, 215,1116,117,219,320,221,1 / 2 / 422,1 / 223,324,125,126,1 / 2 / 327,2$
$28,129,1 / 230,131,2 / 332,133,1134,2 / 335,136,237,138,339,1 / 2 / 3$
$40,1 / 241,242,143,144,1 / 245,2 / 347,548,350,1 / 2$
\#7.Campamulastrumm < Small: C.ammericama>1
 $\mathbb{1 9}, 320,2$ 21, $122,223,324,225,126,327,228,129,330,2 \operatorname{31,3} 32,233,1$ $34,335,136,237,138,339,141,242,143,244,145,347,548,1$
\#8. Cryptocodom <Tred.>1
$1,72, \mathbb{1} 3,14,25,2 \llbracket, 1 / 27,2 / 48,119,210,111,212,113,214,215,1116,1117,2$ $\mathbb{1 9}, 32 \mathbb{2 0}, 221, \mathbb{1} 22, \mathbb{1} 23,324,1125,126,227,228,129,130,1131,232,133,1$ $34,335,1136,237,118,339,240,1141,242,143,144,145,347,548,2$

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#9.Cylimdlrocarpa< <Rege\>/
```

$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25,26,27,58, \mathbb{1} 9,3 \mathbb{1}, 2 \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 7,2$
$\mathbb{1 9}, 320,22 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,327,228, \mathbb{1} 29, \mathbb{1} 30, \mathbb{1} 31,332, \mathbb{1} 33, \mathbb{1}$
$34,335, \mathbb{1} 36,237,138,339,141,242, \mathbb{1} 43,344,345,347,548,1$
\#11. Diosphneera <Buser>1
$\mathbb{1}, \mathbb{1} / 52, \mathbb{1} 3, \mathbb{1} 4,25,2 \quad 6,27,2 / 3 / 4 / 68, \mathbb{1} 9, \mathbb{1} / 2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{2}, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1}$
$16, \mathbb{1} 17,2 \mathbb{1} 9,120,221, \mathbb{1} 22, \mathbb{1} 23,324,125, \mathbb{1} 26,327, \mathbb{1} 28, \mathbb{1} 29,330,1$
$31,3 / 532, \mathbb{1} 33, \mathbb{1} 34,335, \mathbb{1} 36,237,238,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44,1 / 2$
$45,347,548,3$
\#11.Edraiimmthus <(A.DC.) $\mathbb{D C} \mathbb{C}_{0}>1$
$\mathbb{1}, \mathbb{1} / \mathbb{A} / 7 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25,2 \mathbb{2}, \mathbb{1} 8, \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1 2}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1}, 2 \mathbb{1 5}, \mathbb{1} 16, \mathbb{1} 17,2$
$\mathbb{1 9}, 320,221, \mathbb{1} 22,123,324,1 / 225,126,1 / 227,228,1129,130,131,232, \mathbb{1}$
$33,1134,335,1136,237,138,339,1 / 240,141,242,1143,1144,145,146,3$
\#12. Feeria <Buser>/
$\mathbb{1}, 52, \mathbb{1} 3, \mathbb{1} 4,25,2 \mathbb{1}, 27,38, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} 16, \mathbb{1} 17,2$
$19, \mathbb{1} 20,12 \mathbb{1}, \mathbb{1} 22,123,324, \mathbb{1} 25, \mathbb{1} 26,327,228,129,330,131,332,133,1$
$34,335,116,437,138,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44,245,146, \mathbb{1} 49,2$
\#13. Gadelnia <Schonlkima>/
$\mathbb{1}, 2 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25,2 \mathbb{6}, \mathbb{1} / 27,58, \mathbb{1} 9,2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 7,2$
$19,220,22 \mathbb{1}, \mathbb{1} 22,223,324, \mathbb{1} 25,126,227,228, \mathbb{1} 29,1130,1131,332,1133,11$
$34,335, \mathbb{1} 36,237, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,347,548, \mathbb{1} / 2$
\#14. Githopsis < Nintt.>1
$\mathbb{1}, \mathbb{1} / 22, \mathbb{1} 3, \mathbb{1} 4,25,26,1 / 27,2 / 68, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 5, \mathbb{1} \mathbb{1} 6, \mathbb{1}$
$17,2 \mathbb{1} 9, \mathbb{1} 2 \mathbb{2}, 221, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25,126,327,228, \mathbb{1} 29,130,131,332,1$
$33,114435,1136,237,1138,339,1141,242,143,244,1 / 245,1 / 246,3$
$50,1 / 2$
\#15. Hamabunsaya <Nakai>/

$\mathbb{1 9}, 320,22 \mathbb{1}, 422, \mathbb{1} 23,324,125,126,227,228,129, \mathbb{1} 30, \mathbb{1} 31,232,1133,1$
$34,335,136,237,138,339,141,242,143,144,1145,347,548,3$
\#16. Heterocodom < $\mathbb{N}$ utt. $>1$

$19, \mathbb{1} 20,221, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228,129,1130,1131,332,133,1$
$34,335, \mathbb{1} 36,237, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,347,548,3$
\#17. Hommocodom < $\mathbb{D}$. Y . $\mathbb{H}$ omg>/
$\mathbb{1}, \mathbb{1} / 3 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25,26,27,28, \mathbb{1} 9,2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} 16, \mathbb{1}$
$17,2 \mathbb{1 9}, \mathbb{1} 20,221, \mathbb{1} 22,123,324,125,126,227,228, \mathbb{1} 29,1130,131,3$ $32, \mathbb{1} 33,1134,335, \mathbb{1} 36,237,138,339,141,242, \mathbb{1} 43,144,145,347,5$ 48,3

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#18."Ismplhy#la"/
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15,1116,114,2 19,3 20,2 21,1 22,1 23,3 24,1/2 25,1 26,2 27,2 28,1
29,1/2/3 30,1/2 31,3/4 32,1/2 33,1 34,3 35,1 36,2 37,1138,3 39,1
41,2 42,1 43,1/2 &4,1 45,3 47,5 48,2
```

\#19.Jasione <L. $>$ /

$\mathbb{1 9}, \mathbb{1} 20,1121,322, \mathbb{1} 23,324,225, \mathbb{1} 26,227, \mathbb{1} 28,129,330, \mathbb{1} 31,332,233,1$
$34,335, \mathbb{1} 36,237,238,339,141,242, \mathbb{1} 43, \mathbb{1} 44,245, \mathbb{1} 46, \mathbb{1} 49,3$
\#20.Legounsia <Dinramale>/
$\mathbb{1}, \mathbb{1} / 2 / 3 / 52, \mathbb{1} 3, \mathbb{1} \uparrow, 25,2(6,27,58, \mathbb{1} \Phi, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13, \mathbb{1} \mathbb{1}, 2 \mathbb{1 5}, \mathbb{1} \mathbb{1} 6, \mathbb{1}$
$\mathbb{1} 7,2 \mathbb{1} 9, \mathbb{1} 2 \mathbb{O}, \mathbb{1} 21, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,327, \mathbb{1} 28, \mathbb{1} 29, \mathbb{1} 30, \mathbb{1} 31,332, \mathbb{1}$
$33,134,335,1136,237,1138,339,141,242,143,344,2 / 345,347,548,1$
\#21.Michnauxia < $\mathbb{L}^{`}{ }^{9} \mathrm{Her}_{0}>1$
$\mathbb{1}, 2 / 3 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25,26,27,58, \mathbb{1} 9,2 / 310, \mathbb{1} 11,2 \mathbb{1 2 ,} \mathbb{1} 13,2 \mathbb{1} 4,215, \mathbb{1} 16, \mathbb{1}$
$17,2 \mathbb{1 9}, 320,22 \mathbb{1}, 122,123,324,125,126,127,228,129,2 / 330,1131,1 / 2$
$32,1133,1134,335, \mathbb{1} 36,237,138,339,340,241,242, \mathbb{1} 43,144, \mathbb{1} 45,3$
$47,548,3$
\#22.Murlhilbergella < $<$ Feer>/
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25,2(6, \mathbb{1} / 27,2 / 4) 8, \mathbb{1} 9,2 \mathbb{1 0}, \mathbb{1} 1,2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} \mathbb{1}, \mathbb{1}$
$17,219,220,221, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228, \mathbb{1} 29,130,131,332, \mathbb{1}$
$33, \mathbb{1} 34,335, \mathbb{1} 36,237,138,339,240,141,242, \mathbb{1} 43, \mathbb{1} 44,145,347,6$
\#23.Munsschia < $\mathbb{D}$ numort.>1
$\mathbb{1}, 2 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25, \mathbb{1} 6,27,38, \mathbb{1}, 2 \mathbb{1} 0, \mathbb{1} \mathbb{1}, 2 \mathbb{1 2}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$
$\mathbb{1} 9,1120,1121,122,1123,324,125,126,227,2 / 328,129,330,131,232,233,1$
$34,335,116,237,138,339, \mathbb{1} 41,242,143,244, \mathbb{1} 45,347,4$
\#24.Peracarpa<Hooksofo Thnoms.>1
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25,26,27,2 \mathbb{8}, \mathbb{1}, 2 \mathbb{1}, \mathbb{1} 11,2 \mathbb{1}, \mathbb{1} \mathbb{1 3}, 2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$
$\mathbb{1 9}, \mathbb{1} 20,12 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,227,228, \mathbb{1} 29, \mathbb{1} 30, \mathbb{1} 31,332, \mathbb{1} 33, \mathbb{1}$
$34,335,116,337,238,339,141,242,143,144,245,2 / 347,548,350,1$
\#25. Petkovia/

$20,221,122, \mathbb{1} 23,324, \mathbb{1} 25,126,227,228,129,130,131,232,133,134,3$
$35, \mathbb{1} 36,237, \mathbb{1} 38,339,340, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45, \mathbb{1} 46,3$
\#26.Petromarula <Vemt. ex Hedlw. $\mathbb{f} .>1$
$\mathbb{1}, 32, \mathbb{1} 3, \mathbb{1} 4,25,26,27,58, \mathbb{1} 9,3 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} 16, \mathbb{1} 17,2$
$19,320, \mathbb{1} 2 \mathbb{1}, \mathbb{1} 23,1123,324,225,126,227,228,129, \mathbb{1} 30, \mathbb{1} 31,732,233,1$
$34,335, \mathbb{1} 36,237, \mathbb{1} 38,339,141,242, \mathbb{1} 43,144, \mathbb{1} 45,347,548,2$
\#28.PThysoplexis < (Emdll.) Schour>1
 $119,320,221,1122,123,324,225,126,227,228,129,330,231,332,233,1$ $34,335,1136,237, \mathbb{1} 38,339, \mathbb{1} 41,242,143, \mathbb{1} 44, \mathbb{1} 45,347,548,2$
\#29.P@peviocodomia < $\mathbb{F e d} .>1$
 $119,320,221, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228,129,330,1131,332,1133,11$ $34,335, \mathbb{1} 36,237, \mathbb{1} 38,339,141,242, \mathbb{1} 43,244,245,347,548,1$
\#30. Prismatacarpus $<\mathbb{L} \cdot \mathbf{H e r} .>1$
$\mathbb{1}, \mathbb{1} / 2 / 52, \mathbb{1} 3, \mathbb{1} 4,25,2(6,1 / 27,2 / 3 / 48, \mathbb{1} 9,1 / 2 \mathbb{1} 0, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1}, 2 \mathbb{1} 5, \mathbb{1}$ $116,117,219,1 / 220,221, \mathbb{1} 22, \mathbb{1} 23,324,125,126,327,228,1129,1 / 330,1311,3$ $32,133,1134,335,136,237,138,339,141,242,143,344,245,347,1$
\#31. $\mathbb{R}$ apunculus s.s.<(Fourrr.) A.L. Kharadze>/
$\mathbb{1}, \mathbb{1} / 2 / 3 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,25,2(6, \mathbb{1} / 27,58, \mathbb{1} 9,2 / 3 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} / 2 \mathbb{1}, \mathbb{1} / 2 \mathbb{1} 4,2$ $15,1116,117,219,320,221, \mathbb{1} 22,223,324,1 / 225,126,227,228,1$
$29, \mathbb{1} 30, \mathbb{1} 3 \mathbb{1}, 332, \mathbb{1} 33,134,335,136,237,138,339,141,242,11$
$43,144,1145,2 / 347,548,1 / 250,1 / 2$
\#32. $\mathbb{R}$ oucela $<\mathbb{D}$ amm. $>1$
$\mathbb{1}, 2 / 52, \mathbb{1} 3, \mathbb{1} 4,25,26, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1 5}, \mathbb{1} \mathbb{1}, \mathbb{1} 17,2$ $19,320,221,122,123,324,125,126,227,228,129,130,131,332,11$ $33, \mathbb{1} 34,335,136,237, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,347,548,3$
\#33.Sergia < Fedl.>1
$\mathbb{1}, 22, \mathbb{1} 3, \mathbb{1} 4,25,26, \mathbb{1} / 27,58, \mathbb{1} 9,2 / 3 \mathbb{1}, \mathbb{1} 11,2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1} 4,215, \mathbb{1} 16, \mathbb{1}$
$17,219,320,221, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25,1126,227,228,1129,230,1131,3$ $32,233,134,335,136,237,138,339,141,242,143,144,245,347,5$ $4.8,2$
\#34.Sicyocodom <(Feer) J. Damboldt>/
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25,26,27, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 2, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$ $19,320,221, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228,129,330,1131,232,1133, \mathbb{1}$
$34,335,1136,237,138,339,340,241,242,143,144,145,347,548,3$
\#35.Symplhyandra <A.DDC.>1
$\mathbb{1}, \mathbb{1} / 2 \mathbb{2}, \mathbb{1} 3, \mathbb{1} 4,1 / 25,26,1 / 27,2 / 58, \mathbb{1} 9, \mathbb{1} / 2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1}$ $16,117,219,320,221,422,1123,324,125,126,227,228,129,1 / 230,131,2$ $32,1133,134,335,136,237,1138,339,1 / 2 / 340,141,242,143,144,145,3$
$47,548,3$

```
#3G.Trachneliumm<\mathbb{L}>1
```



```
19,1 20,1 21, 11 22,1 23,3 24,1 25,\mathbb{1 26,3 27,2 28,1129,3 30,1 31,5 32,2 33,1}
34,3 35,1 36,2 37,1 38,3 39,1 41,2 42,1 43,1 44,2 45,3 47,5 48,3
#37.Triodamis <\mathbb{Rafi}>1
```



```
17,2 19,3 20,2 21,1 22,2 23,3 24,1 25,1126,2 27,2 28,1 29,2 30,1 31,3
32,1 33,1 34,3 35,2 36,2 37,1 38,3 39,1 41,242,1143,244,245,3 47,5
48,2
#38.Zeungamdra <PP.H. DDavis>/
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```
19,3 20,2 21,1 22,1 23,3 24,1 25,1 26,2 27,2 28,1 29,3 30,2 31,6 32,1 33,1
34,3 35,1 36,2 37,1 38,3 39,3 40,2 41,242,1 43,1 44,1 45,3 47,3 48,3
* END
```

 data fille for Pamkey, SC3)

## *ITEMI $\mathbb{D E S C R I P T I D N S}$

\#1.Campamunnoea <Blunme>/
 $20,121,122, \mathbb{U} 23,224,125,1126,1127,328,129,230,131,132,133, \mathbb{1} 34,2$ $35,1136,237,1138,2 / 439,1141,1142,1$
\#马,Cam@rim@ < $\mathbb{L}_{0}>/$
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1} 5, \mathbb{1}(6,1 / 2$ $17,2 \mathbb{1} 9, \mathbb{1} 2 \mathbb{1}, \mathbb{1} 21, \mathbb{1} 22, \mathbb{1} 23,224,125,126,127,328, \mathbb{1} 29,130,1131,132,2$ $33,134,335,136,237,138,339,141,142,1$
\#3.Codamopsis < Wanli>1
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} \mathbb{4}, \mathbb{1} 5, \mathbb{1} 6, \mathbb{1} / 27,48, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} / 2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1} 4, \mathbb{1} / 2 \mathbb{1} 5, \mathbb{1} 16, \mathbb{1}$ $\mathbb{1 7 , 2} \mathbb{1} 9, \mathbb{1} 20, \mathbb{1} 2 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23, \mathbb{1} 24, \mathbb{1} 25, \mathbb{1} 26, \mathbb{1} 27,328, \mathbb{1} 29, \mathbb{1} 30, \mathbb{1} 3 \mathbb{1}, \mathbb{1}$ $32, \mathbb{1} 33,134,2 / 335,136,237,1138,2 / 3 / 439,141,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1}$
$4.5,114.6,149,2$

 $19,120,121,322,123, \mathbb{1} 24,125,126,327,128,129, \mathbb{1} 30,1313332,233,1$
$34, \mathbb{1} 35, \mathbb{1} 36, \mathbb{1} 37, \mathbb{1} 38, \mathbb{1} 39, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 45, \mathbb{1} 46, \mathbb{1} 49, \mathbb{1}$
\#5.Cyclocodom/
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1}, \mathbb{1}(\mathbb{6}, \mathbb{1} \mathbb{S}, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} 12, \mathbb{1} 13,2 \mathbb{1} 4, \mathbb{1} 15, \mathbb{1} 16, \mathbb{1} 17,2 \mathbb{1} 9, \mathbb{1}$ $20,121,122, \mathbb{U} 23,224,125,1126,127,328,129,130,131,132,133,134,2$ $35,1136,237,1138,1 / 2 / 439,1141,142,1$
\#б.Echimocodom <D. Y. Homg>/
$1, \mathbb{1} / 22, \mathbb{1} 3, \mathbb{1} 4,25, \mathbb{1} 6,27,4 / \sigma \mathbb{8}, \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1}$ $17,2 \mathbb{1 9}, \mathbb{1} 20,221,322, \mathbb{U} 23, \mathbb{1} 24,1125,126,227,228, \mathbb{1} 29,130,131,1$ $32, \mathbb{1} 33,1134,335, \mathbb{1} 36,237, \mathbb{1} 38,239,141,242, \mathbb{1} 43,144, \mathbb{1} 45,146,1$ $49,1 / 2 / 3$
\#7." ${ }^{\text {Himimalcodlom" <Codlomapsis dicemtrifolia>/ }}$
 $20, \mathbb{1} 21,122,123, \mathbb{1} 24, \mathbb{1} 25,126,127,328,129, \mathbb{1} 30, \mathbb{1} 31, \mathbb{1} 32, \mathbb{1} 33,1134,2$
$35, \mathbb{1} 36,237,1138,239, \mathbb{1} 41,242, \mathbb{1} 43, \mathbb{1} 44, \mathbb{1} 45,146,149,2$
\#8.Leptocodom <(Hionk. fi.) Lem. $>1$
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1} 5, \mathbb{1} 6,27,3 / 48, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1} 1,2 \mathbb{2}, \mathbb{1} \mathbb{1 3}, 2 \mathbb{1} 4,2 \mathbb{1 5}, \mathbb{1} 16, \mathbb{1}$ $17,2 \mathbb{1 9}, \mathbb{1} 20,121,122,223,124,125,126,227,328,129,330,131,4$ $32,233, \mathbb{1} 34,335, \mathbb{1} 36,137, \mathbb{1} 38,339, \mathbb{1} 41,242, \mathbb{1} 43,144,145,146,1$ $4 D, 2$

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#\.Ostrowskia< <Regell>/
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33,1 34,3 35,1 36,2 37,1 38,2 39,1 41,2 42,1 43,1 44,2 45,3 47,3
#10.Platycodmm<A.DD.>/
```



```
19,2 20,2 21,1 22,\mathbb{123,2 24,\mathbb{1 25,1}26,1 27,3 28,11 29,2 30,1 31,1 32,2 33,1}
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#11.Pseundocodomapsis <K@mmarov>/
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```
19,3 20,2 21,1122,\mathbb{1 23,1 24,2 25,1 26,2 27,3 28,1129,1130,1 31, 1 32,1133,1}
34,3 35,1 36,2 37,1 38,3 39,1 41,2 42,1 43,1 44,1 45,1 4\sigma,\mathbb{1 49,2}
#12.Lobelia <L.>/
1,1/2/3 2,2 3,2 4,2 5,2 6,2 7,9 8,\mathbb{1 M,2 10,1 11,2 12,113,2 14,2 15,2 16,1}
```



```
32,1/2 33,1 34,3 35,1 36,2 37,1 38,3 39,1 41, 1/2 42,1 43,1/2 44,1 45,\mathbb{1}
46,140,3
* END
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12.1.1. $\mathbb{F}$ FLOWERSW.DAT (Flowers \& Fruits)...Walnlembergeae data sulbset (Delta data fille for Pamkey, SC3)

## *ITEMI $\mathbb{D E S C R I P T I O N S}$

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#1.BBeremice <Tun.>/
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#2.Ceplhalostigmma/
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19,2 20,1/2 21,1 22,1 23,3 24,1 25,1 26,2/3 27,2 28,1129,2 30,1/2 31,4 32,1
33,1 34,2 35,1 36,2 37,1/2 38,3 39,1 41,2 42,1 43,1/2 44,1/2 4.5,1 46,\mathbb{1}
49,2/3
```

\#3. Crateracapsa <Hidlliard \& $\mathbb{B}$.L. Burtt>/
$\mathbb{1}, \mathbb{1} / 2 / 42, \mathbb{1} 3,114,25,2(6,1 / 27,2 / 4 / 5 / 68,119,1 / 210,1 \mathbb{1}, 1 / 212, \mathbb{1} 13,214,2$
$\mathbb{1 5 ,} \mathbb{1} 16, \mathbb{1} 17,2 \mathbb{1 9}, \mathbb{1} 20, \mathbb{1} / 221, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228, \mathbb{1} 29,1130, \mathbb{1}$
$31,232,1133,1134,335,136,237,138,439,141,242, \mathbb{1} 43,144,145,146,2$
\# 4 . Feeria < $\mathbb{B}$ user>/
$\mathbb{1}, 52, \mathbb{1} 3, \mathbb{1} 4,25,2 \quad 6,27,3 \mathbb{S}, \mathbb{1}, \mathbb{1} \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{2}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} \mathbb{1} 6, \mathbb{1} 17,2$
$19,120, \mathbb{1} 21, \mathbb{1} 22,123,324,125,126,327,228,1129,330,1131,332,1133,1$
$34,335,136,437,138,339,141,242,143,144,245,146,149,2$
\#5. Githopssis < Nartt.>1
$\mathbb{1}, \mathbb{1} / 2 \mathbf{2}, \mathbb{1} 3, \mathbb{1} \mathbb{4}, 25,2 \operatorname{6}, \mathbb{1} / 27,2 / 6 \mathbb{6}, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13, \mathbb{1} \mathbb{1}, 2 \mathbb{1 5}, \mathbb{1} 16, \mathbb{1}$
$17,2 \mathbb{1 9}, \mathbb{1} 20,22 \mathbb{1}, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,327,228, \mathbb{1} 29, \mathbb{1} 30,113,332, \mathbb{1}$
$33, \mathbb{1} 34,335,1136,237,1138,339,141,242,143,244,1 / 245,1 / 246,3$
$50,1 / 2$
\#б. Gumillaaea <Thunlim>/
 $20,1 / 22 \mathbb{1}, \mathbb{1} 22,123,324, \mathbb{1} 25, \mathbb{1} 26,327,228, \mathbb{1} 29,1130,1131,332, \mathbb{1} 33,1 / 2$ $34,335, \mathbb{1} 36,237,1138,339,141,242,243,2 / 344,1 / 245,250,1$
\#7. Heterochnaemia <A. $\mathbb{D C}$. $>1$
$\mathbb{1}, \mathbb{1} / 22, \mathbb{1} 3, \mathbb{1} 4, \mathbb{1} / 25,26,1 / 27,28, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1 5}, \mathbb{1} \mathbb{1}, \mathbb{1}$ $17,2 \mathbb{1 9}, \mathbb{1} 20,12 \mathbb{1}, 122,123,324,125,126,227,328,129,1 / 230,1131,232, \mathbb{1}$ $33, \mathbb{1} 34,335, \mathbb{1} 36,237,138,339, \mathbb{1} 41,242,143, \mathbb{1} 44, \mathbb{1} 45, \mathbb{1} 46,149,2$
\#8.Jasiome < $\mathbb{L} .>1$
 $\mathbb{1 9}, \mathbb{1} 20,1121,322, \mathbb{1} 23,324,225, \mathbb{1} 26,227,1128,1129,330,131,332,233,1$ $34,335,1136,237,238,339,141,242,143,144,245,146,149,3$
\#15.Prismatacarpous [LLHer:](LLHer:)1
$\mathbb{1}, \mathbb{1} / 2 / 52, \mathbb{1} 3,14,25,2(6,1 / 27,2 / 3 / 48,19,1 / 210, \mathbb{1} 11,2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1}$
$16,117,8 \mathbb{1} 9, \mathbb{1} / 220,221, \mathbb{1} 22, \mathbb{1} 23,324,125, \mathbb{1} 26,327,228, \mathbb{1} 29,1 / 330, \mathbb{1} 31,3$ $32, \mathbb{1} 33,1134,335,1136,237,138,339,141,242, \mathbb{1} 43,344,245,347, \mathbb{1}$
\#16. $\mathbb{R}$ hinigioplhyllanm <Hicclost.>/
$\mathbb{1}, 42, \mathbb{1} 3, \mathbb{1} 4,25,26,27,48, \mathbb{1}, \mathbb{1} / 2 \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} \mathbb{1 3}, 2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} \mathbb{1} 6,2 \mathbb{1 7}, 2$ $18,2 \mathbb{1 9}, \mathbb{1} 20,1121, \mathbb{1} 22, \mathbb{1} 23,324,125, \mathbb{1} 26,227,228, \mathbb{1} 29,330,131,332,1$
$33,134,335,116,337,238,339,141,242,143,144,145,146,2$
\#17. Raclia $<\mathbb{L} .>1$
$\mathbb{1}, \mathbb{1} / 42, \mathbb{1} 3, \mathbb{1} 4,25,26, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} / 2 \mathbb{1}, \mathbb{1} \mathbb{1}, \mathbb{1} 12, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} 16, \mathbb{1} 17,2$ $\mathbb{1 9}, 220,221,122,1123,324,1125,1126,1 / 227,328,129,130,1131,232,1 / 2$ $33, \mathbb{1} / 234,335,136,237,1138,239,141,242,143,144,145,146,2$

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#18.Siplnocodom<Turez.>/
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$\mathbb{1}, 22, \mathbb{1} 3, \mathbb{1} 4,25,26,27,48, \mathbb{1} 9, \mathbb{1} / 2 \mathbb{1 0}, \mathbb{1} \mathbb{1}, 2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,2 \mathbb{1} 5, \mathbb{1} 16,2 \mathbb{1} 7,2$
$18,219,120,1121, \mathbb{1} 22, \mathbb{1} 23,324,125,126,227,228,129,230,1131,332,1$
$33, \mathbb{1} 34,335,136,237,238,339, \mathbb{1} 41,242, \mathbb{1} 43,144,145,146,2$
\#19.Theilera <E.PThillips>/
$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 4,25,26,27,48, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} \mathbb{1}, 2 \mathbb{1}, \mathbb{1} \mathbb{1} 3,2 \mathbb{1} 4,2 \mathbb{1}, \mathbb{1} 16, \mathbb{1} 17,2$ $19, \mathbb{1} 20,2$ 21, $\mathbb{1} 22,123,324,125,126,227,228, \mathbb{1} 29,330,131,332,133,1$ $34,335,136,237,138,339,141,242,143,144,145,146,149,2$
\#20.Treichelia < Vatke>/
 $\mathbb{1 9}, 220,221, \mathbb{1} 22, \mathbb{1} 23,324, \mathbb{1} 25, \mathbb{1} 26,227,228, \mathbb{1} 29,130,131,332,133,1$ $34,335,136,237,238,339,1411,242,143,244,1145,347,7$
\#21. Walllembergia <Schrad. ex $\mathbb{R o t h}>1$
$\mathbb{1}, \mathbb{1} / 2 / 3 / 72, \mathbb{1} 3,1 \mathbb{1}, 25,26,1 / 27,5 / 88,19,1 / 2 / 310,1111,1 / 212,113,2$ $\mathbb{1 4}, 2 \mathbb{1}, \mathbb{1} 16,117,1 / 2 \mathbb{1} 9,220,1 / 221, \mathbb{1} 22,1 / 223,324, \mathbb{1} 25, \mathbb{1} 26,2 / 3$ $27,228,1129,1 / 2 / 330,1131,1 / 3 / 532,1 / 233,1 / 234,2 / 335,136,237,1$ $38,2 / 319,114,242,143,144,1 / 245,116,1149,1 / 2 / 3$
\#22. Lobelia $<\mathbb{L}_{.}>1$
$\mathbb{1}, \mathbb{1} / 2 / 32,23,24,25,2(6,27,98, \mathbb{1} 9,2 \mathbb{1 0}, \mathbb{1} 11,2 \mathbb{1} 2, \mathbb{1} 13,2 \mathbb{1} 4,215,2 \mathbb{1}, 1$ $17,2 \mathbb{1 9}, \mathbb{1} 20,121,422,123,1 / 224,1$ 25, $1126,327,228,129,330,231,3$ $32,1 / 233,1144,335,136,237,118,339,141,1 / 242,143,1 / 244,145,1$ $4.6,149,3$

* $\mathbb{E N D}$
12.1.1.7 CAMPPAL. $\mathbb{D} A T \mathbb{T}$ (Pollem) oo.Pollem data set (Delta data file for Pamkey, SC3)

```
*ITEMIDESCRIPTIONS
#1.Adem@phncra <Fisclm.>/
```



```
#2.Asymemma/
```



```
#3.Campmamulla/
```



```
#\Uparrow.Cæmppamun\astrunmm<Small>/
1,\mathbb{1}2,\mathbb{1}/2 3,U\mathbb{U},3,S,\mathbb{1},\mathbb{1}/\mathcal{B}9,\mathbb{1}\mathbb{1},\mathbb{1}\mathbb{1},\mathbb{1}12,\mathbb{1}\mathbb{1}3,\mathbb{1}
#5.C\mppamumneea/
```



```
#G.C风marima/
```



```
#7.Codamapsis/
```



```
#8.Cyam@mithus/
```



```
#D.Echimocodom <\mathbb{D.Y. Himg>/}
```



```
#10.Edraiamthus/
```



```
#11.Gadlellia/
1,\mathbb{1}2,\mathbb{1}3,\mathbb{U}\mathbb{Q},\mathbb{S},\mathbb{U}\mathbb{&},\mathbb{1}\mathbb{D},\mathbb{U}\mathbb{10},\mathbb{U}\mathbb{1}\mathbb{1},\mathbb{U}\mathbb{12},\mathbb{U}\mathbb{1},\mathbb{U}
#12.Githmppsis/
```



```
#13.Guminlaeal <Thunlim>/
1,\mathbb{2},\mathbb{1/2 3,\mathbb{1 4,3 5,5 8,1/2 פ,U 10,U 11,U 12,U 13,U}}\mathbf{|}|
#14.Hamabunsaya<Nakai>/
1,\mathbb{1 2,2 3,U }\mathbb{Q},3 5,Z/3 &,\mathbb{1},\mathbb{U}\mathbb{1D},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12,U}\mathbb{1}3,U
```

```
#15.Heteroclnaemia/
```



```
#16.H@mocodom<\mathbb{D.Y. H|mg>/}
```



```
#17."Is@plhyllaa"/
```



```
#18.J`simme <L.>/
```



```
#19.Leg@unsia/
```



```
#20.Leptocodlom/
```



```
#21.Miclhauxxia<<L`Mer.>/
```



```
#22.Munsschiad
```



```
#23.Nammacodlom <Tlmulim>/
1,\mathbb{1}4,\mathcal{B}5,5\mathbb{S},\mathbb{1}/2\mathbb{I},\mathbb{U}\mathbb{1D},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12},\mathbb{U}\mathbb{1},\mathbb{U}
#24.Nesocodion<Thanlim>/
```



```
#25.Ostrowskia/
```



```
#2\sigma.Peracarpa <HHook.If. & Tlmoms.>/
\mathbb{1}\mathbb{1},\mathbb{B}3,\mathbb{U}\mathbb{Q},35,4/5 &,\mathbb{1},\mathbb{U}\mathbb{1D},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12,U}\mathbb{13},\mathbb{U}
#27.P年yteunmma/
```



```
#28.PPhysoplexis/
```



```
#29.Platycodom <A. IDC.>1
```



```
#30.Prismmatocarpus/
```



```
#31.Pseundocodomopsis <K\momol
```



```
#32.R2apumcunus/
```



```
#33.Roellia/
```



```
#34.R隹cel@/
1,\mathbb{1}2,\mathbb{1}\mathbb{B}\mathbb{U}\mathbb{4},\mathbb{B},\mathbb{U}\mathbb{8},\mathbb{1}\mathbb{Q},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12,U}\mathbb{U}3,\mathbb{U}
#35.Symplhyamdra <A. DCC.>/
1,\mathbb{1}2,\mathbb{1}3,\mathbb{1}4,\mathbb{S}5,\mathbb{Q}/5 &,\mathbb{1}\mathbb{D},\mathbb{U}\mathbb{10},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12,U}\mathbb{1}},\mathbb{U}
#36.Trachneliumm <L.>/
1,\mathbb{1}2,\mathbb{U}\mathbb{B},\mathbb{1}/2\mathbb{4},3 S,2/B/4/5 &,\mathbb{1},\mathbb{U}\mathbb{1D},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12},\mathbb{U}\mathbb{1},\mathbb{U}
#37.Walnlembergia/
```



```
#38.L.obelim <l.>/
1,\mathbb{12,}\mathbb{1/4/5 3,\mathbb{14,}1/2 6,2 7,3 8,3/7 1, 1/3 10,2 11, 112,2 13,2}
*END
```

```
12.1.1.8 CAMMPPALC.DAT (Pollem)..Campmmuleae data sulbset (DDelta dlata fille for
Pamkey, SC3)
*ITEMI DESCRIPTIIONS
#1.Adlem@phoora <Fisch.>/
```



```
#2.Asymeunmal
```



```
#3.Campmmunla/
```



```
#\.Cammpmun\astrunmm<Smalli>/
```



```
#11.E.E|ramamthus/
```



```
#11.Gadlellia/
\mathbb{M}\mathbb{1},\mathbb{1}\mathbb{3},\mathbb{U}\mathbb{Q},\mathbb{B}5,\mathbb{U}8,\mathbb{1}\mathbb{Q},\mathbb{U}\mathbb{1D},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12},\mathbb{U}\mathbb{13},\mathbb{U}
#12.Gitlmqpsis/
```



```
#14.HMmalbusaym <Nalkmi>/
```



```
#16.H|mm@codom < DD.Y. Homg>/
```



```
#17."Ilsmplhy|lla"/
```



```
#18.Jasimme <l.>/
```



```
#19.Legounsia/
```



```
#21.Miclhauxia <L\'Her.>/
1,\mathbb{1}2,2\mathbb{B},\mathbb{1}4,\mathcal{B},\mathbb{U}8,\mathbb{1}9,\mathbb{U}\mathbb{10},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12},\mathbb{U}\mathbb{13},\mathbb{U}
#22.Musschia/
```



```
#26.Peracarpa<H|mok.f. & Thamms.>/
```



```
#27.Plnyteumma/
```



```
#28.Phyysopllexis/
```





```
#34.Romcella/
```



```
#35.Symmplhy@mdra <A. DCC.>/
```



```
#36.Tracheliumm<\mathbb{L}>>/
```



```
*\mathbb{END}
```

```
12.1.1.9 CAMMPPALP.DAT (Pallem)o.oPlatycodemeae data subset (Delta data fille for
Pamkey, SC3)
*ITEMI DESCRRIPTIONS
#5.Campamumoea/
```



```
#(6.Camarim@/
```



```
#7.Cod@mmpsis/
```



```
#8.Cyamamtlmus/
```



```
#9.Echimocodom <\mathbb{D.Y. Homg>/}
```



```
#20.Leptocodom/
\mathbb{1}\mathbb{1}2,2/\mathbb{S}3,\mathbb{1}3\mathbb{B},\mathbb{1}7,\mathbb{1}/2,8,\mathbb{1}\mathbb{S},\mathbb{U}\mathbb{1D},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12},\mathbb{U}\mathbb{13,U}\mathbb{U}4,\mathbb{1}
#24,Nesocodlom<Thnolim>/
```



```
#25.(0strowskkial
```



```
#29.Platycodom <A. IDC.>1
```



```
#31.Pseud@cod@mopsis <KKomo>/
1,\mathbb{1}2,\mathbb{Z},\mathbb{U}\mathbb{4},\mathbb{1}7,\mathbb{1}/2/\mathbb{Z}8,\mathbb{1}\mathbb{Q}\mathbb{U}\mathbb{10},\mathbb{U}\mathbb{11,U}\mathbb{U}2,\mathbb{U}\mathbb{1}},\mathbb{U}\mathbb{14},2
#38.Lobelia <L_L.>/
```



```
* ENDD
```

```
12.1.1.10 CAMPPALW.WAT (Pollem)...WaMlembergeae data sumbset (DPlita data finle
for Pamkey, SC3)
*ITEMI IDESCRIPTIIONS
#G.Camamrima/
```



```
#10.E Ilraimmthus/
```



```
#12.Githmpsis/
```



```
#13.Gummillaca< <Thnulim>/
```



```
#15.Heterochaemia/
```



```
#18.Jasimme<ll.>/
```



```
#19.Leg@ajsia/
```



```
#22.Munsschia/
```



```
#23.Nammacodlom<Tlnunlim>/
1,\mathbb{1}|,\mathbb{B}5,5 8,\mathbb{1}2\mathbb{I},\mathbb{U}\mathbb{10},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12,U}\mathbb{U}3,\mathbb{U}
#24.Nesocodion<Thmunim>/
```



```
#30.Prismnatocarpous/
```



```
#33.Roella/
```



```
#36.Tracheliumm<ll.>/
1,\mathbb{1}2,\mathbb{U}3,\mathbb{1}/24,\mathbb{S}5,2/\mathcal{B}/4/5 8,\mathbb{1}\mathbb{Q}\mathbb{U}\mathbb{10},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12,U}\mathbb{13},\mathbb{U}
#37.Warlnlembergia/
1,\mathbb{1}2,\mathbb{1}/2\mathbb{B},\mathbb{1}4,3 5,3/4/5 8,\mathbb{1}\mathbb{Q},\mathbb{U}\mathbb{DC},\mathbb{U}\mathbb{1},\mathbb{U}\mathbb{12},\mathbb{U}\mathbb{1},\mathbb{U}
```

12.1.1.11 CAMPSEIED.DAT (Seeds),oseeds data set (Delta data fill for Pamkey, SC3)

```
*ITEM DESCRIPTIONS
#1.Adem@plhara<A.bunlleymma; A.comfusa; A.lhakusamemsis; A.|iniiifolia>/
1,2/3 2,3/5/7 3,2/4 4,1/2/3/4 5,2 6,2/3 7,1/2 8,1/4 9,1/2 10,1/2 11,1/2/3
#2.Asymeumma <A.japomica; A.michaonxiøidles; A.camescems>/
1,3 2,1/7/M 3,2/4 4,2/3/4 5,2 6,2 7,2 8,1 $,2/6 10,1/2 11,2/3
#3.Az@rima<A.vidlalii>>/
1,\mathbb{12,2/3 3,2/4 4,2 5,2 6,2 7,2/3 8,119,1110, 111,2}
#&.|Bracliycodlom < C.fmstigi&tm>/
```



```
#5.Campamonlastrumm <C.ammericamunm>/
1,3 2,1/4 3,2/4 4,2/3 5,2 6,3 7,1 8,1 1,2 10,1/2 11,2/3
#б."IIberacodom" <Camppamulla arvatica>/
1,2/3 2,7 3,2 4,1 5,2 6,1/2 7,2/3 8,4 \,1110,2 11,11
#7.Scappiflorae <Campmmonla bellidifclia>>
1,2/3 2,7 3,2 4,4 5,2 6,3 7,2/3 8,1 1,7 10,1/2 11,2
#8.Symplhyamdriformmes <Cammpamula betunifolia; C.troegerae>/
1,2/3 2,2/7 3,44,3 5,2 6,2 7,2/3 8,119,7 10, 111,1
#D.Imvolmeratae <C.cervicaria; C.spicata>/
1,2 2,2/9 3,2 &,3/4 5,2 6,2/3 7, 1 8, 19,1 10,1/2 11,2
#10.Ruppestres <C.coriacea No.0314;C.bormmmelleri No.s 0087, 0088, 0089;
C.heteroplhylla No.17; C.calammimthifolia No.10>/
1,3 2,1/2 3,2 4,3 5,2 6,2 7,2/3 8,1 1,1/5 10,1111,1/2
#11.Quimqueloculares <Campamula crispa; C.tomemtosa>/
```



```
#12."Oreocodom" <Campamulla mollis;}\mathbb{C}.jacolbaea; \mathbb{C.edulis;}\mathbb{C}.allsimoinles>/
1,2 2,\mathbb{1/2/7 3,2/4 4,2/4 5,2 6,3 7,2/3 8,1/2 D,2/5/6/7 10,1/2 11,2/3}
#13.C.ffrmm@mekiama<No.0345>/
1,2 2,7 3,4 4,3 5,2 6,2 7,2/3 8,119,7 10,111,\mathbb{1}
#14.Megalocod@m <Campmmula imeurva>/
```



```
#15.C.lammta < Na.34>1
1,\mathbb{12,2/7 3,2 4,3 5,2 6,3 7,2 8,119,1/2 10,1/2 11,2}
#16.C.limgullata <N@.0337>/
```



```
#17.Spimunlosae <Campmmunla mirabilis>/
1,2 2,4/5 3,44,3 5,2 6,2 7,2 8,\mathbb{1 4,5 10, 111, 1}
#18.Tonlipella <Campamunla punmetata var. Ihomdemsis>/
1,2 2,1/2 3,2 4,3 5,2 6,2 7,3 8,4 \,5 10, 1 11, 1
#19.C.swrtori <N@.15>/
1,2/3 2,1/4 3,2 4,3 5,2 6,2 7,3 8,\mathbb{1 M, 110,2 11, 1}
#20.Codmmosphaera <C.thyyrswides>1
1,2 2,2 3,4 4,3 5,2 6,2 7,2 8,119,1110,2 11,1/2
#21.Codlom@psis <C.bunlleyama; C.clematidlea; C.pillosula>/
1,1/2 2,2 3,\mathbb{1/2 4,1/2 5,2 (6,1/2 7,1/2 8,1/4 $,7 10,1/2 11,2}
#22.Craterocapsa <C.momtmma; C.sp.>/
1,3 2,匹/7 3,3 4,1 S,\mathbb{1},\mathbb{1}7,\mathbb{1}8,\mathbb{1}9,5 10,1/2 111,1/2
#23.Cyamamthus <C.lobatms>/
```



```
#24.Cylimalrocarpa <C.severtzowii>/
1,2 2,1/7 3,2/4 4,2/4 5,2 6,3 7,2 8,11 \,4/6 10,2 11,2/3
#25.Diosplnacra< <D.ruumeliama; \mathbb{D.jacquimii ssp. rummeliama>/}
    1,2 2,2/5 3,2/4 4,2/3/4 5,2 6,2/3 7,1/2 8,1 $,1110,1/2 11,2/3
#2G.Edraviamthus <EE.gramimifoliuns; E.serbicuns>/
1,2/3 2,3/8 3,3 4,5 5,2 6,3 7, 1 8,6 $,\mathbb{110,1/2 11,1}
#27.Gadlllia < C.|actifllora>/
1,1/2 2,@ 3,4 4,2/3 5,2 6,2 7,2 8,1 $,1/6/7 10,1111,1
#28.GivTh\proptopsis <G.diiffusa>/
1,2 2,2 3,2 4,2 5,2 6,2 7,1/2 8,1 9,7 10,1 11,2
#29.Is@plny|la < C.tomumasimiama; C.waldsteimianna; C.versicolor; \mathbb{C.zoysii;}
C.femestrellam>>
1,\mathbb{1/2/3 2,1/2/3 3,1/2 4,1 5,1/2 6,1 7,1/2 8,4 9,5/6/7 10,1/2 11, 1}
#30.Jasimme <J.hneldlreichnia; \.hummilis; J.crispa ssp.crispa; J.laevis>/
1,2/3 2,113,2/4 4,2/3/4 5,2 6,2/3 7,1/2 8,119,(6/7 10,1/2 11,3
```

| $1,22,1 / 3 / 93,2 / 44,2 / 45,2(6,37,1 / 28,1 / 24,1 / 510,211,2 / 3$ |  |
| :---: | :---: |
| \#32.Leptocodom <LL.gracilis>/$1,32,3 / 63,24,25,26,2 / 37,28,19,310,211,2 / 3$ |  |
|  |  |
| $\mathbb{1}, 2 / 32,1 / 3 / 93,2 / 44,3 / 45,2(6,2 / 37,2 / 38, \mathbb{1} 9,7 \mathbb{1}, \mathbb{1} \mathbb{1} 1, \mathbb{1} / 2$ |  |
|  |  |
|  |  |
|  |  |
| \#35.Nes©codl $\oplus$ < $\mathbb{N}$.manuriitiomus $>1$ <br>  |  |
|  |  |
| \#36. Peracarpa < P .circaeøidles>/ <br>  |  |
|  |  |
| \#37.Petkovia <Campamulla orphnamidea>/ $1,2 / 32,73,24,15,26,1 / 22,2 / 38,49, \mathbb{1} 10,2 \mathbb{1} 1,1$ |  |
|  |  |
| ```#38.Petrommarula <P.ppimm@{@>/ 1,2 2,2 3,4 4,3 5,2 6,2 7,2/3 8,119,7 10,1111,11``` |  |
|  |  |
| \#39.PThyteuma<<Plnyteumm pyremaicum>1 <br>  |  |
|  |  |
| \# 4 Q.Platycodion $<\mathbb{P}$.gramdifillorum $>1$ $1,32,63,24,25,2 \llbracket, 27,28,4 \oplus, 3 \mathbb{1}, \mathbb{1} 11,2 / 3$ |  |
|  |  |
| \#』1. $\mathbb{R}$ apunculus <C.hnawkimsiama; $\mathbb{C} . a i z \oplus o m ; ~ \mathbb{C} . t r i c h n c e a l y c i m a>/ ~$ $1,2 / 32,1 / 2 / 3 / 5 / 7 / 93,2 / 44,2 / 4 / 5,26,2 / 37,1 / 2 / 38,1 / 29,3 / 510,211,2 / 3$ |  |
|  |  |
| \#42.Mel』mocalyx < Campamola umicolor>/ $1,22,3 / 73,2 / 44,2 / 45,26,2 / 37,2 / 38,1 / 29,310,211,2 / 3$ |  |
|  |  |
| \#43.Pteroplhyllumm < C.primoulifolia < No.12>1 |  |
|  |  |
|  |  |
|  |  |
| \# $45 . \mathbb{R}$ ¢ellla < $\mathbb{R}$.macunllata; $\mathbb{R}$.cilicata>1 |  |
|  |  |
| \# 4 G. Sergia <S.regeliii>/$1,28,23,2 / 44,25,2 \quad 6,27,28,119,3 \mathbb{1 0}, 1 / 211,2$ |  |
|  |  |

```
#&:7.Symmphyy@mdra Inoffmmmmii < No.28>/
    1,2 2,2 3,2 4,3 5,2 6,2 7, 1 8, 19,2 10,1/2 11,1
#&&.Otocalyx <$ymplhywmdra mrmema>1
    1,2/3 2,\mathbb{1/2/4 3,2 4,3 5,2 6,2 7,1/2 8,1 $,1/2 10,111, 1}
#49.Symplhyandra wammeri <N0.0323, 0324>1
1,2 2,2/5 3,4 4,3 5,2 6,2 7,2/3 8,1 1,7 10,111,\mathbb{1/2}
#50.Trachelium <T.caeruleumm>/
1,2 2,2 3,4 &,2/3/4 5,2 6,3 7,1 8,1 $,110,2 11,3
#51.Walmlembergia <W.W.gloriosa; W.amdrosacea; W.comgesta>/
1,2/3 2,\mathbb{1/5 3,2/4 4,\mathbb{1/2/4 5,2 6,2/3 7,1/2 8,\mathbb{1/4}}9,3/5/6 10,1/2 11,1/2/3}
#S2." IHelem@codomn" <W.W.@mgustrifolia>1
```



```
#53."Fermamdeziocdlom" <W.W.berterai; WW.gralhammac; W.|arraimii>/
1,1/2 2,2 3,2 4,1/2 5,2 6,2/3 7,2/3 8,1/4 9,5 10,2 11,1/2
*\mathbb{ND}
```

$12.1 .1 .12 \mathbb{C A M} \mathbb{M} E E I D C . D A T$ (Seeds)...Campamuleae data sulbset (Delta data file for Pamkey, $\mathbb{S C}$ )
*ITEMI $\mathbb{D E S C R I P T I D N S}$
\#1.Ademaplhara < A.bunlleyama; A.comfusa; A.hakusamemsis; A.jiiniifoliaa>/
$1,2 / 32,3 / 5 / 73,2 / 44,1 / 2 / 3 / 45,26,2 / 37,1 / 28,1 / 4 \Phi, 1 / 2110,1 / 211,1 / 2 / 3$
\#2.Asymeuman <A.japomica; A.miclhauxioides; A.camescems>/
$1,32,1 / 7 / 93,2 / 44,2 / 3 / 45,26,27,28,1 \Phi, 2 / 610,1 / 211,2 / 3$
\#3.Az@rima <A.viddaliii>/
$1, \mathbb{1} 2,2 / 33,2 / 44,25,2(6,27,2 / 38,19,110,1111,2$
\# $\uparrow$. IBrachycodlom < C .fastigiata>1
$\mathbb{1}, \mathbb{1} 2,23,2 \varangle, 45,26,37, \mathbb{1} / 28, \mathbb{1} 9,1 / 6 \mathbb{1} 0,1 / 211,2 / 3$
\#5.Campmannlastrum < C.americamumm>/
$1,32,1 / 43,2 / 44,2 / 35,26,37,118,119,210,1 / 2 \mathbb{1} 1,2 / 3$
\#б."IIberocodon" <Campamulla arvatica>/
$1,2 / 32,73,24,15,26,1 / 27,2 / 38,49,110,211, \mathbb{1}$
\#7.Scapifllorae < Campamula loellidififolia>/
$1,2 / 32,73,24,45,2(6,37,2 / 38,19,710,1 / 2 \mathbb{1 1}, 2$
\#8.Symplnyandriformes < Campamula betonifolia; $\mathbb{C} . t r o e g e r a e>/ ~$
$1,2 / 32,2 / 73,44,35,26,27,2 / 38,119,710,1111,1$
\#D.Imvolucratae < C.cervicaria; $\mathbb{C}$. spicata>/
$1,22,2 / 93,24,3 / 45,26,2 / 37, \mathbb{1} 8, \mathbb{1} 9, \mathbb{1} \mathbb{1}, \mathbb{1} / 2 \mathbb{1}, 2$
\#10. Ruppestres < C.coriacea $\mathbb{N a . 0 3 1 4 ; ~ C . b o r m m a c l l e r i i ~} \mathbb{N}$ ©.s $0087,0088, ~ 0089 ;$
C.heteraplhylla Na.17; C.calammimthifoliaa $\mathbb{N}$ ©. $10>1$
$1,32,1 / 23,24,35,26,27,2 / 38,119,1 / 5110,111,1 / 2$
\#11. Quimqueloculares <Campamula crispa; C.tomemtosa>/
$\mathbb{1}, 2 / 32,2 / 4 / 53,24,35,26,27,1 / 28,1 / 49,1 / 5 \mathbb{1}, \mathbb{1} 11,1 / 2 / 3$
\#12."Oreocodom" < Campamula mallis; $\mathbb{C} . j a c o b a e a ; ~ \mathbb{C} . e d u l i s ; ~ C . a l l s i m ø i d e s>/ ~$ $1,22,1 / 2 / 73,2 / 44,2 / 45,26,37,2 / 38,1 / 29,2 / 5 / 6 / 710,1 / 211,2 / 3$
\#13.C.formmanekiama < $\mathbb{N}$ ©.034.5>/
$\mathbb{1}, 22,73,44,35,2 \mathbb{6}, 27,2 / 38,19,710,111, \mathbb{1}$
\#14.Megallocodom <Campamula imeurva>/
$1,32, \mathbb{1} / 2 / 4 / 73,44,35,2(6,27,2 / 38,119,710,111,1$

```
#15.C.l@mata <NO.34>1
1,\mathbb{12,2/7 3,2 4,3 5,2 6,3 7,2 8,119,1/2 10,1/2 11,2}
#16.\mathbb{CDimgunlata <NN.0337>/}
```



```
#17.Spimunlosae <Campmamula mmirabbilis>/
```



```
#18.Tunlipellla <Cammpamulla punctata var. Inomdemsis>/
1,2 2,\mathbb{1/2 3,2 4,3 5,2 6,2 7,3 8,4 5,5 10, 1 11, 1}
#19.C.sartori <NO.15>/
1,2/3 2,1/4 3,2 4,3 5,2 6,2 7,3 8,1 1,1 10,2 11,1
#20.Codl@mosphamera <C.thyyrsoidles>/
1,2 2,2 3,4 4,3 5,2 6,2 7,2 8,119,1110,2 11,1/2
#24.Cylimdrocarpm<C.severizowii>>
1,2 2,1/7 3,2/4 4,2/4 5,2 (1,3 7,2 8,119,4/6 10,2 11,2/3
#25.Dicsphmaera<价.rummeliama; D.jacquimii ssp. rummeliama>/
1,2 2,2/5 3,2/4 4,2/3/4 5,2 6,2/3 7,1/2 8,119,110,1/2 11,2/3
#2G.Edlraiamthus <E.grammimifoliuns; E.serbicus>/
```



```
#27.Gade\Iia<C.\actiflora>/
```



```
#28.Githmpsis <G.diffrusa>/
1,2 2,2 3,2 4,2 5,2 6,2 7,1/2 8,1 9,7 10,1 111,2
#29.|smplnylla < C.tommmasimiama; C.walldsteimiama; C.versicolor; C.zoysii;;
C.femestrellata>/
```



```
#30.J@simme <J.hneldreichini; J.hummilis; J.crispm ssp.crispa; \.laevis>/
1,2/3 2,1 3,2/4 4,2/3/4 5,2 6,2/3 7, 1/2 8,119,6/7 10,1/2 11,3
#31.Legausia <L.falcata Na.37; L.specunlumm-vemeris>/
1,2 2,1/3/9 3,2/4 4,2/4 5,2 6,3 7,1/2 8,1/2 9,1/5 10,2 11,2/3
#33.Michnauxia<<M.tchihmatchewii; M.|aevigata>>/
1,2/3 2, 1/3/9 3,2/4 4,3/4 5,2 6,2/3 7,2/3 8,1 9,7 10, 111,1/2
#34.Munsschia <䧼.wollastomi; M.aurrea>/
1,2 2,2/5 3,2/4 4, 1/2 5,2 6,1/2 7,1 8,1/3 9,6/7 10, 111, 1
```

```
#36.Peracarpm<PP.circaedides>/
1,3 2,1 3,1/2 &,3/4 5,2 6,2/3 7,3 8,\mathbb{19,7 10,1/2 11,2}
#37.Petkovia<Campmmula orplhamidlea>/
```



```
#38.Petrommaru\& <\mathbb{P}.pimmata>/
1,2 2,2 3,4 4,3 5,2 6,2 7,2/3 8,1 1,7 10,1 11, 1
#39.PPhyteunma<\mathbb{Phyteunma pyremaicumm>/}
1,3 2,\mathbb{1/4 3,2/4 }4,2/3 5,2 6,3 7, 1 8,1 $,2 10, 1/2 11,2/3
#&1.Rapummeulus <C.Chawkimsiama; C.aizoom; C.triclhocalycim@>/
1,2/3 2,1/2/3/5/7/9 3,2/4/ 4,2/4 5,2 6,2/3 7,1/2/3 8,1/2 9,3/5 10,2 11,2/3
#&2.Melamocalym <Campamulla umicolor>/
1,2 2,3/7 3,2/4 4,2/4 5,2 6,2/3 7,2/3 8,1/2 1,3 10,2 11,2/3
#43.P^erophyyIlum <C.primullifolia <N@.12>/
1,1/2 2,3 3,2 4,1/4 5,2 6,2 7,1/2/3 8,119,5 10,2 11,2/3
#@\, RTouccla <C.0lralbifolia;, C.erimuss>//
1,2 2,1/2/9 3,24,3/4 5,2 6,3 7,2 8,1/2 9,7 10,1/2 111,2/3
#&|.Sergial <S.regeliii>/
1,2 2,2 3,2/4 4,2 5,2 6,2 7,2 8,1 $,3 10,1/2 11,2
#&7.Symmphyymudra lnoffimmmmiai <N@.28>/
    1,2 2,2 3,2 4,3 5,2 (6,2 7,118,119,2 10,1/2 11, 1
#\8.0tocalyx <Symplhy@mdra armmem@>/
    1,2/3 2,1/2/4 3,2 4,3 5,2 6,2 7,1/2 8,119,1/2 10, 111, 1
#\9.Symphyymmdra wammeri <N@.0323, 0324>1
    1,2 2,2/5 3,4 4,3 5,2 6,2 7,2/3 8,\mathbb{1 D,7 10, 1 11, 1/2}
#50.Trachelium <T.c@erouleum>/
    1,2 2,2 3,4 4,2/3/4 5,2 6,3 7,118,1 9,1110,2 11,3
    *\mathbb{ND}
```

 for Pamkey, SC3)
*ITEMI $\mathbb{D E S C R I P T I O N S}$

## \#23.Cyamamthnus <C.llolbatuns>1

$\mathbb{1}, \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} 8,25,26,27,38, \mathbb{1} 9,711,2 \mathbb{1}, 2$
\#32.Leptocodom <Lu.gracilis>/
$1,32,3 / 63,24,25,26,2 / 37 ; 28,19,310,211,2 / 3$
\#35. Nescocodom <N.mauritiamus>1
$1,2 / \mathbb{1} 2, \mathbb{1} 3, \mathbb{1} / 2 \mathbb{4}, \mathbb{1} 5,2 \mathbb{2}, \mathbb{1} / 27,2 \mathbb{Z}, 4 \Phi, 7 \mathbb{1}, 1 / 2 \mathbb{1}, \mathbb{1}$
$\# \triangle Q . P$ latycodam $<\mathbb{P}$.gramdifloronm>1
$1,32,63,24,25,2(6,27,28,49,310,1111,2 / 3$
\# 4 . $\mathbb{R}$ ©ellla $<\mathbb{R}$.maculata; $\mathbb{R}$.cilinata>/
$\mathbb{1}, 2 / 32,3 / 83,3 \mathbb{1}, \mathbb{1} 5 ; \mathbb{1} 6, \mathbb{1} 7, \mathbb{1} 8,59, \mathbb{1} \mathbb{1 0}, \mathbb{1} / 2 \mathbb{1}, \mathbb{1}$

* $\mathbb{E N D}$
12.1.1.14 $\mathbb{C A M S E I E I D W} . \mathbb{D A T}$ (Seeds)...Walnlembergeae data sulbset (DDelta data file for $\mathbb{P}$ Pamkey, $\mathbb{S C}$ )

```
*ITEM DESCRIPTIIDNS
#3.Az@rima<A.vid|alii>1
1,\mathbb{12,2/3 3,2/4 4,2 5,2 6,2 7,2/3 &,1 $, 11 10,1111,2}
#22.Craterocapsa <C.momtmma; C.sp.>/
```



```
#26.Edraiamthus < <E.gramimifolius; E.serbicus>/
```



```
#28.Githmppsis <G.adiffrusa>/
1,2 2,2 3,2 &,2 5,2 6,2 7,1/2 8,19,7 10,1111,2
#3D.J@siome <J.helldreichnii; J.hnumnilis; J.crispa ssp.crispa; J.\aevis>/
1,2/3 2, 1 3,2/4 4,2/3/4 5,2 (,2/3 7,1/2 &,\mathbb{1 Q,@/7 10, 1/2 11,3}
#31.Leg@usia <ll.fallcata Na.37; L.speculumm-vemeris>/
1,2 2,1/3/4) 3,2/4, &,2/4 5,2 (1,3 7,1/2 8,1/2 9,1/5 110,2 111,2/3
#3&.MMusschinia<M.woliastomi; M.@urrea>/
```



```
#35.Nesccodon<\mathbb{N}.mamuritiamus>/
```



```
#45.RRocllaa <R.mmaculata; R.ciliata>/
```



```
#50.Traclhelium <T.c风erumleum>/
    1,2 2,2 3,4 4,2/3/4 5,2 6,3 7, 1 8, 1 $, 1 10,2 11,3
#51.Wa\nlembergia <W. gloriosa; W.amolrosacea; W.comgesta>/
    1,2/3 2,1/5 3,2/4 4,1/2/4 5,2 6,2/3 7,1/2 8,1/4 9,3/5/6 10,1/2 11,1/2/3
#52."Helemacod@m" <WW.amgustifolia>/
```



```
#53."TFermamdeziocd@m" <W.Werterबi; W.grahmmam; W.lamrraimiii>/
    1,1/2 2,2 3,2 &,1/2 5,2 6,2/3 7,2/3 8,1/4 D,5 10,2 11,1/2
    *END
```


### 12.1.2.1. ASTERALE.CMU (Coplnemetic Matric for $\mathbb{A S T E R A L E} . \mathbb{U P} \mathbb{G})$




( $\mathrm{l}=$ living material; $\mathrm{h}=$ herbarium material; $\mathrm{p}=$ photographs )
1.Adenophore Fiscln.
A.divaricata; Eddie 96086. (ex RBGE 875003). cult. (h,l,p)
A. remotiflora; Eddie 96087. (ex RBGE 900973). cult. (h,l,p)
2.Asymeuman Griseb. \& Schemk.
A. limoniifolium; Papanicolou 283. Greece (h)
A. limoniifolium; Strid 23822. Turkey (h)
A. limoniifolium; Hartvig 10585. Greece (h)
A. canescens; Gustavsson 4134. Greece (h)
3.Azorina Feer
A.vidalii; RBGK 4548404814. cult. (l, d, p)
4. Wracky codon Fed.
B.fastigiatus; Eddie 87053. ex. RBGE (Univ. of Cordoba) (h,)
B.fastigiatus; Eddie 85054. ex RBGE (hern C.Baeritz). (h)
5.Companula L. (essemtially Sect.Mediuma)
C. aizoon; J. Persson 1729. Greece (h)
C. alliariifolia; Archibald 250.300.Turkey (h)
C. alliariifolia; RBGE 360064. cult. (h)
C. alpina; Hartvig 10019. Greece (h)
C. andrewsii; Eddie 86010. Greece (h,l,p)
C. barbata; Archibald 251.700. Italy (h)
C. barbata; RBGE 760194.cult. (h)
C. bellidifolia; RBGE 770282. cult. (h)
C. betulifolia; Archibald 252.000-2/4-5. Turkey (h,l)
C. bornmuelleri; Archibald 252.300-2.Turkey (h,l)
C. celsii; Eddie 86001. Greece (h,1,p)
C.cervicaria; Hartvig \& Christensen 6492 (h).
C. collina; Archibald 253.600.Turkey (h)
C. collina; RBGE 693700. cult. (h)
C. coriacea; Archibald 253.800. Turkey (h,l)
C. crispa; Archibald 253.901.Turkey (h,l)
C. cymbalaria; Strid 23799. Turkey (h)
C. foliosa; Hartvig; 6592. Greece (h)
C. formanekiana; Strid 16549 (h)
C. glomerata; Eddie 86009. Greece (h,l,p)
C. glomerata; Eddie 86012. London (h,l,p)
C. grossekii; Univ. of London. cult. (h)
C. hawkinsiana; Archibald 256.001.Greece (h,l)
C. hawkinsiana; Baden \& Franzen 1138. Greece (h)
C. incurva; Archibald 256.800. Greece (h,l)
C. lactiflora; Archibald 257.500.Turkey (h)
C. lingulata; Greuter 11177. Bulgaria (h)
C. oreadum; Archibald 259.700.Greece (h)
C. oreadum; Strid 10077. Greece (h)
C. orphanidea; Archibald 259.800.Greece (h)
C. orphanidea; Papanicolou. 282. Greece (h)
C. patula; Univ.of London. cult. (h)
C. pyramidalis; Eddie 86019. ex RBGK. cult. (h,p,l)
C. raddeana; RBGE 510212. cult. (h,l)
C. radicosa; Gustavsson 3780. Greece (h)
C. rapunculoides; Univ. of London.cult. (h)
C. rhomboidalis; Archibald 262.250. France (h)
C. rhomboidalis; RBGE 760537. cult. (h)
C. rupestris; Archibald 262.300.Greece (h)
C. rupicola; Archibald 262.400. Greece (h)
C. rupicola; Franzen 589. Greece (h)
C. sarmatica; RBGE 820077. cult. (h)
C. saxatilis; Eddie 86011. Greece (h,l,p)
C. saxifraga; RBGE 694317. cult (h)
C. scheuchzeri; RBGE 490009. cult. (h)
C. stricta; Strid 23621. Turkey (h)
C. sparsa; Hartvig 4456. Greece (h)
C. topaliana; Archibald 265.000. Greece (h,l)
C. topaliana; Eddie 86003-4. Greece (h,l,p)
C. topaliana; Eddie 86006-7. Greece (h,1,p)
C. trachelium; Hertvig 4335. Greece (h)
C. tymphaea; Moller \& Petersen 1283. Greece (h)
C. tymphaea; Hartvig 6731. Greece (h)
C. aucheri; Archibald 251.500. Turkey (h,l)
C. spatulata; Strid 15172. Greece (h)
C. spatulata; Strid 10031. Greece (h)
C. spatulata; Hartvig 6933. Greece (h)
C. spatulata; Eddie 86008. Greece (h,l,p)
C. thessala; J.S.Andersen 10057. Greece (h)
C. trichocalycina; Greuter 15487. Greece (h)
C. tridentata; Archibald 265.400. Turkey (h)
C. troegerae; Archibald 265.500. Turkey (h)
C. velebitica; Strid \& Papanicolou 16634 (h)
C. versicolor; Hartvig 10795. Greece (h)
C. waldsteiniana; Archibald 266.000.Yugoslavia (h)
C. zoysii; Archibald 266.101. Austria (h)
6.Cowapormallastrumo Small
C.americanum; Eddie 96050. cult. (h,l.p)

## 7. Counarivar $\mathbb{L}$.

C.canariensis; Eddie; 87068. ex RBGE (Davis 67409). (h,l,p)
C. rotundifolia; RBGE 693922. cult. (h)
C. bulleyana; RBGE 760331. cult. (h)
C. cardiophylla; RBGE 500271. cult. (h)
C. viridiflora. ex. Univ. of London. cult. (h)
C. ovata; Univ. of London. cult. (h)
C. clematidea; Acad. Sci. Lithuania. cult. (h)
C. handeliana; Eddie 86015. ex RBGK. cult. (h,l.p)
C. dicentrifolia; Eddie 96022. ex RBGE. cult. (h,l,p)
C. lanceolata; Eddie 96023. ex RBGE. cult. (h,l,p)
C. convolvulacea; Eddie 96091. (ex Scottish Rock Garden Club). cult. (h,l,p)

## 9.Craterocapsa Hinliard \& B.L. Burte

C. congesta; Hirst 0448. Lesotho (h)
C. congesta; Hirst 0408. Lesotho (h)
C. cf. montana; Hirst 0216. Lesotho. (h)
10. Cyannowth was Wanl. ex Bemth.
C. lobatus; RBGE 771923. cult. (h)
C. lobatus; RBGE 570349. cult. (h)
C. lobatus; Sherriff 7496. (h)
C. sp.; Eddie 96082. origin unknown. cult (h,l,p)

## 11. Cytivalrocoupa Regel

C. severtzowii; Eddie 87047. ex RBGE (Popov 223). (h)

## 12. Diossphaera Buser

D. rumeliana; Greuter 15881. Greece (h)
D. rumeliana; Strid 9055 . Greece (h)
13. Edraimath us (A.DC.) DC.
E. graminifolius; Hartvig 10447. Greece (h)
E. graminifolius; Strid 19029. Greece (h)
E. graminifolius; Baden 883. Greece (h)
E. parnassicus; Gustavsson 6895. Greece (h)
14. Feeria Buser
F. angustifolia; Eddie 87001 (ex. S.Jury). Morocco. (h)
15.Gadellia Schullkina
G. lactiflora; RBGE 583773. cult (h)
G. lactiflora; RBGE 693714. cult. (h,l,p)
16. Githoppsis Nutt.
G. diffusa; Eddie 87051.ex RBGE (Langdon). (h)
G. calycina; Eddie 87.052. ex RBGE (Hellewr \& Brown). (h)
17. Heaveabrasaya Nakai
H. asiatica; Eddie 96018. ex RBGE. cult. (h,1,p)
H. rariflorum; Eddie 87071 (ex. Rancho Santa Ana, 40828). (h).

## 19.Homocodon D.Y. Homg

H. brevipes; Eddie 87072. ex RBGE (Forrest 7846). (h)

## 20.Jasione $\mathbb{L}$.

J. heldreichii; Univ. of London. cult. (h)
J. montana; Eddie 87100 . Suffolk. (h,p)
J.laevis; Eddie 96035. cult. (h,l,p).
J.crispa; Eddie 96083. cult. (h,l,p)
21.Legousia Duramde
L. speculum-veneris; Eddie 87003. cult. (h)
L. speculum-veneris; Eddie 96034. (ex Paris) cult.(h)
L. falcata; Eddie 96017. cult. (h,l,p)
22. Leptocodom (Hionk. fio) Lem.
L.gracilis; Eddie 87059. ex RBGE (Cave). (h)
L.gracilis; Eddie 87.060. ex RBGE (Ludlow \& Sherriff). (h)
L.gracilis; Eddie 96021. ex RBGE. cult. (h,l,p)
23. Michowusia L'Her.
M. laevigata; Archibald 677.200. Turkey (h)
M. tchihatchewii; Archibald 677.300. Turkey (h)
M. tchihatchewii; Strid 24078. Turkey (h)
24.Musschiou IDumart.
M. aurea; RBGE 760217. cult. (h,l,p)
M. aurea; ex Botanischer Garten der Justus-Liebig Univ. cult. (h,1,p)
M. wollastoni; RBGE 801834. cult. (h,l,p)
25. Nesocodon Thunlim
N. mauritianus. Eddie 86.022, ex. Univ. of Dublin. (h,p,l)
26.Ostrowskia Regel
O. magnifica; RBGK. SD.1342. USSR. (h,p,).
27.Peracarpa Hook.f. \& Thams.
P. circaeoides; Eddie 87069. ex RBGE (Yamazaki). (h).
P. carnosa; Eddie 87070. ex RBGE (Prain). (h)
28. Petromarula Vemto ex Hedlw. 1 o
P. pinnata; Stamatiadou 17344. Greece (h)
P.pinnata; Eddie 96066 (ex Pankhurst). Greece. (h)
29.Playteumsal.
P. spicatum; Eddie 96090.(ex RBGE 770151). cult. (h,l,p)
30.Physoplexis (EmdI.) Schwr
P. comosus; RBGE 2626. cult. (h,l,p)
31.Plautycodon A.IDC.
P. grandiflorum; ex. Univ. of London. cult. (h)
P. grandiflorum; Acad. Sci. Lithuania 653. cult (h,p,l)
P. grandiflorum; Eddie 96076. Nantes. cult. (h,l,p)
32.Roucela $\mathbb{D}$ um.
R. drabifolia; Stamatiadou 16761. Greece (h)
R. erinus; Strid 8599. Greece (h)
R. drabifolia; Eddie 86002. Greece (h,l.p)
R. drabifolia; Eddie 86005. Greece (h,l,p)
R. erinus; Eddie 96016. cult. (h,l)

## 33.Sergia Fedl.

S. regelii; Eddie 87048. ex RBGE (Popov \& Vedensky). (h)

## 34.Symppleyamadra $\mathbb{A} . \mathbb{D C}$.

S. wanneri; Strid \& Georgiadou 13601. Greece (h)
S. hoffmannii; Univ. of London. cult. (h)
S. odontosepala; Eddie 87001. ex RBGK. cult. (h,p)
S.zangezura; RBGE 685139. cult. (h,p)

## 35. Trachelium $\mathbb{L}$.

T. caeruleum; Eddie 87004. origin unknown. cult. (h)
36. Wandenbergia Schradl. ex Roth
W. angustifolia; RBGK 4517004396. cult. (h,p)
W. marginata; RBGK 3306833002 . cult. ( $\mathrm{h}, \mathrm{p}$ )
W. gracilis; RBGK 0178500788 . cult (h,p)
W. gracilis; Eddie 86013. ex RBGK. cult. (h)
W. mathewsii; RBGK 2457202274. New Zealand (h)
W. ceracea; RBGK 2077802106. Australia (h)
W. gloriosa; RBGK 2367701868. Australia (h)
W. undulata; Eddie 86014. ex RBGK. cult. (h,p)
W. berteroi; ex Ricci. Chile. (h)
W. larrainii; Eddie 96058 (ex Ricci). Chile (h,l.p)
W. grahamae; ex Ricci. Chile. (h)
W. androsaceae; Hirst 0317. Lesotho. (h,l)


[^0]:    Fig.21. Principal coordinates 1 and 3 for the Pollen (Camppal.DAT) data set and opposite.

[^1]:    " The scientist has to face the fragmentation of physical facts with courage. He has to scan a multitude of possible links that could make sense out of apparent chaos. I would maintain that he needs the more dispersed (undifferentiated) structure of low-level vision in order to project the missing order into reality".

