Taxonomic Studies on the Satureja complex (Labiatae).

by A. Doroszenko

Ph. D. Edinburgh University and
Royal Botanic Garden, Edinburgh

I declare that the work presented herein is entirely my own except where otherwise credited.

A. Doroszenko

12th. May 1986

Abstract

The Satureja complex has hitherto been treated in two ways: either as one large omnibus genus of c. 240 species divided into sections or else these sections raised to generic rank. The recent opinion adopts the former treatment for the New World representatives and generally the latter treatment for the Old World representatives. The present investigation has, therefore, concentrated on the generic limits within the complex to achieve a consistency of treatment on a world basis.

The introductory chapter establishes the place of Satureja s.l. in the Labiatae, outlines the scope of the study, presents a historical review of the complex, and discusses the theoretical concept of the genus and its application to the study of Satureja s.l. It is concluded that historically Satureja s.l. has usually been divided into several genera. The present morphological and anatomical studies also suggest the adoption of a narrow generic concept. A synopsis of the 17 accepted genera is presented. These genera are divided into 4 groups: the Satureioid genera comprising Satureja L. s.s., Gontscharovia Boriss. and Euhesperida Brullo & Furnari; the Micromerioid genera comprising Micromeria Benth., Brenaniella A. Doroszenko and Killickia A. Doroszenko; the Calaminthoid genera comprising Calamintha Miller, Clinopodium L., Acinos Miller and Cyclotrichium Manden. & Scheng.; and the American genera comprising Gardoquia Ruiz & Pav., Obtegomeria A. Doroszenko, Montereya A. Doroszenko, Piloblephis Rafin., Hesperothymus A. Doroszenko, Xenopoma Willd. and Diodeilis Rafin.

A detailed account on leaf anatomy presented in the second chapter shows that anatomical structure provides consistent generic and sectional characters. The Satureioid genera have isolateral palisade parenchyma, while all the other genera, with few exceptions, have dorsiventral palisade parenchyma. In *Micromeria*, sections *Micromeria*, *Cymularia* and *Pineolentia* are distinguishable by abundant sclerenchymatous fibres in the mid-vascular bundle, and sections *Micromeria* and *Pineolentia* by sclerenchymatous leaf marginal veins. The epidermis, collenchyma, bundle sheath, stomata and glands are of lesser taxonomic importance. The ecological effects on leaf morphology and anatomy are discussed. A Scanning Electron Microscope study of nutlets revealed few characters of value at the generic level, but these characters were frequently of use at the specific level. Many of the species nutlets are mucilaginous, but no consistent pattern of myxospermy was found within genera. General discussions on gross floral morphology, pollination syndromes, gynodioecy and chromosome numbers (a complete list of literature reports is included) conclude the chapter.

The final chapter, the Taxonomic Account, includes keys to the genera and species, a full synonymy, and citation of types, illustrations and distributions. However, no species descriptions are included except for novelties (*Micromeria cinerea*, *Brenaniella rungwensis*, *Acinos nanus*, *Gardoquia impressa* and *G. cutervoensis*), though data on the states of 70 characters are codified and presented in an appendix. These data form the basis of a numerical analysis, the results of which broadly support the taxonomic arrangement adopted here. Newly created genera are *Brenaniella* (a previously described but unnamed group of African species hitherto included within *Satureja*), *Killickia* (for 3 South African endemics), *Obtegomeria* (previously *Satureja* sect. *Obtectae* Epling & Jativa), *Montereya* (monotypic, Californian) and *Hesperothymus* (formerly *Satureja* sect. *Hesperothymus* Epling & Jativa). *Micromeria* sect. *Madagascarensis* (3 Madagascaran species), 9 sections in *Gardoquia*, 6 sections in *Xenopoma* and 2 sections in

Diodeilis are newly described; these are based mainly on vegetative and inflorescence characters. A large number of new combinations are made.

Acknowledgement

This work was funded by an SERC grant and it is gratefully acknowledged. I thank Prof. P. H. Davis, Edinburgh University, Mr. I. C. Hedge, Royal Botanic Garden, Edinburgh, and Dr. P. M. Smith, Edinburgh University, for their invaluable assistance, helpful advice and constant encouragement throughout the duration of my studies. I thank Prof. W. Greuter and Dr. Hakki, Berlin, Dr. R. Harley, Kew, and Dr. S. Edwards, Manchester, for assistance during visits to their respective institutes; the trustees of the Edinburgh Botanic Garden Trust for funding the visit to Berlin Botanic Garden herbarium and field studies in Spain; the Directors, curators and staff of B, BM, C, E, FM, G, Hb. Huber-Morath, HUJ, K, LA in UC, LD, M, MANCH, NY, P, UC, W, WU and Z for the loan of specimens. I also thank my parents for their generous financial support, warm encouragement and interest at all times.

Chapter 1

Chapter 2 Anatomy and Morphology

Chapter 3. Taxonomic account

Appendix

Chapter 1

Chapter 1

1.1. Introduction

This chapter introduces Satureja s.l. in the context of the Labiatae as a whole. Since the time of Linnaeus Species Plantarum (1753) there has been little dispute about the affinity of the broad group here called Satureja s.l. However, within this group there has been much disagreement, primarily on generic limits. Therefore the group of interest here is clearly indicated and terms such as "Satureja s.l.", "Satureja s.s." and "Satureioid genera" are defined below. A short outline of the scope of the thesis is also presented.

The differences of opinion on generic limits has is roots in the history of discovery in Satureja s.l. and the viewpoint of various authors. Clearly Linnaeus in Scandinavia would have seen the group differently from Kunth who assessed the Humboldt and Bonpland collections from South America. With this in mind a detailed historical discussion is presented.

The final section of this chapter deals with the concept of the genus, both in the theoretical context and in its application to the study of Satureja s.l.

1.2. The Place of Satureja s.l. in Labiatae

In Linnaeus Species Plantarum (1753) the Class Didynamia Gymnospermia, equivalent to much of the modern-day Labiatae, was not divided into suprageneric taxa. Species now included in Satureja s.l. were distributed amongst Satureja L., Clinopodium L., Thymus L. and Melissa L. The latter three were placed consecutively, with Origanum amongst them, while Satureja was placed some distance away, separated by many genera now considered not to be closely related to Satureja s.l.

Bentham in his Labiatarum (1832-35) divided the family into eleven tribes (Ocimoideae, Menthoideae, Monardeae, Satureineae, Melissineae, Scutellarineae, Prostanthereae, Nepeteae, Stachydeae, Prasieae, Ajugoideae) with *Satureja* s.l. divided amongst Satureineae and Melissineae. These tribes were circumscribed as follows (genera which contain species which are now considered to belong to *Satureja* s.l. are preceded by an asterisk):

Satureineae

Calyx 5-toothed, equal or bilabiate to 3/2. Corolla tube exannulate, calyx or bracteoles imbricating, shorter than or scarcely longer, limb sub-bilabiate, upper lip flat, entire or emarginate to bifid, lower lobes entire. Stamens straight, divergent or scarcely ascending, equal or upper shorter or abortive. Anthers not divided.

Bystropogon, *Pycnanthemum*, *Monardella*, *Amaracus*, *Origanum*, *Majorana*, *Thymus*, * *Satureja*, *Hyssopus*, *Collinsonia*, *Cunila*

Melissineae

Calyx 13-, rarely 10-nerved, 5-toothed, bilabiate to 3/2 or rarely equal. Corolla tube exannulate, little exserted, limb bilabiate, lips flat or the upper (in *Glechon*) galeate. Stamens ascending, upper shorter or abortive.

Hedeoma, * *Micromeria*, * *Melissa*, * *Gardoquia*, *Glechon*, *Keithia*, *Thymbra*, *Dicerandra*, *Pogogyne*, *Lepechinia*.

The division of *Satureja* s.l. amongst two tribes was abandoned in favour of a single tribe, Satureieae, in Benthams second revision of Labiatae in De Candolles Prodromus (1848). He divided the tribe into four sub-tribes plus a group of anomalous genera, with the following arrangement (the asterisk again indicates species of *Satureja* s.l.):

Sub-tribe Elsholtzieae

Stamens 4. Anther locules confluent, at the shedding of pollen ovate-reniform or orbicular.

Pogostemon, *Dysophylla*, *Colebrookia*, *Tetradenia*, *Elsholtzia*

Sub-tribe Menthoideae

Corolla sub-actinomorphic. Stamens spreading, never connivent. Anthers bilocular.

Perilla, *Preslia*, *Mentha*, *Lycopus*

Sub-tribe Thymeae

Corolla bilabiate (lips sometimes obscure), inside of tube naked. Stamens distant or divaricate, never connivent. Anthers bilocular.

Cunila, *Zataria*, *Bystropogon*, *Pycnanthemum*, *Monardella*, *Origanum*, *Thymus*

Sub-tribe Melisseae

Corolla bilabiate, inside of tube naked. Stamens 4 or 2, ascending from the base and divergent at the apices, or connivent arctuate-ascending under the upper lip (rarely sub-parallel?). Anthers bilocular. Genera very characteristically very exquisitely distinct [exquisitis distincta].

* *Satureja*, * *Micromeria*, * *Calamintha*, * *Gardoquia*, *Thymbra*, *Melissa*, *Dicerandra*, *Pogogyne*, * (1 species with a query) *Hedeoma*, *Keithia*.

Anomalous genera

Glechon, *Hyssopus*, *Collinsonia*, *Sphacele*, *Cuminia*, *Dekinea*, *Lepechinia*, *Horminum*

Subsequent revisions of the supra-generic taxa have remained basically the same. Most differences have concerned the rank of undisputed groups. Briquet (1896) recognised a much more broadly circumscribed tribe Stachydoideae divided into 12 sub-tribes. This tribe is more or less Benthams Satureieae, Monardeae, Nepeteae and Stachydeae united into one. Briquets sub-tribe Satureieae was divided into 5 groups: A. Melissinae, B. Hyssopinae, C. Thyminae, D. Menthinae, and E. Perillinae. The Melissinae was composed of the following genera: *Ziziphora*, *Hedeoma*, *Hedeomoides*, *Melissa*, *Satureja*, *Saccocalyx*, *Kurzamra*, *Conradina*, *Pogogyne*, *Ceranthera*, *Thymbra* and *Amaracus*, in that order. *Satureja* s.l. thus became one large omnibus genus.

1.3. Definition of taxa

The foregoing has given some idea of the position of *Satureja* s.l. in the family. The close relationship of the American genus *Hedeoma* should be particularly noted. From here *Satureja* s.l. can be more closely defined and the scope of the study outlined.

The shortened synopsis of the whole group given below will aid in understanding the terms used.

Old World genera

Satureioid genera
1. *Satureja*
2. *Gontscharovia*
3. *Euhesperida*

Micromerioid genera
4. *Micromeria*
5. *Brenaniella*
6. *Killickia*

Calaminthoid genera
7. *Calamintha*
8. *Clinopodium*
9. *Acinos*
10. *Cyclotrichium*

New World genera

"American" genera
11. *Gardoquia*
12. *Obtegomeria*
13. *Xenopoma*
14. *Diodeilis*
15. *Montereya*
16. *Hesperothymus*
17. *Piloblephis*

Satureja s.l. refers to the entire group of genera listed above, be they thought of as distinct genera, as is my opinion, or thought of as being one genus. Thus *Satureja* s.l. is equivalent to *Satureja* L. sensu Briquet (1896). A description of the broad group is as follows:

Satureja s.l.

Habit very diverse but mostly perennial shrubs. Leaves very diverse. Calyx tubular to obconical, tube straight to curved, hairy or naked in throat, 10-15-nerved; 5-toothed, 3 upper and 2 lower; upper teeth usually shorter than lower, rarely united, straight or curving upward; lower teeth nearly always straight, rarely curving upward, ciliate or not. Corolla tube longer than lobes, annulate or not, rarely resupinate; upper lip nearly always emarginate, rarely entire; lower lip divided into three lobes, sometimes the middle one bifid; stamens 4, didynamous, anterior pair longer, included within corolla upper lip or shortly exserted, sometimes long-exserted beyond corolla; filaments nearly always glabrous; thecae 2, without appendages, mostly divergent, sometimes parallel. Style gynobasic, stigma lobes 2, equal or unequal.

Satureja s.s. = Satureja L. sensu Bentham in the Prodromus (1848) excluding sect. Pycnothymus (=Piloblephis here). The Linnaean genus Satureja L. (type species S. montana L.) also included species of Micromeria. Satureja s.s. is equivalent to sect. Tragoriganum Benth. sensu Briquet (1896) and half of sect. Sabbatia Briq. (1896), the names hortensis to bachtiarica inclusive. All species following bachtiarica belong to Micromeria.

Satureioid, Micromerioid and Calaminthoid genera are explained by reference to the synopsis above. "American genera" is used interchangably with "New World genera" and includes those numbered 11 to 17 in the synopsis. The American genera may be thought of as a single, distinct group of similar rank as the Satureioid, Micromerioid and Calaminthoid genera.

Satureja L. (without qualification) is the generic name as used by various authors where no indication of scope is given.

1.4. Outline of the scope of the study

The most important aim of this study was to provide an up-to-date, worldwide account of Satureja s.l. The number of species has increased by 80% since the last worldwide revision (Briquet, 1896), from 130 species to approximately 240 species. There is much more known of distribution, anatomy, pollen, chromosomes, gynodioecism, breeding systems, pollinators, etc., and much improved instrumentation to study these. A new revision was therefore very necessary.

At the specific level, and in arranging these into species groups, there has been broad agreement. However the rank that these species groups should be given has produced the most argument. Therefore, this revision is biased toward an investigation of the generic limits within Satureja s.l. The modern differences of opinion persist mainly because of a restricted viewpoint of Satureja s.l., since most recent investigations have been linked to the writing of Floras. However, these differences have their roots in the quite different approaches to the problem by two nineteenth century botanists, Bentham and Briquet, who both took on the immense task of summarising the relationships in the entire family Labiatae. These differences of opinion still persist today, so that two different generic arrangements are being used simultaneously in different parts of the world. Clearly this situation is unsatisfactory. Thus one of the main parts of this study was to investigate this controversy.

With such a large group, very little experimental work was possible. Therefore the bulk of the study was concerned with a "traditional" morphological herbarium investigation. After preliminary observations of character variation and study of the literature, a list of important taxonomic characters was compiled. For each species every character on the list was investigated and the information codified in a large table. This rather laborious procedure ensured that every species was studied in a comparable manner and that a thorough knowledge was gained of all the species. Where difficulties had arisen in the past, e.g. for the Satureja montana complex and the Calamintha gracilis group, further, more detailed morphological studies were made.

Preliminary work by G. Ertem (unpublished data) showed that there were important differences in leaf anatomy in Satureja s.l. Hand-sections prepared for a large number of species confirmed the taxonomic importance of leaf anatomy at the generic level. There are also important ecological implications arising from these results.

The nutlets of 67 species were studied with the Scanning Electron Microscope for surface micro-characters and 148 species tested for mucilage. Both investigations revealed characters of minor importance at the generic level.

No attempt was made to investigate chemical constituents since varieties of the same species vary greatly in composition (Genova & Balinova, 1970), and also composition changes during the day and from season to season.

Chromosome investigations were also not attempted because of a lack of living material of those species which needed investigating most, i.e. the American species. Lack of time was also a factor. However, a large number of counts were drawn from the literature.

Gynodioecism is very common in the Labiatae. Therefore, particular attention was given to the fertility of the flowers to find out the extent of gynodioecism in Satureja s.l. This investigation is particulary important in the discussion on relating the 4-staminate genera of the Satureja group with the closely related 2-staminate genera of the Hedeoma group. The study shows that the relationship is closer than hitherto thought. A discussion of the generic basis and evolution of gynodioecism reveals the importance of pollinators. Measurements made in many species show that there is a marked reduction in size in all of the floral parts in female flowers. Dissection of the corollas of all the species has indicated how length of the tube, width of the throat, the position and density of hairs, size and position of stamens, and colour is apparently adaptive to particular pollinators.

Because of the large number of species in Satureja s.l. the formal taxonomic account has had to be shortened into a synoptic form. A generic key and keys to the species within genera are of the bracketed type, again for the sake of compactness. I have attempted to make the synonymy as comprehensive as was practical, so that all relevant names of sub-specific rank and above have been included. A few important varietal names have also been included. The exclamation mark notation indicating personal examination of type material has been adopted. Species descriptions were originally included in the thesis. However, the bulk of the thesis was becoming so great that it was felt the descriptions had to be omitted. The data tables and keys compensate somewhat for this omission. Descriptions are provided for new species only. A list of the specimens seen for each species has also been omitted for reasons of excessive bulk.

The data tables formed the basis of a numerical analysis. Computer programs were written to input the data, calculate similarity values for all pairs of species using the general coefficient of Gower (1971), and clustering of species by group pairs sorting. Generally, the results of the numerical analysis agree with those obtained using traditional, intuitive methods.

1.5. Historical Review of *Satureja* s.l.

1.5.1. Introduction

Satureja s.l. as it is understood today, is a very large group. Obviously the component species were not all discovered at once, so the known species at the time of a revision strongly influenced the generic treatment. Since the group is so large the historical details of discovery of new species, a species placement in the existing arrangements of the time, and modifications in the light of new discovery are very complex. In this historical review I hope to simplify the complexities so that the trends in generic arrangement are emphasised. Nevertheless, since there have been so many wide differences of opinion, which I feel cannot be glossed over, the reader may find this history rather difficult to follow. I would encourage constant reference to the shortened synopsis above and the synopses of Benthams Labiatarum (1834) and Prodromus (1848).

1.5.2. The Earliest Years (1753-1825)

It was inevitable in the early years of scientific taxonomy that the species sent to Linnaeus or known by him personally would not allow an accurate assessment of the Plant Kingdom as a whole. Linnaeus Species Plantarum (1753) included only 9 species belonging to *Satureja* s.l., i.e. under 4% of the now known species. Nevertheless his generic arrangement is very interesting. Four genera are of interest: *Satureja* L., *Clinopodium* L., *Thymus* L. and *Melissa* L.

(a) *Satureja* L. included 9 species: 3 belong to *Satureja* s.s., 2 to *Micromeria* Benth. sect. *Micromeria*, and the rest are now placed in *Pycnanthemum*, *Thymus* and *Cunila*. Note that these last three genera were placed in the tribe Satureineae along with *Satureja* in Benthams Labiatarum (1834).

(b) *Clinopodium* L. comprised 3 species: the very common and widespread *C. vulgare* L. and species now placed in *Pycnanthemum* and *Hyptis*.

(c) The eight species of *Thymus* L. included two species now placed in *Acinos* Miller.

(d) *Melissa* L. included four *Calamintha* species and one of *Micromeria* sect. *Pseudomelissa*.

This taxonomic arrangement was more or less maintained in subsequent editions of Species Plantarum and Linnaeus Systema Vegetabilum into the nineteenth century, though anomalous species were removed and newly discovered species added.

Satureja L. was placed some distance from the other three genera. The 13th. edition of Systema Vegetabilum (1774) distinguished the two groups thus:

Calyx ± equal, 5-toothed
Satureja L.
Calyx ± bilabiate
Thymus L., *Clinopodium* L., *Melissa* L.

This division is equivalent to the following:

1. *Satureja* L., *Micromeria* Benth. sect. *Micromeria*
2. *Clinoodium* L., *Calamintha* Miller, *Acinos* Miller *Micromeria* Benth. sect. *Pseudomelissa*

The 4th. edition of Species Plantarum edited by Willdenow (1800) included 23 species belonging to *Satureja* s.l.; all but two were Mediterranean in origin. Ths preponderance of Mediterranean species had a clear effect: since the European species groups were so easily discernible, these groups were described as genera, and what is termed here the "narrow generic concept" was established in the Old World.

Before proceeding with a discussion of developments in the nineteenth century, two important works of the eighteenth century must be commented upon. These support a narrow generic concept in the Old World. The first is Millers abridged 4th. edition of The Gardeners Dictionary (1754). The taxonomic importance of this work was quite ignored until Druce (1914) drew attention to it. Miller validly published 260 new generic names in the Dictionary, amongst them *Acinos* and *Calamintha*. The Linnaean system of binomials was not used consistently (not until the 8th. edition of 1768) but the extensive polynomial synonymy in Species Plantarum helped considerably to identify the Miller species. Miller included four genera of *Satureja* s.l.: *Acinos*, *Calamintha*, *Satureia* (sic) and *Clinopodium*. The first three genera are, as far as I can ascertain, circumscribed exactly as they are in Flora Europaea (1972), i.e. in a narrow, strict sense. *Satureia* sensu Miller is equivalent to *Satureja* s.s. as defined above under "Definition of Terms", i.e. without the inclusion of *Micromeria*. *Clinopodium* sensu Miller is rather more confused, including *Clinopodium* sensu L., an *Acinos* species, a *Nepeta* L., a *Pycnanthemum*, and three other unidentified species. Millers arrangement is taxonomically superior to Linnaeus even though the Dictionary was never intended to be a comprehensive compilation of all plants. As far as I can ascertain none of Millers species belonging to *Satureja* s.l. are American.

The second important work I would like to highlight is Moenchs Methodas Plantas (1794). This is really a local Flora but is remarkable in that the taxonomic arrangement is exactly equivalent to that of Flora Europaea (1972). Moench used the Linnaean binomial system but deliberately did not use Linnaean names; he used Tournefortian ones wherever possible. This resulted in numerous illegitimate names as defined by the present Code of Botanical Nomenclature. His generic arrangement of *Satureja* s.l. consisted of *Satureja*, *Sabbatia* Moench, *Clinopodium*, *Acinos* and *Calamintha*. Moench separated *Satureja* sensu L. (1753) into *Satureja* s.s. and

Sabbatia. *Sabbatia* Moench, equivalent to *Micromeria* Benth. sect. *Micromeria*, is illegal since it is a later homonym of *Sabbatia* Adans. (1763) in the Gentianaceae.

Discovery of new American *Satureja* s.l. was not entirely static during the latter half of the eighteenth century. Ruiz & Pavon (1794) validly published *Gardoquia* without descriptions but with a clear illustration of *G. multiflora*. This species was quite distinct from anything known of *Satureja* s.l. in the Old World. Kunth in Bonpland & Humboldts Nova Genera et Species Plantarum (1817) added 10 more species to this Central and South American genus. *Xenopoma* was proposed by Willdenow in 1811 to accommodate an anomalous species (*X. viminea*) which had been rather uncomfortably placed in *Satureja* since the 2nd. edition of Species Plantarum (1764).

In summary, by the first quarter of the nineteenth century the generic arrangement was as follows:

Satureja sensu Miller or Moench   or *Satureja* sensu L.
Sabbatia Moench

Clinopodium sensu L.
Calamintha sensu Miller or Moench   or sub *Melissa* sensu L.
Acinos sensu Miller or Moench   or sub *Thymus* sensu L.

Gardoquia Ruiz & Pavon
Xenopoma Willd.

The number of species of Labiatae increased rapidly through the period 1753-1825, but the arrangement of successive editions of Species Plantarum and Systema Vegetabilum remained basically the same. Little account was taken of the innovations of Miller, Moench, Ruiz & Pavon, Persoon (1807), and others. So by the 16th. edition of the Systema (1825) edited by Sprengel the taxonomic treatment looks decidedly old-fashioned and very inadequate. The poor treatment of *Thymus* is a case in point.

1.5.3. *Order from Disorder (1826-1836)*

The Labiatae had become so disorganised that Lindley (1829) complained that the Labiatae had "become the disgrace of Botany". It was around 1826 that Bentham began preliminary studies toward a complete revision of the family. Benthams Labiatarum Genera et Species was published in 13 parts between 1832 and 1835. The tribal arrangement of the Labiatarum has already been outlined above. It would be beneficial now to take a closer look at the generic treatment since the Labiatarum really is the beginning of the modern phase of Labiate taxonomy.

In the following synopsis of the genera comprising *Satureja* s.l., the comments in square brackets indicate the modern status of the sections and species. The number in round brackets is the number of species.

Tribe Satureineae

Satureia L.

Sect. 1. *Satureia* (6) [= *Satureja* s.s. *S. rupestris* (=*Micromeria thymifolia*) also placed here was thought intermediate between *Satureja* and *Melissa* (*Calamintha*)]

Sect. 2. *Tragoriganum* (1) [*S. thymbra* only]

Sect. 3. *Pycnothymus* (1) [=*Piloblephis*. Bentham had his doubts about the placement of this section in *Satureja*]

Tribe Melissineae

Micromeria Benth.

Sect. 1. *Hesperothymus* (6) [=*Hesperothymus* mihi, plus one species of *Diodeilis* (*D. glabella*) and a species of *Conradina*]

Sect. 2 *Piperella*

Sub-sect. *Gerontogeae* (21) [= *Micromeria* sect. *Micromeria*]

Sub-sect. *Australasicae* (3) [all belong to *Mentha*]

Sub-sect. *Americanae* (3) [= *Xenopoma*]

Sect. 3. *Pseudomelissa* (2) [= *Micromeria* sect. *Pseudomelissa*]

Melissa L.

Sect. 1. *Calamintha* (6) [5 species = *Calamintha*, 1 = *Micromeria* sect. *Pseudomelissa*]

Sect. 2. *Calomelissa* (1) [= *Diodeilis*]

Sect. 3. *Acinos* (6) [= *Acinos* Miller]

Sect. 4. *Clinopodium* (5) [1 species = *Clinopodium*, 3 species = *Calamintha*, 1 species = *Cyclotrichium*]

Sect. 5. *Meliphyllum* (4) [= *Melissa* s.s.]

Sect. 6. *Macromelissa* (2) [1 species = *Calamintha*, 1 species = *Gardoquia*]

Sect. 7. *Heteromelysson* (1) [= *Calamintha*]

Gardoquia Ruiz & Pavon (22) [= *Gardoquia*]

In notes after his description of *Micromeria* Bentham says that this new genus is closely allied to *Satureja* and *Melissa*. After the description of *Melissa* he writes:

> "The circumscription of this [*Melissa*] and the nearly related genera of *Hedeoma*, *Micromeria*, *Gardoquia*, and *Keithia* is attended by much difficulty; and it might, perhaps, have been a clearer classification, if the whole had been considered as forming one extensive genus, as in the case of *Salvia*, *Hyptis*, *Teucrium*, etc."

and also

> "I am fully aware that there are many species which may nearly as well placed in either of two or more sections or genera."

Note how Benthams treatment compares with the shortened synopsis of the arrangement adopted in this thesis. Bentham has Satureioid, Micromerioid (but includes the American *Xenopoma*), Calaminthoid, and the American genera (represented by the large genus *Gardoquia*). He also places *Satureja* L. distant from the rest of the genera, maintaining the opinion of Linnaeus (1753).

1.5.4. Consolidation and Clarification (1836-1848)

Bentham with his Labiatarum now complete had a solid foundation upon which to base further revisions. Problems that had arisen were now much easier to deal with. New species could be more easily placed within the framework of the family.

Discovery of new species continued apace during the years between the Labiatarum and Benthams second account of Labiatae in De Candolles Prodromus (1848). Notable amongst the many publications during this period is Webb & Berthelots monumental Phytologia Canariensis (1844) which added a large number of *Micromeria* species. Prominent also were Boissiers Diagnoses published in parts between 1842 and 1859.

Major changes were made in the treatment of *Satureja* s.l. in the Prodromus. The most important are the placement of the entire *Satureja* s.l. complex into the same tribe (Satureieae) and the removal of the Calaminthoid genera and *Calomelissa* from *Melissa* L. Other major changes are:

a) *Satureja*

i) *S. rupestris* is removed to *Micromeria* sect. *Pseudomelissa*.

ii) Although the sectional arrangement remains there is still doubt about *S. rigida* Bartr. which Bentham says may be related to *Pogogyne*. There is indeed a clear similarity in habit, but in leaf structure especially there is a marked difference.

b) *Micromeria*

The sectional arrangement has been reorganised.

i) Sect. *Piperella* - 38 of the 41 species belong to

Micromeria sect. *Micromeria*, and one to *Micromeria* sect. *Pseudomelissa* (*M. capitellata*). Bentham placed *M. staminea* in a sub-group of its own based on the long-exserted, divergent stamens, noting the similarity to *Calamintha* sect. *Clinopodium*. This species and *M. origanifolia* were later removed to *Calamintha* sect. *Cyclotrichium* Boiss. by Boissier (1879). Sub-sect. *Australasicae* is removed to *Mentha*.

ii) Sect. *Xenopoma* - This is equivalent to *Micromeria* sect. *Piperella* sub-sect. *Americanae* of the Labiatarum. Bentham adds *M. bonariensis* here, which he says may belong to *Hedeoma* [= *H. multiflorum* (Irving, 1980)].

iii) Sect. *Hesperothymus* - As in the Labiatarum but with *M. glabella* removed to *Calomelissa*.

iv) Sect. *Pseudomelissa* - Remains as defined in the Labiatarum but now with seven species.

c) *Calamintha*

Bentham adopts the arrangement first proposed by Miller (1754) by combining the Calaminthoid genera into one genus. He divides the genus into 5 sections: *Calamintha*, *Calomelissa*, *Acinos*, *Clinopodium* and *Heteromelysson*. These sections are circumscribed in a similar way as in the Labiatarum, though of the six species included in sect. *Calomelissa*, two species actually belong to *Gardoquia* and one to *Conradina*. Bentham also notes that the suffrutescent species of sect. *Calomelissa* are similar to sect. *Gardoquia* and the herbaceous species to *Micromeria*.

d) Gardoquia

Other than in a change in the sequence of the species, the circumscription is the same as in the Labiatarum.

Four distinct genera are thus again adopted in the Prodromus, even closer to the generic groupings of Satureioid, Calaminthoid, Micromerioid, and American genera than the treatment in the Labiatarum.

1.5.5. Building on the Foundation (1848-1896)

In this part of the history of Satureja s.l. I shall briefly described the period between De Candolles and Engler & Prantls encyclopaedic works, highlighting the major developments on the foundation that Bentham laid.

There was no work to challenge Benthams treatment until Kuntzes Revisio Genera Plantarum (1891). However, Kuntzes treatment did not really catch on. Briquets account in Engler & Prantls Naturlichen Pflanzenfamilien (1896) was much more influential.

Before discussing these two major works some mention must be made of Boissiers Flora Orientalis (vol. 4, 1879). This very important regional Flora had a clear effect on the treatment of Satureja s.l. by Briquet (1896). Boissier followed Bentham by placing all the Old World Satureja s.l. into 3 genera: Satureja, Micromeria and Calamintha. Satureja sensu Boiss. is equivalent to Satureja s.s. The genus was divided into 5 sections based primarily on calyx labiation and nervation. Micromeria was divided into 3 sections: sect. Cymuligera, for one small Turkish annual, sect. Eumicromeria (sect. Micromeria to be nomenclaturally correct), and sect. Pseudomelissa. Calamintha was also divided into 3 sections: sect. Eucalamintha, i.e. sect. Calamintha, sect. Cyclotrichium (the name refers to the characteristic annulus of hairs in the corolla tube), and sect. Acinos. Calamintha sensu Boissier is thus equivalent to my own Calaminthoid genera shifted down in rank.

Nymans Sylloge Florae Europeae (1855), though published only a short time after the monumental Prodromus, shows a great deal of independent thought. Thymeae sensu Nyman (1855) is similar in concept to Satureieae Bentham (1848), containing Horminum, Melissa, Clinopodium, Satureja, Origanum, Thymus, Thymbra and Hyssopus. His circumscription of Melissa is similar to Benthams original concept in the Labiatarum, and Satureja sensu Nyman goes back to the old Linnaean idea of uniting Satureja s.s. with Micromeria.

In Nymans Conspectus Florae Europeae (1881) all the tribes other than Thymeae remain virtually unchanged. Thymeae sensu Nyman (1881) now accomodates Origanum, Thymus and Thymbra only, and a new tribe, Melisseae, is created to encompass Hyssopus, Horminum, Melissa, Clinopodium, Calamintha, Micromeria and Satureja. Calamintha is divided into 2 sections, Eucalamintha and Acinos, and Micromeria is divided into 3 sections, Pseudomelissa, Eumicromerieae and Piperellae. As we will see later, this arrangement had a clear effect on Briquets treatment (Briquet, 1896).

All the works cited above are European. This is mainly because little of note was going on the in the New World studies that concern Satureja. However, one cannot pass on without mentioning the labours of Asa Gray. His Synoptical Flora of North America (1886) is a useful summary of his ideas. Satureja sensu A. Gray (1886) = Satureja sensu Bentham (1848); Micromeria sensu A. Gray (1886) includes sect. Hesperothymus Benth. (1848) only; Calamintha is somewhat different in including only two sections: sect. Clinopodium to accomodate the introduced C. calamintha [=Clinopodium vulgare L.], and sect. Calamintha which combines European introductions of Calamintha s.s. and the American species belonging to genera I am here calling Diodeilis and Montereya.

Up to this point the impression may have been given that

Briquet was the first to unite the Satureja complex into one genus, i.e. Satureja s.l., and that there was no precedent for this arrangement. In fact Kuntze (1891) beat Briquet to it. Kuntze, however, argued in favour of Clinopodium L. rather than Satureja L. and listed all the species here included within Satureja s.l. under the generic name Clinopodium. The reader is referred to the taxonomic account of Clinopodium for further details on this nomenclatural difference of opinion. But let it be said here that if a broad view is taken Satureja would have been preferable to Clinopodium. Satureja L. was always more broadly circumscribed than Clinopodium L. from Linnaeus Species Plantarum (1753) until after Benthams account in De Candolles Prodromus (1848).

Without question Briquets account of Satureja s.l. has been the most influential after Bentham. In order to justify his very broad view of Satureja s.l., Briquet launches into an attack of Benthams treatment of the Melissinae. He writes:

> "Bentham has seized on a criterion in the classification of the genera in the Melissinae like none other in the rest of the family. Had he considered his Monardeae, Ajugoideae and Ocimoideae with the same principles, groups like Salvia, Teucrium and Hyptis should have been split into numerous genera, which would have been at least better delimited against one another than for example Micromeria, Satureja, Gardoquia and Calamintha. Having decided on which principle one would use in the differentiation of the genera in a family one must logically stick to it. Then it is of the greatest importance, Bentham also accepting these principles, that because there is a gradual transitional series, obligate relationship must be placed in one genus. It is easy to see that if one later separates that kind of systematically related group into different genera, one gives the reader the completely wrong idea of the existing inter-relationship of the different groups. Practicality is also not gained by this differentiation of the genera, since during determination a species can sometimes be placed between 2, 3, or even 4 genera because of doubt and in each of these separated groups one must apply it in a very uncertain manner."

These remarks are totally unfair and sometimes completely inaccurate. Bentham did not "seize on a criterion" at all. As has already been mentioned Bentham recognised that it may be better to consider Melissa, Hedeoma, Micromeria, Gardoquia and Keithia "as forming one extensive genus, as in the case in Salvia, Hyptis, Teucrium, etc.", and was fully aware of the limitations of his 1834 revision. Obviously after more than a decade of extra study Bentham decided that he was justified in keeping these genera separate in the Prodromus. One cannot compare the method used to divide up Satureja s.l. with Salvia, Teucrium, Hyptis, etc. since they have evolved differently and have different patterns of variation. To say that Salvia may be split into several genera which would be better delimited than Micromeria, etc. is debatable. Salvia may at first appear to be divisible into distinct genera, but modern opinion generally concludes that there are too many intermediates to justify splitting the genus. As for "because there is a gradual transitional series, obligate relationship must be placed in one genus", this can be taken too far. As for practicality, Briquets arrangement does not really improve matters; rather I would say that the relationships within the complex become more obscure.

Let us now consider in more detail Briquets arrangement of Satureja s.l. to see whether it is any better than that of Bentham. Satureja sensu Briquet is equivalent to the four genera of Benthams Prodromus, Satureja, Micromeria, Calamintha and Gardoquia, united into one large omnibus genus, divided into 14 sections. The circumscription of these sections show a curious mixture of good original thought and complete lack of appreciation of the ideas of various authors. I shall take each of the 14 sections in turn, in the order Briquet had them, and discuss their similarity to previous accounts.

i) & ii) Sect. Tragoriganum Benth. and sect. Pycnothymus Benth. are as defined in the Labiatarum.

iii) Sect. Sabbatia Briq. is equivalent to Satureja sensu L.

(1753), i.e. *Satureja* s.s. and *Micromeria* sect. *Micromeria* united. Thus Briquet completely misses the significance of *Sabbatia* Moench (1794), which was to separate *Satureja* s.s. from *Micromeria* sect. *Micromeria*.

iv) Sect. *Cymularia* Briq. = *Micromeria* sect. *Cymularia* Boiss.

v) Sect. *Piperella* Briq. is quite different from *Micromeria* sect. *Piperella* Benth. Benthams section is equivalent to *Micromeria* sect. *Micromeria* whereas Briquet has created a section to accomodate just two species, *S. piperella* and *S. croatica*. Sect. *Piperella* Briq. is very flimsily distinguished from sect. *Sabbatia* and is not very consistent with the rest of his sectional treatment.

vi) Sect. *Cyclotrichium* = *Calamintha* sect. *Cyclotrichium* Boiss. Briquet clearly spells out the resupinate nature of the corolla.

vii) Sect. *Xenopoma* = *Micromeria* sect. *Xenopoma* Benth. It seems that Briquet was not able to examine all the species in this section since *S. bonariensis* is still included here even though Bentham had long before suggested this may belong to the diandrous genus *Hedeoma*.

viii) Sect. *Hesperothymus* = *Micromeria* sect. *Hesperothymus* Benth. The misplaced species of *Conradina* in Benthams account is removed to its correct genus by Briquet.

ix) Sect. *Gardoquia*. Briquet follows Benthams account in the Labiatarum (1834) very closely.

x) Sect. *Pseudomelissa* combines the accounts of *Micromeria* sect. *Pseudomelissa* of Bentham (1848) and Boissier (1879).

xi) There is a good piece of original thought in Briquets treatment of section *Calamintha*. He shows here a rather broad concept for *S. calamintha* (mostly drawn from his Labiees des Alpes Maritime, 1891) and a narrower concept for the rest of the species.

xii) Sect. Calomelissa is divided into three sub-sections: Glabellae [= Herbaceae Benth.], Coccineae [= Fruticosae Benth.] and Mimuloideae [= Montereya mihi].

xiii) Briquet has a broad species concept in sect. Clinopodium.

xiv) Briquets broader species concept than Bentham in Acinos brings it into line with modern thinking.

1.5.6. Modern Times (1896 to the present)

The claim by Briquet that a clearer appreciation of the affinities between the various species groups of Satureja s.l. is obtained by his treatment is a very debatable point. Rather it seems to me that all the modern day confusion about Satureja s.l. stems directly from his work. In 20th. century Floras most American and African writers have followed Briquet, while most of the rest of the world have stuck with Bentham. There has been a more serious result of Briquets work: since Satureja sensu Briquet is conveniently vague, some authors when in doubt about affinities have dumped species into Satureja. However, I have a great deal of sympathy with these authors since it a daunting task indeed to assess such a large group as Satureja s.l.

The important 20th. century works are too numerous to list, so I have selected a few which indicate the trends most clearly.

The most prominent author by far on the American scene has been Carl Epling. Not only did he produce accounts of the entire South American Labiatae, he also wrote many generic revisions, including two of Satureja for South America (Epling, 1927; Epling & Jativa, 1966) and one synoptic account for North America (1966). Epling followed Briquet in uniting all the American species into one genus, Satureja, divided into eleven sections: Gardoquia, Xenopoma, Calomelissa, Hesperothymus, Pycnothymus, Discolores, Anomales, Sphenostachys, Obtectae, Occidentalis and Arenosae. The first five sections have been discussed earlier and are similar to Briquets account. The other six sections each accommodate just one anomalous species. A number of authors, mainly of North American State Floras, have tried to place their species of Satureja s.l. into Micromeria, Calamintha or Clinopodium, e.g. Jepson (1926), Shinners (1961) and Small (1903), following the account of Grays North American Flora. However, the restricted number of species covered by these works decreased their influence quite considerably. Nearly all State Floras in the last twenty years have followed Epling.

Though a European author writing in a European publication, Briquet (1896) had remarkably little impact on European authors after him. The great majority have retained the arrangement of Bentham (1848). Flora Europaea (1972) includes Satureja s.s., Acinos, Calamintha, Clinopodium and Micromeria, all understood in a narrow strict sense. A similar treatment has been adopted in Flora of Turkey (Davis, 1982), Flora Iranica (Rechinger, 1983), Flora U.R.S.S. (Shishkin, ed., 1954), the Botanical Survey of India (Mukerjee, 1940), and Flora Sinica (1977), the most influential in their respective areas. Thus recent Flora writers in the whole of Eurasia have adopted a common opinion of Satureja s.l.

In Africa the situation is a little more complicated. Baker in Flora of Tropical Africa (1900) adopted Benthams narrow generic concept. Unfortunately there have been no African Floras with such a wide geographical coverage since. The Floras of French colonies in North Africa have been mostly directly influenced by Briquet, e.g. Negre (1962), Quezel & Santa (1963), whereas many other African Floras, though also adopting one genus, Satureja s.l., have done so because of a very restricted number of species within their area and the consequent difficulties of placing these in the context of the whole Satureja complex worldwide. Amongst this second group are accounts by Hutchinson & Dalziel (1963), Binns (1968), Brenan (1954) and Killick (1961).

1.6. Defining the Generic Limits within *Satureja* s.l.

1.6.1. The Theoretical Concept of the Genus

Thoughts and objects are being constantly organized by us all into convenient "pigeonholes" so that they may be synthesized into a coherent thought pattern or heirarchy of association. The question that arises here is: is the genus just one of these conceptual "pigeonholes", convenient for organizing data, or is it, in the biological context, of greater significance than this?

There is basically a three-fold answer to why the genus as a category is used. Firstly, the genus describes and gives recognition to the pattern of variation in the group of concern. Secondly, it implies naturalness of relationship and, in biological systems, consanguinity. Thirdly, and just as importantly, it is a practical system to assist identification and communication.

Expanding on the first of these points, it is plain that the way that the genus is defined depends on the variability of the characters and their correlation with one another in the group concerned. One genus may have extraordinary variability in habit and other vegetative features yet is relatively invariable in floral morphology, e.g. *Gardoquia*, whereas in another, e.g. *Satureja* s.s., vegetative and floral features are much less variable. Therefore one cannot devise a formula to distinguish the genus from species, tribe or family. This is self-evident when one considers the processes which produce these categories. The question of whether the processes which produce species or sub-species are the same as those which produce genera, families, etc. was addressed by Stebbins (1971). He showed that various character differences were diagnostic at specific, generic, familial and ordinal levels. For example the perianth biseriate versus uniseriate is diagnostic at the specific level with *Sagina* nodosa versus S. decumbens, at the generic level with Agrimonia versus Sanguisorba (Rosaceae), and at the familial level with Portulacaceae versus Chenopodiaceae. Many other examples are given. The implication is that the processes which produce species, genera, families, etc. are the same since the patterns of diversity are the same at all levels and that there are no peculiar characteristics of any of the categories. This cannot be tested experimentally for the higher categories, since the time required for the major groups to become recognizable takes too long. However, the well known processes responsible for evolutionary diversity at the sub-specific level, i.e. gene mutation, genetic recombination, chromosomal rearrangements, etc. and then selection of these, are, by implication, applicable to all levels because of the similarities in the patterns of diversity at all levels. So a genus or family arises when a particular combination of characters becomes so successful that it is retained in a series of related evolutionary lines that have become diversified in various directions.

Numerous definitions of the genus have been proposed and it would be useful to cite a few of these. Legendre & Vaillancourt (1969) asserted that the genus is "a monophyletic group of species that occupies a given adaptive zone". Legendre (1971) changed this definition to "a group of species with a genetic information content sufficiently similar that occupies a given adaptive zone". This is a significant change. Although the development of the genus must be understood in evolutionary terms the circumscription of a genus must be determined on phenetic similarity. The concept of phyletic closure, i.e. where all species descended from a common ancestor must be included in the genus, would be impossible in most cases to apply or be certain of. Legendre (1971) points out that a biological classification is not intended to be a perfect representation of an evolutionary tree. In reality the genus, or any biological taxon, is a compromise. It is impossible to adequately represent an evolutionary tree, which is a multi-dimentional system, by a two-dimentional taxonomic heirarchy. A similar compromise must also be made if a phenetic approach to classification is adopted. Cain (1956) defines the genus as "a natural group of species, monophyletic, and arbitrarily delimited". As was indicated above, since no formula can be devised I would agree that the genus is arbitrarily delimited. Porter (1959) also agrees here, stating that "no rule of thumb that will always apply can be set down". As for the genus being monophyletic one would agree that ideally this would be the case. But how can one guarantee the genus will be monophyletic? The short answer is: one cannot. However, a genus is more likely to be monophyletic if an extensive phenetic study of the component species has been carried out so that true homologies of characters may be discovered, uncovering parallelisms and convergencies. The final definition I would like to discuss is that of Mayr (1969), who has a phylogenetic concept of the genus. His definition is: "A category for a taxon including one species or a group of species, presumably of common phylogenetic origin, which is separated from similarly related units (genera) by a decided gap, the size of the gap being in inverse ratio to the size of the unit (genus)." I would agree with Legendres assessment of the definition (Legendre, 1972) that knowledge about the common phylogenetic origin is based on cladistic, unverifiable assumptions and that the determination of the size of the genus is entirely up to the worker. Love (1963) also points out that the size of genera is no good indication of degree of artificiality. A large genus may be very heterogeneous but not necessarily so, and heterogeneity is also met with in small genera. However, I would not agree with Love that "whereas hybridization is possible between species of a genus, hybridization between genera should be excluded". Though he does temper this by saying that frequent natural hybridization between genera implies the genera are not well defined and should be revised, and easy artificial hybridization does not necessarily mean they are in the same genus, I would not agree that hybridization is in any way more "reliable" than morphological information. Knobloch (1972) refers to a list of 2993 intergeneric hybrids, and one interfamilial hybrid, with about half showing some fertility. Even considering that some are spurious, these figures are probably an underestimate, since only a small fraction of plant species has been investigated. Therefore hybridization between genera (or lack of it) should not be over-emphasized.

Although the genus is impossible to absolutely define (Sherff, 1940), this is not a strong arguement to abandon the use of the taxon. It is a simple device to put a limit on certain known variation. Similarly, the species. The notion that the species is the "basic" taxonomic unit seems to me illogical. A "basic unit" implies that the species may be absolutely defined; but the species cannot be absolutely defined, just as the genus cannot be absolutely defined. The taxa of species, genus, family, etc. are just increasingly inclusive groups, but since they are in some manner described and defined on the known variation are very useful in summarizing that variation and to indicate naturalness of relationship. This leads on to the third point made above about the genus being a practical system for identification and communication. Linnaeus was the first to use the binomial system consistently. The two names were to be used as an alternative to a short diagnosis, the first part being the generic name which was also the first word in the diagnosis, and the second part being a descriptive name usually chosen not from Linnaeus diagnosis, but was either drawn from various earlier works, or describes some conspicuous feature, or its distribution. The practicality of this simple system is shown by its rapid adoption by taxonomists after Linnaeus first edition of Species Plantarum (1753). However, Sherff (1940) quotes L. H. Bailey who says "we would have gained much in simplicity of literature, in clarity and of popular usage, if we had a mononymy or other arrangement instead of a taxonomic dionymy". I would agree with Sherff that this statement is probably true, but a mononymy gives no immediate indication of relationship, so the advantages of the binomial system as outlined above far outweigh its disadvantages as implied by Bailey.

1.6.2. The Principles of Studying Genera

To engender any confidence in a generic revision or study, the entire group throughout its range must be investigated. In many revisions too many unnecessary splits of genera have been made because of a restricted viewpoint of the variation of that genus. As much data as possible should be compiled on morphology, anatomy, cytology, geography, etc. The interpretation and method of assessment of these data have caused most of the recent discussion in taxonomy. Taking a rather simple view there are basically two schools of thought: the pheneticists and the phylogeneticists. The phenetic school forms groups based on the overall resemblance of taxa, based on as many, equally weighted characters as possible. The groups thus formed do not imply any evolutionary pathway. The phylogenetic school tries to construct evolutionary pathways inferred from a taxons present characteristics, and those supposed to be of most recent common descent are used to form groups. Both purport to show natural relationships. Duncan (1980), who is an avowed cladist, lists several weaknesses of the phylogenetic method. He states that it is not possible to produce a unique cladogram since, as there is frequent use of contemporaneous organisms only, there are many uncertainties and difficulties in estimating the direction of evolution of characters. Phenetic classification makes no a priori assumptions of primitiveness of characters or of the direction of evolution of a group. In phenetic taxonomy primitive characters and possible evolutionary pathways are proposed after a classification has been devised. Even then such a proposed pathway is in most cases highly circumstantial. Phenetic taxonomy thus seems to me to be the more satisfactory approach.

Any study of a genus should take account of the generic concepts in the rest of the family and aim for a consistency of treatment as much as possible. This does not mean, however, that similar importance must be placed on certain characters in every genus. Each genus has diversified in a characteristic way, independent of another genus. However, since two closely related genera are probably of common phylogenetic origin they tend to vary in certain characters in a similar manner. This is very clearly seen in Satureja s.l. and is the basis of most of the differences of opinion in interpretation of the group. The main problem is parallel and convergent evolution between the genera within the Satureja complex.

Some taxonomists believe that the genus should have at least one diagnostic character so that it may be clearly delimited. This is really a typological concept which has its roots in Aristotelian logic that looked for the "essence" of things, an approach which Linnaeus adopted. Such a typological concept is not compatible with phenetic taxonomy which looks for overall similarity based on as many unweighted characters as possible. The former idea is a monothetic one, whereas phenetic classification is based on polythetic principles, where no single character is essential for a species, for example, to be included in a genus, but that a group of species which has been grouped together on account of overall similarity circumscribes the genus. This is essentially a synthetic approach. Briquet comments in his revision of Satureja s.l. in Naturlichen Pflanzenfamilien (1896), "that because there is a gradual transitional series, obligate relationship must be placed in one genus." He then gives some examples of characters which, when taken on their own, indeed show a transitional series from one genus to another. For example, he says that Micromeria is supposed to be differentiated from Satureja s.s. by the former having a 13-nerved calyx and the latter only 10, and then states that the difference is trivial since there is a complete series beween 10-nerved and 13-nerved depending upon where the intercostal veins unite. The fact that he picks on certain characters as being not good to separate genera suggests that his view was that a genus should have at least one character which is diagnostic of it, and if they do not then two supposed genera should be united. Bentham, on the other hand, by his many comments in the Labiatarum (1834) on genera or sections appearing natural, must have been guided more by overall similarity than by diagnostic characters alone. It is interesting to note that Briquet almost never gives much description of leaves and habit, with nearly all of the description of corolla and calyx. However, it is frequently the case that the most obvious characteristics of genera and sections recognised by various authors are in the leaves, e.g. the conduplicate leaves of Satureja s.s. and the thick-margined, entire leaves of Micromeria sect. Micromeria; but it must be noted here that these taxa have been formed not on these characters alone but by overall similarity. Briquets work has had a very unfortunate effect on later workers in the group, an effect which Briquet himself strove to avoid, i.e. to give "the reader the completely wrong idea of the existing relationship of the different groups". Flora writers especially have been very inconsistent in the treatment of the group. In America and Africa for the most part workers have followed Briquet, whereas elsewhere workers have followed Bentham. This may seem to be inevitable considering the usually restricted viewpoint of Flora writers. Therefore this new revision will hopefully point the way to a more consistent worldwide monographic treatment.

Chapter 2

Anatomy and Morphology

Chapter 2. Anatomy and Morphology

2.1. Introduction

Of the very few anatomical studies on the *Satureja* complex, most have been about one or a few species from a specified region (e.g. Caballero, Jimenez & Perez de Paz, 1978) or incidentally as part of a wider survey (e.g. Heinrichter, 1884). These earlier studies do not concentrate on the taxonomic importance or significance of anatomy solely within *Satureja* s.l. The following account will attempt to gather together all the available information on leaf and nutlet anatomy for *Satureja* s.l.

2.2. Leaf Anatomy

There has been some reservation about the significance of leaf organization in view of the many reports of large structural differences in the same species of sun and shade leaves (McDougall & Penfound, 1928; Stalfelt, 1956) and mesic and xeric leaves (Starr, 1912). Various environmental factors contribute to leaf xeromorphy, including heat, cold, wind, light intensity, and soil nutrients (Sheilds, 1950). The xeromorphic adaptions most commonly exhibited by leaves include reduced size, high volume to surface area, leaf loss in the dry season, revolution or folding, increased density of hairs, increased number of glandular hairs, stomata in cavities or grooves often lined with hairs, thickening of cuticle, thickening of epidermal cell walls, enlargement of epidermal cells, strong development of palisade mesophyll, increase in cell layers of palisade mesophyll, decrease in intracellular volume in spongy mesophyll, occurrence of a hypodermis, abundant development of sclerenchyma, collenchyma and xylem, thickening of vessel cell walls, reduced size and number of hydathodes, and an increase in the stomatal frequency (Russell, 1895; Maximov, 1929; Evenari, 1938; Oppenheimer, 1960; Pyykko, 1966; Parker, 1968; Rudall, 1980). The illustrations in the papers by Starr (1912), McDougall & Penfound (1928) and Stalfelt (1956) show, however, that although shade and sun leaves have these above-mentioned differences, the pattern of the tissues nearly always remains the same. Leaves with a dorsiventral arrangement of palisade mesophyll (e.g. fig. 2.7) in shade or mesic forms nearly always remains so in sun or xeromorphic forms. Rarely there is a transition to an isolateral pattern of palisade mesophyll (e.g. fig. 2.41) in sun and xeric forms, e.g. in Populus deltoides Marsh. and Prunus virginiana L. (Starr, 1912). Leaves with isolateral palisade in mesic forms probably remain so in xeromorphic forms.

Heinrichter (1884) noted that Satureja mutica Fisch. & Mey. had an isolateral arrangement of palisade parenchyma. Etienne (1930), however, showed that the Micromeria species he investigated all had dorsiventral palisade mesophyll. Preliminary anatomical data on 36 species of Satureja s.l. obtained by G. Ertem (unpublished; summarized in Table 2.12) also revealed clear differences in mesophyll composition and mid-vein bundle structure. It was these data and the very obvious differences in leaf morphology which prompted a more detailed investigation throughout the Satureja complex.

2.2.1. Materials and Methods

Herbarium material was used throughout this investigation. A very simple procedure was used to prepare leaf sections:

i) boil leaves for 2-5 minutes in water with two drops of detergent;

ii) place leaves in 5% KOH (aq.) solution for 5 minutes;

iii) wash leaves thoroughly in at least two separate beakers of cold water;

iv) place leaves in FAA [70% ethanol, 5% acetic acid, 5% formalin (aq.)] overnight or for at least four hours;

v) section the leaves freehand, holding the leaf between pieces of pith;

vi) using a fine brush, place the sections into 10% sodium hypochloride (aq.) solution in a watchglass until the section is bleached and clear, then transfer to water to remove the bleach;

vii) transfer the sections to a watchglass containing 1% Safranin (aq.) solution for 15-20 seconds (the time depends on the thickness of the section and concentration of the Safranin);

viii) transfer sections to clean water and wash off excess stain;

ix) mount in glycerol for semi-permanent slides.

The time required to rehydrate the leaves very much depends on the hardness and thickness of the leaf. However, within the time limits given above, softer leaves did not seem to be damaged if boiled longer than is minimally required to rehydrate them. The KOH treatment further softens the tissues by loosening the bonds between cells. This second treatment may be omitted when dealing with the thin-leaved species but is beneficial when sclerophyllous leaves are to be sectioned. The FAA treatment hardens and fixes the leaf so that the cells are not squashed when sectioned.

Transverse leaf sections were prepared for representatives of nearly all genera of the <u>Satureja</u> complex. In the descriptions, the shapes of cells are as viewed in transverse section.

2.2.2. Results

2.2.2.1. Satureja L. s.s.

2.2.2.1.1. Epidermis

In all 12 species investigated the cells are small and oblong. Wall thickening varies. In the laminar part of the epidermis there is only a slight thickening in S. spicigera. The other species show a distinct thickening of the walls, and in S. wiedemanniana, S. hortensis and S. bzybica very markedly so, especially in the outermost wall. The cuticle is rather thin in S. cuneifolia, S. spicigera and S. hortensis. In the other species the cuticle is very thick, extremely so in S. coerulea where it is as thick as the epidermis. The laminar epidermis and cuticle are very similar on both sides of the leaf.

Around the central vascular bundle the epidermal cells are usually very much smaller, rounder in section, and with very much more thickened walls; this is especially pronounced in S. coerulea. The cuticle around the vascular bundle is also thicker.

2.2.2.1.2. Palisade

The palisade consists of dorsiventrally elongated, thin-walled cells. In Satureja s.s. it is always isolateral in arrangement, i.e. there is a layer of palisade adjacent to both the upper and lower epidermis. When there is more than one cell layer the cells tend to be arranged end to end between layers. The upper palisade tends to be better developed than the lower palisade. The proportion of upper and lower palisade is usually similar, but the upper palisade is more compact with smaller air spaces. This difference in development is most marked in S. spicigera and S. bzybica. However, in S. thymbra and S. coerulea both palisade layers are poorly developed. See Table 2.1.

Table 2.1

Species	Palisade mesophyll				Spongy mesophyll	
	Cells in UP	%	Cells in LP	%	Cells in SM	%
S. hortensis	1	35	1	35	2-3	30
S. thymbra	1(-2)	30	1	20	4-5	50
S. salzmannii	2	50	2	50	0	0
S. spicigera	1	40	1	20	3-4	40
S. coerulea	1-2	20	1-2	30	c.4	50
S. macrantha	1	40	1	30	2-3	30
S. bzybica	1	30	1	30	3-4	40
S. aintabensis	2	40	2	40	1-2	20
S. spinosa	2	50	2	50	0	0
S. wiedemanniana	3	50	3	50	0	0
S. montana	2-3	50	2-3	50	0	0
S. cuneifolia	3	50	3	50	0	0

UP = upper palisade mesophyll; LP = lower palisade mesophyll; SM = spongy mesophyll; % = percentage of the mesophyll of the leaf lamina thickness.

2.2.2.1.3. Spongy mesophyll

Spongy mesophyll consists of rounded to rather irregular, rarely rather oblong (S. spicigera) cells with thin walls, and large air spaces (usually) in comparison to the air spaces of the palisade. In Satureja s.s., when present, the spongy mesophyll is always sandwiched between two layers of palisade mesophyll. In proportions and numbers of cells across the layer the spongy mesophyll varies greatly. See Table 2.1.

2.2.2.1.4. Mid-vein region collenchyma

The mid-vein vascular bundle is usually flanked above and below by collenchyma cells. Collenchyma is probably derived from parenchyma (Esau, 1965) but distinguished by possessing thickened, though unlignified, cell walls. In shape and disposition collenchyma varies considerably.

Only one species of those investigated, S. salzmannii, seems to be without collenchyma (fig. 2.41).

The three closely related species S. cuneifolia, S. spinosa and S. wiedemanniana all have very few dorsiventrally elongated cells, typically 1 to 4, above the vascular bundle (see fig. 2.40) bridging the gap between the upper epidermis and the vascular bundle. Below the vascular bundle these three species either have a small layer of collenchyma or again have very few, but rounded, collenchyma cells.

In S. spicigera, above the vascular bundle there is a thin layer of ± rounded-celled collenchyma, sometimes becoming slightly lignified next to the vascular bundle, and below there is a single layer of collenchyma adjacent to the epidermis only; thin-walled parenchyma cells separate the collenchyma from the vascular bundle. In all other species there is no separating band of parenchyma.

The remaining species have more or less developed bands of collenchyma above and below the vascular bundle. S. coerulea is remarkable for the very thickened cell walls of the collenchyma attached to the lower epidermis. The collenchyma in S. bzybica and S. macrantha above and below all has a very pronounced wall thickening. Collenchyma in S. hortensis is highly developed below the vascular bundle, taking up 50% of the total leaf thickness at the mid-vein region (see fig. 2.39).

2.2.2.1.5. Bundle sheath

In all the species investigated the bundle sheath consists of small, rather rounded cells. The walls are always unthickened, except for a slight thickening noted in S. cuneifolia.

2.2.2.1.6. Vascular bundle

The size of the vascular bundle varies greatly (see Table 2.2). In section, the bundle is usually oval, though ± rounded in S. cuneifolia. Sclerenchyma is usually entirely absent in the mid-vein vascular bundle (see Table 2.2). Sclerenchyma is also absent in the lateral vein vascular bundles in all these species except S. bzybica where the outermost two lateral veins have highly developed sclerenchyma, taking up 80-90% of these vascular bundles. In S. coerulea the sclerenchyma is slightly more developed with a couple of vessels only below the mid-vein phloem but highly developed in all the lateral veins, taking up about 75% of the bundle in section. In the remaining three species sclerenchyma is well developed in the mid-vein. In S. spinosa the sclerenchyma is in two bundles, one on either side of the xylem, encompassing 50% of the vascular tissue in total. In S. wiedemanniana there is a thick cap of sclerenchyma above the xylem taking up 50-70% of the vascular tissue. The strongest development of sclerenchyma is in S. salzmannii where 90% of the vasculature is this tissue, with the xylem and phloem (in a ratio of 3:1) above it (see fig. 2.41). In all the other species (except S. spinosa, where the ratio is 3:1) the ratio of xylem to phloem is approximately 1:1.

2.2.2.1.7. Stomata

In 11 species investigated, all had the diacytic stomatal type (see fig. 2.35 to 2.38), by far the most common type in Labiatae (Metcalfe & Chalk, 1979). Apart from in S. coerulea where the stomata are slightly raised up and level with the very thickened cuticle, the stomata are level with the epidermal walls. Table 2.2 gives an indication of the proportion of stomata near the middle part of the leaf on either side, calculated from counts made from leaf sections.

2.2.2.1.8. Glands

Three types of gland have been found in Satureja s.s. Type 1 (fig. 2.60), always sunken into a little pit, has a small stalk cell supporting a large spherical, single-celled gland. The second, type 2 (see fig. 2.59), is very much larger and is usually visible to the naked eye. A large, thin-walled epidermal cell supports 4-16 glandular cells which are surrounded by a large spherical envelope of glandular secretion. These glands may be yellow or red in colour. The first type was found on both sides of the leaf in all the species of Table 2.2. The second type was found in every species on both sides except in S. coerulea where this type is confined to the lower side of the leaf. A third type was found only on the upper side of the leaf in S. aintabensis (see fig. 2.62). The epidermal cell to which the gland is attached is very small. A short stalk supports a single-celled club-shaped gland only slightly larger than the stalk cell.

Table 2.2

Species	M.V.S.	M.V.B.%	Stomata Above%	Stomata Below%	Type
S. hortensis	-	40	50	50	D
S. thymbra	-	35	/	/	D
S. salzmannii	+	60-70	40	60	D
S. spicigera	-	40	67	33	D
S. coerulea	+	40	40	60	?
S. macrantha	-	50	60	40	D
S. bzybica	-	30	71	29	D
S. aintabensis	-	50	/	/	D
S. spinosa	+	35	40	60	D
S. wiedemanniana	+	30-40	54	46	?
S. parnassica	?	?	?	?	D
S. montana	-	30-40	49	51	D
S. cuneifolia	-	20	44	56	D

D = diacytic; / = present but proportions unknown; ? = unknown; M.V.B.% = proportion of mid-vascular bundle of leaf thickness at the mid-vein; M.V.S. = sclerenchyma in mid-vascular bundle; + = present; - = absent.

2.2.2.2. Gontscharovia Boriss.

The single species of the genus, G. popovii, is illustrated in figure 2.42.

The upper and lower epidermis is of small, oblong cells with thick walls, especially the outer; around the vascular bundle the cells become rounded and the walls even thicker. The cuticle is very thick. The palisade is isolateral with spongy mesophyll confined to around the vascular bundle. Near the vascular bundle the upper palisade is of one cell layer and well developed with few air spaces, taking up 30-40% of the leaf thickness. The lower palisade is much less well developed, being 20-25% of the leaf thickness and with more air spaces. The spongy mesophyll is 3-5 cells thick, rather irregular in shape and with quite large air spaces. Collenchyma above the vascular bundle consists of a layer 5-6 cells wide and 2-3 cells deep. The cell walls are extremely thickened so that their lumen is quite small. Below the vascular the bundle the collenchyma is about a dozen cells wide and 5-6 cells deep. Adjacent to the epidermis the cell walls are extremely thickened, becoming much less so toward the vascular bundle. The bundle sheath is of very small, thin-walled cells. In the mid-vein, sclerenchyma is absent or a few cells may be present above the xylem, but these may be lignified collenchyma cells. Sclerenchyma is extremely well developed in all the lateral veins, taking up to 80-90% of the vein in cross-section. Stomata are of the diacytic type, with 59% on the upper side, more or less level with the epidermis. Glands of types 1 and 2, exactly as found in <u>Satureja</u> s.s. species, are on both sides of the leaves.

2.2.2.3. <u>Saccocalyx satureoides</u> Coss. & Dr.

The epidermis on both sides consists of rounded to oblong cells with very thick walls. The epidermis is little different above and below the vascular bundle. The cuticle is very thick. Palisade parenchyma is isolateral, without any spongy mesophyll. Above and below, the palisade consists of 3 cell layers of small oblong cells which are rather loose, with large air spaces. In the mid-vein region there is no collenchyma above or below the vascular bundle. The bundle sheath has cells with slightly thickened walls and are small and rather oblong in shape. Sclerenchyma is strongly developed, taking up 80% of the vascular bundle. The xylem and phloem, in about equal amounts, is situated atop the sclerenchyma. Stomata are of the diacytic type with 29% on the upper side of the leaf. Glands similar to types 1 and 2, as found in Satureja s.s., were found on both sides of the leaf, the large punctate glands (type 2) always sunken in a pit.

2.2.2.4. Euhesperida Brullo & Furnari

Sections of both species were prepared.

2.2.2.4.1. Epidermis

E. linearifolia has small, squarish epidermal cells with extreme wall thickening. About 50% of the epidermal cells support glandular or eglandular hairs. In E. thymbrifolia the cells are rather more oblong but again have very thick walls, especially the outer wall. The leaf is less densely eglandular and glandular hairy than E. linearifolia. In both species the cuticle is rather thin.

2.2.2.4.2. Palisade

The palisade is isolateral and well developed but spongy mesophyll is entirely absent in both species. Both upper and lower palisade is of 2-3 cell layers. The cells are rather broadly oblong in E. linearifolia but much narrower and more compact in the other species.

2.2.2.4.3. Collenchyma

In both species above the mid-vascular bundle, there is a single layer of only a few thick-walled cells. In E. thymbrifolia adjacent to the lower epidermis, is a single layer with very thick walls, and between that layer and the bundle sheath are large rounded cells with somewhat thickened walls. The upper palisade is not interrupted by collenchyma in E. thymbrifolia, but a layer of small, round, thick-walled cells link the vascular bundle with the lower epidermis.

2.2.2.4.4. Bundle sheath

In E. linearifolia the cells are small and thin-walled. The cells are even smaller, with slightly thickened walls in E. thymbrifolia.

2.2.2.4.5. Vascular bundle

In both species the bundle is flattened and oval in section. In E. thymbrifolia the mid-vein bundle is situated in the lower third of the leaf and is only 15% of the leaf thickness, whereas in the other species the bundle takes up 35-40%. Sclerenchyma is entirely absent in both species.

2.2.2.4.6. Stomata

The stomata are slightly raised above the level of the epidermis, with about 1/3 situated on the upper side of the leaf.

2.2.2.4.7. Glands

Large punctate glands (type 2), like those in Satureja s.s., are on both sides of the leaf in both species. Type 1 (fig. 2.60) has been found on the upper side of the leaf in E. linearifolia only. A third type (designated type 7 in the figures; see fig. 2.67) was noted from both sides of the leaf in both species. An epidermal cell, square in cross section, with extremely thickened walls, supports a small stalk cell which in turn supports a spherical, club-shaped glandular cell. In *E. linearifolia* there is an extra ring of thickening around the top of the epidermal cell.

2.2.2.5. *Micromeria* Benth.

The results from *Micromeria* sect. *Micromeria* and sect. *Pseudomelissa* are presented separately since there are marked differences in their leaf anatomy.

2.2.2.5.1. *Micromeria* sect. *Micromeria*

Seven species were studied: *M. cristata* (see fig. 2.7), *M. parvifolia*, *M. kerneri*, *M. ovata*, *M. punctata*, *M. schimperi* and *M. longiflora*.

2.2.2.5.1.1. Epidermis

There is a marked difference between the upper and lower epidermis. The upper epidermal cells are quite large, oblong in shape, and with a very thickened outer wall. The lower epidermal cells are much smaller, being only 1/2 as thick in *M. cristata* and *M. parvifolia*, and 1/4 as thick in the rest. The lower epidermis has a similar pattern of wall thickening but it is much less marked.

2.2.2.5.1.2. Palisade

The palisade is dorsiventral in arrangement with a single layer of cells, taking up about 50% of the leaf thickness in most species. In *M. schimperi* and *M. longiflora* the palisade is more developed with narrower oblong cells, taking up 60-65% of the leaf thickness.

2.2.2.5.1.3. Spongy mesophyll

The spongy mesophyll tends to be composed of small, irregularly shaped cells. Air spaces between the cells may be large, as in *M. parvifolia* and *M. ovata*, or small, as in *M. cristata* and *M. longiflora*.

2.2.2.5.1.4. Collenchyma

In *M. cristata* there is no collenchyma above the mid-vascular bundle. In the other species there is only a small amount, with the most thickened walls in those cells adjacent to the epidermis and becoming less thickened toward the vascular bundle. The cells are round in section, about the size of the upper epidermal cells. Most of the area below the mid-vascular bundle is composed of rather thin-walled collenchyma cells smaller than the collenchyma above the bundle. Again, however, *M. cristata* differs and has only a few collenchyma cells below the vascular bundle adjacent to the epidermis.

2.2.2.5.1.5. Bundle sheath

The sheath is quite distinct. The cells are oval-oblong with very slightly thicker walls than the mesophyll.

2.2.2.5.1.6. Vascular bundle

The mid-vascular bundle is either oval in section (*M. cristata*, *M. kerneri*, *M. ovata* and *M. punctata*) or almost round (the other three species). In all species the mid-vein bulges out very markedly and yet the vascular bundle takes up only about 50% of the leaf thickness at the mid-vein.

Sclerenchyma above the mid-vein xylem is entirely absent in most species. A few fibres were noted above the xylem in *M. parvifolia* and *M. kerneri* only. In contrast, below the phloem, sclerenchyma is very strongly developed in all the species, with 50-75% of the whole bundle composed of this tissue. The marginal veins in all of the species are composed entirely of sclerenchyma.

2.2.2.5.1.7. Stomata

Nearly all the species had no stomata on the upper side of the leaf but many on the lower side. M. cristata was exceptional with 22% of the total stomata on the upper side. In this species the stomata are raised above the level of the epidermis while in all the other species the stomata are level with the epidermis. Stomata of the diacytic type were noted in M. cristata, M. parvifolia, M. kerneri and M. ovata. See also fig. 2.37 (Ertem; unpublished).

2.2.2.5.1.8. Glands

Table 2.3 below lists the various types of gland found.

Table 2.3

	Upper side	Lower side
M. cristata	14	3,12,13,14
M. parvifolia	14	2b,3,14
M. kerneri	2b,3,14	2b,3
M. ovata	3	2b,3,14
M. punctata	14	2b,3,14
M. schimperi	14	2b,3,14
M. longiflora	2b,3	2b,3

In M. cristata, gland type 12 is rather smaller than those found in Cyclotrichium (see fig. 2.71). Type 14 (see fig. 2.72) is found at the midrib in M. kerneri and very rarely on the upper side of the leaf in M. schimperi.

2.2.2.5.2. Micromeria sect. Pseudomelissa

The species investigated were M. frivaldskyana, M. taygetea, M. hydaspidis and M. fruticosa.

2.2.2.5.2.1. Epidermis

M. frivaldskyana was the only species in which the upper and lower epidermal cells are similar. Here the cells are very small, rounded, and with thick walls. The cuticle is as thick as the epidermis. In the other three species there is a marked difference between the upper and lower epidermal cells. In M. taygetea and M. hydaspidis the upper laminar epidermal cells are large oval-oblong, with moderately thickened walls, while the lower epidermal cells are small, oblong, only 1/4-1/5 the thickness of the upper cells in M. taygetea, and 1/3 the thickness in M. hydaspidis. M. fruticosa is quite different in that almost every epidermal cell supports a 1-3-celled hair. The cells supporting these hairs on the upper side are small, oblong-oval and thin-walled. The lower epidermis has cells only 1/2 the size of the upper, but in thickness the lower epidermis is only slightly less than the upper. The cuticle is thin in all three species.

The epidermis above and below the vascular bundle has rounded cells, usually smaller than the laminar epidermal cells. There is extreme thickening of the cell walls in M. frivaldskyana and M. hydaspidis, and much less thickening in the other two species.

2.2.2.5.2.2. Palisade

All four species have dorsiventral palisade mesophyll. It consists of 2, rarely 3, cell layers of small, narrow oblong, tight-packed cells in M. fruticosa that take up about 60% of the leaf thickness, and only a single layer of cells in the other species which takes up 50% of the leaf thickness. In these latter species, M. hydaspidis has rather tight-packed palisade, but in the others the palisade is rather loose with quite big air spaces.

2.2.2.5.2.3. Spongy mesophyll

This tissue consists of 3-4 layers of very irregular cells. All species have large air spaces between the cells with the exception of *M. fruticosa* which has rather small air spaces.

2.2.2.5.2.4. Collenchyma

Above the mid-vein bundle there is very little collenchyma, typically only a small wedge of small, round, very thick-walled cells. *M. taygetea* differs in having only one or two large oval collenchyma cells above the mid-vein bundle. Below the mid-vein bundle most of the tissue is collenchyma. The cells are round, larger and thinner walled, except adjacent to the epidermis, than the upper collenchyma.

2.2.2.5.2.5. Bundle sheath

The cells are always small, oval to rounded, and thin-walled.

2.2.2.5.2.6. Vascular bundle

The shape varies from round in *M. taygetea*, semi-circular to crescent-shaped in *M. hydaspidis*, and a flattened oval in the other two species. The bundle takes up about 1/3 of the leaf thickness at the mid-vein. Sclerenchyma is entirely absent in all veins.

2.2.2.5.2.7. Stomata

Two species, *M. hydaspidis* and *M. fruticosa*, seemed to have no stomata on the upper side of the leaf. *M. hydaspidis* had many on the lower side, level with the epidermis, but *M. fruticosa* very few slightly raised above the level of the epidermis. The other two species had stomata on both sides of the leaf raised up above the level of the epidermis, *M. frivaldskyana* with 18% on the upper side, and *M. taygetea* with 13%. The sub-stomatal spaces in *M.*

fruticosa were very small. The stomata were noted as being of the diacytic type in M. hydaspidis and M. frivaldskyana.

2.2.2.5.2.8. Glands

The following types of gland were found:

Table 2.4

	Upper side	Lower side
M. frivaldskyana	int. 1 & 9	int. 1 & 9,2b
M. taygetea	11	int. 1 & 9,2b,11
M. hydaspidis	int. 1 & 9,2b	int. 1 & 9,2b
M. fruticosa	2b,14	2b,14

In M. taygetea, type 11 (fig. 2.69) is very common but those intermediate between types 1 (fig. 2.60) and 9 (fig. 2.65) are very rare.

2.2.2.6. Killickia A. Doroszenko

The only species investigated, of the three in the genus, was K. pilosa.

The upper epidermis consists of large oblong cells with very thickened walls, especially the outer wall. The lower epidermis is only 1/4 as thick as the upper, with oblong, thick-walled cells, though not as thick as the upper epidermal cells. Above and below the mid-vascular bundle the epidermal cells are small and square with extreme wall thickening.

The palisade mesophyll is dorsiventral, with compact, broad, oblong cells, taking up 40-50% of the lamina thickness. The spongy mesophyll has approximately 4 cell layers of large irregular-rounded cells.

The mid-vein is strongly developed, bulging well below the level of the lamina. The vascular bundle is about 25% of the leaf thickness at the mid-vein. Collenchyma above this bundle is of 3 layers, c. 6 cells wide, with extreme thickening of the walls so that the cell lumen is almost closed. Most of the area below the vascular bundle is also taken up by collenchyma. Only next to the epidermis is the wall thickening as extreme as it is above the vascular bundle; the other cells are much larger and thinner walled. There is no sclerenchyma in any of the vascular bundles. A few slightly lignified collenchyma cells may be present above the mid-vascular bundle.

Stomata are diacytic and level with the epidermis; 91% are on the lower side of the lamina.

Punctate glands of type 2b (see fig. 2.58) are on both sides of the leaf. Glands similar to type 1 (see fig. 2.60), though not sunken, are on the upper side, and glands of type 9 (see fig. 2.65) on the lower side.

2.2.2.7. Brenaniella A. Doroszenko

Two species were investigated, B. robusta and B. myriantha.

2.2.2.7.1. Epidermis

The upper epidermis consists of large, oblong, thick-walled cells. The lower epidermis is only 1/3 the thickness of the upper. Above and below the vascular bundle the cells are very small, lens-shaped, with very thick walls. The cuticle is quite thin.

2.2.2.7.2. Palisade

The palisade mesophyll is dorsiventral, taking up about 40% of the leaf thickness. In B. robusta the cells are very narrow oblong while in B. myriantha the cells are much broader.

2.2.2.7.3. Spongy mesophyll

Both species have 4-5 layers of cells. The cells are small and irregularly shaped in *B. robusta*, but rather oblong in *B. myriantha*.

2.2.2.7.4. Collenchyma

The whole mid-vein region above and below the vascular bundle contains collenchyma. The cells are small next to the epidermis, enlarged toward the vascular bundle. The cells are all rather smaller in *B. myriantha* than *B. robusta*.

2.2.2.7.5. Vascular bundle

The bundle is about 1/3 of the leaf thickness. Xylem and phloem are in approximately equal amounts. There is no sclerenchyma at all in the bundles of *B. robusta*, but a few fibres were noted above the xylem and below the phloem in *B. myriantha*.

2.2.2.7.6. Stomata

No stomata were found on the upper side of the lamina. The many stomata below are diacytic, slightly raised above the epidermis in *B. robusta*, and more or less level with the epidermis in *B. myriantha*.

2.2.2.7.7. Glands

Glands of a type intermediate between type 1 (see fig. 2.60) and type 9 (see fig. 2.65) were found on the upper side of the leaf in both species, and on the lower side in *B. robusta* only. In *B. robusta* these glands are only found above and below the vascular bundles. On the lower side of the leaf there are glands similar to type 1 sunken into pits, and punctate glands of type 2b (see fig. 2.58) in *B. myriantha*.

2.2.2.8. Calamintha Miller

Two species were investigated: C. rouyana and C. uhligii.

2.2.2.8.1. Epidermis

The laminar epidermal cells on the upper side are small, oval-oblong, with very thick walls, especially the outer walls. The lower epidermis is only 1/3-1/2 as thick as the upper epidermis in C. rouyana, and 3/4 as thick in C. uhligii, but the cells are similar in shape and wall thickening. Above the mid-vascular bundle in C. rouyana the cells are more rounded but not with much more thickened walls, while below the mid-vein the cells are twice the size of the other epidermal cells on the lower side, rounded in shape and with much more thickened walls. In C. uhligii both above and below the mid-vein the cells are small, rounded, and with very thick walls. The cuticle is quite thin in both species.

2.2.2.8.2. Palisade mesophyll

The palisade is dorsiventral with a single layer of broad oblong cells taking up 50% of the leaf thickness in C. rouyana and 35-40% in C. uhligii.

2.2.2.8.3. Spongy mesophyll

The spongy mesophyll in C. rouyana has irregularly shaped cells with large air spaces between them, but is more compact in C. uhligii, with irregular oblong to squarish cells. The mesophyll is 3-4 cells deep.

2.2.2.8.4. Collenchyma

Above the mid-vascular bundle, collenchyma is almost absent in C. rouyana with 2-3 rounded cells only, but in C. uhligii there is a broad band of small, round, thick-walled cells. Most of the area below the mid-vascular bundle in both species is composed of quite large collenchyma cells with not very thickened walls. The cells tend to be smaller and thicker walled adjacent to the epidermis.

2.2.2.8.5. Vascular bundle

The mid-vein bundle is only 1/3 the leaf thickness, round in section in *C. rouyana* and a broadly flattened oval in the other species. There is no sclerenchyma at all in *C. rouyana*, though a few fibres were noted below the phloem of the mid-vein in *C. uhligii*.

2.2.2.8.6. Stomata

In both species the stomata are diacytic. No stomata were found on the upper side of the leaf in *C. uhligii*, but 23% on the upper side in *C. rouyana*.

2.2.2.8.7. Glands

The many types of gland found are summarized in Table 2.5 below.

Table 2.5

	Upper side	Lower side
C. rouyana	int. 1 & 9,2b,3	int. 1 & 9,2b,3,10
C. uhligii	6	3,2b,13

The glands intermediate between types 1 (fig. 2.60) and 9 (fig. 2.65) have an apical cell less spherical than type 1 but not as narrow as type 9. In *C. uhligii*, the gland designated type 3 has a rather smaller apical cell than that drawn in figure 2.62.

2.2.2.9. *Acinos* Miller

Four species were investigated: *A. corsicus*, *A. nanus*, *A.*

alpinus and A. pseudosimensis.

2.2.2.9.1. Epidermis

A. corsicus is the only species in which both upper and lower epidermis consist of small oblong cells of similar size with equally thickened walls. In the other three species the upper epidermal cells are quite large, oblong to squarish in section, and with rather thickened walls, and the lower epidermis only 1/2, 1/10-1/5, and 1/2 the thickness of the upper epidermis in A. nanus, A. pseudosimensis and A. alpinus, respectively. The lower epidermal cell walls are less thickened than the upper in these three species. The cuticle is thick in A. corsicus and A. nanus, but thin in the other two species.

2.2.2.9.2. Palisade

In A. corsicus the palisade is more or less dorsiventral around the mid-vein vascular bundle but becomes isolateral towards the margins. The upper palisade has two layers of broad oblong, thin-walled cells. The lower mesophyll has 3-5 cell layers, rather similar to the upper palisade in being arranged in regular rows, but is much looser around the mid-vein and only becomes compact toward the margins.

The other species are clearly dorsiventral in arrangement. The upper palisade is most strongly developed in A. nanus which has 2 cell layers of thin-walled, markedly elongated, oblong cells without obvious air spaces, taking up slightly more than half of the leaf thickness. The palisade is of one cell layer in the other species. In A. alpinus the palisade is rather poorly developed with rather broad oblong cells with large air spaces between them.

2.2.2.9.3. Spongy mesophyll

The cells are small and irregular in all species except *A. corsicus*. The approximate number of cell layers is 5-6 in *A. nanus*, and 4 in the other two species. The air spaces are only large in *A. alpinus*.

2.2.2.9.4. Collenchyma

A. corsicus usually has no collenchyma above or below the mid-vein vascular bundle. Rarely an elongated cell similar to the palisade with slightly thickened walls is present above the mid-vein.

Collenchyma is strongly developed above and below the vascular bundle in the other three species. The cell walls are especially thickened in the cells adjacent to the lower epidermis, so much so in *A. pseudosimensis* that the cell lumen diameter is less than the wall thickness.

2.2.2.9.5. Bundle sheath

The bundle sheath is hardly, or not, distinguishable from the small, thin-walled parenchyma cells adjacent to the vascular bundle.

2.2.2.9.6. Vascular bundle

The bundle is a flattened oval in section, taking up 40-50% of the leaf thickness in *A. alpinus* and 25-30% in the others.

Sclerenchyma is entirely absent in all traces in *A. alpinus* and *A. pseudosimensis*. In *A. corsicus* sclerenchyma is absent from the mid-vein and all lateral veins, but has a thick marginal vein apparently entirely composed of sclerenchyma fibres. *A. nanus* has a similar marginal vein and also has sclerenchyma in all the vascular traces, taking up 50% of the bundle tissue.

2.2.2.9.7. Stomata

In all four species, the stomata are of the diacytic type. The proportion of stomata on the upper side of the leaf varies considerably; none at all was seen in *A. pseudosimensis*, while 27% and 52% was found in *A. alpinus* and *A. corsicus*, respectively.

2.2.2.9.8. Glands

Refering to figs. 2.58 to 2.65, which illustrate the gland types, the following was found:

Table 2.5

	Upper side	Lower side
A. corsicus	1,4	1,3,4
A. nanus	1,4	1,2
A. alpinus	1	1,5,6
A. pseudosimensis	1,3	2b,3,4,9

In *A. nanus* the gland designated type 2 is similar in appearance to that drawn in fig. 2.59 but is smaller, not much larger than type 1, and not sunken into a pit.

2.2.2.10. *Cyclotrichium* Manden. & Scheng.

Four species were investigated: *C. leucotrichum*, *C. niveum*, *C. stamineum* and *C. haussknechtii*.

2.2.2.10.1. Epidermis

The epidermis is rather variable. *C. niveum* is the only species which has all cells on both upper and lower sides of the lamina that are of similar shape and size. The cells are very small, oblong, with thickened walls. *C. leucotrichum* and *C. haussknechtii* have large oval-oblong cells with thick walls on the upper side, and on the lower side the epidermal cells are only 1/3 as thick and thinner walled. In *C. stamineum* the upper epidermal cells are small, oblong-oval with somewhat thickened walls. The lower epidermal cells are a little smaller, but similar otherwise. Above and below the mid-vascular bundle the cells are much smaller in all species, either squarish or round in section and much thicker walled.

2.2.2.10.2. Palisade

The palisade of C. niveum is isolateral while the rest are clearly dorsiventral, but in all the species the cells are small and oblong. Both upper and lower palisade in C. niveum consists of two (rarely 3) compact cell layers. The palisade in C. leucotrichum and C. haussknechtii is usually of two layers, while C. stamineum is usually of one layer.

2.2.2.10.3. Spongy mesophyll

There is no spongy mesophyll in C. niveum. In the other species 40-50% of the leaf thickness is this tissue in 3-4 cell layers. C. leucotrichum has irregular-oblong cells which tend to be arranged dorsiventrally, but the air spaces are quite large. The other two species have irregularly shaped cells with large air spaces between.

2.2.2.10.4. Collenchyma

Above the mid-vascular bundle is a small wedge of collenchyma, usually only a few cells wide in 3-4 layers. The cells are small, round, with very thick walls, especially so in C. haussknechtii. Most of the area below the mid-vein bundle is composed of collenchyma. The cells are usually larger and thinner walled.

2.2.2.10.5. Bundle sheath

The cells are small, rounded to oblong-oval, and thin-walled.

The sheath is quite distinct only in C. leucotrichum.

2.2.2.10.6. Vascular bundle

In all species, the bundle is oval in section, taking up about 1/3 of the leaf thickness. Sclerenchyma is entirely absent in C. leucotrichum and C. niveum. A few fibres were noted below the phloem in the other two species. A few collenchyma cells may be slightly lignified above the xylem in C. haussknechtii.

2.2.2.10.7. Stomata

Diacytic stomata were noted in C. leucotrichum and C. stamineum. All the species have fewer stomata on the upper side of the leaf (see Table 2.7).

2.2.2.10.8. Glands

Table 2.7 details the different types of gland found.

Table 2.7

	Upper side	Lower side	Stomata % on upper side
C. leucotrichum	3,6,7a,12	2,6,12	21
C. niveum	2b,3,7a	2b,3,7a	41
C. stamineum	3,7a,9	2b,3,7a,9	34
C. haussknechtii	7a,12	2b,7a,12	27

In C. leucotrichum the punctate gland, type 2 (fig. 2.59), is small and of similar size to the punctate gland of type 2b (fig. 2.58). Gland type 12 (fig. 2.71) on the lower side of the leaf is commonest around the mid-vein. In C. niveum, type 7a (fig. 2.76) is rather taller than average, while type 3 (2.62) is smaller than usual.

2.2.2.11. *Gardoquia* Ruiz & Pavon

22 species were studied and are listed in Table 2.8.

2.2.2.11.1. *Epidermis*

The upper epidermis usually consists of rather small oblong cells in transverse section. However, there are notable differences in some species: *G. sericea* and *G. sericifolia* have squarish-oblong cells; *G. clivorum* and *G. tomentosa* have large-oblong cells; *G. multiflora* has long, thin, narrow-oblong cells; and *G. micromerioides* has small and squarish cells.

The majority of species have a much thinner lower epidermis. In most cases the thickness ratio is about 2 or 3 to 1. A more marked difference was noted in G. sericea (5:1) and *G. pulchella* (4:1) and a less marked difference in *G. incana*, *G. mathewsii* (fig. 2.42), *G. multiflora* and *G. discolor* (fig. 2.46) (all c. 4/3:1). There is no great difference in thickness in *G. gilliesii* (fig. 2.43), *G. plicatula* (fig. 2.44), *G. mexicana*, *G. micromerioides* and *G. weberbaueri*. The shape of the lower epidermal cells is usually similar to the upper epidermis, except for in *G. mexicana* and *G. tomentosa* where the cells are much squarer in section.

Most species have very thick-walled cells in the upper epidermis, especially the outermost wall, and this is most marked in *G. plicatula*, *G. sericifolia*, *G. acutifolia*, *G. sericea*, *G. gilliesii* and *G. pulchella*. However, the walls are rather thin in *G. weberbaueri*, *G. taxifolia*, *G. incana*, *G. domingensis* and *G. striata*. The lower epidermis cell walls are usually a little less thickened than the upper, except in *G. taxifolia* where the lower side has thicker walls. Only in *G. sericea* and *G. pulchella* are the lower epidermal cell walls a great deal thinner than the upper.

The epidermal cells above and below the mid-vein are usually rounded, and generally smaller and thicker walled than the laminar epidermal cells. This difference in wall thickening is most marked on the lower side of the leaf.

The cuticle is usually thin and unremarkable. G. clivorum and G. striata, however, have a rather thick cuticle.

2.2.2.11.2. Palisade

G. micromerioides has isolateral palisade parenchyma, while all the rest have dorsiventral palisade. Some specimens of G. pallida (see fig. 2.45), G. striata and G. incana have some dorsiventrally arranged, oblong cells adjacent to the lower epidermis with large air spaces between these cells.

The palisade is usually of one cell layer, but G. weberbaueri tends to have a double layer. Most species have broad-oblong palisade cells, but are narrow-oblong in G. sericifolia, G. plicatula, G.cercocarpoides, G. gilliesii, G. micromerioides, G. mexicana, G. pallida, G. domingensis and G. tomentosa.

2.2.2.11.3. Spongy mesophyll

The spongy mesophyll is quite distinct in all species, except in G. micromerioides which has none. The cells are usually irregular in shape with quite distinct air spaces between them. However, in G. pulchella, G. weberbaueri, G. revoluta and G. discolor the spongy mesophyll is compact and arranged in regular layers, and as mentioned above some species have a few palisade-like cells within the spongy mesophyll. The approximate number of cells across the spongy mesophyll is given in Table 2.8.

2.2.2.11.4. Mid-vein region collenchyma

The collenchyma above the mid-vein bundle is usually of only a few small, rounded, thick-walled cells, in 1-3 layers. However, in G. mathewsii collenchyma is strongly developed above the mid-vein (see fig. 2.42). Very often the collenchyma becomes slightly lignified and merges into a layer of an unusual type (for *Satureja* s.l.) of sclerenchymatous fibre which has a very large lumen (see Table 2.9). Below the mid-vein bundle the whole area is usually composed of collenchyma. The cells are rounded, mostly larger than the collenchyma above the vascular bundle, and thick-walled, especially adjacent to the epidermis. Exceptions are *G. domingensis*, which has only a single layer of tiny, very thick-walled cells adjacent to the epidermis, and *G. micromerioides*, which has a narrow wedge of cells without especially thickened walls except at the epidermis.

2.2.2.11.5. Bundle sheath

The sheath cells are small, usually merging into the collenchyma or spongy mesophyll, and usually thin walled.

2.2.2.11.6. Vascular bundle

The mid-vein bundle is oval or round in section, sometimes rather crescent-shaped, and is about 35-40% of the leaf thickness at the mid-vein. The only notable departures from this were in *G. domingensis*, which has a very small, round bundle, and *G. striata* which has a very large bundle that takes up 75% of the leaf thickness.

As has been previously mentioned, sclerenchyma in the mid-vein is of two types, a very small lumen type and a large lumen type, though in many species there is a transition between them. Most species have a large cap of sclerenchyma above the xylem and a broad layer below the phloem. Rarely there are only very few fibres. In *G. multiflora* there are typically 0-2 very narrow fibres above and below the bundle. Only four species were noted to have no sclerenchyma at all (see Table 2.9). *G. discolor*, though having no sclerenchyma above the vascular bundle, has a well developed band of sclerenchyma below the phloem (see fig. 2.46).

The details of the mid-vascular bundle are given in Table 2.9.

Table 2.8

Species	Palisade % of leaf thickness	Spongy (no. cells across)	Glands	
			Above	Below
G. multiflora	40	c.4	c.14	2b,14,int.1 & 15
G. mexicana	40-45	5-6	1	1,2b
G. seleriana	35	c.5	c.15	1,2b
G. acutifolia	50	c.4	-	2b
G. cercocarpoides	40-50	c.5	2b,15	2b,c.14,15
G. tomentosa	50	3-4	5,14,17	2b,c.12,17
G. pulchella	35-40	3-5	14	2b,3
G. mathewsii	50	3-4	?	2b,15,16
G. incana	50	c.4	14	2b,c.14
G. domingensis	40	c.5	2a,c.14,15,c.17	2b,c.3,c.14
G. pallida	50	c.4	1,2b	1,2b
G. gilliesii	50	c.5	2b,c.9	2b,c.9
G. taxifolia	40-60	3-4	15	2b,c.14,c.15
G. weberbaueri	60	c.3	15	2b,15
G. clivorum	40	4-5	8	2b,9
G. sericea	40-50	3-4	18	2b,15,18
G. sericifolia	40	5-6	2b,c.4,c.14	2b,c.14,c.17
G. revoluta	50-75	c.2	14	2b,14,16
G. plicatula	35	c.6	15,17	2b,c.9,17
G. striata	35-40	4-5	-	1,2b
G. discolor	40	c.4	?	2b
G. micromerioides	100	0	1,2b	1,2b

2.2.2.11.7. Stomata

Nearly all species have no stomata on the upper side of the leaf. Only *G. gilliesii* and *G. micromerioides* were noted to have approximately 14% and 55%, respectively, of the total stomata near the middle of the leaf on the upper side. The stomata on the lower side are usually slightly raised above the level of the epidermal cells. A few species have stomata level with the epidermis. Diacytic stomata were noted in *G. micromerioides*, *G. mexicana*, *G. striata* and *G. multiflora*. The sub-stomatal space in *G. seleriana* and *G. acutifolia* is exceptionally small, but in *G. domingensis* it is very large. The subsidiary cells of *G. taxifolia* are very small.

Table 2.9

Species	V.B.	V.B. shape	Sclerenchyma	
			Above	Below
G. multiflora	35	O-C	V.few S	V.few S
G. mexicana	35	O	None	None
G. seleriana	30	C	Few L	S
G. acutifolia	35	FO	Few S	S
G. cercocarpoides	35	O	L	S
G. tomentosa	30	R	S-L	S
G. pulchella	35	R	L	S
G. mathewsii	35	R	L	±S
G. incana	35	O	S-L	S
G. domingensis	25	R	L	S-L
G. pallida	35	FO	None	None
G. gilliesii	35	R	S-±L	S
G. taxifolia	35	O	S-L	S
G. weberbaueri	40	O	S-L	S
G. clivorum	40	±R	S-L	S
G. sericea	35	O	V.few S	S
G. sericifolia	40	O	Few L	S
G. revoluta	35-40	O	None	None
G. plicatula	40	R	V.few S	S
G. striata	75	±O	S-L	S-L
G. discolor	40	R	None	S
G. micromerioides	35	FO	None	None

V.B. % = proportion of dorsiventral thickness of vascular bundle to whole leaf thickness at mid-vein; V.B. shape = vascular bundle shape in section; C = crescent-shaped; FO = flattened oval; O = oval; O-C = intermediate between oval and crescent-shaped; R = round; Sclerenchyma - S = small lumen fibres present; L = large lumen fibres present; S-L = transition between small and large fibres present.

2.2.2.11.8. Glands

Table 2.8 summarizes the numerous different types found. In *G. multiflora*, the glands intermediate between types 1 (fig. 2.60) and 15 (fig. 2.73) are unusual in being sunken into a pit, and in *G. taxifolia*, a gland similar to type 15 on the lower side of the leaf is also sunken, but into a shallow pit. On the upper side, near the mid-vein in *G. plicatula*, glands similar to type 15 but with very large gland cells were found. A very small form of type 14 (fig. 2.72) was found on the upper side of the leaf in *G. tomentosa* and on the lower side of *G. sericifolia*. Also in *G. incana*, glands of type 2b (fig. 2.58) are exceptionally small. Glands were found to be very rare or absent on the upper side of the leaf in *G.*

acutifolia, G. pulchella, G. taxifolia, G. weberbaueri and G. striata.

2.2.2.12. Obtegomeria caerulescens (Benth.) A. Doroszenko

The upper epidermis consists of rather oblong and thick-walled cells in section. Above the mid-vein the cells become more squarish and thicker walled. The lower epidermal cells are similar to the upper in shape but thin-walled on the lamina and thick-walled around the mid-vein. The cuticle is thick, especially on the upper side. The palisade parenchyma is dorsiventral, with one layer of cells. The spongy mesophyll is rather compact with oblong cells arranged in c. 4 regular layers. Collenchyma above and below the mid-vein consists of only a single layer of thick-walled cells adjacent to the epidermis. Between the collenchyma and xylem and phloem are small parenchyma cells with unthickened walls. The mid-vascular bundle is oval, taking up 30-35% of the leaf thickness, and equally divided amongst xylem and phloem. There is no sclerenchyma. Stomata are diacytic and only found on the lower side of the leaf. Glands of types 1 and 3 were found on both sides, and type 2b (fig. 2.58) on the lower side of the leaf only.

See fig. 2.47 for a T.S. drawing of the leaf.

2.2.2.13. Xenopoma Willd.

The 16 species listed in Table 2.10 were examined.

2.2.2.13.1. Epidermis

The shape and size of the epidermal cells tend to be similar within the sections of Xenopoma. The species of sect. Xenopoma have a thick upper epidermis, consisting of large square to oblong cells, with very thick outer walls. The lower epidermis is only 1/4-1/2 as thick as the upper, with cells similarly shaped, but with rather less thickened walls. In X. alpestris (see fig. 2.48) the cells below the mid-vein are a little smaller and thicker walled than the laminar cells, otherwise the cells above and below the mid-vein are similar. X. schusteri (see fig. 2.49) has squarish to upright oblong, very thick walled cells, and X. viminea has irregularly rounded, very thick walled cells above the mid-vein. Below the mid-vein both have small, rounded, thick-walled cells.

The upper epidermis in sections Ceratominthe, Pauciflorae, Prostratae and Sphenostachys (see fig. 2.55) nearly always has small cells, oval to oblong in shape, with rather thickened walls. Exceptions are X. boliviana (sect. Ceratominthe) (see fig. 2.50), which has very small squarish-oblong cells, and X. darwinii and X. tenella (both sect. Prostratae) which have large oval or oval-oblong cells. In these four sections the lower epidermis is generally a little thinner, usually 1/2 to almost as thick. However, in X. darwinii, X. tenella and X. nubigena the lower epidermis is only about 1/4-1/3 as thick. The epidermis above the mid-vein is no different from the upper laminar epidermis in X. chandleri, X. nubigena and X. darwinii, but tends to be of smaller, rounder, and thicker walled cells in the other species. Below the mid-vein the epidermal cells are nearly always smaller than the laminar cells, rounded and very thick walled.

In the remaining section, Spicatae, the two species are rather different in their epidermides. X. fasciculata has large squarish upper epidermal cells (see fig. 2.53), with very thick outer walls. The lower epidermis is only 1/4-1/3 as thick, with small, oval-oblong cells. X. mutabilis has thick-walled, rounded to oval upper epidermal cells (see fig. 2.54). The lower epidermis has thinner walled cells of similar shape but is only half as thick as the upper epidermis. Both species have very small, rounded, very thick walled cells above and below the mid-vein.

2.2.2.13.2. Palisade

The palisade mesophyll is always dorsiventral, consisting of a single, 1-cell layer, except for in X. darwinii which tends to have 2 layers. In nearly all species the palisade takes up about 45-50% of the leaf thickness, but in X. brevicalyx the proportion is rather less at about 35-40% (see fig. 2.51).

2.2.2.13.3. Spongy mesophyll

The number of cells across the spongy mesophyll and its compactness varies considerably; (2-)3-4(-6) cells across is most common. Figures 2.48 to 2.55 give some impression of its variability.

2.2.2.13.4. Collenchyma at the mid-vein

Collenchyma is found both above and below the mid-vein bundle except in X. darwinii which has collenchyma only below. Most species have a rather narrow wedge of small, rounded, thick-walled cells above the vascular bundle, and reduced even to a couple of cells only in X. alpestris, X. viminea, X. nubigena and X. tenella. A very broad, distinct band of cells, about three cells thick, is found in X. mutabilis (see fig. 2.54).

The whole area below the mid-vein bundle is composed of collenchyma. These cells tend to be larger than the upper collenchyma, rounded and thick-walled (though sometimes only very thick-walled adjacent to the epidermis). X. darwinii is again exceptional in having only a few, small, rounded cells, with very slightly thicker walls than those of the spongy mesophyll.

2.2.2.13.5. Vascular bundle

Nearly all the species have more or less rounded bundles. Only X. fasciculata, X. vana, X. parvifolia and X. mutabilis have oval bundles, strongly flattened in the last two species. In proportion to the leaf thickness at the mid-vein, the bundle ranges from 25-45%. See Table 2.10 for details.

Sclerenchyma fibres are absent in all the species of sections Ceratominthe, Prostratae and Pauciflorae, save for a single fibre noted at the base of the phloem in X. nubigena, and three groups of 2 fibres, possibly phloem fibres, at the base of the phloem in a specimen of X. odora (see fig. 2.52). The two species of sect. Spicatae and the one species of sect. Sphenostachys have a few fibres above the xylem, but a broad, distinct layer of sclerenchyma right round the base of the phloem. Sclerenchyma is rather variable in sect. Xenopoma. X. schusteri has none above the xylem but a thick layer of narrow lumen fibres below the phloem. X. alpestris has a broad cap of fibres above and below the bundle, while X. viminea has a narrow vertical chain of fibres, 1-2 cells wide, connecting the epidermis and xylem, and a broad, distinct layer of fibres below the phloem.

2.2.2.13.6. Stomata

There are no stomata on the upper side of the leaf, except in X. darwinii which had about 42% on the upper side. The stomata were slightly raised above the level of the epidermis, except again in X. darwinii where they were more or less level with the epidermis. Diacytic stomata were noted in X. nubigena, X. tenella, X. darwinii, X. axillaris and X. parvifolia.

2.2.2.13.7. Glands

The gland types found are summarized in Table 2.10 (see also figs. 2.58 to 2.77). Both species of sect. Spicatae have an unusually small form of punctate gland similar to type 2b (fig. 2.58). Glands are rare on the upper side in X. odora, as are type

14 (fig. 2.72) on the upper side of the leaf in X. boliviana.

Table 2.10

Species	%V.B.	Glands Upper	 Lower
X. viminea	30	2b,14	2b,14
X. schusteri	30	2b	2b
X. alpestris	30-35	-	2b
X. axillaris	30-35	2b,c.14	2b,c.14
X. boliviana	30-35	2b,14	2b,14
X. odora	40	1,c.15	1,2b
X. parvifolia	25	2b	2b,c.9
X. fasciculata	40	15	2b,14
X. mutabilis	30-35	?	2b
X. brevicalyx	25	2b,c.9	2b,9
X. darwinii	25	2b,3,14	2b,3,14
X. tenella	25	14	2b,3,14,16
X. vana	25-30	2b,3,c.14	2b,c.3
X. nubigena	40	2b,3	2b,3,14
X. chandleri	35	2b,3,14,16	2b,3,14,16
X. cylindristachys	45	-	2b,14

%V.B. = vascular bundle thickness as a percentage of whole leaf at the mid-vein.

2.2.2.14. Piloblephis rigida Rafin.

The upper epidermis has large oblong-oval cells that are very thick walled, not just in the outer wall but equally in all the walls. The lower epidermal cells are smaller, oblong to squarish, only half as thick as the upper epidermis, but almost as equally thick walled. Above and below the mid-vein the epidermal cells are similarly sized or a little smaller than the laminar cells.

The palisade parenchyma is dorsiventral, with a single layer of small, oblong cells. The palisade is only about 30-35% of the total lamina thickness. Spongy mesophyll is approximately 2-4 cells across, very irregular in shape, and with very large air spaces between the cells.

The mid-vein is very broad, with an oval vascular bundle which is about a third as thick as the leaf. Collenchyma above and below the vascular bundle is confined to a single layer of cells adjacent to the epidermis, with cells of a size similar to the epidermal cells. Between the collenchyma and the vascular bundle are small, unthickened parenchyma cells. Xylem and phloem is equally divided in the mid-vascular bundle. The phloem cells are unusually large and enormously thickened in the walls so that the lumen has all but disappeared. No sclerenchyma was noted anywhere in the leaf.

Stomata are on the lower side of the leaf only, more or less level with the epidermis.

No glands were seen on the upper side of the leaf. On the lower side, glands similar to type 3 (fig. 2.62) are quite common.

A transverse section of the leaf is illustrated in fig. 2.57.

2.2.2.15. Hesperothymus A. Doroszenko

The anatomy of both species of the genus were studied.

2.2.2.15.1. Epidermis

The upper epidermis in H. brownei has very large oval cells, emphasized by the thinness of the leaf, which are only slightly thickened, especially in the outer wall (see fig. 2.56). The lower epidermis is only half as thick with much smaller oblong cells, slightly thickened in the walls. H. douglasii has large oblong cells with thick outer walls on the upper side. The lower epidermis is only 3/4 as thick as the upper but similar otherwise. The epidermis above the mid-vein in H. brownei has cells very similar to the laminar cells, if a little smaller, but in H. douglasii the cells are small, round, and very thick-walled. In both species, below the mid-vein the cells are very small, rounded, and very thick walled.

2.2.2.15.2. Palisade

Both species have dorsiventral palisade with one layer of very broad oblong cells, taking up about 35% of the leaf thickness in H. douglasii and 40% in H. brownei.

2.2.2.15.3 Spongy mesophyll

H. brownei has rather large, rounded, fairly compact cells in the spongy mesophyll. The tissue is only 2-3 cells across. In H. douglasii the mesophyll is about 3-4 cells across, with irregular cells and large air spaces between them.

2.2.2.15.4. Collenchyma at the mid-vein

In both species there are rather few rounded and little-thickened collenchyma cells connecting the upper epidermis and vascular bundle. The whole area below the mid-vein is composed of small, rounded cells, with slightly thickened walls. The cells adjacent to the lower epidermis in H. douglasii are, however, more markedly thickened.

2.2.2.15.5. Vascular bundle

Both species have a small, round bundle, one third as thick as the leaf at the mid-vein. No sclerenchyma fibres are present in any part of the leaf.

2.2.2.15.6. Stomata

Stomata were only found on the lower side of the leaf, and are of the diacytic type. In H. brownei they tend to be more or less level with the epidermis, while in H. douglasii they are slightly raised.

2.2.2.15.7. Glands

Types 1 and 2b were noted on both sides of the leaf in H. brownei. In H. douglasii, on the upper side, glands similar to type 9 were found, and on the lower side, glands of types 2b and 14.

2.2.2.16. Diodeilis Rafin.

The anatomy of the first six species listed in Table 2.11, of 8 in the genus, was studied.

2.2.2.16.1. Epidermis

The upper epidermal cells are generally small oval-oblong with thick walls. Only *D. glabella* has rather large oval-oblong cells, with just a little thickened walls.

The lower epidermis usually has rather smaller cells, similarly shaped or a little more oblong than the upper epidermis, though in *D. dentata* the cells on both sides are similar in size.

Above the mid-vein the cells are generally smaller, rounder or squarer, with thicker walls. However, in *D. coccinea* and *D. ashei* all the upper epidermal cells are similar. Below the mid-vein the epidermal cells are small, rounded, and thick walled in all species.

2.2.2.16.2. Palisade and spongy mesophyll

All species basically have dorsiventral palisade, but in the woody section *Diodeilis* there is a much weaker distinction between palisade mesophyll and spongy mesophyll than in sect. *Herbaceae*.

In sect. *Diodeilis* palisade takes up about 50% of the leaf thickness. *D. coccinea* and *D. ashei* both have spongy mesophyll with dorsiventrally arranged cells. *D. dentata*, however, has more clearly distinguishable palisade with very irregular spongy mesophyll cells that have large air spaces between them.

The spongy mesophyll in sect. *Herbaceae* is quite distinct, taking up about half of the leaf in *D. arkansana*, 60% in *D. georgiana*, and 70-75% in *D. glabella*. Palisade in *D. glabella* is particularly weak, with a single layer of very small oblong cells.

2.2.2.16.3. Collenchyma at mid-vascular bundle

Sect. Diodeilis has no collenchyma above the mid-vascular bundle, and very few, rounded, thick-walled cells below the bundle. Sect. Herbaceae, on the other hand, has a few, but distinct, collenchyma cells capping the bundle. Below the bundle the collenchyma varies from a small wedge of round cells in D. georgiana, to about half the vein area composed of large, round cells with little thickened walls in D. arkansana, and most of the vein area below the bundle composed of large, round, thin-walled cells in D. glabella.

2.2.2.16.4. Bundle sheath

The bundle sheath is quite distinct in sect. Diodeilis, with small, oval to rounded cells with not or slightly thickened walls. In sect. Herbaceae, though less prominent, the sheath is still easily distinguishable from the mesophyll, having small to quite large, rounded, thin-walled cells.

2.2.2.16.5. Mid-vein bundle

The bundle in sect. Diodeilis is round, about 35-40% of the leaf thickness at the mid-vein, and situated in the lower half of the vein. In sect. Herbaceae, D. glabella and D. arkansana have small, oval bundles, and D. georgiana has a large, semi-circular or crescent-shaped bundle, that take up 25-30%, 30% and 40% of the leaf thickness at the mid-vein, respectively.

Sclerenchyma is absent in D. dentata, D. arkansana, D. glabella and D. procumbens, and only a few fibres were noted below the phloem in D. coccinea and D. ashei. However, D. georgiana has a distinct band of sclerenchyma below the phloem, and only a few weakly lignified cells above the xylem.

2.2.2.16.6. Stomata

The proportion of the total stomata on the lower side of the leaf is summarized in Table 2.11. Diacytic stomata were noted in D. coccinea, D. georgiana, D. arkansana and D. glabella. Additionally, a leaf epidermal peel also revealed diacytic stomata in D. procumbens.

Table 2.11

	Stomata % lower side	Glands Above	 Below
D. coccinea	78	2b,16	2b,14,16
D. ashei	77	2b,c.7a	2b,c.7a
D. dentata	100	2b,7a,12,14	2b,12
D. georgiana	100	1,2b	1,2b
D. arkansana	49	2b,19	2b,19
D. glabella	95	2b,19	2b,19
D. procumbens	100	c.14	2b,c.14

2.2.2.16.7. Glands

The various types of gland found are summarized in Table 2.11. D. coccinea has a small form of type 16, and D. dentata has a small form of type 12, on both sides of the leaf.

2.2.3. Summary of Anatomical Data obtained by G. Ertem

The information summarized in Table 2.12 and the illustrations reproduced in figs. 2.1 to 2.38 were extracted from preliminary notes of G. Ertem. My own investigations have largely complemented and expanded on Ertems work.

2.2.3.1.

Table 2.12 Legend. Palisade: Iso = isolateral; Dorsi = dorsiventral. Mid-vein bundle: Tissues encountered in a T.S. through mid-vein from the top to bottom: C = collenchyma; S = sclerenchyma; X = xylem; P = phloem. Marginal vein: - = absent; / = present.

2.2.3.2.

Table 2.12. Summary of Anatomical Data obtained by G. Ertem.

Species	Palisade	Mid-vein bundle	Marginal vein
Satureja L.			
S. montana L.	Iso	CXPC	-
S. cuneifolia Ten.	Iso	CXPC	-
S. spinosa L.	Iso	CXPC	-
S. macrantha C.A. Mey.	Iso	CXPC	-
S. hortensis L.	Iso	CXPC	-
S. thymbra L.	Iso	CXPC	-
S. spicigera (C. Koch) Boiss.	Iso	CXPC	-
S. parnassica Heldr. & Sart.	Iso	CXPC	-
Micromeria Benth. sect. Micromeria			
M. juliana (L.) Benth. ex Reichenb.	Dorsi	CSXPSC	✓
M. cristata (Hampe) Griseb.	Dorsi	CSXPSC	✓
M. myrtifolia Boiss. & Hohen.	Dorsi	CSXPSC	✓
M. cremnophila Boiss. & Hohen.	Dorsi	CSXPSC	✓
M. marginata (Sm.) Chater	Dorsi	CSXPSC	✓
M. nervosa (Desf.) Benth.	Dorsi	CSXPSC	✓
M. graeca (L.) Benth.	Dorsi	CSXPSC	✓
M. densiflora Benth.	Dorsi	CSXPSC	✓
M. battandieri (Briq.)	Dorsi	CSXPSC	✓
M. macrosiphon Coss.	Dorsi	CSXPSC	✓
M. lanata (Chr. Sm. ex Link) Benth.	Dorsi	CSXPSC	✓
M. benthamii Webb & Berth.	Dorsi	CSXPSC	✓
Micromeria sect. Pineolentia P. Perez			
M. pineolens Svent.	Dorsi	CSXPSC	✓
Micromeria sect. Cymularia Boiss.			
M. cymuligera Boiss. & Hausskn.	Dorsi	CSXPSC	-
Micromeria sect. Pseudomelissa Benth.			
M. thymifolia (Scop.) Fritsch	Dorsi	CXPC	-
M. dalmatica Benth.	Dorsi	CXPC	-
M. dolichodonta P.H. Davis	Dorsi	CXPC	-
M. libanotica Boiss.	Dorsi	CXPC	-
M. fruticosa (L.) Druce	Dorsi	CXPC	-
M. mollis Benth.	Dorsi	CXPC	-
M. pulegium (Roch.) Benth.	Dorsi	CXPC	-
M. carica P.H. Davis	Dorsi	CXPC	-
Acinos Miller			
A. rotundifolius Pers.	Dorsi	CXPC	-
Cyclotrichium Manden. & Scheng.			
C. origanifolium (Labill.) M. & S.	Iso	CXPC	-
Clinopodium L.			
C. vulgare L.	Dorsi	CXPC	-
C. umbrosum (M. Bieb.) C. Koch	Dorsi	CXPC	-
Calamintha Miller			
C. grandiflora (L.) Moench	Dorsi	CXPC	-
C. sylvatica Bromf.	Dorsi	CXPC	-

2.2.33.

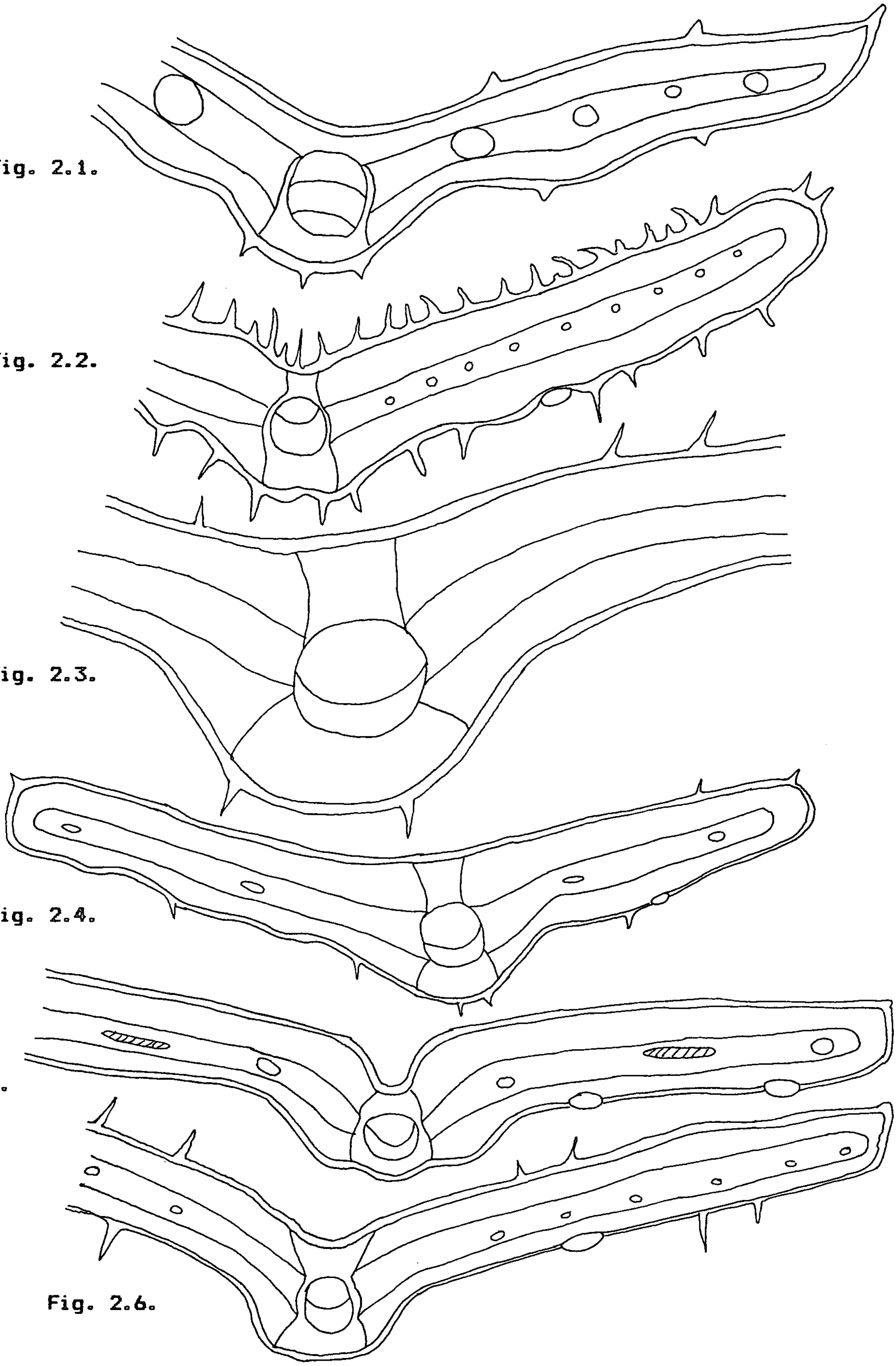


Fig. 2.1.

Fig. 2.2.

Fig. 2.3.

Fig. 2.4.

Fig. 2.5.

Fig. 2.6.

Fig. 2.1 Satureja montana. Fig. 2.2 S. cuneifolia. Fig. 2.3 S. parnassica. Fig. 2.4 S. macrantha. Fig. 2.5 S. spicigera. Fig. 2.6 S. thymbra.

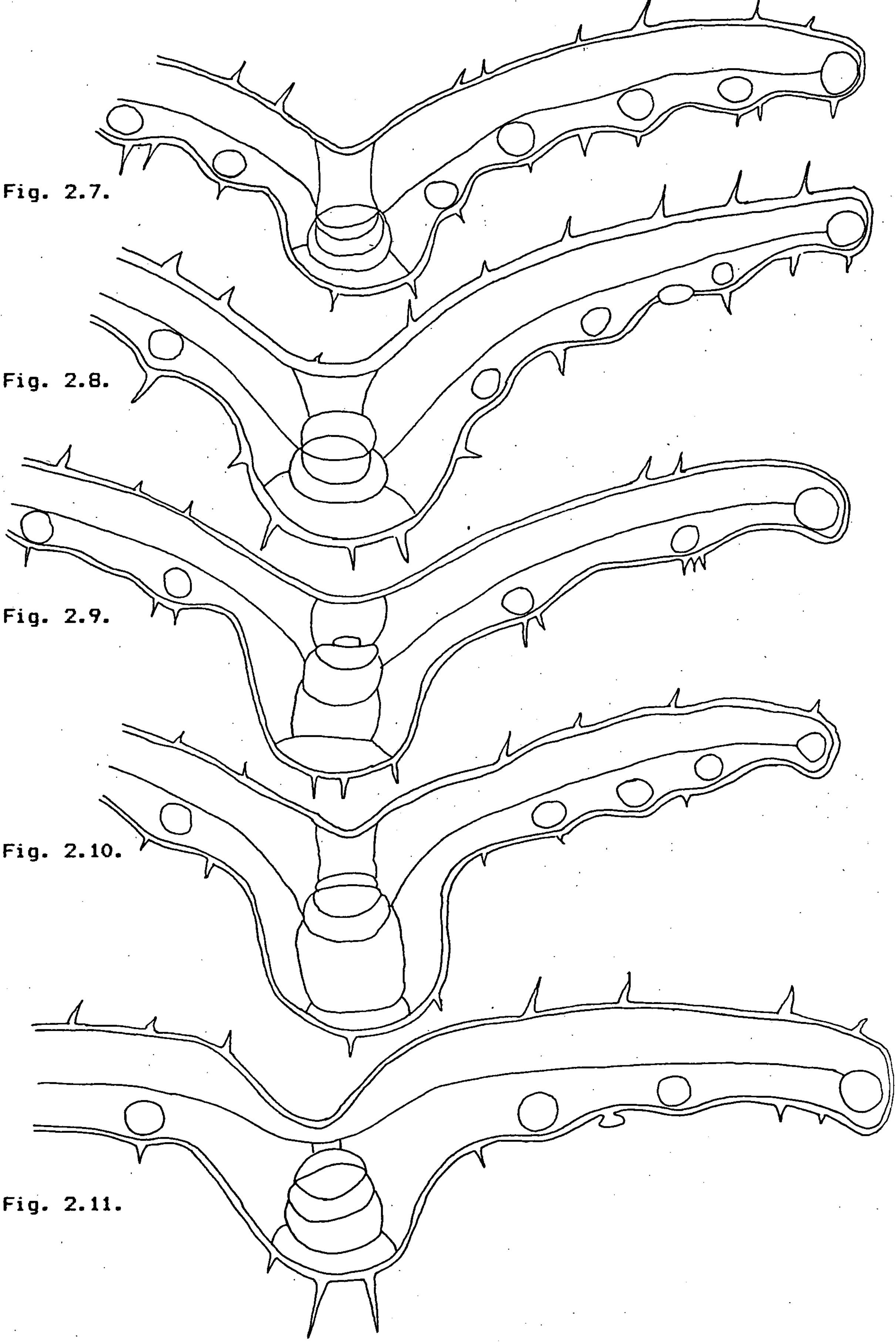


Fig. 2.7 Micromeria juliana. Fig. 2.8 M. myrtifolia. Fig. 2.9 M. graeca. Fig. 2.10 M. nervosa. Fig. 2.11 M. amana.

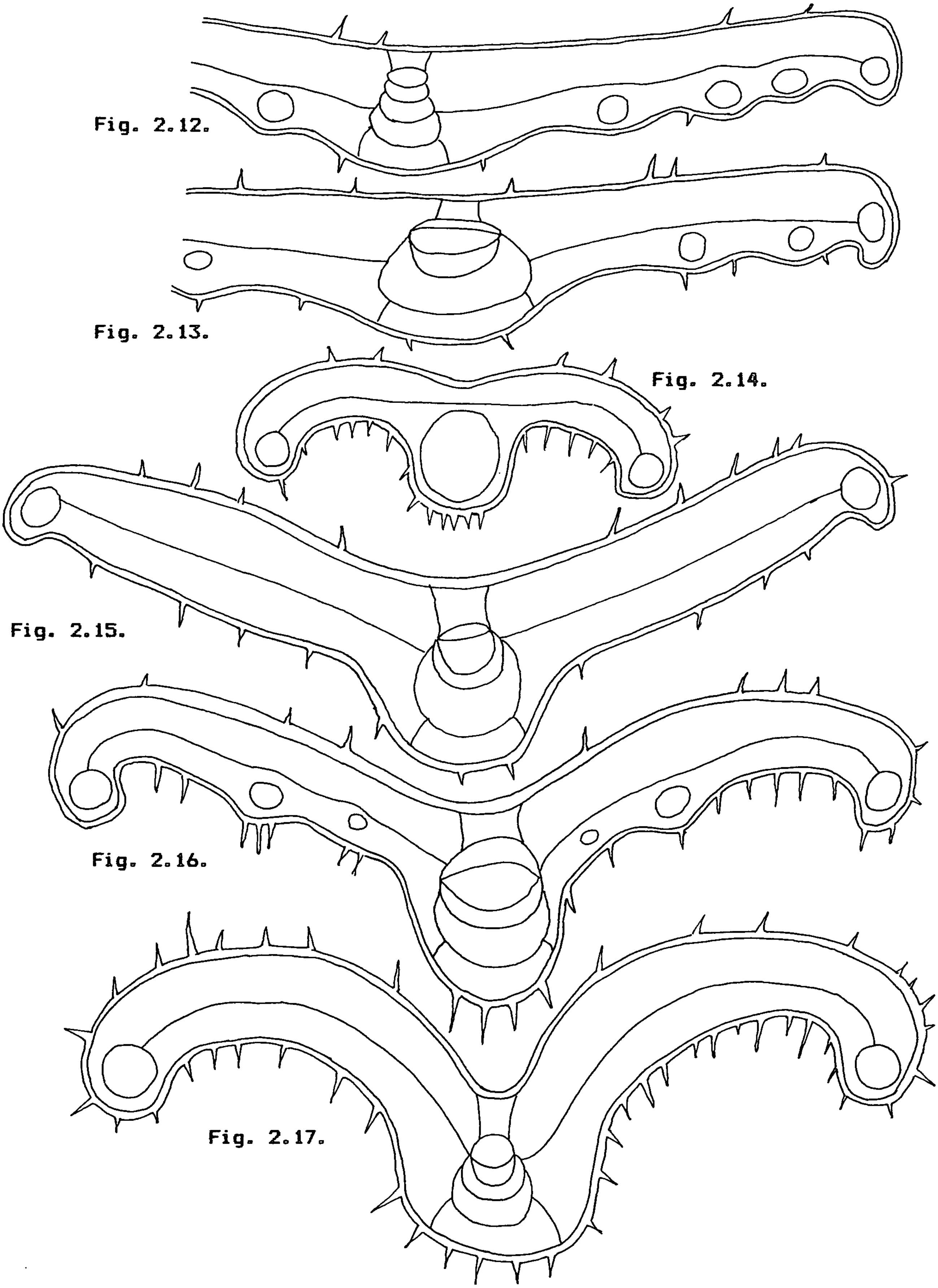


Fig. 2.12 Micromeria marginata. Fig. 2.13 M. cristata. Fig. 2.14 M. battandieri. Fig. 2.15 M. macrosiphon. Fig. 2.16 M. densiflora. Fig. 2.17 M. lanata.

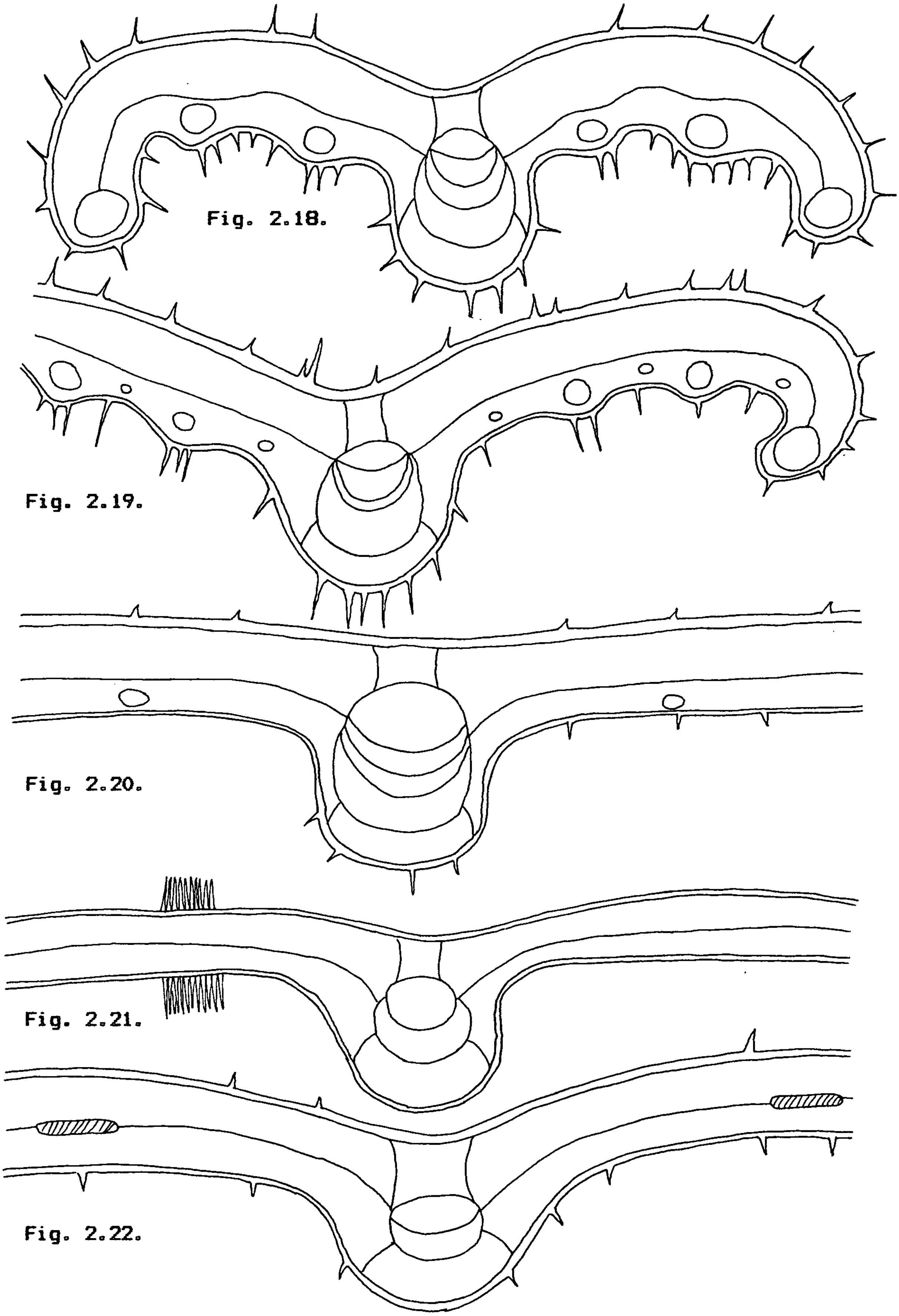


Fig. 2.18 Micromeria benthamii. Fig. 2.19 M. pineolens. Fig. 2.20 M. cymuligera. Fig. 2.21 M. fruticosa. Fig. 2.22 M. pulegium.

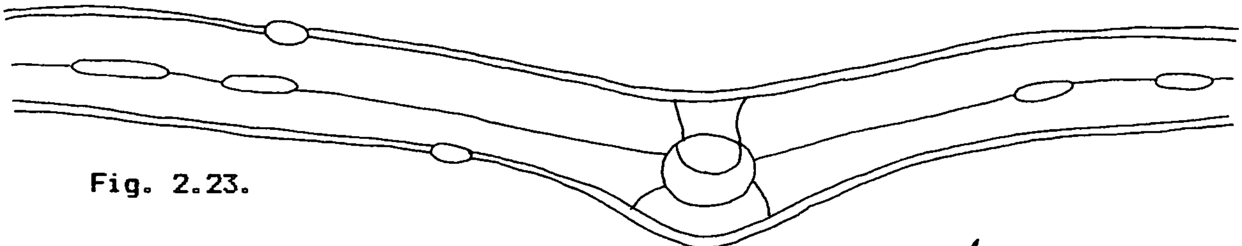


Fig. 2.23.

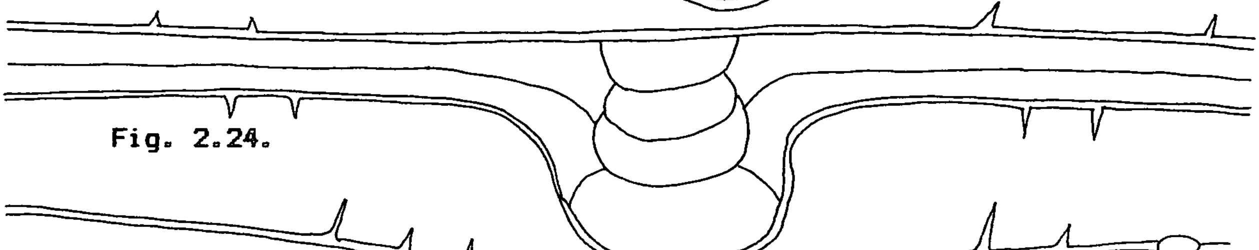


Fig. 2.24.

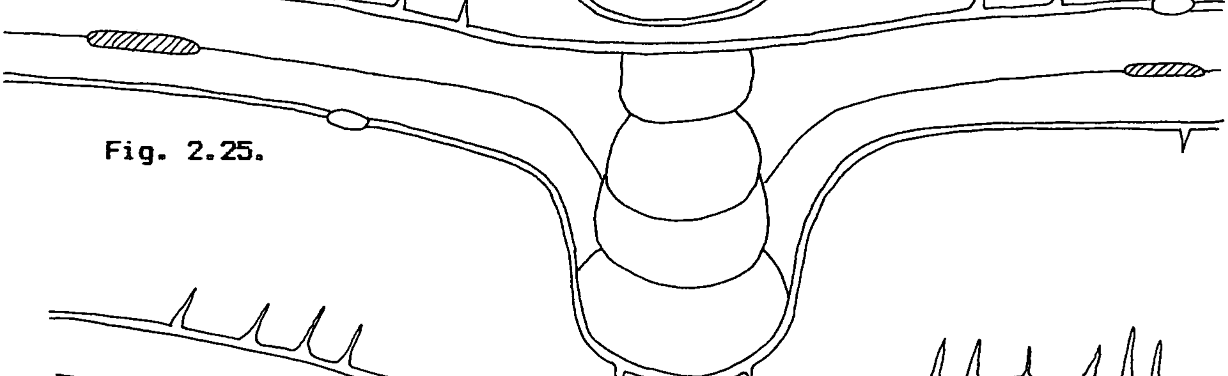


Fig. 2.25.

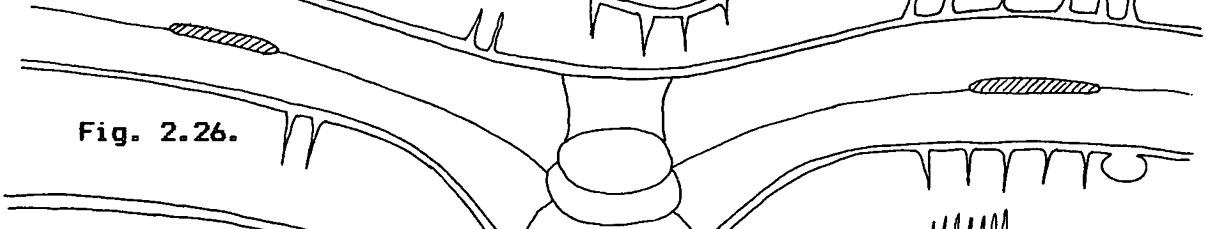


Fig. 2.26.

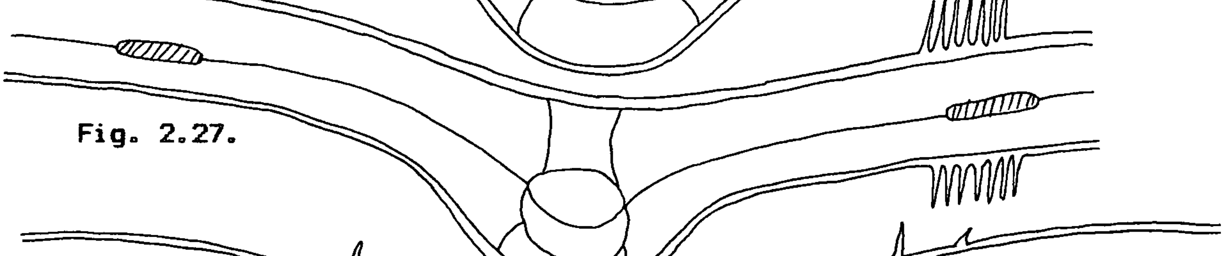


Fig. 2.27.

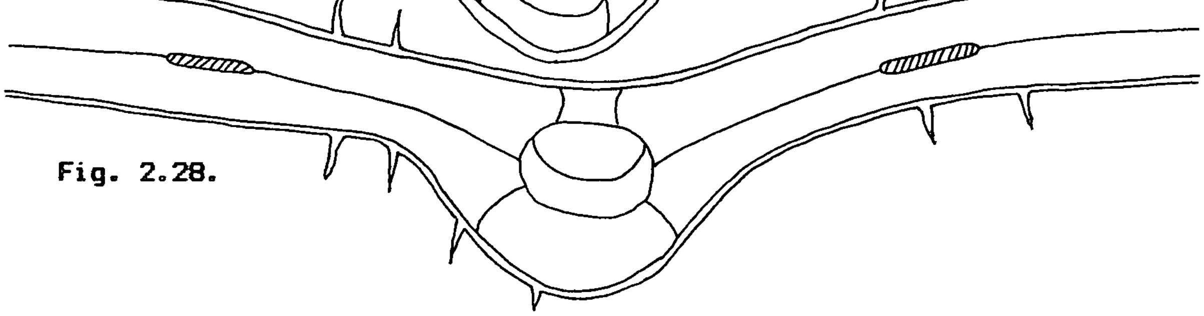


Fig. 2.28.

Fig. 2.23 *Micromeria thymifolia*. Fig. 2.24 *M. dalmatica*. Fig. 2.25 *M. mollis*. Fig. 2.26 *M. dolichodonta*. Fig. 2.27 *M. libanotica*. Fig. 2.28 *M. carica*.

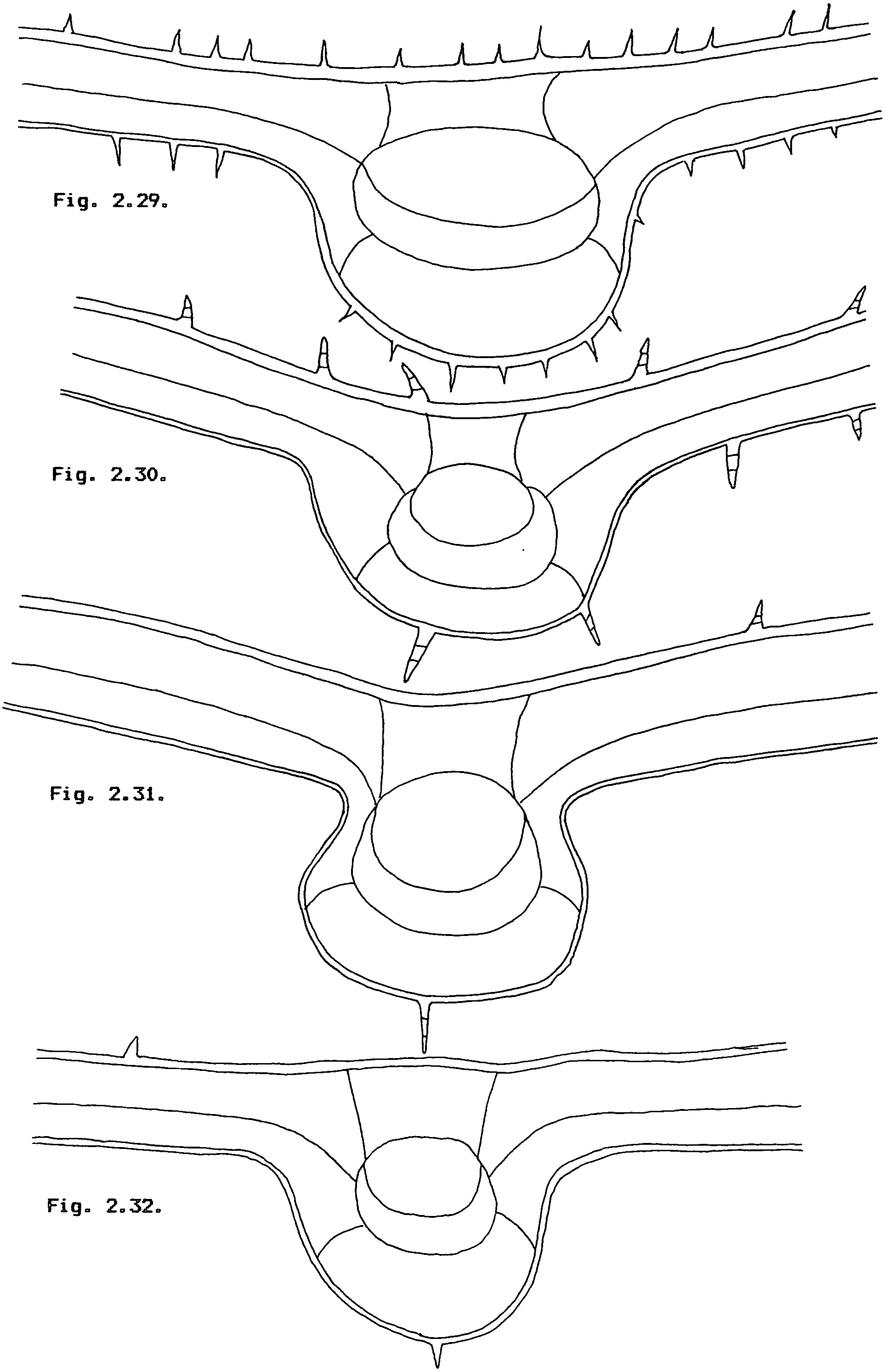


Fig. 2.29.

Fig. 2.30.

Fig. 2.31.

Fig. 2.32.

Fig. 2.29 Calamintha grandiflora. Fig. 2.30 C. sylvatica. Fig. 2.31 Clinopodium vulgare. Fig. 2.32 C. umbrosum.

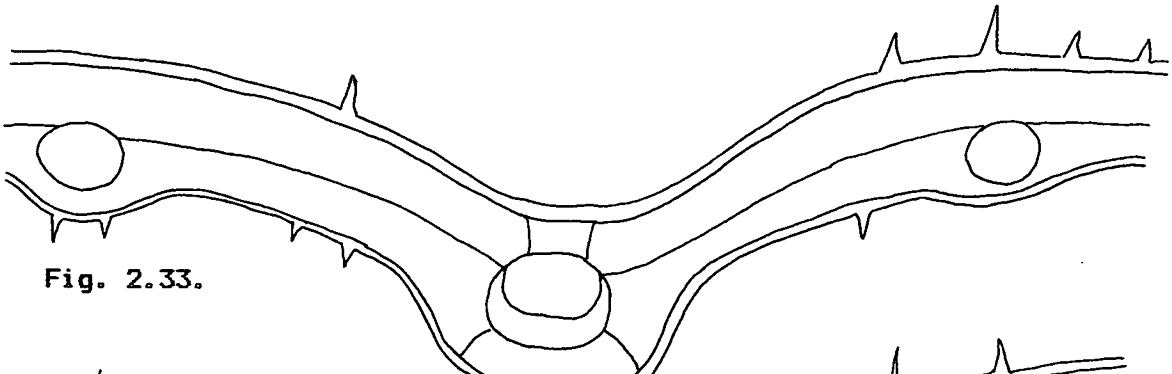


Fig. 2.33.

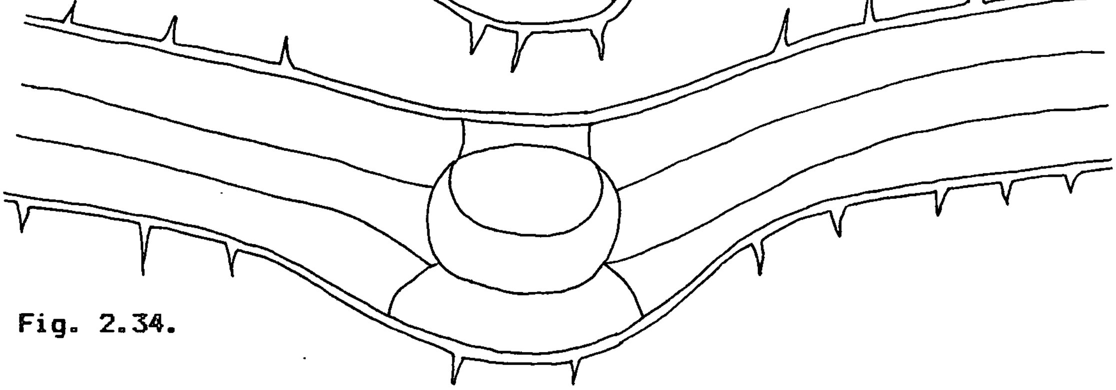


Fig. 2.34.

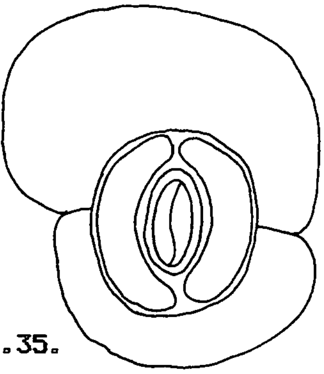


Fig. 2.35.

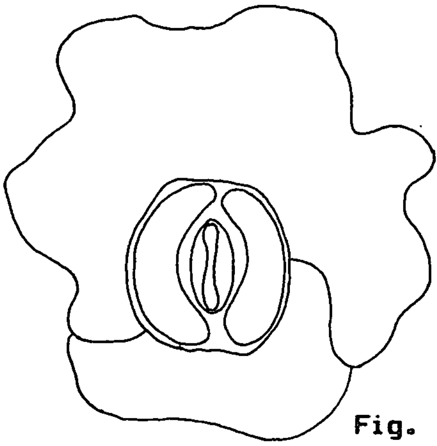
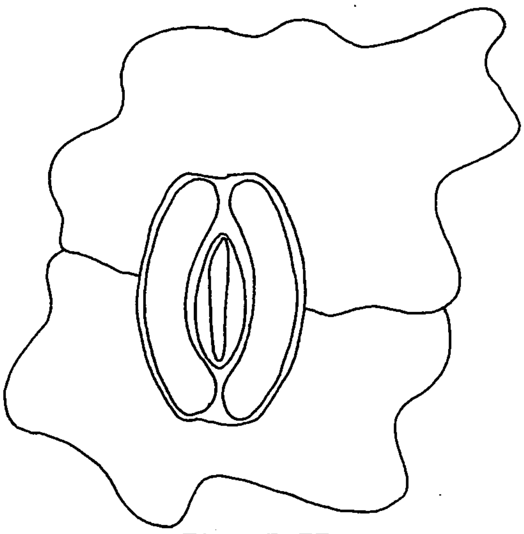


Fig. 2.36.



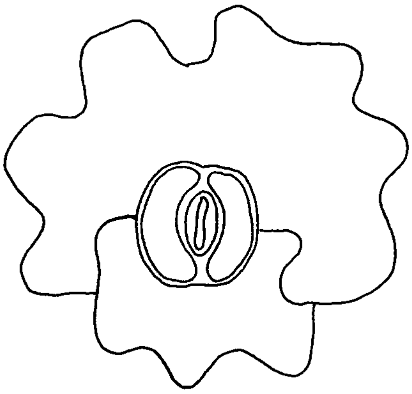


Fig. 2.38.

Fig. 2.37.

Fig. 2.33 Acinos rotundifolius.
Fig. 2.34 Cyclotrichium origanifolium.

Stomata. Fig. 2.35 C. origanifolium. Fig. 2.36 Satureja parnassica.
Fig. 2.37 Micromeria marginata. Fig. 2.38 Calamintha grandiflora.

.2.4.

Fig. 2.39 Satureja hortensis.

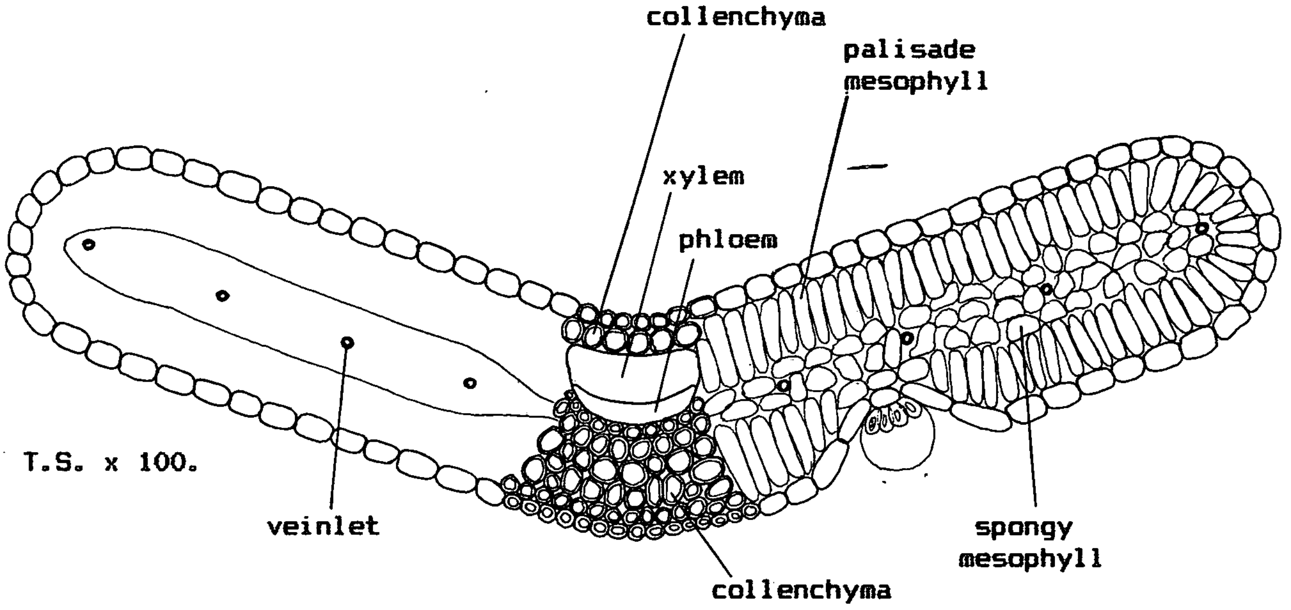


Fig. 2.40 Satureja spinosa.

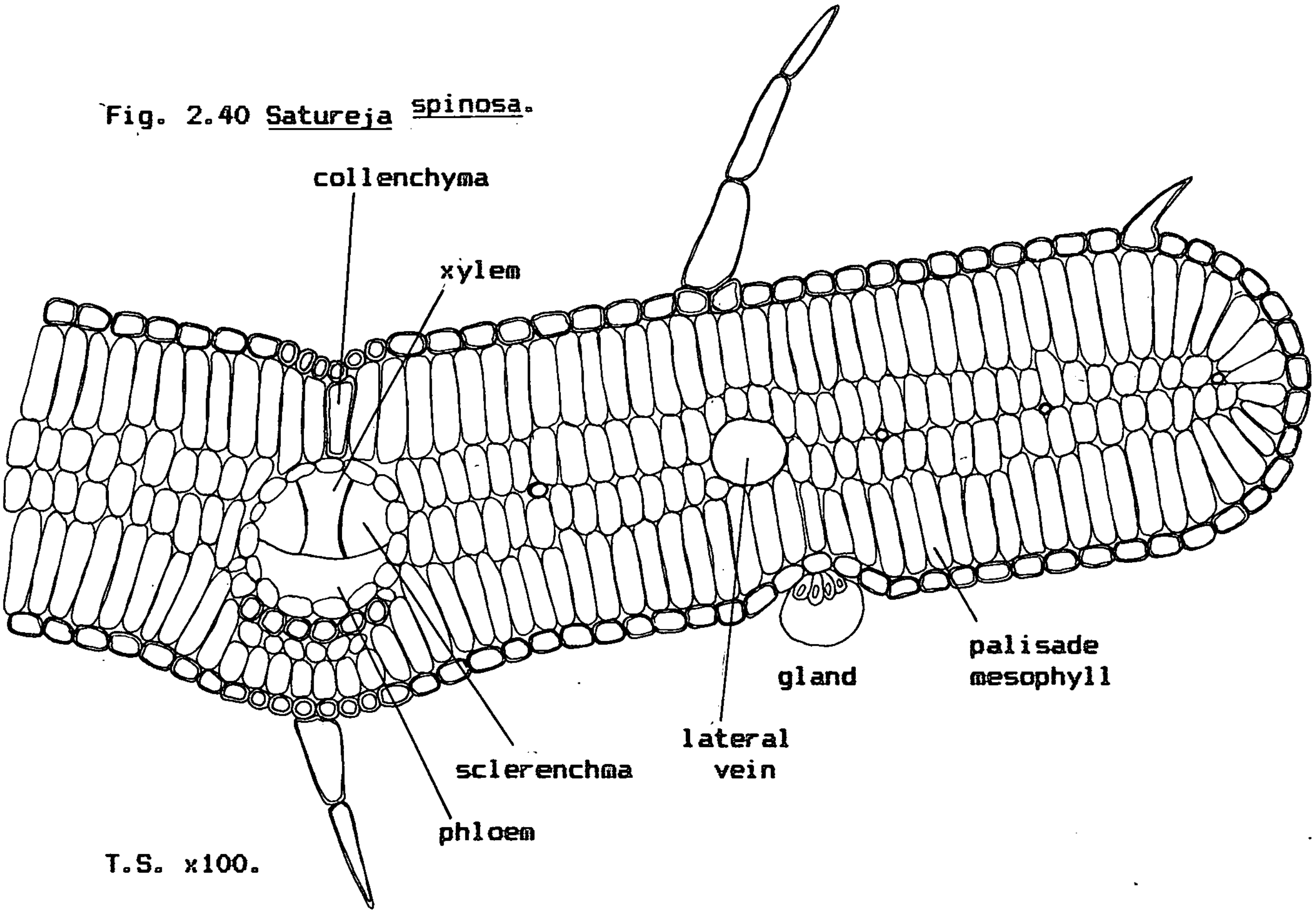
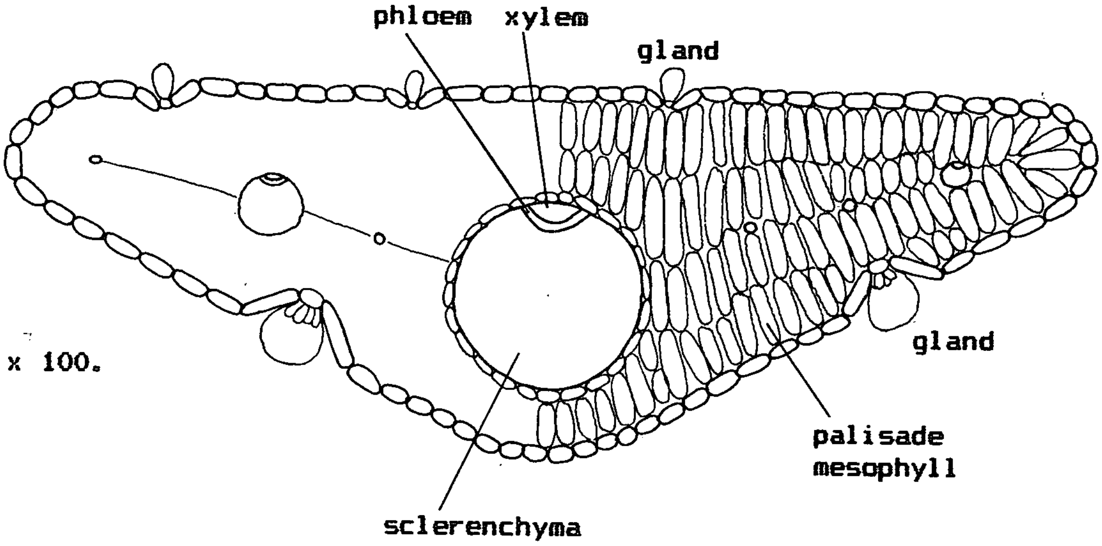
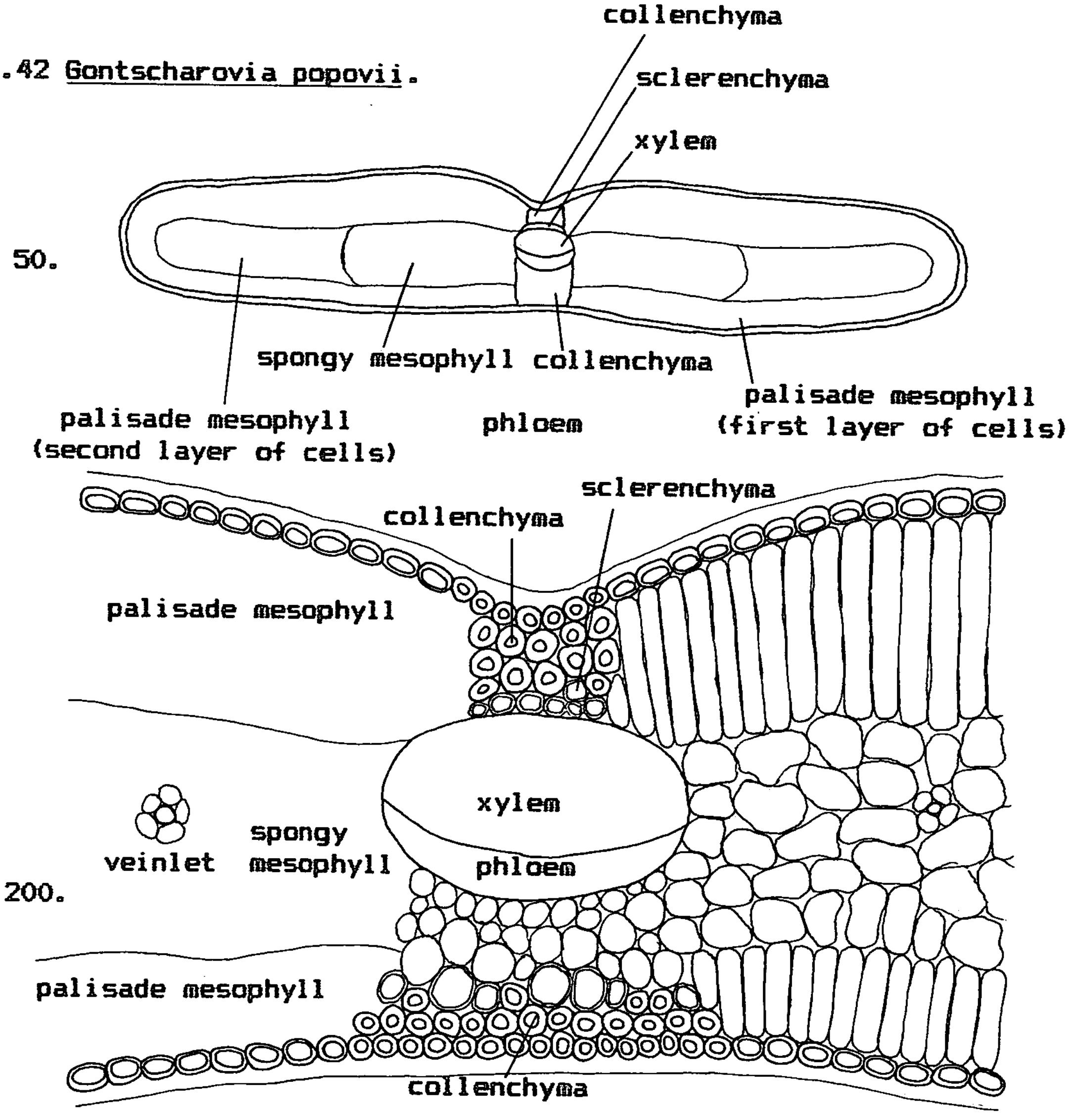


Fig. 2.41 Satureja salzmannii.



T.S. x 100.

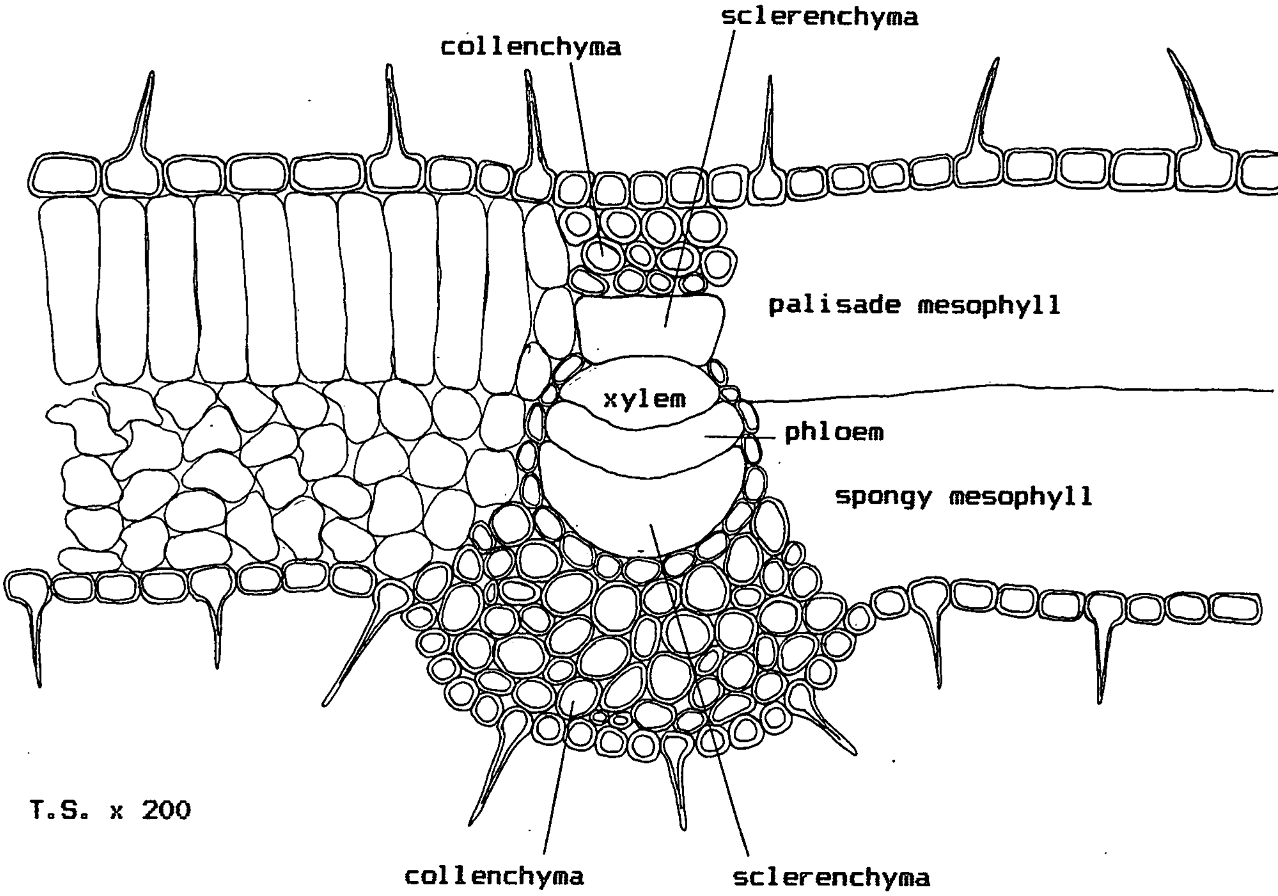
Fig. 2.42 Gontscharovia popovii.



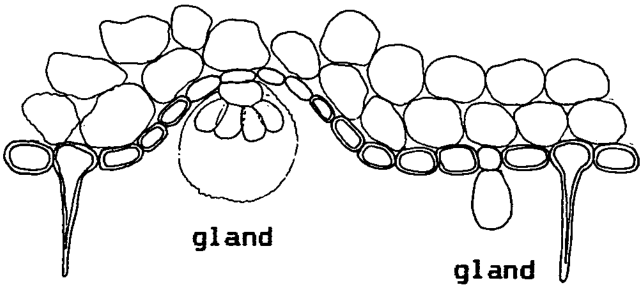
T.S. x 50.

T.S. x 200.

Fig. 2.42a Gardoquia mathewsii



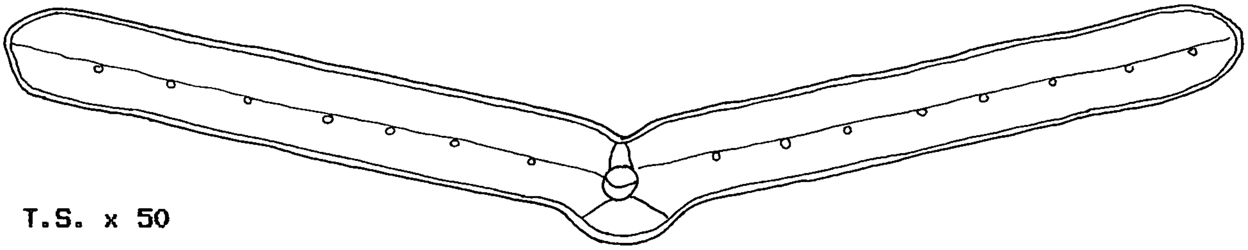
T.S. x 200



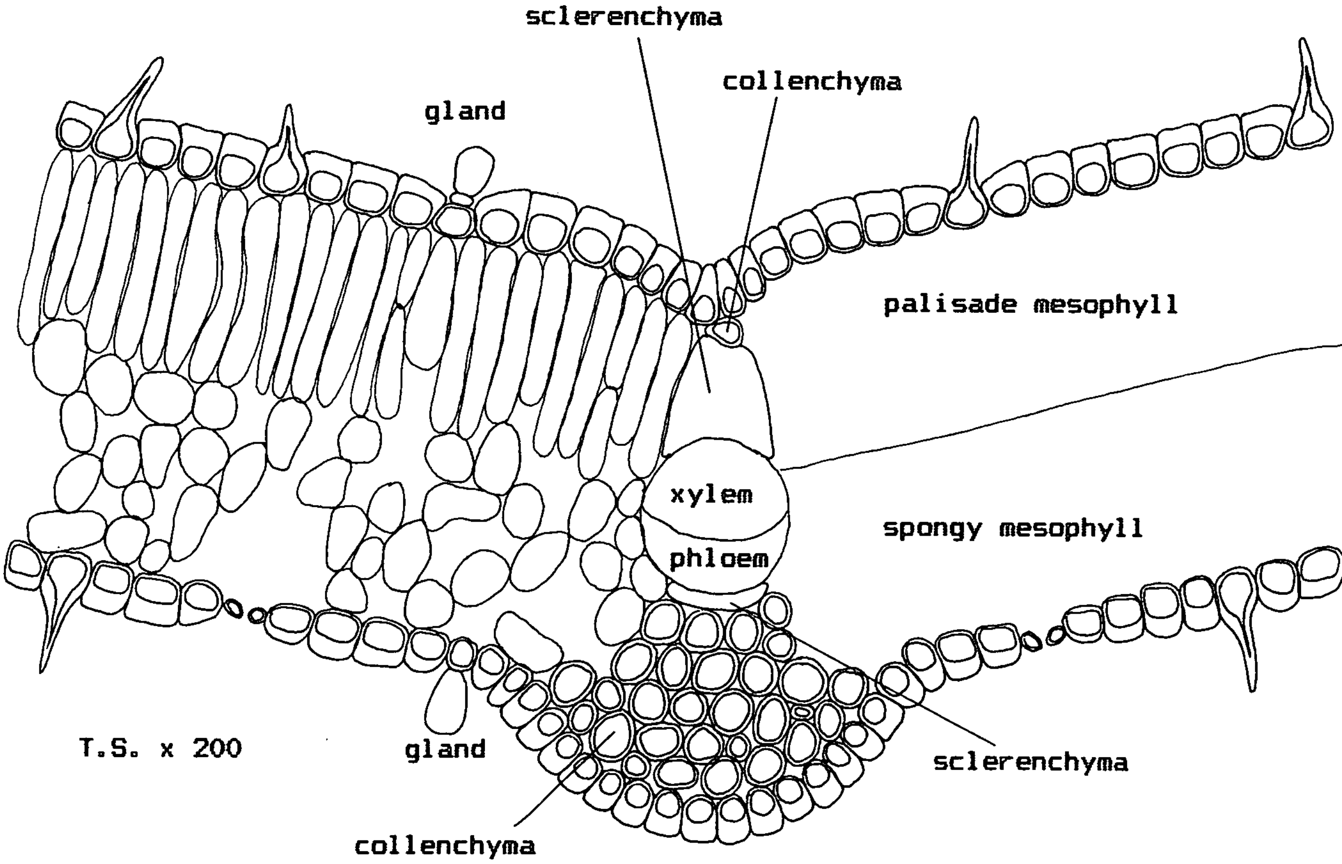
T.S. Portion of lower epidermis x 200

Fig. 2.42b Gardoquia mathewsii

Fig. 2.43a <u>Gardoquia gilliesii</u>



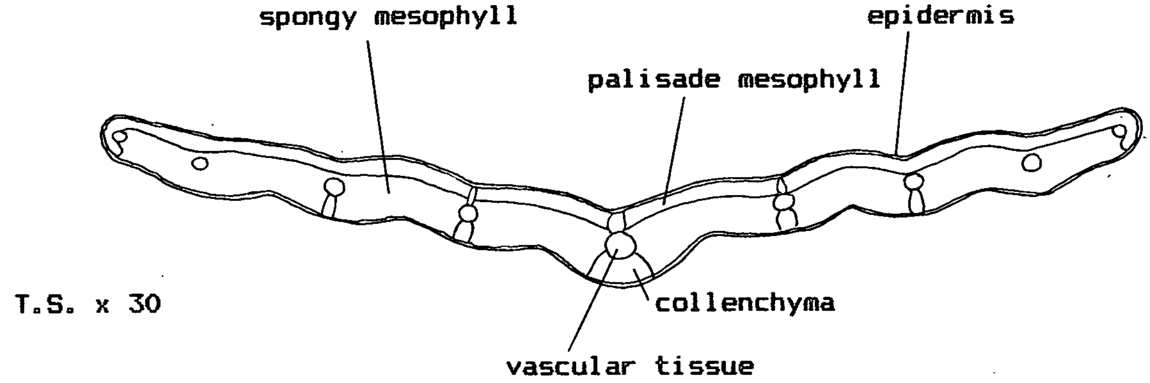
T.S. x 50



T.S. x 200

Fig. 2.43b <u>Gardoquia gilliesii</u>

Fig. 2.44a Gardoquia plicatula



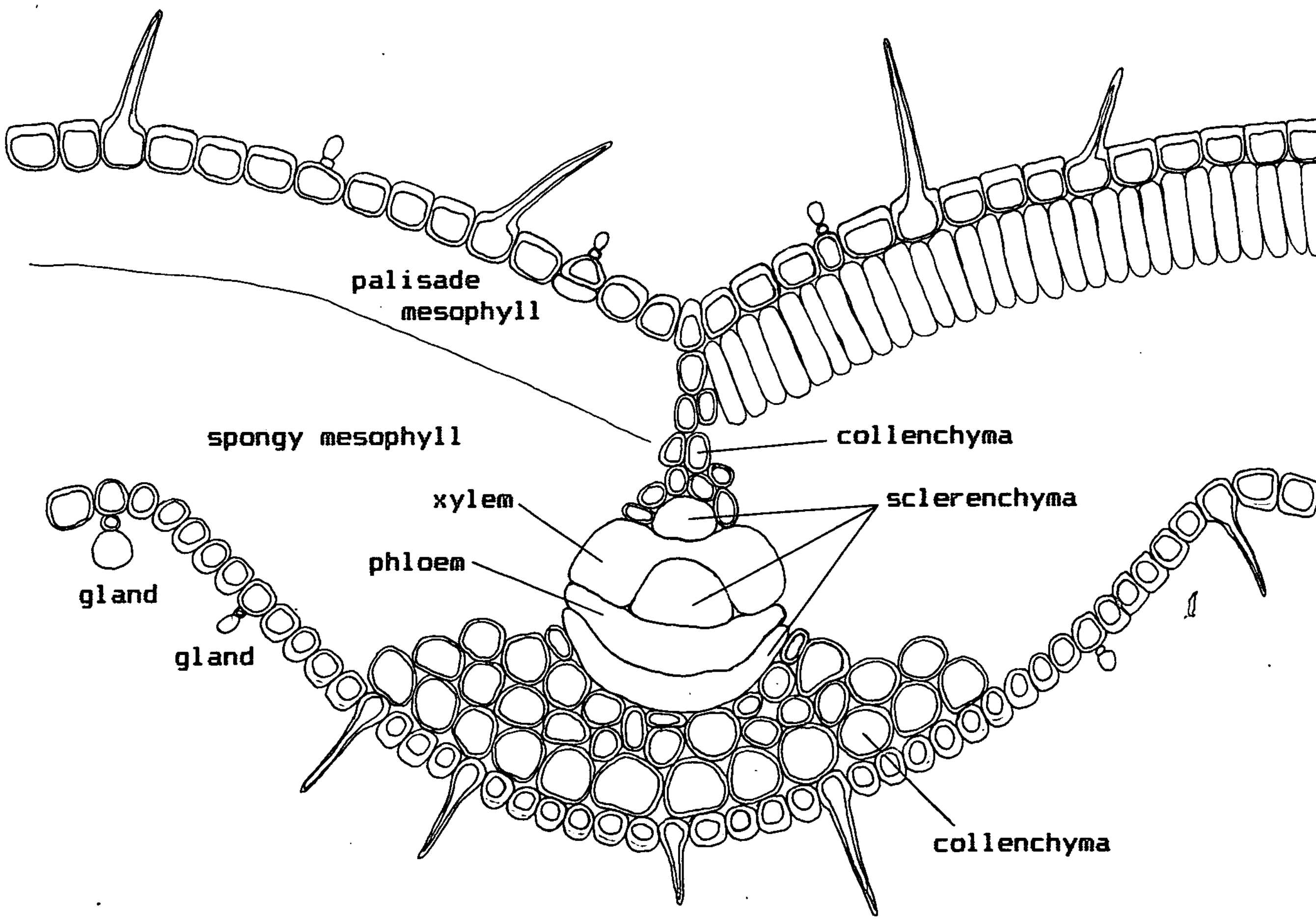
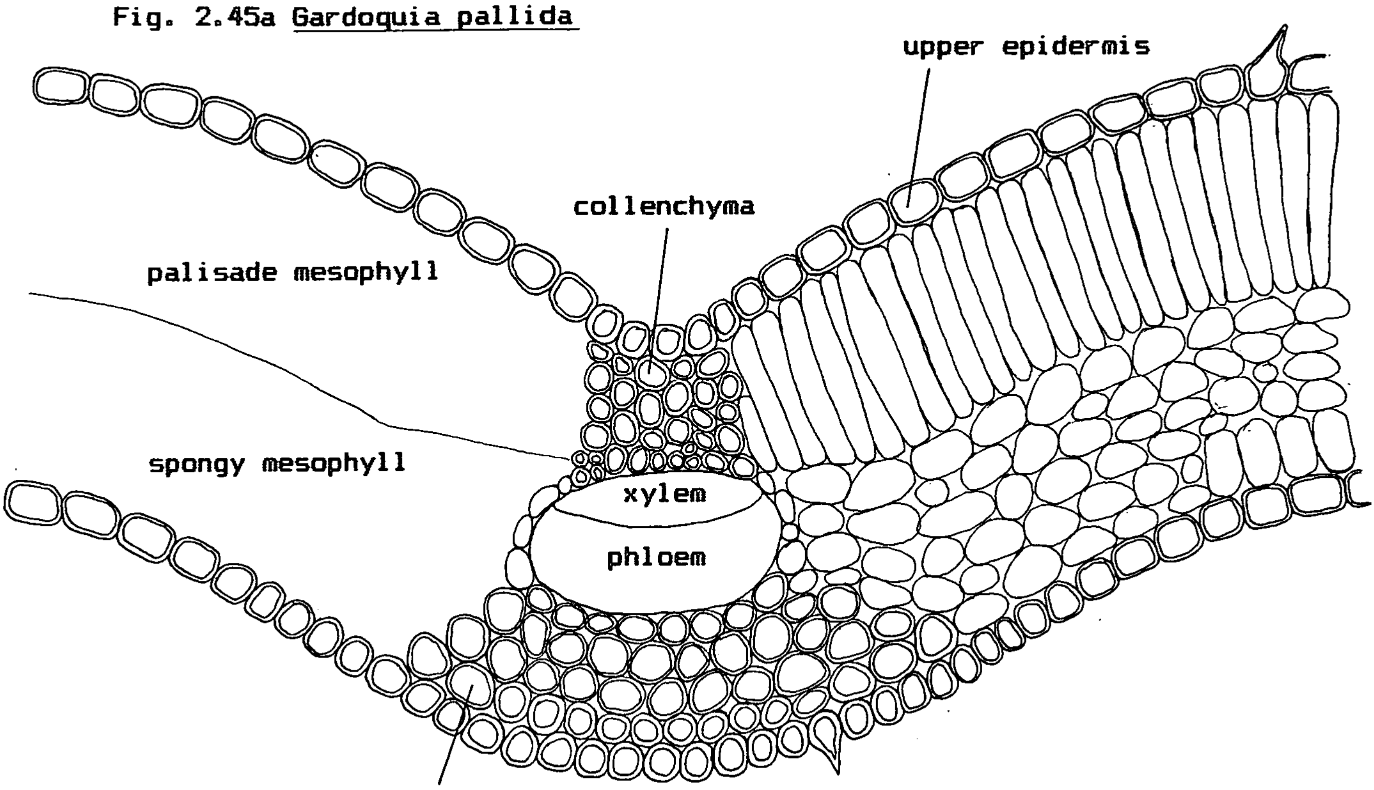
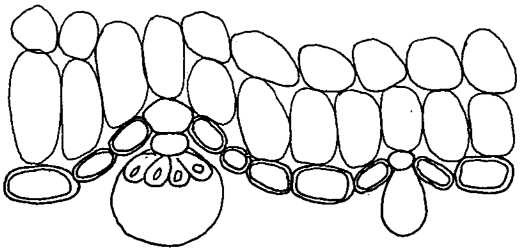


Fig. 2.44b Gardoquia plicatula. T.S. x 200

Fig. 2.45a <u>Gardoquia pallida</u>



T.S. x 200



T.S. Portion of lower epidermis x 270

Fig. 2.45b <u>Gardoquia pallida</u>

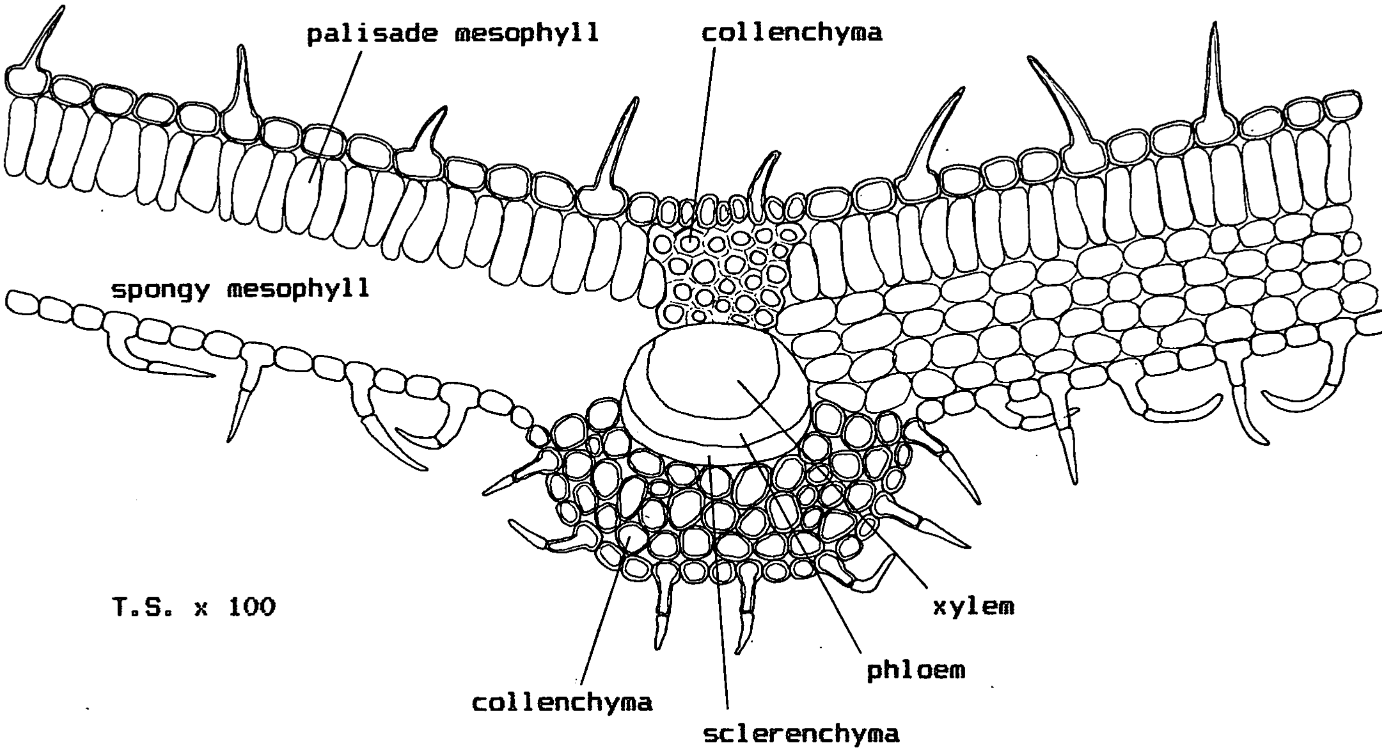
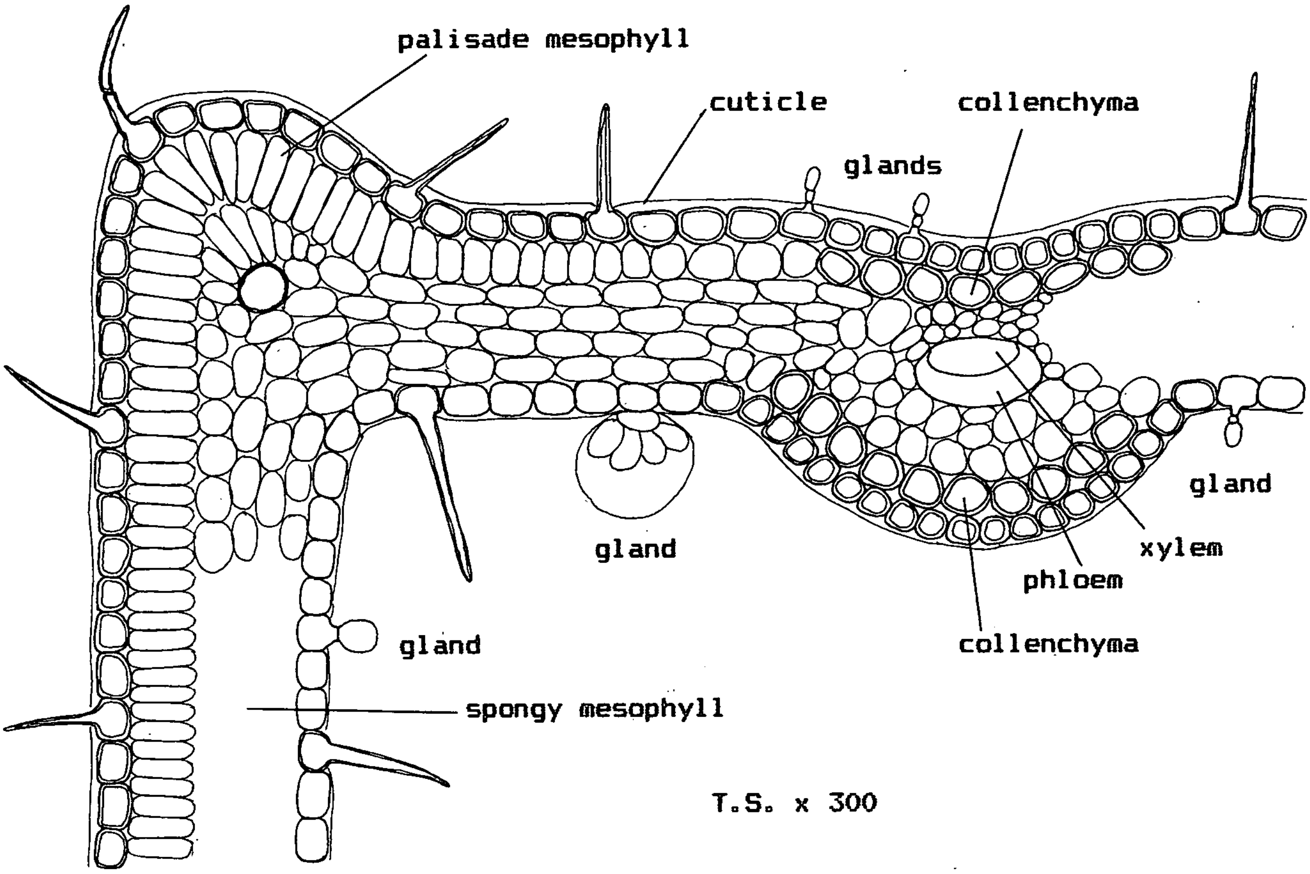


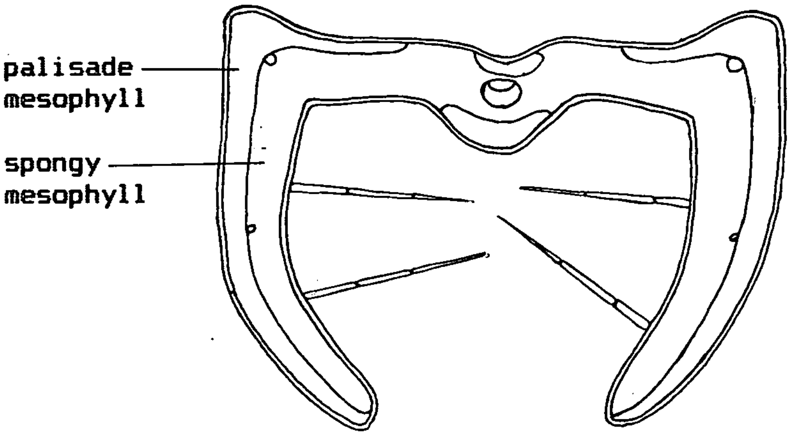
Fig. 2.46 Gardoquia discolor

Fig. 2.47a Obtegomeria caerulescens



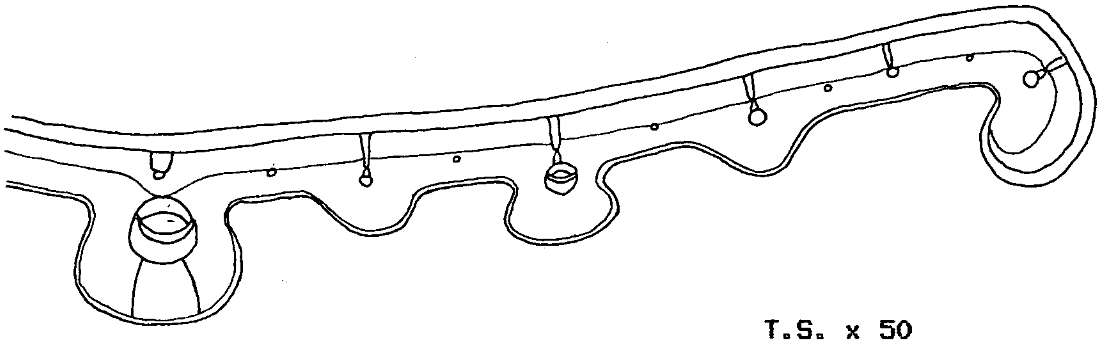
T.S. x 300

Fig. 2.2.47b Obtegomeria caerulescens



T.S. x 100

Fig. 2.48a <u>Xenopoma alpestris</u>



T.S. x 50

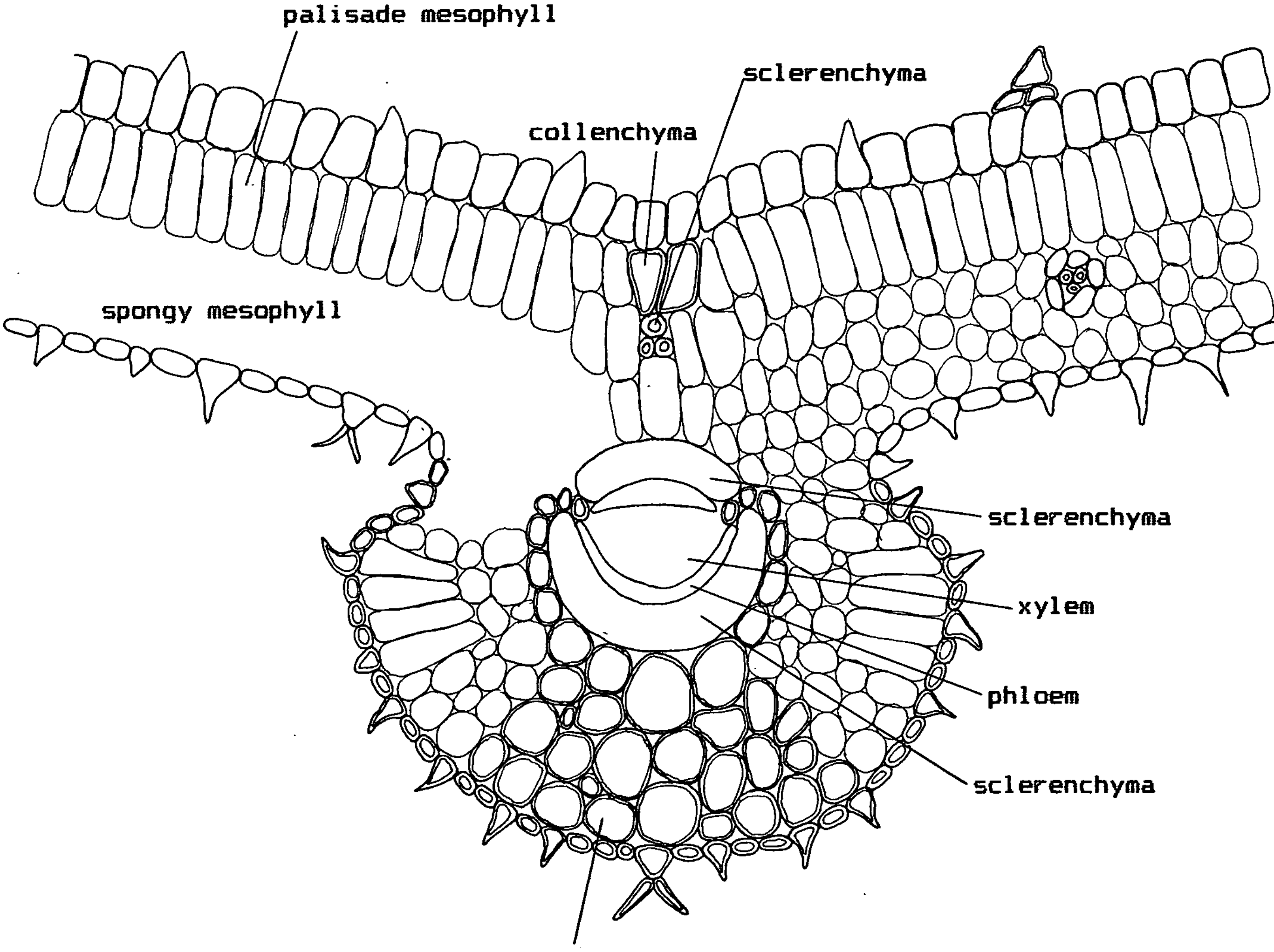
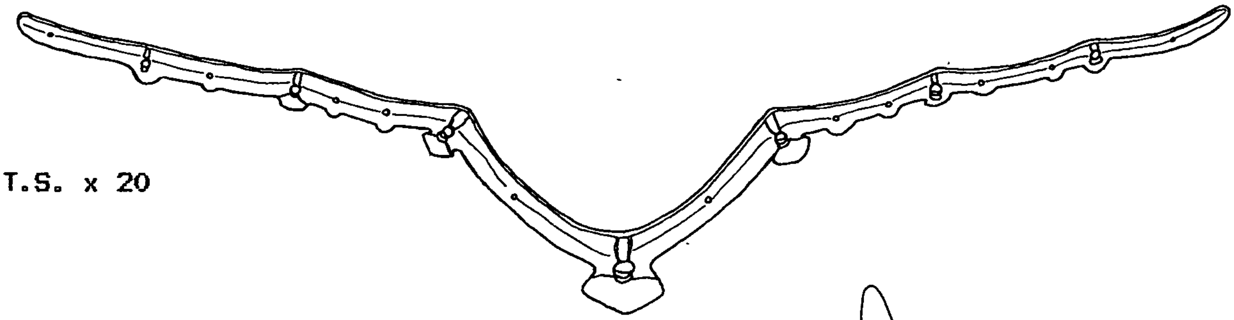


Fig. 2.48b <u>Xenopoma alpestris</u>. T.S. x 200

Fig. 2.49a *Xenopoma schusteri*

T.S. x 20



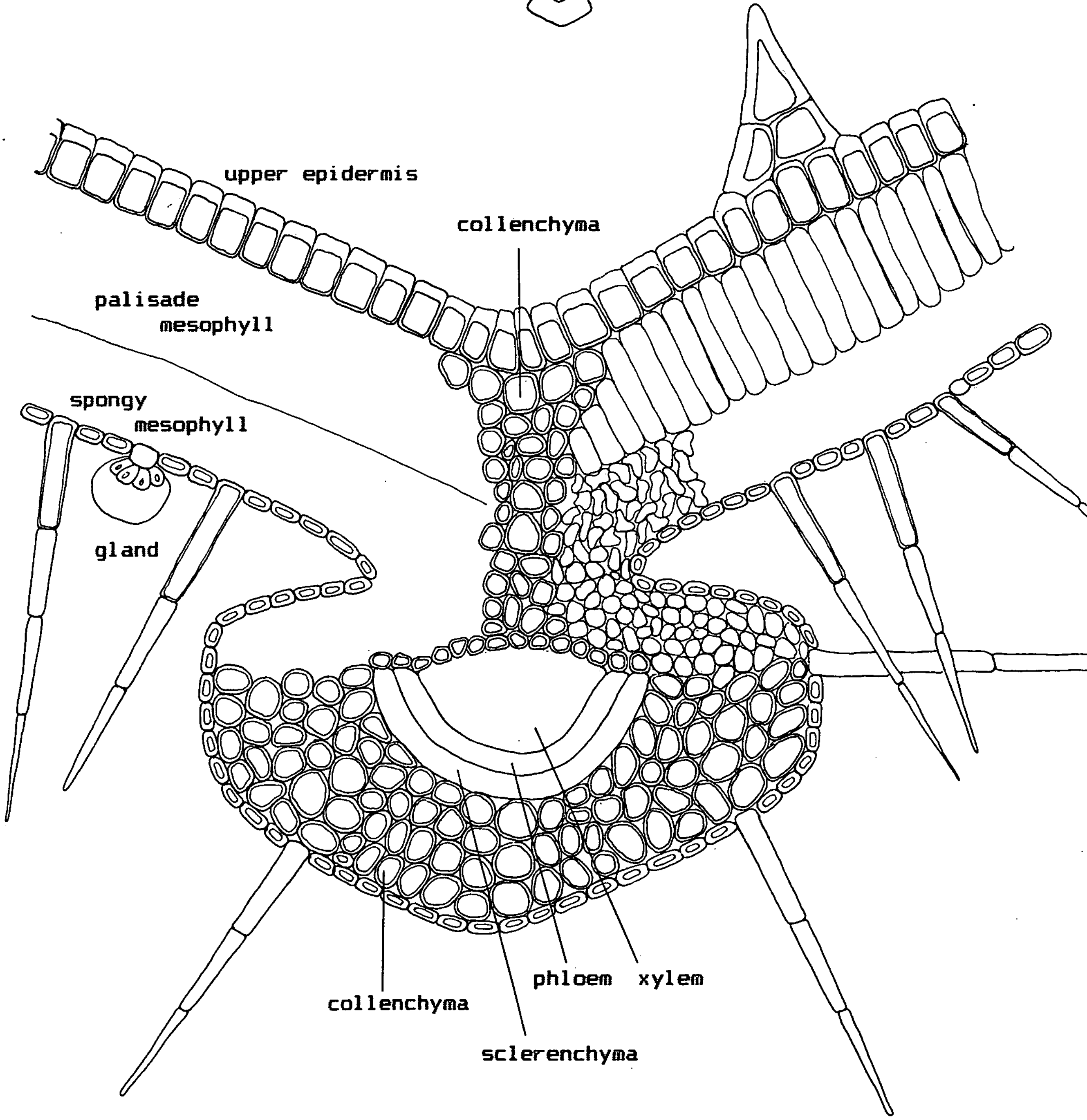
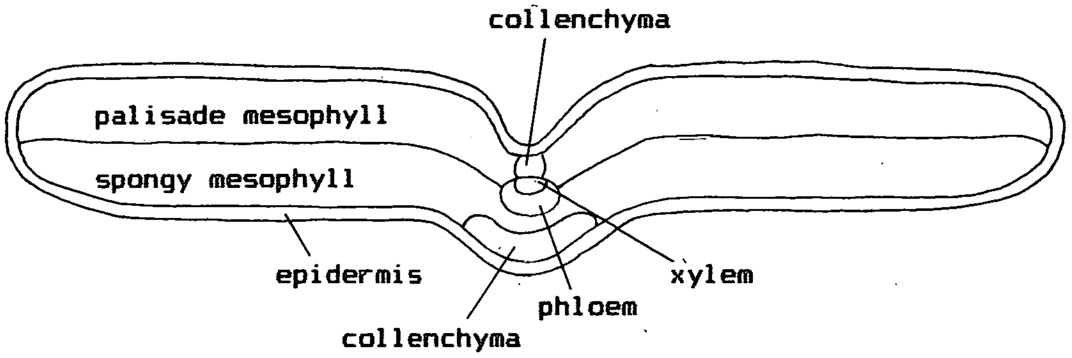


Fig. 2.49 *Xenopoma schusteri* T.S. x 200

Fig. 2.50a Xenopoma boliviana



T.S. x 100

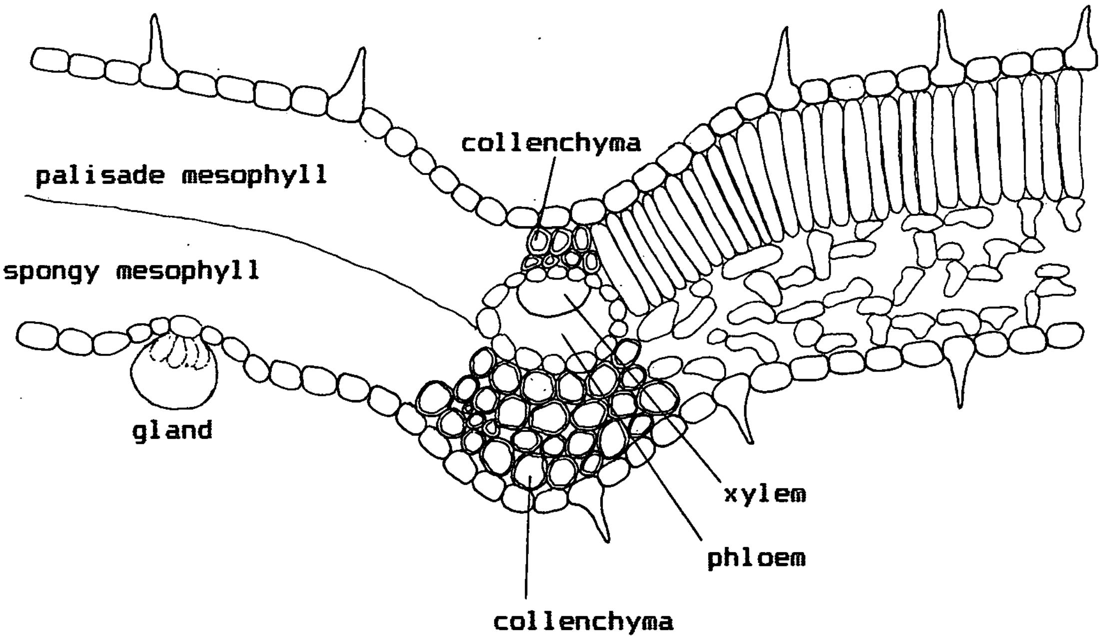
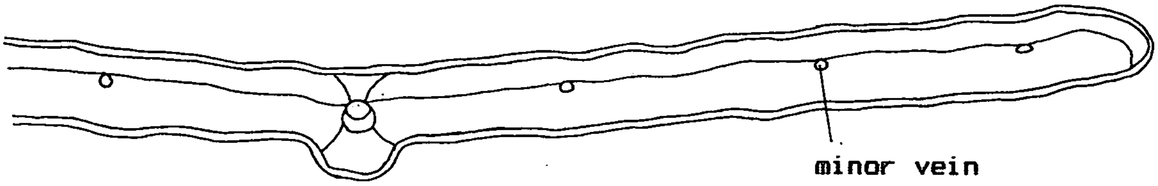


Fig. 2.50b Xenopoma boliviana T.S. x 200

Fig. 2.51a Xenopoma brevicalyx



T.S. x 50

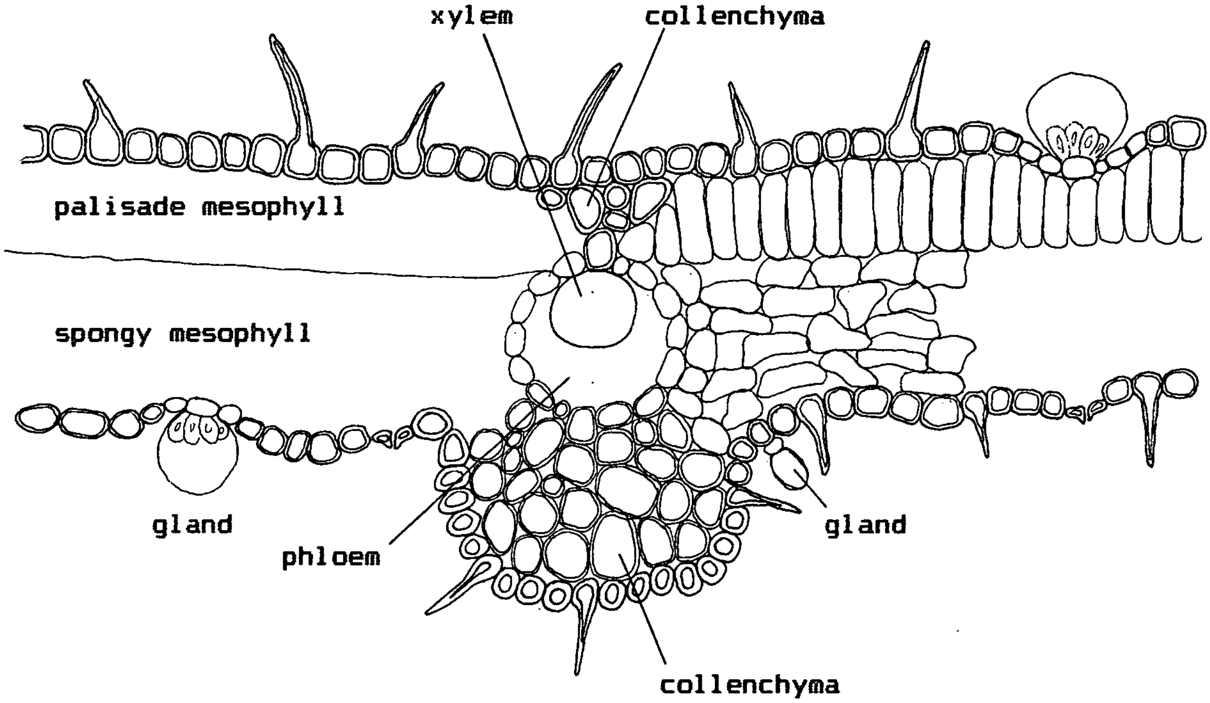
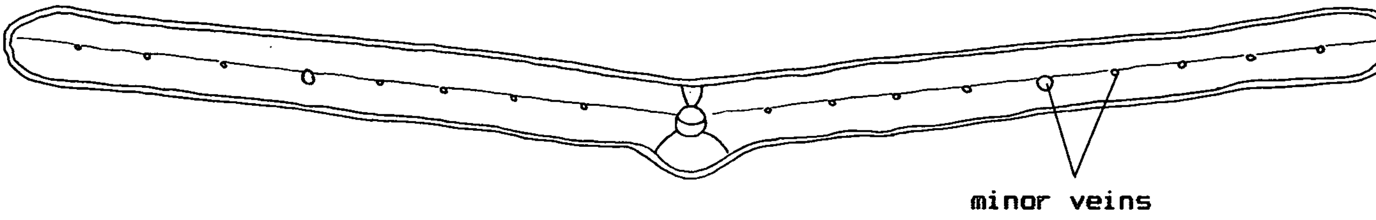


Fig. 2.51b Xenopoma brevicalyx T.S. x 200

Fig. 2.52a *Xenopoma odora*



T.S. x 50

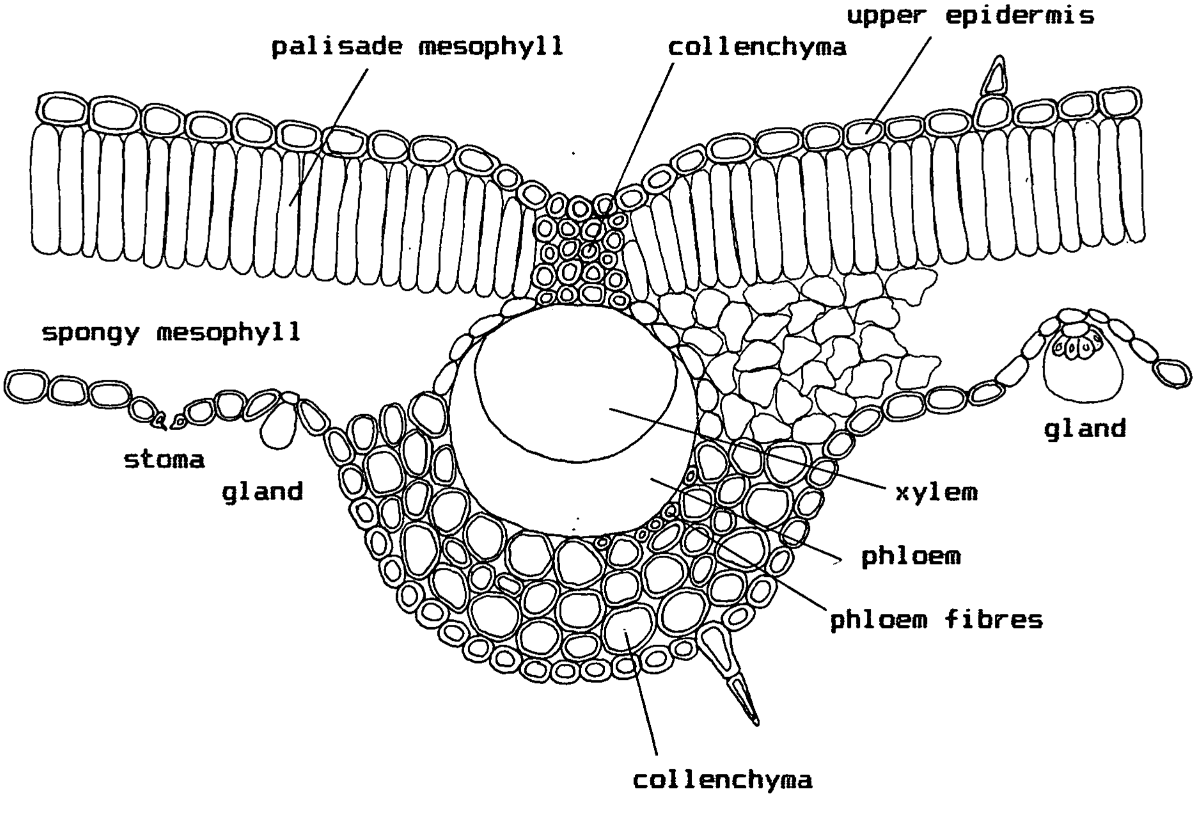
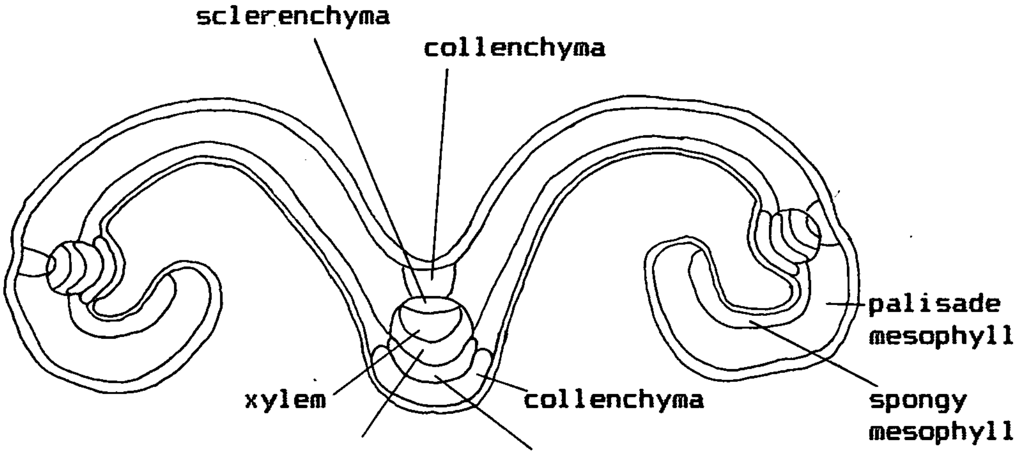


Fig. 2.52b *Xenopoma odora* T.S. x 200

Fig. 2.53a <u>Xenopoma fasciculata</u>



T.S. x 100

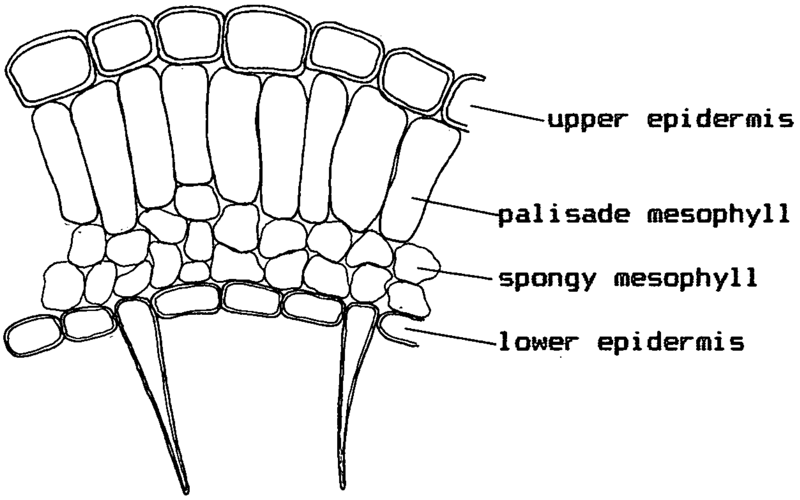


Fig. 2.53b <u>Xenopoma fasciculata</u>, portion of lamina, T.S. x 400

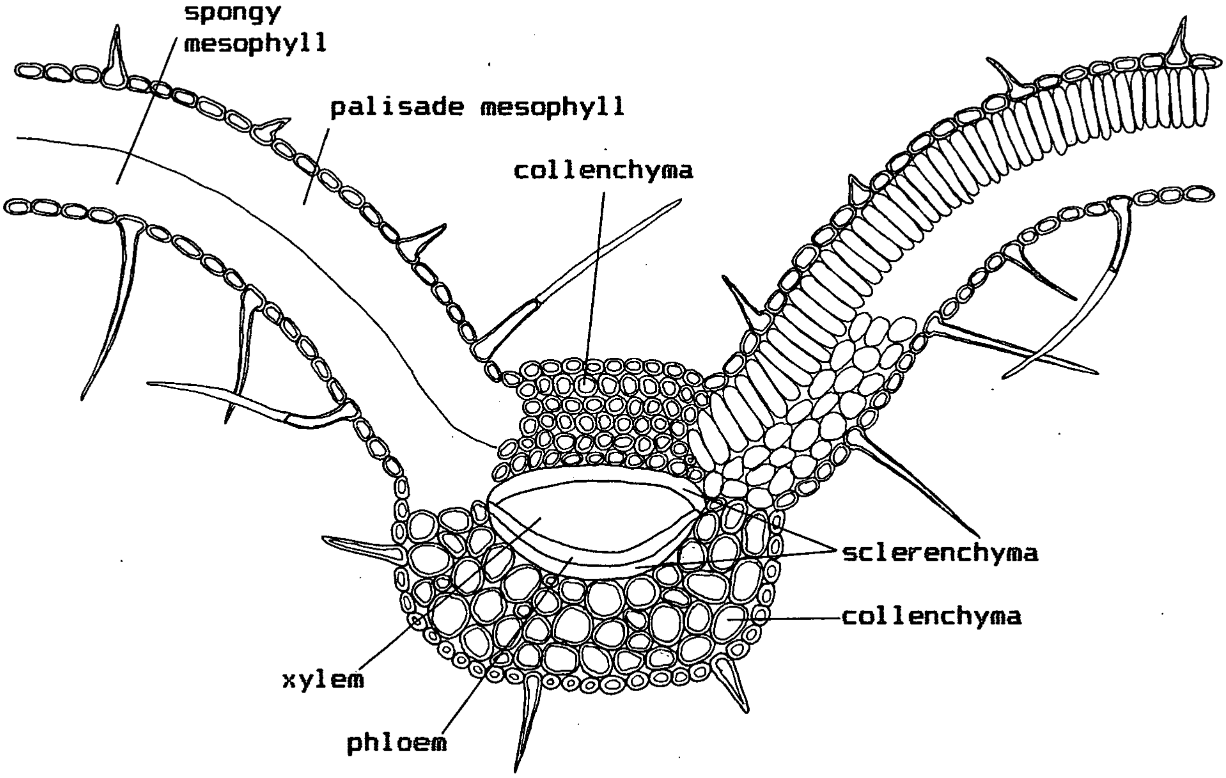


Fig. 2.54 <u>Xenopoma mutabilis</u>, T.S. x 100.

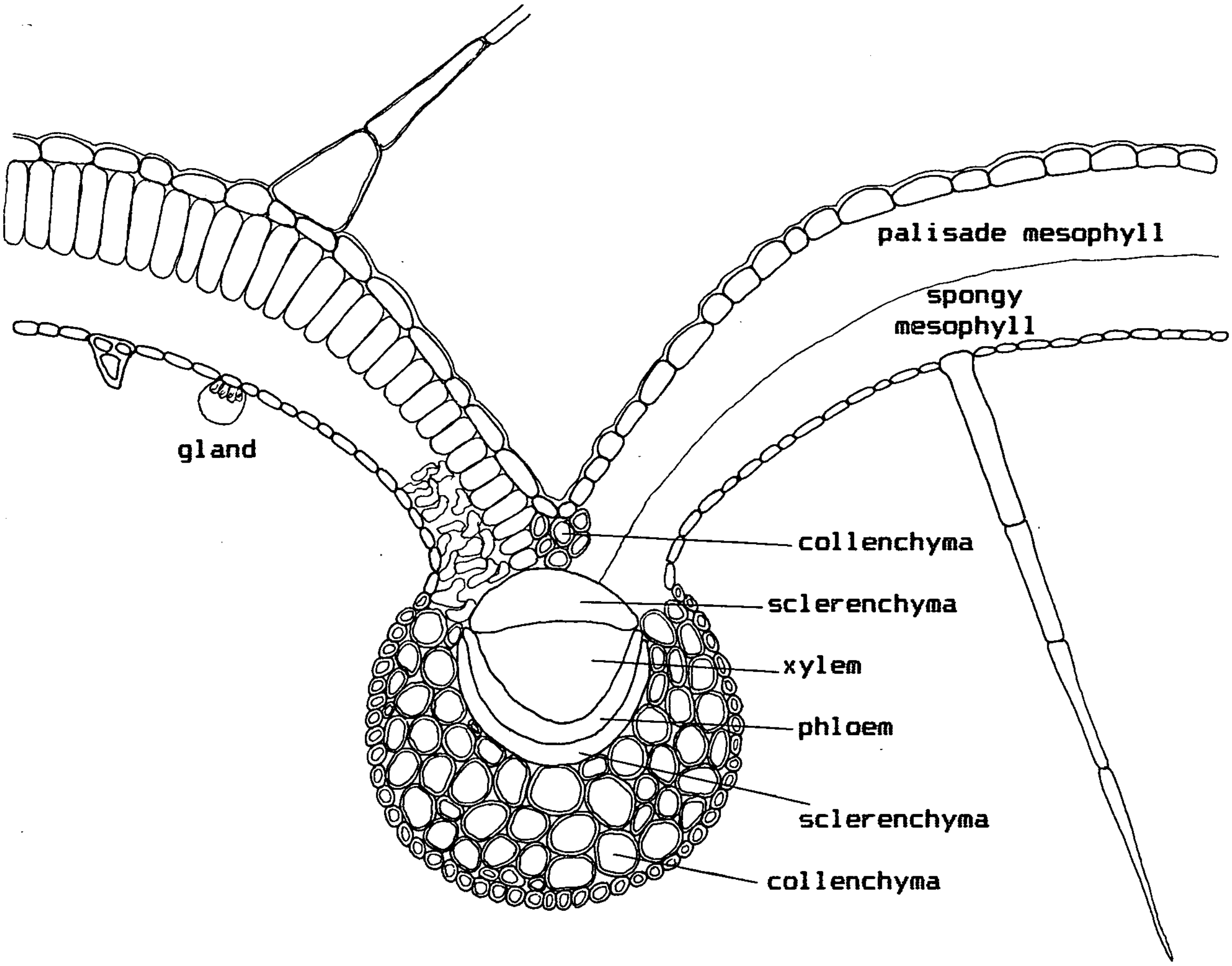
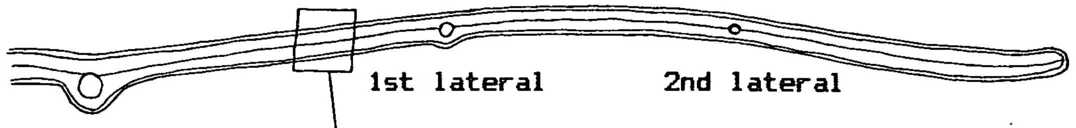


Fig. 2.55 Xenopoma cylindristachys, T.S. x 100

Fig. 2.56a Hesperothymus brownei



T.S. x 25

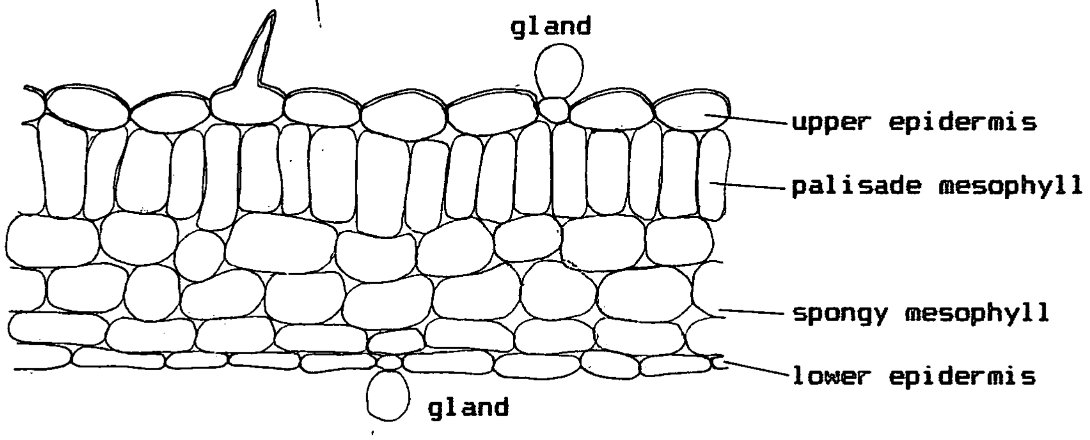


Fig. 2.56b Hesperothymus brownei, T.S. portion of leaf lamina, x 250

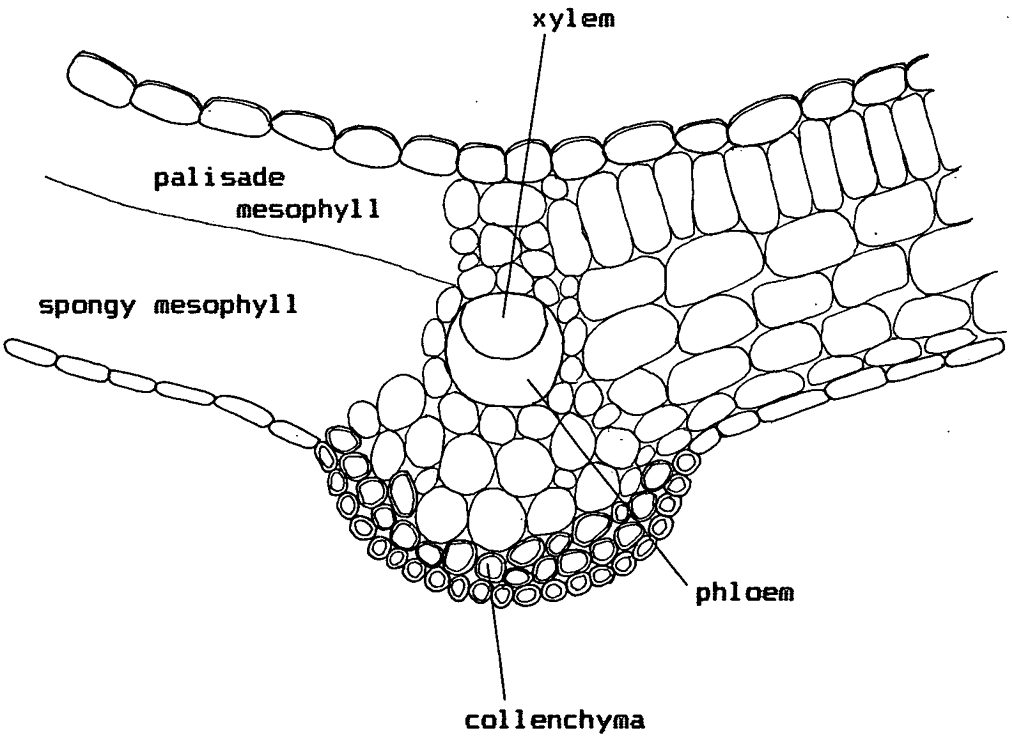
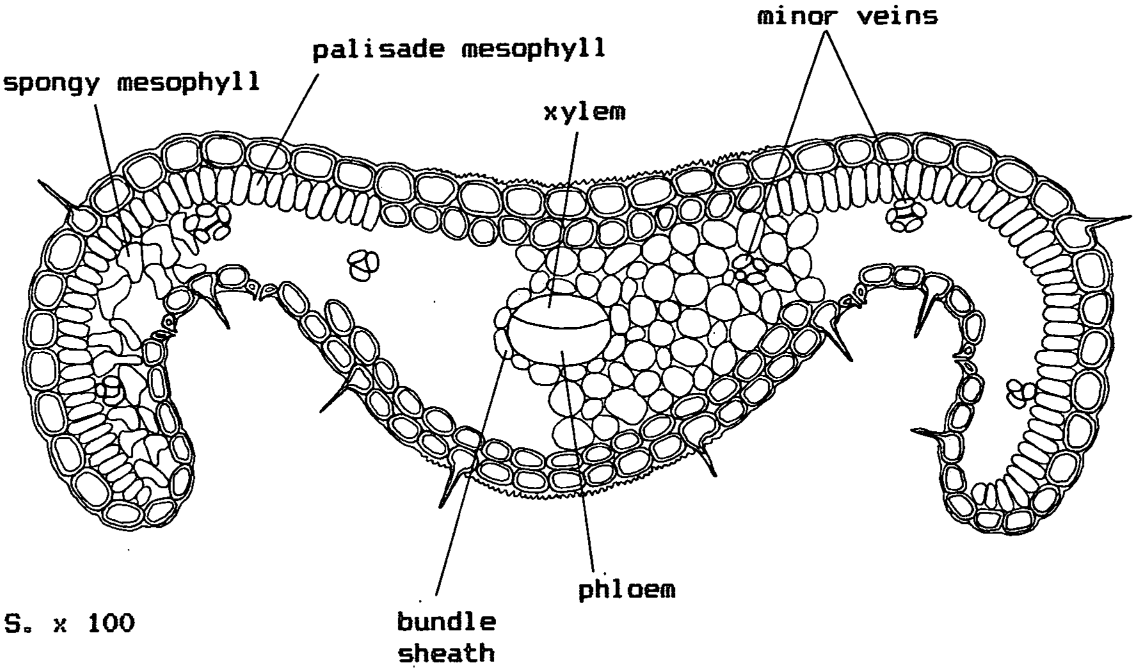
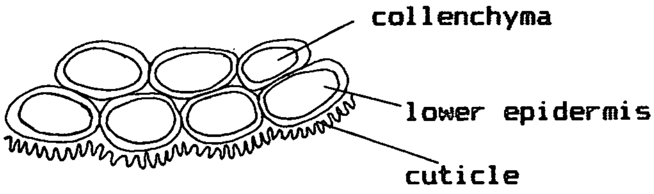


Fig. 2.56c Hesperothymus brownei, T.S. x 250

Fig. 2.57 Piloblephis rigida



T.S. x 100



T.S. portion of lower epidermis below the mid-vein, x 300

Leaf glands.

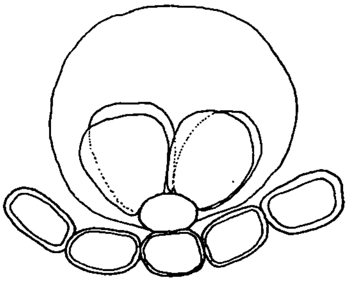


Fig. 2.58. Type 2b.

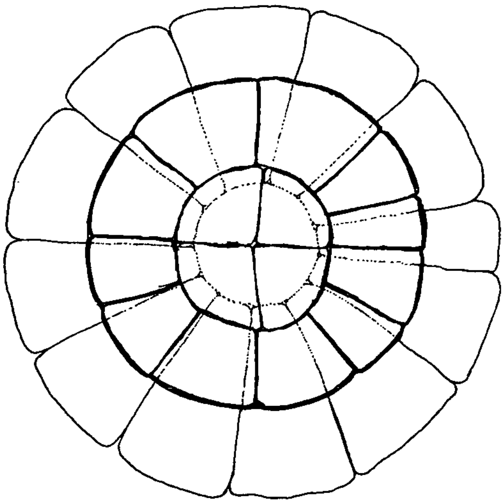


Fig. 2.59a. Type 2, from above.

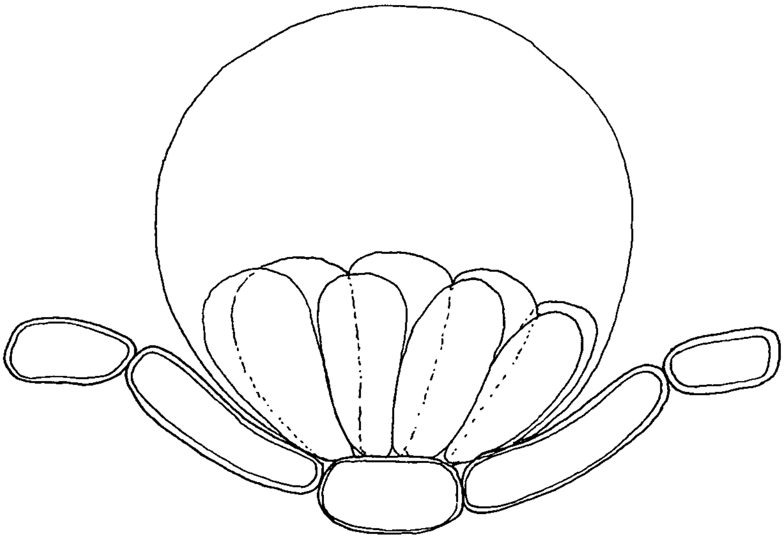


Fig. 2.59b. Type 2, side view.

Leaf glands.

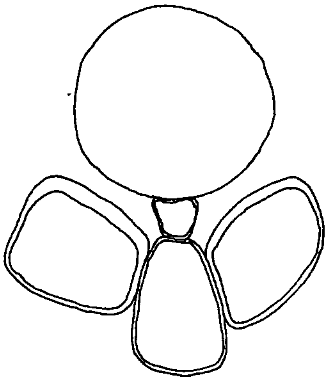


Fig. 2.60. Type 1.

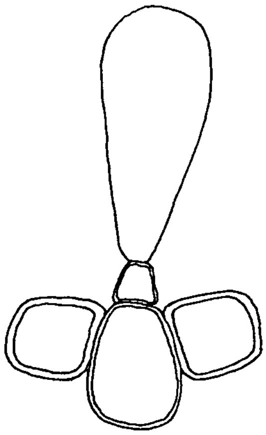


Fig. 2.61. Type 4.

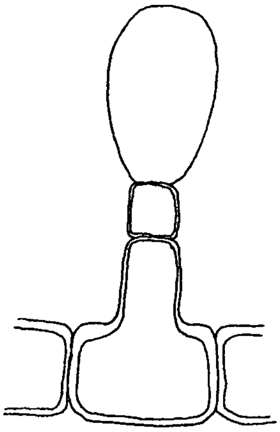


Fig. 2.64. Type 5.

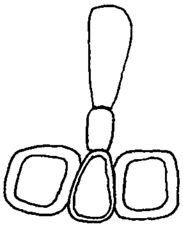


Fig. 2.62.
Type 3.

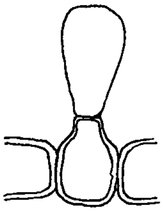


Fig. 2.63.
Type 6.

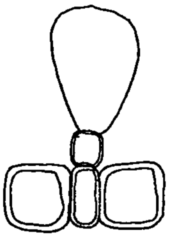


Fig. 2.65. Type 9.

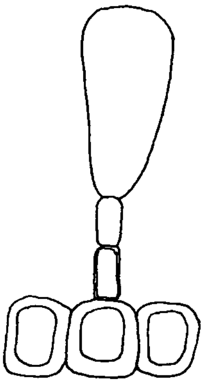


Fig. 2.66. Type 8.

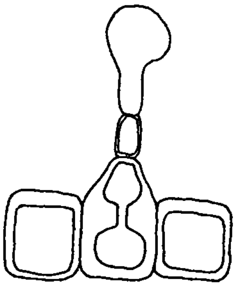


Fig. 2.67. Type 7.

Leaf glands.

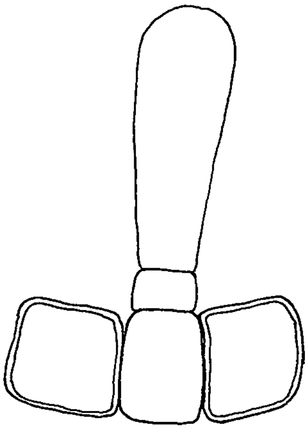


Fig. 2.68. Type 10.

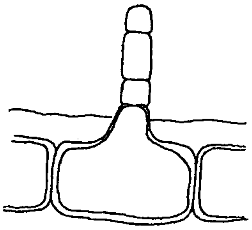


Fig. 2.69. Type 11.

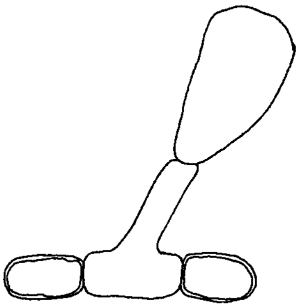


Fig. 2.70. Type 13.

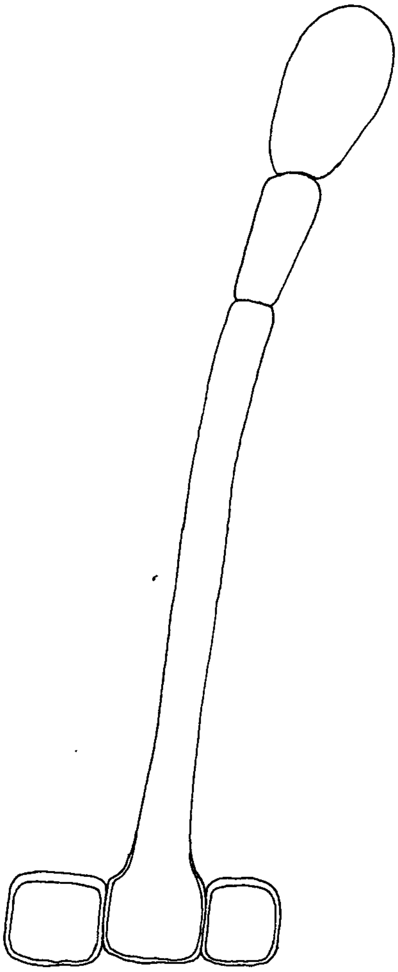


Fig. 2.71. Type 12.

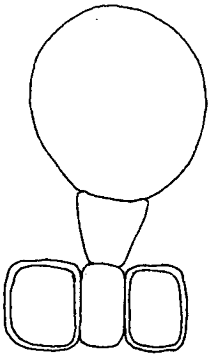


Fig. 2.72. Type 14.

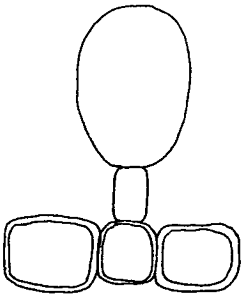


Fig. 2.73. Type 15.

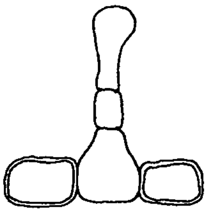


Fig. 2.74. Type 18.

Leaf glands.

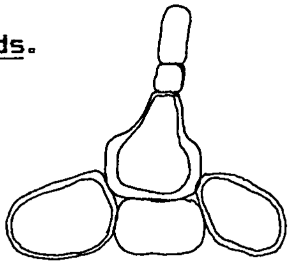


Fig. 2.75. Type 17.

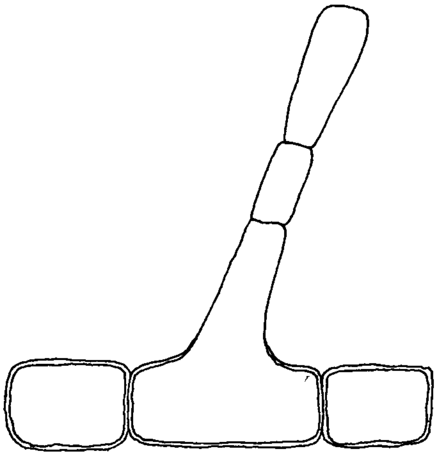


Fig. 2.77. Type 16.

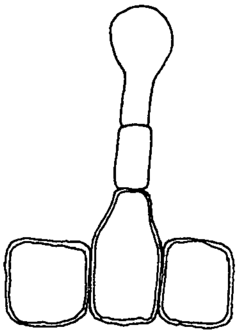


Fig. 2.76. Type 7a.

2.2.5. The Taxonomic Value of Leaf Anatomy

2.2.5.1. a) Epidermis

Though interesting in respect to modifications caused by ecological influences, the epidermis is rather poor in providing useful taxonomic characters. That is not to say that the epidermis is invariable; it is, in fact, very variable. The problem is that in the majority of genera there is a gradual transitional series between extremes. Most frequently the cells are small, oblong to oval, sometimes squarish, with the outer wall markedly thickened, and the lower epidermis clearly of smaller cells than the upper.

There are occasions when the epidermis provides useful diagnostic characters. The cells of the upper and lower epidermides are quite similar in Acinos corsicus and Cyclotrichium niveum, whereas the upper epidermis has much larger cells in the other species of their respective genera.

The sole case when epidermal characters may be useful at the sectional level is in Xenopoma. However, even here the epidermis is not entirely similar within sections. The details are rather lengthy so the reader is referred to page 64.

2.2.5.2. b) Mesophyll

The Satureioid genera (Satureja s.s., Euhesperida, and Gontscharovia) and Saccocalyx all have isolateral palisade parenchyma. All the other genera have dorsiventral palisade, though there are isolated exceptions. Acinos corsicus has more or less isolateral palisade towards the leaf margins, and Cyclotrichium niveum and Gardoquia micromerioides have entirely isolateral palisade.

Cyclotrichium may have a complete transitional series from dorsiventral palisade, to isolateral with clear development of spongy mesophyll, to complete absence of spongy mesophyll. C. haussknechtii and C. stamineum have dorsiventral palisade with clear distinction between palisade and spongy mesophyll. C. leucotrichum has a clear layer of upper palisade mesophyll, but the spongy mesophyll is less distinct than the other two species, having dorsiventrally arranged irregular-oblong cells with large air spaces between them. C. origanifolium has isolateral palisade with spongy mesophyll sandwiched in the middle (Ertem, unpublished; see fig. 2.34). Finally, C. niveum has isolateral palisade with no spongy mesophyll. It is difficult to draw a line between dorsiventral and isolateral in this genus. However, it may be that C. niveum, which has linear leaves quite unlike any other Cyclotrichium species, is the only one with constantly isolateral palisade. The others may be basically dorsiventral. It may be that the mesophyll in C. origanifolium seen by Ertem is similar, if not identical, to C. leucotrichum, which would illustrate my point of the difficulty of drawing a line between isolateral and dorsiventral.

All the Satureioid genera and Saccocalyx have narrowly elliptic, oblanceolate, or linear leaves, with conduplicate ptyxis, or more rarely linear, channelled leaves. The non-Satureioid genera tend to have flat, ovate to lanceolate leaves. In some genera, especially Micromeria and Piloblephis, the leaves may be narrowly elliptic or linear but then they have revolute ptyxis. Aside from the few above-mentioned exceptions, palisade structure correlates well with gross morphology, and supports the distinction of the Satureioid genera.

As regards the relative proportions of palisade and spongy mesophyll and the compactness and numbers of cells across the spongy mesophyll, one must keep in mind the many reports on the strong influence of climate, especially exposure to sun and air humidity, on the structure of the mesophyll (Starr, 1912; McDougall & Penfound, 1928; Nius, 1931; Schröder, 1938; Stålfelt, 1956). From the data gathered in my own study I cannot confirm or refute these authors' conclusions, but there is no reason to doubt that their results also have general application to Satureja s.l. Generally, leaves of more xeric conditions have smaller intercellular volume in the spongy mesophyll and a greater proportion of palisade. The pattern of the mesophyll tissues usually remains the same no matter the climatic conditions a leaf may develop in. Nevertheless, Russell (1895) reports that in Calamintha clinopodium (= Clinopodium vulgare L.) plants gathered from around Paris had heterogeneous mesophyll and those from Provence had mesophyll entirely of palisade. However, one wonders how accurate this observation was since the present study has not discovered any species with heterogeneous mesophyll, and Ertem (unpublished; see Table 2.12) reports C. vulgare with dorsiventral palisade.

The species with isolateral palisade may or may not have spongy mesophyll sandwiched between the palisade layers. In Satureja s.s. my own results differ somewhat from those of Ertem (unpublished). Whereas Ertem found spongy mesophyll present in all the species she studied, I found that all species of the montana complex (S. montana, S. spinosa, and S. cuneifolia were studied by us both) and S. salzmannii had no spongy mesophyll (see Table 2.1). It seems probable, therefore, that the development of spongy mesophyll in Satureja s.s. is strongly influenced by ecological factors.

Heinrichter (1884) concluded that isolaterality was probably inherited and derived from dorsiventrality. The constancy of isolateral palisade in the Satureioid group and dorsiventral palisade in the rest of the Satureja s.l. complex indicates that palisade structure is genetically determined rather than solely influenced by climate. Throughout the Mediterranean region at least, the distributions of Satureioid and non-Satureioid genera largely coincide, and occupy similarly arid habitats. A short review by Pyykkö (1966) of papers dealing with isolaterality shows that this form of palisade is associated with arid climates. The Satureioid genera nicely support this observation. A few species in Satureja s.l. support the hypothesis that isolateral palisade is derived from dorsiventral palisade. All the Acinos species studied have dorsiventral palisade except A. corsicus. It seems reasonable to conclude that in this case isolaterality is indeed derived from dorsiventrality, not merely since A. corsicus is "odd-man-out" but because this species is specialised in other leaf characters also, such as the strong marginal vein. Additional support comes from Gardoquia and Diodeilis. Some specimens of G. pallida, G. striata, and G. incana have a few dorsiventrally arranged cells adjacent to the lower epidermis, whilst usually these species conform to the pattern throughout the genus (except G. micromerioides) of clearly dorsiventral palisade. In Diodeilis the distinction between palisade and spongy mesophyll is much weaker in the woody section Diodeilis than the herbaceous section Herbaceae. Dorsiventrally arranged cells in the spongy mesophyll were noted in D. coccinea and D. ashei.

2.2.5.3. c) Collenchyma

The amount and disposition of collenchyma varies considerably in Satureja s.l. Most commonly this tissue is confined to above and below vascular bundles, and is particularly well developed around the mid-vein bundle. This perivascular collenchyma is nearly always less well developed above the bundles than below. Collenchyma is rarely entirely absent. Using the classification of Duchaigne

(1955), in every case the collenchyma is of the "annular" type, which has uniformly thickened walls.

At the generic level the disposition of collenchyma is of little taxonomic value, but is useful in distinguishing the two sections of Diodeilis. Sect. Diodeilis has no collenchyma above the mid-vein while sect. Herbaceae has a distinct cap of collenchyma cells.

At the specific level collenchyma is frequently of value. There are too many cases to list in full here, but a few examples might be mentioned. In Satureja s.s. only one species, S. salzmannii, has no collenchyma. A similar situation is found in Acinos corsicus. The large size of the collenchyma cells above the mid-vein distinguishes Micromeria taygetea from the other Micromeria sect. Pseudomelissa species investigated. Extreme wall thickening of collenchyma cell walls adjacent to the lower epidermis is characteristic of Acinos pseudosimensis and also Killickia pilosa. Lignification and the merging of collenchyma with a peculiarly large-lumen form of sclerenchyma is characteristic of a number of Gardoquia species (see Table 2.8). Lemesle (1928) also noted complete sclerification of the stem collenchyma in G. gilliesii and G. incana.

2.2.5.4. d) Bundle sheath

The bundle sheath is usually rather unremarkable and does not provide any noteworthy features of taxonomic value.

2.2.5.5. e) Vascular bundle and sclerenchymatous tissue

The shape of the mid-vein bundle is of little taxonomic importance. Usually it varies from round to oval in section, or more rarely crescent-shaped. The proportion of xylem and phloem also seems of little use, but the presence or absence of sclerenchyma and its disposition is of great value at sectional and specific levels. Sclerenchyma is always associated with vascular bundles or as the sole constituent of marginal veins; I have never seen isolated sclerenchymatous fibres in the mesophyll.

The most striking feature of use at the sectional level is the presence or absence of marginal veins. These veins, composed entirely of sclerenchymatous fibres, are present in all species of Micromeria sect. Micromeria and Micromeria sect. Pineolentia, and Acinos corsicus and A. nanus. They are large enough to be seen with the naked eye in undissected leaves.

Sclerenchyma provides a consistent diagnostic character to distinguish the two main groups of species in Micromeria. This treatment recognises 5 sections in Micromeria, but four of them, sect. Micromeria, sect. Pineolentia, sect. Cymularia, and sect. Madagascarenses, based upon morphological data, seem more closely related; the remaining sect. Pseudomelissa is set distinctly apart from these. On anatomical data this division is well supported. Sect. Micromeria and its associated sections have strong development of sclerenchyma below the phloem and fewer fibres, rarely none, above the xylem. There is a complete absence of sclerenchyma in all vascular traces in sect. Pseudomelissa. Taking both my own study and that of Ertem together, a very wide range of Micromeria species was studied and yet this correlation has held.

In Xenopoma, species of sects. Ceratominthe, Prostratae, and Pauciflorae have no sclerenchyma or almost none, but sects. Spicatae, Sphenostachys, and Xenopoma have a broad band of fibres at least below the mid-vein phloem.

The amount of sclerenchyma varies greatly in Satureja s.s., Acinos, and Gardoquia, so there are many cases at the species level in these genera where this tissue provides valuable diagnostic characters.

The value of marginal veins is undoubted; the veins are a constant feature in Micromeria sect. Micromeria and sect. Pineolentia and the two Acinos species mentioned above. However, there is an extensive literature concerned with the effects of climate on the development of mechanical tissue. The general conclusion is that mechanical tissue increases with increasingly xeric conditions. With this in mind, I have tried to concentrate on large, striking differences rather than possibly inconsequential details. I think it has been shown that sclerenchyma can be relied upon to provide a useful diagnostic character.

2.2.5.6 f) Stomata

Diacytic stomata were the only type found, which is by far the most common in the Labiatae (Metcalfe & Chalk, 1979).

Of the 86 species for which data is available, 70 species had more than 60% of the total stomata on the lower side of the leaf, 14 species with more or less equal numbers of stomata on either side (i.e. between 40% and 60% of total stomata on one side), and only 2 species had more stomata on the upper side. So it appears that the proportion of stomata on either side of the leaf has no great taxonomic value.

In Satureja s.l. as a whole about half the species have stomata level with the epidermis and half with slightly raised stomata. Sunken stomata were never seen. Particular genera within Satureja s.l. tend to have either raised or level stomata but never absolutely one or the other type. For example, Satureja s.s. tends to have stomata level with the epidermis, whereas Gardoquia and Xenopoma mostly have raised stomata.

2.25.7. g) Glands

There is a wide variety of gland types, the majority of which are not confined to any particular genus. Although this study has enumerated 20 different types of gland (see Anatomical Results; figs. 2.58 to 2.77) it is very difficult to support the contention that gland types provide useful indicators of taxonomic affinity. For example, can it really be said that the so called gland type 9 found in Cyclotrichium can be equated with what appears to be a similar gland in Gardoquia? On a morphological basis these genera are poles apart. Nothing is known about the ontogeny of these glands, and even if this was known, similar glands in different genera may not indicate any close affinity. So where might glands be of value? The results indicate that glands are of value in two ways: firstly there are glands characteristic of the entire Satureja s.l. complex; secondly there are very rare types of gland restricted to particular genera or species.

The most characteristic glands of the entire complex are the punctate, multicellular, sessile glands similar to types 2 and 2a. These are also characteristic of a number of other genera outside the Satureja s.l. complex (Ettiene, 1930; Metcalfe & Chalk, 1950; Caballero, Jimenez, & Perez de Paz, 1978).

To illustrate the usefulness of the rare gland, three examples might be mentioned: the first illustrates a gland restricted to a related group of genera, the second to a particular genus, and the third to a single species. Gland type 6 is restricted to the Calaminthoid genera Calamintha, Acinos, and Cyclotrichium. Gland type 7 is found in both species of Euhesperida only and not in any of the closely related Satureioid genera. Gland type 11 is confined to the single species Micromeria taygetea.

2.2.6. Ecological Effects on Leaf Morphology and Anatomy

A large proportion of Satureja s.l. species could reasonably be classed as xerophytes, but strictly one cannot say that a plant is a xerophyte from anatomical data alone since although the classical anatomical features may be present the plant may not physiologically be xerophytic (Maximov, 1931; Stocker, 1957; Pyykkö, 1966). In fact, the opposite can be true in that a plant may not show any obvious anatomical adaptations to dry conditions yet be physiologically well adapted (Lemée, 1946). Xeromorphic structures may also be induced by influences other than water deficiency such as heat, cold, strong winds, excessive radiation, salt (particularly NaCl), and excesses or deficiencies of soil nutrients. Paradoxically, too much water may produce xeromorphic features, and suboptimal water supply may lead to increased mesomorphy (Lundkvist, 1956). Stocker (1960, p.91) provides a short review on this subject, emphasising anatomical papers, and Levitt (1980) emphasises the physiological aspects of environmental stress. Therefore, the term "xeromorph" may be more accurate than "xerophyte" in the following discussion (Seddon, 1974).

The majority of Satureja s.l. inhabit 3 broad climatic zones: Mediterranean or mediterranean-like i.e. parts of California, Chile, and S. Africa; Irano-Turanian; and S. American high alpine. Admittedly this is rather simplistic, but the point is that most species have to endure longer or shorter periods of drought characteristic of these climatic zones, aggravated by high insolation and low temperatures in high alpine plants. Only a few species are probable hygrophytes, including the species of Hesperothymus, Diodeilis of Eastern North America, and those of Micromeria sect. Madagascarenses which grow on the margins of marshes.

One thing is clear: there is no set anatomical pattern of adaptation to environmental stress. In one species it may be the epidermis that is more developed, in another it may be strong development of sclerenchyma. It is apparent that there is a system of compensation occurring; for example, epidermis development may compensate for sclerenchyma development. Nevertheless, as has been shown in the previous section, definite tissue patterns still emerge characteristic of genera, sections, species groups or individual species. Presumably this is because of the plant's underlying genetic constitution.

Without regard to the effectiveness of various xeromorphic adaptations, whether these adaptations actually reduce water loss or render the leaf more resistant to water loss, I would like to outline those features typical of <u>Satureja</u> s.l. and how the different species cope with or react to similar environmental stresses. The presumption is, as has already been mentioned, that the xeromorphic characters seen are, in fact, in response primarily to water stress; this presumption gives a reasonable basis for discussion.

2.2.6.1. <u>Leaf fall</u>

There is very little direct evidence that leaf fall is a significant factor as a drought-avoiding mechanism in <u>Satureja</u> s.l. Some herbarium specimens have a large proportion of their leaves missing and though this may be due to poor drying or rough handling it is likely that a good proportion were collected with their leaves missing. It appears that the lower leaves tend to be shed first. Oppenheimer (1960) showed that this is a very widespread phenomenon, citing <u>Phlomis viscosa</u>, <u>Teucrium polium</u>, <u>Thymus</u>

capitatus, and Salvia triloba as Labiate examples. Mooney et al. (1977) cite three further examples from Salvia.

Montenegro et al. (1979) showed that there are two types of leaf in Gardoquia gilliesii; there are large dolichoblast leaves in the winter and small brachyblast leaves during the dry summer. Both types coexist during early summer (September to December) and then the dolichoblast leaves are shed as drought becomes severe. The brachyblast leaves gradually dehydrate to about 15% water by weight during the summer, and remarkably quickly recover after the first rains in April. Brachyblasts begin to grow about six weeks later and by October have grown into dolichoblasts, with new axillary brachyblasts developing. The summer and winter forms of G. gilliesii appear so different that they have been described as separate species (G. gilliesii and G. chilensis).

2.2.6.2. Indumentum and Epidermis

The indumentum is very variable both in size of hairs and their density. The hairs are always simple, except in Cyclotrichium niveum (see fig. App. 1e), Calamintha candidissima, and species of Xenopoma sect. Xenopoma with dendroid hairs (see fig. 2.48). Simple hairs may be single-celled and no more than tiny triangular outgrowths of the epidermis (e.g. Gardoquia pallida, fig. 2.45) or up to half as long as the leaf thickness (e.g. G. plicatula, fig. 2.44). Multi-cellular, simple hairs may be fairly short and robust (e.g. Satureja spinosa, fig. 2.40) or long and thin (e.g. Obtegomeria caerulescens, fig. 2.47). Usually the hairs are straight and more or less erect, though sometimes they are recurved or curly (e.g. G. discolor, fig. 2.46).

Numerous widespread species are known to have much more pubescent forms in xeric habitats (Johnson, 1975), and it is clear that an increased density of hairs bestows an ecological advantage on these forms. However, Levin (1973) warns about not being too dogmatic on this observation. Eberhardt (1903) showed experimentally for a large range of species that a denser indumentum was developed in drier conditions. It is reasonable to suggest that some advantage is also achieved by the hairs in Satureja s.l. species, in probably three main ways: by maintaining a boundary layer of still air transpiration may be decreased (Johnson, 1975), by providing shade from strong sunlight for the tissues beneath leaf temperature might be reduced, and by providing a possible absorbing surface for dew which is subsequently taken up by the leaf (Barthlott & Capesius, 1974).

Practically all Satureja s.l. species have leaf hairs of some sort. The pubescence is usually sparse enough for the leaf surface to be visible. Usually the indumentum is much denser on the lower side, which would tend to diminish the importance of hairs as a sun-shading adaptation. However, since the majority of stomata are also found on the lower side of the leaf, the hairs may play a more important role in control of transpiration. A striking example is seen in the species of Gardoquia sect. Tomentosae and G. discolor where the lower leaf surface is much more densely hairy than the upper side. These species do not have stomata on the upper side of the leaf. Very dense indumentum on both sides is characteristic of some species, including Satureja aintabensis, Micromeria fruticosa, Calamintha candidissima, Cyclotrichium niveum, and Piloblephis rigida.

The correlation between hair density and dryness of habitat is by no means clear in Satureja s.l. As has been said, most species are found in dry places such as stony mountain slopes, rock crevices, and cliffs. Densely pubescent species and sub-glabrous species are equally likely to be found in these habitats. The conclusion one must come to is that pubescence is only one of a whole battery of possible xeromorphic adaptations. A lack of hairs is of itself only as important as its contribution to transpiration or temperature control in the whole leaf system.

The epidermis and its vestiture should be considered together since functionally one often compensates for the lack of development of the other. Dr. Baas in a personal communication to Metcalfe (1983) noted that "it is unusual to find all of the putative xeromorphic characters occuring together in any one species. Indeed he suggests that there may be an 'anatomical compensation' that keeps them apart. As examples it may be noted that a dense covering of hairs is usually associated with a thin cuticle and raised rather than sunken stomata."

The adaptational trends in the epidermis related to xeric conditions include reduction in cell size (Eberhardt, 1903; Maximov, 1929), increased thickening of walls, especially the outer walls, cuticle thickening (Kamp, 1930), and presence of mineral crystals. Confirming what Baas has said, no species in Satureja s.l. has all these features, but one usually compensates for the other. For example, Satureja coerulea has small oblong cells with thickened walls and an extremely thick cuticle, but no hairs, while S. aintabensis has small cells with only slightly thickened walls, a thin cuticle, and an extremely dense indumentum. This compensation of thin cuticle with dense indumentum can also be seen in both species of Euhesperida. The majority of Satureja s.l. species do not have such a dense indumentum but have thick-walled epidermal cells. A thickening of the walls may or may not reduce transpiration but will certainly increase mechanical strength of the leaf. More will be said about this under the heading

"Mechanical tissue".

Martin & Juniper (1970) caution that there is no simple relationship between rate of water loss and cuticle thickness, pointing out that structure and chemical composition are more important. They quote a result of Gäumann and Jaag (1935) which showed that though the cuticle is of similar thickness in the hart's tongue fern (Phyllitis scolopendrium) and the conifer Abies sibirica the former species lost 57 times more water per unit area of leaf. To me this comparison is rather meaningless because of the large anatomical differences between the two species. However, the result again draws attention to the fact that xerophytism is a complex interaction of many component tissues each contributing a part of the total transpiration resistance or desiccation tolerance.

Pyykkö (1966), in a study of Patagonian xeromorphic plants, found that generally speaking those species with the thickest cuticle were from the driest habitats, citing a large number of papers confirming this observation. Metcalfe (1983) provides a short review of papers relating to cuticular thickness. The situation in the Satureja complex is less clear-cut since few species have a markedly thickened cuticle, though most species live in equally xeric conditions. However, there is a clear tendency for the Satureioid genera to have a thick cuticle notwithstanding the cases of Satureja aintabensis and Euhesperida species mentioned above.

Practically every species I have seen shows a marked reduction in size and thickening of walls in cells around the mid-vascular bundle. Possibly this is an adaptation in response to the proximity of the main water conducting tissue to the leaf surface, or merely provides additional mechanical strength. However, Gardoquia striata has larger cells above the vascular bundle.

No particular attention was paid to the presence or absence of mineral crystals, though Metcalfe (1983) in a review on their taxonomic significance shows that they have some value. Small crystals are fairly frequent throughout the Satureja complex but the only case to catch my eye was the extremely dense packing of crystals in the upper epidermis of Cyclotrichium haussknechtii. A reduction of water loss might be obtained by a decrease in the water potential of these cells.

2.2.6.3. Mechanical tissue

The tissues which contribute to mechanical strength in leaves are primarily collenchyma, sclerenchyma, and xylem. A thick-walled epidermis and a thick cuticle may provide additional strength. There is an extensive literature dealing with the ecological importance of mechanical tissue, and the reader is referred to Pyykkö (1966) and Metcalfe & Chalk (1983) where the subject is ably reviewed.

The main function of such tissue is in wilting and bending resistance. Maximov (1929) showed that frequently xeromorphs are not very efficient at preventing water loss by transpiration but were well suited to tolerate desiccation. A strong development of mechanical tissue would prevent the collapse of the mesophyll by wilting. Furthermore, since most xeromorphs are of open habitats, including nearly all of Satureja s.l., and are subject to buffetting by the wind, leaf rigidity is advantageous. Few Satureja s.l. species have large leaves, longer than, say, 3 centimetres, so supporting the weight of the leaf itself is probably a minor role for the mechanical tissue. The major stresses are probably external, such as the wind.

The previous section showed that sclerenchyma can be relied upon to provide a useful taxonomic character, particularly in *Micromeria*. Even though a wide range of *Micromeria* species was examined the underlying genetic control of sclerenchyma was clear, but without proper experiments it is impossible to determine the proportion of mechanical tissue produced by genetic make-up and induced by external stresses. However, keeping the aforesaid in mind, patterns of development of mechanical tissue can be seen in certain genera which are apparently related to environmental factors, which may or may not be genetically fixed by natural selection.

In *Satureja* s.s., sclerenchyma is most developed in species of the driest habitats, such as *S. coerulea*, *S. wiedemanniana*, *S. spinosa*, and *S. salzmannii*. However, in general, there is an inverse correlation of collenchyma with sclerenchyma, though *S. coerulea* is exceptional in having both well developed collenchyma and sclerenchyma. This pattern of stronger sclerenchyma in drier habitats is not found in the closely related *Euhesperida*. The two species, one from the Judaean desert and the other from Northern Libya, have no sclerenchyma and little collenchyma, the major mechanical development being in the epidermis.

The collenchyma is rather invariable in *Calamintha* and *Clinopodium*, and sclerenchyma is absent or nearly absent in these genera. *Acinos* is a little more interesting. *A. nanus*, a dwarf, montane species from Crete and the East Aegaean island of Samos, has strongly developed sclerenchyma in all vascular traces plus a marginal vein entirely composed of sclerenchymatous tissue, whereas the closely related species *A. rotundifolius*, widely distributed around the Mediterranean at altitudes of 50 m to 2500 m, is, according to a drawing by Ertem (see fig. 2.33), entirely lacking in sclerenchyma in all veins. The specimen studied by Ertem (Davis 21810) has no indication of the altitude at which it was collected. However, it may well be that the strong development of mechanical tissue in *A. nanus* is related to the very dry, mountain-top localities the species inhabits.

In the New World genera *Gardoquia* and *Xenopoma* it is difficult to see any relationship between mechanical tissue and environmental conditions. Table 2.9 shows that the majority of *Gardoquia* species have well developed sclerenchyma. The four species without sclerenchyma have related species from the same or nearby localities with well developed sclerenchyma. A clear lack of mechanical tissue is seen in the species of *Hesperothymus*. *H. brownei* is commonly found in swamps, ditches and woods, and *H. douglasii* is a woodland plant. These damp conditions, an unusual habitat for *Satureja* s.l. species, are clearly related to the absence of sclerenchyma and poor development of collenchyma.

2.3. Fruit Morphology

2.3.1. Introduction

The fruits of Labiatae are very variable, and within Satureja s.l. this is also the case. Most reports to date, however, have merely presented short descriptions and often rather simple nutlet drawings (e.g. Fabre & Nicoli, 1965; Wojciechowska, 1966; Schermann, 1966). I have not been able to find any reports on the taxonomic significance of nutlet pericarp sculpturing, though Wojciechowska (1966) has presented data on pericarp anatomy. Little is also known on the structure of hairs and glands present in many species of the Satureja complex. It was to fill this gap that a Scanning Electron Microscope (SEM) study was carried out.

Acknowledgement.

I am grateful to the staff of the SEM Unit of the Electrical Engineering Department, Edinburgh University, for the use of their microscope facilities and generous assistance in preparation of specimens.

2.3.2. Method.

Dry, mature nutlets were stuck on to SEM stubs and coated with gold in a vacuum chamber in the standard manner. No special preparation of the nutlets was necessary before coating.

The following is a list of the species prepared with the source specimen in brackets:

> Satureja thymbra (Collector?), S. montana (Cavara 1132), S. spinosa (Greuter 7753), S. macrantha (Foroughi 13978), S. bzybica (Grossheim s.n.), S. bachtiarica (Bornmuller 4264), S. spicigera (Davis 24899 & Polunin), S. coerulea (Stribrny 8/1905), S. hortensis (Ricasoli s.n.)
>
> Gontscharovia popovii (Schmid 2419)

Calamintha grandiflora (O. Polunin 8265), *C. nepeta* ssp. *glandulosa* (Uslu 4304), *C. pamphylica* (Davis 14420), *C. kilimandschari* (Volkens 1194), *C. debilis* (Regel 989)

Clinopodium vulgare (Davis 1761), *C. atlanticum* (Davis 55524)

Acinos rotundifolius (Jackson 5102), *A. nanus* (Heldreich s.n.), *A. suaveolens* (Stribrny 5/1893), *A. pseudosimensis* (Harris 2249)

Cyclotrichium origanifolium (Darrah 348)

Micromeria sect. *Micromeria*
M. graeca (Thomas 43), *M. nervosa* (Stebbing 88), *M. juliana* (Davis 47879), *M. marginata* (Reverchon 130), *M. inodora* (Faure 1/12/1935), *M. lanata* (Burchard 34), *M. cinerea* (Nasher IH32)

Micromeria sect. *Cymularia*
M. cymuligera (Haussknecht s.n.)

Micromeria sect. *Pseudomelissa*
M. thymifolia (Maly 4481), *M. mollis* (Davis 23883 & Polunin), *M. pulegium* (Fl. Aust. Hung. 2953), *M. nepalensis* (Gardner 1199), *M. barosma* (Forrest 17077), *M. euosma* (Forrest 10574), *M. hydaspidis* (Stewart 23536), *M. capitellata* (Koelz 10753), *M. abyssinica* (Wood Y1143)

Killickia compacta (Hilliard & Burtt 7876)

Brenaniella myriantha (Richards 6728), *B. cacondensis* (Gossweiller 2861)

Gardoquia multiflora (Elliot 195), *G. macrostema* (E.K. Balls 4055), *G. seleriana* (Heyde & Lux 4/1892), *G. tomentosa* (E.K. Balls 7147), *G. cercocarpoides* (M.T. Dawe 728), *G. impressa* (E.K. Balls 7079), *G. sphenophylla* (Killip & Smith 24443)

Xenopoma viminea (Fuertes 1527), *X. alpestris* (Ekman 13557), *X. schusteri* (Ekman 13702), *X. parvifolia* (Reales 1952), *X. odora* (Ugent & Cardenas 12/4/1963), *X. nubigena* (Hartweg 1336), *X. axillaris* (Bang 1125), *X. brevicalyx* (Sandemann 2524), *X. chandleri* (E.K. Balls 9125), *X. cylindristachys* (Hutchison & Wright 3869), *X. mutabilis* (Lehmann 5829)

Diodeilis coccinea (Torrey 1534), *D. georgiana* (Curtiss s.n.), *D. procumbens* (Pringle 8895), *D. amissa* (Gentry 7146)

Piloblephis rigida (Curtiss 5847)

Hesperothymus brownei (Triana s.n.), *H. douglasii* (Franklin Expedition s.n.)

2.3.3. Results

The terminology adopted here to describe various parts of the fruit wall, illustrated in fig. 2.78, are those of Wojciechowska (1966).

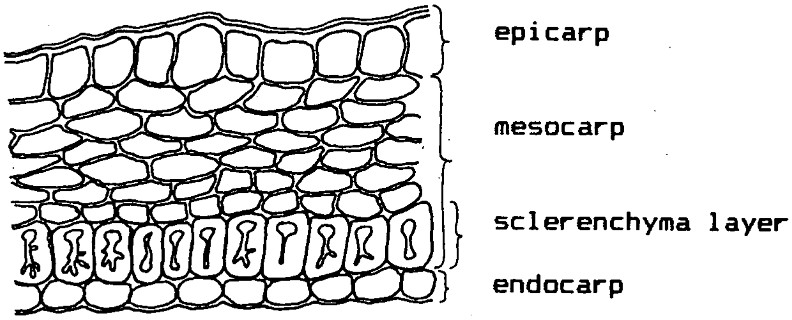


Fig. 2.78. Transverse section of the pericarp.

To obviate the need to add further identifying numbers to the SEM photographs, the plates will be referred to by the numbers already on the prints. After the scale bar and "30KV" (the filament voltage), the next two numbers are the stub number and the slide number. The plates are identified by these two numbers; e.g. stub number 12, slide number 14 = Pl. 12.14 = Killickia compacta.

2.3.3.1. Satureja s.s.

The shape is very variable, ranging from very broadly ovoid (S. spinosa, Pl. 10.14) to oblong (S. coerulea, Pl. 11.2).

All the species except S. hortensis have a minutely reticulate surface pattern. What one is seeing are the walls of dead epicarp cells. This is quite clearly seen in S. thymbra (Pl. 11.1 & 11.19). S. hortensis has much larger epicarp cells, rather oblong in outline (see Pl. 11.8). Transverse sections of the pericarp of S. hortensis and S. montana, illustrated by Wojciechowska (1966; Plates XXIX & XXX), clearly show these differences in cell size.

All species, other than S. hortensis, have minute stalked glands at least at the apex. These glands can be seen with a binocular microscope at x20.

Of the 9 species investigated, 4 have punctate glands. The glands are of two types: large, almost hemispherical glands (see Pl. 11.8) as found in S. hortensis, and rather smaller, more spherical glands as in S. bzybica (Pl. 12.17), S. spicigera (Pl. 11.5), and S. montana (Pl. 10.10). If one knows what to look for, the large glands of S. hortensis can just be made out at x20 with a binocular microscope.

2.3.3.2. Gontscharovia

The single species, G. popovii, has oblong nutlets, with a subobtuse apex. There are no trichomes or glands. The surface is extremely minutely reticulate (see Pl. 20.33).

2.3.3.3. Micromeria sect. Micromeria

The shape varies from ovoid (M. lanata, Pl. 14.8; M. inodora, Pl. 14.5), oblong (M. marginata, Pl. 14.6), to elliptic (M. cinerea, Pl. 20.31).

All the species have a characteristic reticulate surface pattern with linear, parallel depressions. Plates 13.1 and 14.4 show these very clearly.

There were no glands or trichomes in the species I investigated.

2.3.3.4 Micromeria sect. Cymularia

The single species of the section, M. cymuligera, is sub-orbicular in shape. The epicarp cells are large, areolate when viewed from the surface (see Pl. 18.15), and overlying much smaller cells of the mesocarp. Either age or preparation of the specimen destroys most of the epicarp so the surface appears to have a minutely reticulate pattern (Pl. 18.14). There are no trichomes or punctate glands.

2.3.3.5. Micromeria sect. Pseudomelissa

The shape is very variable, ranging from ovoid (e.g. M. euosma, Pl. 18.12), oblong (e.g. M. nepalensis, Pl. 17.9), to oblong-elliptic (e.g. M. pulegium, Pl. 17.8).

The majority of species have a minutely reticulate pericarp surface. M. capitellata (Pl. 18.19) and M. hydaspidis (Pl. 18.17) on the other hand have large epicarp cells, the latter clearly overlying smaller cells of the mesocarp (see Pl. 18.16). In M. thymifolia the surface is almost completely covered in broadly triangular papillae (Pl. 17.5). These papillae, at least they seem to be more like papillae than hairs (see Pl. 17.6), overlie small cells of the mesocarp (see top right of Pl. 17.6).

Three of the species investigated have trichomes. M. pulegium has large, flat, triangular hairs at the nutlet apex and on the adaxial median edge (Pl. 17.8), and M. mollis has tiny, 2-celled hairs (they appear glandular under a light microscope) primarily at the nutlet apex (Pl. 17.3). The papillae of M. thymifolia have already been mentioned above.

Two species, M. nepalensis (Pl. 17.9) and M. euosma (Pl. 18.12), have large sessile glands at the nutlet apex. These apparently multicellular glands are different in form to those in Satureja s.s. Plates 18.13 and 17.10 show that the glands are much larger, not at all sunken, and quite distinct from the epicarp.

2.3.3.6. Brenaniella

Both species investigated have narrowly oblong nutlets, with acute apices (see Pl. 12.12 and 12.10). The surface is minutely reticulate, with small papillae, especially toward the apex. There are no hairs or glands.

2.3.3.7 Killickia

The nutlets of K. compacta are very large, ovoid in shape (Pl. 12.14). The surface is minutely reticulate, with minute trichomes arising from the centre of many epicarp cells (Pl. 12.15). Thick, prominent longitudinal veins are also noteworthy. There are no glands.

2.3.3.8 Calamintha

All the species are ovoid, sometimes very broadly so (C. pamphylica, Pl. 15.14).

Large areolate epicarp cells are found in C. debilis (Pl. 15.10) and C. nepeta (Pl. 15.12 and 15.13). The other three species investigated have a minutely reticulate surface.

There are no hairs or glands.

2.3.3.9 Clinopodium

Both species are sub-orbicular in shape (Pl. 16.1). The surface is minutely reticulate (Pl. 16.16), and there are no trichomes or punctate glands.

2.3.3.10 Acinos

The nutlets in all the species are narrowly ovoid in shape. The base narrows sharply in A. suaveolens (Pl. 19.24) and A. rotundifolius (Pl. 19.26).

The walls of collapsed epicarp cells are very prominent in A. rotundifolius (Pl. 19.20) and A. nanus (Pl. 19.26). Close-up views of A. pseudosimensis (Pl. 19.23) and A. suaveolens (Pl. 19.25) also reveal large epicarp cells.

There are no hairs or glands.

2.3.3.11. Cyclotrichium

C. origanifolium has narrowly ovoid nutlets with a rounded apex (Pl. 20.29). The surface is minutely reticulate (Pl. 20.30) and there are no trichomes or punctate glands.

2.3.3.12 Gardoquia

The shape varies greatly, from ovoid, with a rounded apex (e.g. G. multiflora, Pl. 2.11), to oblong with an obtuse apex (G. impressa, Pl. 2.7), an acute apex (G. cercocarpoides, Pl. 1.1), or a long, apiculate apex (G. sphenophylla, Pl. 7.8).

There are three distinct forms of surface pattern: minutely reticulate (G. macrostema, Pl. 3.17), colliculate (G. multiflora, Pl. 2.11), and areolate-reticulate (all the other species investigated).

None of the species studied had trichomes or punctate glands.

2.3.3.13 Xenopoma

Of all the genera in the Satureja complex, Xenopoma must have the most variable nutlets. Eleven species were studied to cover most of this variation. The shape varies from broadly ovoid (e.g. X. nubigena, Pl. 4.23) to narrowly oblong (e.g. X. alpestris, Pl. 9.1), the apex rounded (e.g. X. brevicalyx, Pl. 4.20) to apiculate (e.g. X. schusteri, Pl. 5.31).

The nutlet surface features are also very variable. X. schusteri (Pl. 5.32), X. alpestris (Pl. 9.3), and X. brevicalyx (Pl. 4.20) have more or less parallel furrows running longitudinally. X. odora is pustulate over the whole nutlet surface except for at the very apex (Pl. 7.4). All the other species have a reticulate surface pattern. The reticulations are due to large epicarp cells overlying smaller mesocarp cells in X. chandleri (Pl. 9.18), X. cylindristachys (Pl. 8.12), and X. axillaris (Pl. 7.7).

X. alpestris (Pl. 9.1), X. viminea (Pl. 5.33), and X. brevicalyx (Pl. 4.20) have distinctive triangular hairs. In all three species the hairs are covered in tiny waxy pustules (Pl. 4.22 and Pl. 5.35).

None of the species have punctate glands.

Another feature of note are the thin, membranous wings at the base of the nutlets unique to X. schusteri (Pl. 5.31).

2.3.3.14. Diodeilis

The shape varies from suborbicular (D. georgiana, Pl. 6.3) to ovoid (e.g. D. amissa, Pl. 9.4).

The surface features of the annual D. amissa is at variance with the rest of the genus. This species has large epicarp cells relative to its very small size (c. 0.8 mm compared to 1.4-1.8 mm for the others). The other species have a much finer reticulate pattern (Pl. 6.3, 4.26, and 9.0).

None of the four species investigated have trichomes or punctate glands.

2.3.3.15 Hesperothymus

The nutlets of the two species of the genus are vastly different from one another. H. brownei has suborbicular nutlets (Pl. 8.15) whilst H. douglasii has ovoid nutlets (Pl. 8.16).

The nutlet surface of H. brownei is deeply ruminate, with a dense incrustation of crystaline-like wax deposits (Pl. 8.14), but H. douglasii has a smooth surface or with small reticulations (Pl. 8.17).

An extreme close-up of the nutlet surface of H. brownei reveals tiny spherical gland-like structures (Pl. 8.14). These glands are absent in douglasii. Neither species has trichomes.

2.3.3.16 Piloblephis

The single species, P. rigida, has ovoid nutlets with a rounded apex (Pl. 3.19). Small reticulations cover the whole nutlet surface. There are no trichomes or glands.

2.3.4. Discussion

Realising now the great variability of the nutlets in Satureja s.l. and the small sample studied, due caution has to taken in extrapolating from the results obtained. Sixty seven species were examined, i.e. somewhat over one quarter of the known species.

The shape of the nutlets has been found to be very variable, even within genera, and, as a consequence, is of little value in distinguishing genera. At the sectional level, the almost spherical nutlets of the monotypic Micromeria sect. Cymularia might be mentioned. As far as I am aware, no other Micromeria has suborbicular nutlets. At the specific level, on the other hand, nutlet shape is often of value, especially in such genera as Gardoquia, Hesperothymus, and Xenopoma.

Only four types of nutlet surface pattern were found. By far the most common was the reticulate pattern. The size of the lacunae varied greatly, from very small (e.g. Micromeria euosma, Pl. 18.13) to very large (e.g. Acinos rotundifolius, Pl. 19.26), with all intergradations between. The other three surface types are quite rare: the sulcate type in three species of Xenopoma, the ruminate type of Hesperothymus brownei, and the colliculate type of

Gardoquia multiflora. As in the case of nutlet shape, surface patterning was of little taxonomic value at generic level but often useful at specific level. There is, however, one clear exception. The nutlets of *Micromeria* sect. *Micromeria* have a reticulate surface, but the lacunae are more or less linear (Pl. 13.1) and not rounded as in other species.

Useful generic characters have been found in trichomes and glands. All *Satureja* s.s. species, except *S. hortensis*, have minute stalked glands. These glands, easily seen with a x20 binocular microscope, are not found in any other genus.

The large triangular hairs found in *Xenopoma* are restricted to some species of this genus. Six of the twenty species in *Xenopoma* have such hairs.

The distribution of hairs in *Micromeria* is very interesting but the sample I chose from *Micromeria* really gives a false impression as to their importance. The table below indicates the number of species which do or do not have hairs and/or glands.

	Glabrous	Non-gland. hairs	Glandular hairs	Sessile glands	Nutlets unknown
Sect. *Micromeria*	32	2			12
Sect. *Pineolentia*	1				1
Sect. *Madagascarenses*					3
Sect. *Cymularia*	1				0
Sect. *Pseudomelissa*	5	9	2	3	1

The table shows clearly that sect. *Micromeria* and the more nearly related sections *Pineolentia* and *Cymularia* tend to have glabrous nutlets, while sect. *Pseudomelissa*, quite distinct in vegetative features from these other sections, tends to have hairy nutlets or nutlets with sessile glands.

Twenty five of the 68 American species of the *Satureja* complex were investigated in this SEM study and only one, *Hesperothymus* *brownei*, was shown to have very minute sessile glands. Twenty more species studied by light microscopy did not reveal any more species with glands. This is not to say that glands might not be there since those of *H. brownei* were completely missed by light microscopy owing to their very small size.

Only two Old World genera have punctate glands: *Satureja* s.s. and *Micromeria* sect. *Pseudomelissa*. The glands are rather different in morphology in each genus. It is difficult to describe the differences, but reference to Plates 11.8, 10.10 (*Satureja*) and Pl. 18.12 (*Micromeria*) shows them to be quite distinct. There are three *Micromeria* species with sessile glands; *M. euosma* and *M. nepalensis*, included in this SEM study, and also *M. wardii*, a close relative of *M. nepalensis*. *M. barosma*, a species closely related to *M. euosma* (Kudo, 1929), does not appear to have any glands. It seems clear that the taxonomic value of punctate glands lies at the specific rather than the generic level.

The attachment scar was found to be of little interest since in all species examined there are no very marked differences of structure. The attachment scar is always quite small and is of two intergrading forms: the reniform type (e.g. *Gardoquia multiflora*, Pl. 2.11; *Satureja spinosa*, Pl. 10.14; *Calamintha pamphylica*, Pl. 15.14), and where there are two small attachment zones of similar shape, usually ovate to orbicular, either side of the median line (e.g. *Satureja hortensis*, Pl. 11.6; *Acinos suaveolens*, Pl. 19.24).

Perusing the numerous nutlet drawings by Schermann (1966) reveals a great variation in attachment scar structure thoughout the Labiatae. It seems that the uniformity in attachment scar structure in *Satureja* s.l. may be useful in distinguishing the complex as a whole from other Labiatae but does not assist in assessing generic limits within the group.

In conclusion, it seems that nutlet morphology is of limited taxonomic value in determining generic limits within Satureja s.l. It may be that pericarp anatomy is more useful, but the few transverse sections presented by Wojciechowska (1966) do not encourage optimism in this line of enquiry either. Wojciechowska's diagram of the relationships in the Labiatae based upon nutlet structure does not match up with arrangements based upon vegetative and floral features, though this may be due to the nutlet characters she chose. For example, she relates Calamintha alpina [=Acinos alpinus] to Satureja s.s. but Calamintha acinos [=Acinos arvensis] to Nepeta. A generic key presented by Schermann (1966) based upon nutlet morphology and anatomy keys Satureja s.l. out twice. Of the genera which key out in the same couplets (Glechoma, Hedeoma, Hyssopus, Origanum, Mentha, Koellia, Perilla, and Lavandula) most are not closely related to Satureja s.l., i.e. based upon whole plant morphology.

2.4. Nutlet mucilage

2.4.1. Introduction

Myxospermy, the production of mucilage by seeds or fruits, is a very widespread phenomenon in flowering plants (Grubert, 1974). In the Labiatae secretion of mucilage on wetting of the nutlets is quite frequent. The nutlet pericarp consists of cells which exude mucilage, often very abundantly. Grubert (1974) compiled about a dozen reports from the myxospermic literature for Satureja s.l., confirming some of these reports but not greatly increasing the number of species investigated. Therefore, with a view to determining the possible taxonomic significance of myxospermy in the Satureja complex, 148 species were tested for mucilage.

2.4.2. Method

For the most part the number of nutlets available for each species was very restricted, but from these few the most mature nutlets were chosen. The nutlets were soaked in warm distilled water for some minutes and observed under a x20 binocular microscope.

2.4.3. Results

The results, summarised below, use the following abbreviations: SM = semi-mature; IM = immature. If no indication of maturity is given the nutlet may be assumed to be fully mature. The source specimen is indicated in square brackets.

In the majority of cases it was found that after two or three minutes wetting the mucilage cells had swollen to their maximum extent.

2.4.3.1. Acinos

A. arvensis [Polunin 8255] - thick layer of clear mucilage.

A. nanus [Heldreich s.n.] - thin layer of ± papillose, clear mucilage.

A. pseudosimensis [Harris 2249] - thin layer of papillose mucilage, with a few fine threads near apex.

A. rotundifolius [Jackson 5102] - thick layer of clear mucilage; mucilage cells long, triangular, without spirals.

A. simensis [A.S.Thomas 1186] - no mucilage.

A. suaveolens [Stribrny 5/1893] - thick layer of triangular papillae, with spiral fibres

A. troodii [Davis 1856] - rather thin layer of small, triangular papillate mucilage cells with spiral fibres.

2.4.3.2. Calamintha

No mucilage was found in the following species: C. barosma [McLaren 193], C. betulifolia [Huber-Morath 9609], C. candidissima [Munby 62], C. confinis [d'Argy s.n.], C. cretica [Greuter 7675], C. debilis [Regel 989], C. grandiflora [Polunin 8265], C. incana [Davis 2002], C. kilimandschari [Volkens 1194], C. rouyana [Porta & Rigo 6/8/1885], C. tauricola [Davis 16225], C. uhligii [Liebenberg 1660A].

C. longicaulis [Shrestha & Bista 11579] - thin layer of yellowish mucilage; cell walls obvious.

C. nepeta ssp. glandulosa [Uslu 4304] - thick layer of clear mucilage.

C. pamphylica [Davis 14420] - apex and abaxial side covered in small hemispheres of very clear mucilage.

C. robusta [Collector?] - very thin layer of clear mucilage.

C. sylvatica [Sennen 1018] - no mucilage? (perhaps minutest amount).

2.4.3.3. Clinopodium

C. atlanticum [Davis 55524] - thin layer of clear mucilage.

All the following species revealed no mucilage: C. chinense [Wilson 810], C. gracilis var. multicaule [Taquet 5850], C. micranthum [Mizushima 817], C. umbrosum [Stewart 2647], C. vulgare [Davis 1761].

2.4.3.4. Diodeilis

D. amissa [Gentry 7146] - thick layer of clear mucilage.

D. coccinea [Torrey 1534] - small papillose mucilage cells.

The following species had no mucilage: D. dentata [Bozeman 1136], D. georgiana [Curtiss s.n.], D. procumbens [Pringle 8895].

2.4.3.5. Gardoquia

No mucilage: G. cercocarpoides [M.T.Dawe 728], G. discolor [Kuntze 1640], G. elliptica (SM) [Pennell 14401], G. gilliesii (SM) [Elliot 162], G. macrostema [Balls 4055], G. sericea (IM) [Mathews 1521], G. seleriana [Heyde & Lux 4/1892], G. taxifolia [Knight 558].

Thick layer of clear mucilage: G. impressa [Balls 7079], G. rugosa [Ferreyra 13299], G. tomentosa [Balls 7147], G. vargasii [Vargas 9472].

Thin layer of clear mucilage: G. acutifolia [Mathews 1521], G. multiflora [Elliot 195].

Minute amount of mucilage: G. pallida (IM) [Bang 1227], G. pulchella [Stork & Horton 9956], G. plicatula (SM) [Macbride & Featherstone 2238].

G. sphenophylla [Killip & Smith 24443] - few easily visible mucilaginous strands.

2.4.3.6. *Hesperothymus*

H. brownei [Triana 2037] - small amount of dense mucilage.

H. douglasii [Franklin Exp. s.n.] - no mucilage.

2.4.3.7. *Killickia*

K. compacta [Hilliard & Burtt 7876] and *K. reptans* [Hilliard 8094] have no nutlet mucilage.

2.4.3.8. *Micromeria* sect. *Cymularia*

M. cymuligera [Haussknecht s.n.] - thin layer of clear mucilage.

2.4.3.9 *Micromeria* sect. *Micromeria*

Thick layer of clear mucilage: *M. battandieri* [Davis 58316], *M. biflora* [Reading Univ./BM Exp. 424], *M. briquetii*, *M. conferta* [Davis 50334], *M. cremnophila* [Davis 23], *M. cristata* [Velenovsky 8/1887], *M. cypria* [Davis 2995], *M. elliptica* [Davis 47562], *M. inodora* [Faure 1/12/1935], *M. kerneri* [Murbeck 29/7/1891], *M. lanata* [Burchard 346], *M. lepida* [Bramwell 2011], *M. macrosiphon* [Bramwell, Richards & Murray 275], *M. microphylla* [Dörfler 48], *M. nervosa* [Reverchon 130], *M. parviflora* [Dörfler 154], *M. persica* [Alava 10739], *M. sinaica* [Davis 8600], *M. tenuis* ssp. *linkii* [Burchard 237].

Thin layer of clear mucilage: *M. filiformis* (IM) [Bianor 1422], *M. fruticulosa* [Ross 179], *M. graeca* [Ross 178], *M. herpyllomorpha* [Bourgeau 126], *M. hochreutineri* (IM) [Kralik 52], *M. hysoppifolia* [Burchard 27], *M. juliana* [Davis 47879], *M. lachnophylla* [Bourgeau 255], *M. marginata* [Reverchon 130], *M. myrtifolia* [Akman 159], *M. teneriffae* (IM) [Noë 1478], *M. weilleri* [Maire 4/1937].

Minutest amount of mucilage: *M. congesta* [Haussknecht s.n.], *M. contardoi* [Pichli-Sermolli 2684], *M. croatica* (SM) [Herb. Norm.

3460], *M. serbaliana* (IM) [Kinross 9/1945].

2.4.3.10. *Micromeria* sect. *Pseudomelissa*

Thin layer of clear mucilage: *M. carica* [Davis 14322], *M. dolichodonta* [Davis 16356], *M. hydaspidis* [Stewart 23536], *M. libanotica* [Davis 9943], *M. nepalensis* [Gardner 1199].

No mucilage: *M. cilicica* [Eig & Zohary 17/8/1931], *M. dalmatica* [Stribrny 7/1907], *M. euosma* [Forrest 10574], *M. frivaldskyana* [Stiefelhagen 22/7/1909], *M. fruticosa* [Reverchon 686], *M. pulegium* [Fl. Exs. Aust.-Hung. 2953], *M. taygetea* [Davis 2/10/1938], *M. thymifolia* [Crichiutti s.n.], *M. wardii* [Elliot 14234].

M. mollis [Davis 23883 & Polunin] - a rather thick layer of brownish, dense mucilage. *M. capitellata* [Koelz 10753] -a thick layer of clear mucilage.

2.4.3.11. *Brenaniella*

All the following species produce a thin layer of clear mucilage: *B. cacondensis* [Gossweiller 2861], *B. masukuensis* [Geilinger 2413], *B. myriantha* var. *myriantha* [Richards 6728], *B. wellmannii* (IM) [Kassner 2895].

2.4.3.12 *Piloblephis*

P. rigida [Curtis 5847] produces no mucilage.

2.4.3.13 *Satureja*

No mucilage: *S. cilicica* [Darrah 335], *S. coerulea* [Stribrny 8/1905], *S. cuneifolia* [Sennen Pl. Esp. 825], *S. icarica* [Runemark & Snogerup 12460], *S. intermedia* [Lamond 5149], *S. macrantha* [Foroughi 13978], *S. montana* [Cavara 1132], *S. mutica* [Sintenis 947], *S. parnassica* [Davis 312], *S. spicigera* [Davis 24899 &

Polunin], *S. spinosa* [Greuter 7753], *S. thymbra* [Baytop, Baytop & Cubukcu 9789], *S. wiedemanniana* [Manissadjian 540].

A very thin layer or a minute amount of mucilage: *S. bachtiarica* [Bornmuller 4264], *S. bzybica* [Grossheim s.n.], *S. hortensis* [V. Ricasoli s.n.], *S. obovata* [Sennen Pl. Esp. 950].

2.4.3.14. *Xenopoma*

No mucilage: *X. alpestris* [Ekman 1355], *X. axillaris* [Bang 1125], *X. boliviana* (SM) [Lippmann 25/6/1970], *X. brevicalyx* [Sandeman 2524], *X. nubigena* [Hartweg 1336], *X. schusteri* (SM) [Ekman 13702], *X. vana* (IM) [Weberbauer 7259], *X. viminea* [Fuertes 1527].

A thick layer of mucilage: *X. chandleri* [Balls 9125], *X. cylindristachys* [Hutchison & Wright 3869], *X. ganderi* [Moran 13293], *X. odora* [Ugent & Cardenas 12/4/1963].

A minute amount of mucilage: *X. ekmaniana* [Holdridge 1248], *X. mutabilis* [Lehmann 5829], *X. parvifolia* [Reales 1952].

2.4.4. Discussion

The results show that production or non-production of mucilage by nutlets tends to be characteristic of a genus, more so in Old World than New World genera. Amongst the Calaminthoid genera, *Calamintha* and *Clinopodium* tend to have no mucilage (Schenk, 1877), whereas all *Acinos* species, apart from the African *A. simensis*, have mucilaginous nutlets (see also Swarbrick, 1971; Hegi, 1927). A thick layer of clear mucilage is characteristic of Micromeria sect. *Micromeria*, while sections *Cymularia* and *Pseudomelissa* tend to exude only a thin layer or no mucilage at all. The Micromerioid genera *Killickia* and *Brenaniella* produce no mucilage and a small amount respectively. Satureja s.s. in nearly all species does not have myxospermic nutlets; those which exude mucilage do so only in the smallest amounts. The two largest American genera have a mixture of both mucilaginous and non-mucilaginous species, the distribution of which does not appear to correspond with described sections or species groups. In Diodeilis all species, other than the annual D. amissa, have no mucilage.

There is circumstantial evidence that immature nutlets produce less mucilage than fully mature ones. In nearly all Micromeria sect. Micromeria species tested a thick layer of clear mucilage was produced, but four species produced the minutest amount only. The specimens available for two of these four only provided immature nutlets. Similarly in Gardoquia, the immature nutlets either produced no mucilage or a minute amount only while the tendency in mature nutlets is to produce a definite layer in this genus.

Mucilaginous cells are sometimes restricted to certain parts of the nutlet. In Calamintha nepeta ssp. glandulosa the mucilage cells seem to be found only on the abaxial side and at the apex. Micromeria congesta produced only a tiny amount near the nutlet apex. This phenomenon of localised mucilage cells has also been seen in certain species of Prunella L. (Grubert, 1974).

Cellulosic spirals in the mucilage are rare in Satureja s.l. They have been seen only in Acinos suaveolens and A. troodii. Schenk (1877) has also reported spirals in A. alpinus. The fine threads seen in a number of other species are mucilage cell walls.

Zohary (1937) found in Palestine that myxospermy tends to be found in winter annuals, mostly from the Saharo-Sindian region of the flora and other arid parts. In Satureja s.l., however, the amount of mucilage is not clearly related to aridity of habitat. Species of both Satureja s.s. and Micromeria sect. Micromeria generally inhabit similarly arid habitats, yet the former usually produces no mucilage but the latter abundantly so.

Various ideas have been proposed on the ecological importance of myxospermy. Mucilage may either cement the fruit to the ground or aid in attachment to the outside of animals (epizoochory). In support of the first suggestion: a plant which reaches maturity and produces viable nutlets would probably be living in a favourable habitat, so the nutlets it sheds would likely grow well in the same spot. This might be important in arid environments where favourable growing areas may be small. In desert areas it is less likely that myxospermy is involved in epizoochoric dispersal since rain is infrequent, and when it does rain sand grains would probably adhere to the nutlet. Such a coating of sand would prevent animal dispersal. Galinat (1950) has shown also that for *Micromeria juliana* and *Satureja hortensis* the mucilage has very poor adhesion to flat surfaces. Fuller & Hay (1983) have presented convincing evidence that *Salvia columbariae* is protected from desert granivores by the mucilage gluing sand grains around the nutlets.

2.5. Chromosomes

No cytological work was possible in the present study. However, a large number of chromosome counts have been compiled from the literature. These investigations are so biased toward the Old World genera that conclusions on trends in the whole Satureja complex would be very poorly founded. Nevertheless, within the Satureioid, Micromerioid, and Calaminthoid groups there is enough information to speculate on basic chromosome numbers.

Many of the chromosome reports present no more than a count and cite the voucher specimen. Presumably this is partly because the chromosomes in most species are very small, 1.0-2.0 µm at metaphase being quite typical, and practically indistinguishable from one another. One is therefore restricted to comparing numbers of chromosomes rather than morphology in most cases.

2.5.1. Satureioid genera

All the counts available are of Satureja s.s. The genus is divisible into two groups: the annual S. hortensis with 2n=48, and the rest of the genus, all perennials, with 2n=30.

It appears that in the cultivated varieties of S. hortensis there is some instability of chromosome number, with Vaarama (1949) reporting 2n=45 and Reese (1953) reporting 2n=46, 47, and 48. Vaarama (1949) noted apparently normal seed production, so hybridisation seems a less likely reason for the lower count. Reese (1953) suggests that the variable number may be due to B chromosomes. It is probable that S. hortensis is a polyploid with basic number x=12 or 6. Mechelke (1954) presents an illustration of 48 chromosomes at metaphase; 40 chromosomes are all very similar but eight others are distinguished by their small size. Tetraploidy or octoploidy are, therefore, both possible. Gill (1981) suggests the species is tetraploid.

The rest of the genus, with nearly all reports of 2n=30, seemed simpler to interpret until Borsos (1970) put a spanner in the works by reporting S. kitaibelii (S. montana ssp. kitaibelii) with 2n=12. Lovka, Susnik, Löve & Löve (1971) and Markova (1983) reported S. montana ssp. kitaibelii with 2n=30, as so do six other reports of S. montana. (See also Delay, 1947 [n.v.] who reports 2n=12 for S. montana.) There are three ways to deal with Borsos' count of 2n=12: the count is an error, or the specimen was identified incorrectly as S. kitaibelii, or Borsos is correct in all respects. Unless Borsos' technique was really atrocious (very unlikely) I cannot imagine a count as low as 12 being in error, and misidentification of a common Balkan species is also unlikely, especially with the backing of a herbarium of 500,000 specimens (BUC) and the facilities of the Botanic Garden of Bucurest. So I tend to believe the count is accurate.

A scheme integrating 2n=48, 2n=30, and 2n=12 must be very speculative without detailed investigation. Nevertheless there can be no harm suggesting one. Polyploidy seems to be the linking factor. With two basic numbers, x=5 and x=6, S. hortensis could be an octoploid with x=6, Borsos' count of S. kitaibelii a diploid with x=6 or a diploid with aneuploidy with x=5, and the rest hexaploids with x=5. Genera with multiple basic numbers are not uncommon as we shall see in the Micromerioid and Calaminthoid genera.

2.5.2. Micromerioid genera

Chromosome numbers are available for a wide range of Micromeria species, and there is a single count for Bremaniella.

Morton (1962) suggests that *Satureja robusta* (*Brenaniella robusta*) with 2n=42 is a hexaploid of basic number x=7. From a drawing presented by Morton the chromosomes are all very similar, rod-shaped, 1.5-2.0 µm long at metaphase.

The great majority of *Micromeria* sect. *Micromeria* species have 2n=30, with doubling to 2n=60 reported by Dahlgren et al. (1971) in *M. filiformis*. The count of 2n=20 obtained for *M. graeca* by Bjorkqvist (1969) is difficult to believe, especially after Cenci (1968) published 2n=60 for the same species. If Bjorkqvist is correct then the basic number for *Micromeria* sect. *Micromeria* is more likely to be x=5 than x=15. The count of 2n=26 for *M. inodora* (Cardona, 1973) is most easily explained by aneuploidy derived from 2n=30, and the count by Cardona & Contandriopoulos (1983) of 2n=48 could be an autopolyploid of 2n=26 with the loss of 4 chromosomes.

In *Micromeria* sect. *Pseudomelissa*, the Mediterranean species *M. dalmatica* and *M. thymifolia* have 2n=20, and the Himalayan *M. capitellata* has 2n=50. A basic number of x=5 would link these two groups; in fact, this same number could link sect. *Micromeria* with sect. *Pseudomelissa*. A unified system for *Micromeria* based on x=5 can be achieved by assuming frequent polyploidy, the majority being hexaploid, some tetraploid, and a few decaploid and even dodecaploid. Polyploidy at such high levels would be much more tolerant of aneuploidy such as proposed in *M. inodora*.

2.5.3. Calaminthoid genera

The Calaminthoid genera are an excellent example of an aneuploid series. In outline the genera have the following numbers:

Acinos	2n=18 (rarely 22, 36, 18+3B)
Clinopodium	2n=20 (rarely 10, 36, 38, 40)

Calamintha 2n=20, 22, 24 (also 18, 40, 42, 48, 72)

Unfortunately there are no counts available for Cyclotrichium.

Acinos is almost uniformly 2n=18, suggesting a basic number of x=9. Only the East African A. pseudosimensis has 2n=22. Polyploidy seems to be uncommon, contrasting with Calamintha (see above), and noted only in a Samos population of A. rotundifolius (Bothmer, 1970). The report by Loon & Setten (1982) of B chromosomes is the only one for the entire Satureja complex.

Although nearly every count in Clinopodium is 2n=20 and the basic number is apparently x=10, the count obtained by Chuksanova & Kaplanbekova (1971) of 2n=10 for C. integerrimum (C. vulgare ssp. vulgare) suggests that the basic number is likely to be x=5 for the whole genus. Higher polyploids are known in C. vulgare and C. umbrosum, accompanied also in the latter species by aneuploidy.

Calamintha is a cytologically complicated genus. There seems to be multiple basic numbers of x=9, 10, 11, and 12. Polyploidy and polyploidy accompanied by aneuploidy also adds to the wide range of numbers reported. The great variability of form in C. nepeta seems to be at least partially explained by its propensity for polyploidy and aneuploidy.

2.5.4. American genera

There is very little information on the American species: two counts published [Hesperothymus douglasii (2n=20) and Diodeilis arkansana (2n=20)] and three more in press [one Xenopoma (2n=46) and two Gardoquia species (2n=46 and 2n=48)]. It would be unwise to speculate on basic chromosome numbers from such scanty knowledge.

The following table lists all chromosome reports for <u>Satureja</u> s.l. that I have been able to personally examine. There are about a dozen other reports cited in various reference works (e.g. the many volumes of Regnum Vegetabile devoted to chromosome numbers, and Fedorov, 1969) which have not been checked and are not listed below. None of these excluded reports make any difference to the conclusions reached on basic chromosome numbers. The abbreviations of herbaria are according to Holmgren, Keuken & Schofield, Index Herbariorum, ed. 7 (1981), Utrecht.

2.5.5.

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
Acinos				
A. alpinus (L.) Moench	Tirol, Austria	KIEL, Reese s.n.	Reese (1953)	2n=18
A. alpinus (L.) Moench	Povazsky Inovec, Czechoslovakia	SLO, Majovsky s.n.	Majovsky (1974)	2n=18
A. alpinus (L.) Moench	Pancarevo, Bulgaria	VIL, Markova HH-L221	Markova (1974)	2n=18
A. alpinus (L.) Moench	Sierra de Albarracia, Prov. Teruel, Spain	LD, LIVU, N.0426	Löve & Kjellquist (1974)	2n=18
A. alpinus (L.) Moench	Cortina, Italy	COLO, Love & Love N 605	Löve & Löve (1982)	2n=18
A. alpinus (L.) Moench ssp. alpinus	Alpi Apuani, Italy	PI, Garbari et al., H.B.P. 406/1980	Giordani, Miceli, & Monti (1980)	2n=18
A. alpinus (L.) Moench ssp. dinaricus Šilic	Prenj, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=18
A. alpinus (L.) Moench ssp. majoranifolius (Miller) Ball	Prijepolje, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=18
A. alpinus (L.) Moench ssp. meridionalis (Nym.) Ball	Vallee du Galbe, Pyrenees, France	NEU	Favarger & Kupfer (1968)	2n=18
A. alpinus (L.) Moench ssp. meridionalis (Nym.) Ball	Sierra Nevada, Spain	SEV 37768, Ubera	Ubera (1979)	2n=18
A. alpinus (L.) Moench ssp. meridionalis (Nym.) Ball	Katafyton, Greece	C, Strid 13156	Strid & Franzen (1983)	2n=18
A. arvensis (Lam.) Dandy	Mölln, Germany	Scheerer s.n.	Scheerer (1940)	2n=18
A. arvensis (Lam.) Dandy	Lund, Sweden	LD	Löve & Löve (1944)	2n=18
A. arvensis (Lam.) Dandy	Bergen, Holland	U, Gadella & Kliphuis 2167	Gadella & Kliphuis (1966)	2n=18

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
A. arvensis (Lam.) Dandy	Vinicky, Czechoslovakia	SLO, Majovsky s.n.	Majovsky et al. (1970)	2n=18
A. arvensis (Lam.) Dandy	Elbasan-Hysgete, Albania	LD, Strid 1102	Strid (1971)	2n=18
A. arvensis (Lam.) Dandy	Gower, England	DHM, Morton s.n.	Morton (1973)	2n=18, diploid
A. arvensis (Lam.) Dandy	Durham, England	DHM, Morton 4682	Morton (1973)	2n=18, diploid
A. arvensis (Lam.) Dandy	Serrania de Cuenca, Prov. Cuenca, Spain	LD, LIVU, N.0466	Löve & Kjellquist (1974)	2n=18
A. arvensis (Lam.) Dandy	Bessapara hills, Bulgaria	VIL, Markova MM-L70	Markova (1974)	2n=18
A. arvensis (Lam.) Dandy (forma villosa)	Paramun, Bulgaria	VIL, Markova MM-L215	Markova (1974)	2n=18
A. arvensis (Lam.) Dandy	Konitsa-Pentalophon, Greece	U 20339, Loon & Snelders	Loon & Snelders (1979)	2n=18
A. arvensis (Lam.) Dandy	Sheki, Azerbaidzhan, U.S.S.R.	L, Wieffering 18662	Kliphuis & Wieffering (1979)	2n=18
A. arvensis (Lam.) Dandy	Horning Hills, Ontario, Canada	WLU, Gill Can. 48	Gill (1981)	n=9, diploid
A. arvensis (Lam.) Dandy	Mt. Busludza, Bulgaria	U, Loon & Setten 25100	Loon & Setten (1982)	2n=18, 18+3B
A. hungaricus (Simk.) Šilic	See A. alpinus ssp. majoranifolius		Papes & Šilic (1981)	
A. orontius (K.Maly) Šilic	Konjic, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=18
A. pseudosimensis (Brenan) Doroszenko	Cameroon Mt., Cameroon	GC, Morton K1007	Morton (1962)	2n=22, diploid
A. rotundifolius Pers.	Samos, Greece	LD, Runemark & Snogerup 19589	Bothmer (1970)	2n=36, tetraploid
A. rotundifolius Pers.	Samos, Greece	LD, Runemark & Snogerup 16944	Bothmer (1970)	2n=36, tetraploid
A. suaveolens (S. & S.) Don f.	Mt. Pangaion, Greece	C, Strid 844	Strid (1980)	2n=18
A. suaveolens (S. & S.) Don f.	Mt. Olympus, Greece	C, Strid 11028	Strid & Franzen (1983)	2n=18
Calamintha				
C. acinos (L.) Clairv.	See Acinos arvensis (Lam.) Dandy		Scheerer (1940) Majovsky et al. (1970) Markova (1974)	
C. alpina (L.) Lam.	See Acinos alpinus (L.) Moench		Reese (1953) Markova (1974) Majovsky (1974)	
C. ascendens Jord.	See Calamintha sylvatica ssp. ascendens		Strid (1971) Morton (1973) Löve & Löve (1981)	

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
C. clinopodium Benth.	See Clinopodium vulgare L.		Scheerer (1939) Mehra & Gill (1968) Majovsky (1970) Gill (1971) Vij & Kashyap (1976)	
C. exigua (S. & S.) Hal.	See Acinos rotundifolius Pers.		Bothmer (1970)	
C. glandulosa (Req.) Benth.	See Calamintha nepeta ssp. glandulosa		Papes & Silic (1981)	
C. grandiflora (L.) Moench	Valais, Switzerland	NEU, Wieffering s.n.	Wieffering (1969)	n=11
C. grandiflora (L.) Moench	Massif Central, France	Cult. Grignon	Favarger (1969)	2n=22
C. grandiflora (L.) Moench	Pirin Mt., Bulgaria	VIL, Markova MM-L50	Markova (1974)	2n=22
C. nepeta (L.) Savi	Malaga, Spain	LD, Kraft 44	Bjorkqvist, et al. (1969)	2n=24
C. nepeta (L.) Savi	Kruj, Albania	LD, Strid 0745	Strid (1971)	2n=40
C. nepeta (L.) Savi	Eynsham, England	Hb. Morton, Morton 4787	Morton (1973)	2n=48, tetraploid
C. nepeta (L.) Savi	Corfe Castle, England	Hb. Morton, Morton 4860	Morton (1973)	2n=72, hexaploid
C. nepeta (L.) Savi	Uludere, Bulgaria	VIL, Markova MM-L212	Markova (1974)	2n=18
C. nepeta (L.) Savi ssp. glandulosa (Req.) P.W.Ball	Petreto, Corsica	No details	Contandriopoulos (1964)	2n=20
C. nepeta (L.) Savi ssp. glandulosa (Req.) P.W.Ball	Pruhonice, Czechoslovakia	Pruhonice, Holub 1963	Holub, Mesicek & Javurkova (1970)	2n=24
C. nepeta (L.) Savi ssp. glandulosa (Req.) P.W.Ball	Pirin Mt., Bulgaria	VIL, Markova MM-L31	Markova (1974)	2n=20
C. nepeta (L.) Savi ssp. glandulosa (Req.) P.W.Ball	Petko Slaveikovo, Bulgaria	VIL, Markova MM-L52	Markova (1974)	2n=20
C. nepeta (L.) Savi ssp. glandulosa (Req.) P.W.Ball	Zivogosce, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=42
C. officinalis Moench	See Calamintha nepeta ssp. glandulosa		Holub, Mesicek & Javorka (1970) Markova (1974)	
C. sylvatica Bromf.	Mt. Szarvasko, Hungary	No details	Baksay (1958)	2n=24, diploid
C. sylvatica Bromf.	Isle of Wight, England	DHM, Morton 5087	Morton (1973)	2n=24, diploid
C. sylvatica Bromf. ssp. ascendens (Jord.) P.W.Ball	Mallorca, Balearic Is.	LD, Kraft JK-M 11; 12; 149	Strid (1971)	2n=48
C. sylvatica Bromf. ssp. ascendens (Jord.) P.W.Ball	Tytherington, England	Hb. Morton, Morton 4817	Morton (1973)	2n=48, tetraploid
C. sylvatica Bromf. ssp. ascendens (Jord.) P.W.Ball	Brixham, England	Hb. Morton, Morton 4869	Morton (1973)	2n=48, tetraploid

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
C. sylvatica Bromf. ssp. ascendens (Jord.) P.W.Ball	Barnstaple, England	DHM, Morton 5008	Morton (1973)	2n=48, tetraploid
C. sylvatica Bromf ssp. ascendens (Jord.) P.W.Ball	Toscano, Italy	COLO, Löve & Löve N720	Löve & Löve (1982)	2n=48
C. umbrosa (M. Bieb.) Fisch &	See Clinopodium umbrosum		Mehra & Gill (1968) Gill (1971) Saggoo & Bir (1981) Krishnappa & Indiramma (1982)	
Clinopodium				
C. integerrimum Boriss.	See Clinopodium vulgare ssp. vulgare		Chuksanova & Kaplanbekova (1971)	
C. laxiflorum (Hayata) Shimizu	Yushanchienhan, Taiwan	TAI, Hsu 3996	Hsu (1968)	2n=20
C. umbrosum (M. Bieb.). C. Koch	Nainital, India	PUN, Gill 7380	Mehra & Gill (1968) Gill (1971)	n=10
C. umbrosum (M. Bieb.) C. Koch	Mussoorie, India	PUN, Saggoo 23983	Saggoo & Bir (1981)	n=18
C. umbrosum (M. Bieb.) C. Koch	Pauri-Garhwal, India	PUN, Saggoo 24200	Saggoo & Bir (1981)	n=19
C. umbrosum (M. Bieb.) C. Koch	Karnataka, India	CCB, Indiramma & Krishnappa 330	Krishnappa & Indiramma (1982)	2n=38
C. vulgare L.	Moltenort-Laboe, Germany	KIEL	Scheerer (1939)	2n=20
C. vulgare L.	Lund, Sweden	LD	Löve & Löve (1944)	2n=20
C. vulgare L.	Kral, Czechoslovakia	SLO, Majovsky s.n.	Majovsky (1970)	2n=20
C. vulgare L.	Gulmarg, India	PUN, Gill 7477	Mehra & Gill (1968) Gill (1971)	n=10
C. vulgare L.	Backovo, Asenovgrad, Bulgaria	SOM, Ivanova MM-L30	Markova & Ivanova (1971) (also Markova & Ivanova, 1972)	2n=20
C. vulgare L.	Cirencester, England	Hb. Morton, Morton 4715	Morton (1973)	2n=20, diploid
C. vulgare L.	Durham, England	Hb. Morton, Morton s.n.	Morton (1973)	2n=20, diploid
C. vulgare L.	Mussoorie, India	PUN 3508	Vij & Kashyap (1976)	n=20, tetraploid
C. vulgare L.	S. do Gerez, Portugal	U 21424	Loon & de Jong (1978)	2n=20
C. vulgare L.	S. da Estrella, Portugal	U 21425	Loon & de Jong (1978)	2n=20
C. vulgare L.	Sheki, Azerbaidzhan, U.S.S.R.	L, Wieffering 18603	Kliphuis & Wieffering (1979)	2n=20
C. vulgare L.	Horning Mills, Ontario, Canada	WLU, Gill Can.166	Gill (1981)	n=10, diploid

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
C. vulgare L.	Mt. Stoletov, Bulgaria	U, Loon & Setten 25082	Loon & Setten (1982)	2n=20
C. vulgare L.	Gazibaba, Yugoslavia	Cult. Skopje	Sopova & Sekovski (1983)	2n=20
C. vulgare L.	Mt. Olympus, Greece	C, Strid et al. 12510	Strid & Franzen (1983)	2n=20
C. vulgare L. ssp. arundanum (Boiss.) Nym.	Euboea, Greece	LD, Runemark 11709	Bothmer (1967)	2n=20
C. vulgare L. ssp. arundanum (Boiss.) Nym.	Progradec, Albania	LD, Strid 0905	Strid (1971)	2n=20
C. vulgare L. ssp. arundanum (Boiss.) Nym.	Elbasan-Mysgete, Albania	LD, Strid 1101	Strid (1971)	2n=20
C. vulgare L. ssp. arundanum (Boiss.) Nym.	Athos, Greece	U 20484	Loon & Löve (1980)	2n=20
C. vulgare L. ssp. arundanum (Boiss.) Nym.	Kupres, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=20
C. vulgare L. ssp. arundanum (Boiss.) Nym.	Toscana, Italy	COLO, Löve & Löve N707	Löve & Löve (1982)	2n=20
C. vulgare L. ssp. orientale Bothmer	See Clinopodium vulgare ssp. arundanum		Bothmer (1967) Strid (1971)	
C. vulgare L. ssp. vulgare	Kara-Kalinskii, Turkmeniskai S.S.R.	ASH, Nikitina 458	Chuksanova & Kaplanbekova (1971)	2n=10
Diodeilis				
D. arkansana ((Nutt.) Doroszenko	Tobermory, Ont., Canada	WLU, Horton, MA 3696	Gill (1981)	n=10, diploid
Gardoquia				
G. incana Ruiz & Pav.	Tarma San Ramon, Peru	K, Palmer 73	Harley & Heywood (in press)	2n=46
G. tomentosa Kunth	Chimborazo, Ecuador	K, Hart 1637	Harley & Heywood (in press)	2n=48
Hesperothymus				
H. douglasii (Benth.) Doroszenko	Rockwood, Oregon, USA	WLU, Horton MA 3381	Gill (1981)	n=10, diploid
Micromeria				
M. benthamii Webb & Berth.	Mt. Costantino, Gran Canaria	O, cult. 66-1159	Borgen (1970)	2n=30
M. biflora (Buch.-Ham.) Benth.	Kilimanjaro, Tanzania	EA, K, S, UPS, Hedberg 1223	Hedberg (1957)	2n=30
M. biflora (Buch.-Ham.) Benth.	Nainital, India	PUN, Gill 7489	Mehra & Gill (1968) (also Gill, 1971)	n=15

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
M. biflora (Buch.-Ham.) Benth.	Pachmarhi, India	PUN	Bir & Saggoo (1981)	n=15, diploid
M. capitellata Benth.	Pachmarhi, India	PUN, Saggoo 20866	Saggoo & Bir (1981) Bir & Saggoo (1981)	n=25
M. cremnophila Boiss. & Heldr.	Kruj, Albania	LD, Strid 0743	Strid (1971)	2n=30
M. cremnophila Boiss. & Heldr.	E of Prenjas, Albania	LD, Strid 0803	Strid (1971)	2n=30
M. cristata (Hampe) Griseb.	Znepole, Bulgaria	VIL, Markova MM-L88	Markova (1974)	2n=30
M. dalmatica Benth.	Lovcen, Krstac, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=20
M. ericifolia (Roth.) Bornm.	See M. varia Benth.		Loon (1974)	
M. filiformis (Ait.) Benth.	Isla Dragonera, Balearic Is.	LD, MHF 302	Dahlgren, et al. (1971)	2n=30
M. filiformis (Ait.) Benth.	Eremita de Betlem Balearic Is.	LD, MHF 924	Dahlgren, et al. (1971)	2n=30, 60
M. filiformis (Ait.) Benth.	Eremita de Betlem Balearic Is.	LD, MHF 1004	Dahlgren, et al. (1971)	2n=30
M. filiformis (Ait.) Benth.	Mallorca, Balearic Is.	BC, BC 617271	Cardona & Contandriopoulos (1980)	n=15
M. graeca Benth.	Vejer de la Frontera, Spain	LD, Bjorkqvist Sp. 24	Bjorkqvist et al. (1969)	2n=20
M. graeca Benth. ssp. tenuifolia (Ten.) Nym.	No data	No data	Cenci (1968)	2n=60
M. helianthemifolia Webb & Berth.	Bco. Berriol, Gran Canaria	O, cult. 67-887	Borgen (1969)	2n=30, diploid
M. inodora (Desf.) Benth.	Ivice, Spain	BC, Cardona s.n.	Cardona (1973)	2n=26
M. inodora (Desf.) Benth.	Eivissa, Balearic Is.	BC & MARS, Cardona & Contandriopoulos 81-343	Cardona & Contandriopoulos (1983)	2n=48
M. juliana (L.) Benth.	Naxos, Greece	LD, Runemark & Snogerup 10625	Strid (1965)	2n=30
M. juliana (L.) Benth.	Amorgos, Greece	LD, Runemark & Snogerup 12238	Strid (1965)	2n=30
M. juliana (L.) Benth.	Arnissa, Greece	U 20308, Loon & Snelders s.n.	Loon & Snelders (1979)	2n=30
M. juliana (L.) Benth.	Ulcinj, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=30
M. juliana (L.) Benth.	Leptokarya, Greece	C, Strid 674-76-02	Strid (1981)	2n=30
M. juliana (L.) Benth.	Pontestazzemese, Italy	COLO, Löve & Löve N736	Löve & Löve (1982)	2n=30
M. myrtifolia Boiss. & Hohen.	Naxos, Greece	LD, Runemark & Snogerup 10611	Strid (1965)	2n=30

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
M. myrtifolia Boiss. & Hohen.	Naxos, Greece	LD, Runemark & Snogerup 9984	Strid (1965)	2n=30
M. myrtifolia Boiss. & Hohen.	Ikaria, Greece	LD, Runemark & Snogerup 1424	Strid (1965)	2n=30
M. myrtifolia Boiss. & Hohen.	Ikaria, Greece	LD, Runemark & Snogerup 12520	Strid (1965)	2n=30
M. myrtifolia Boiss. & Hohen.	Sitia, Crete	LD, Runemark & Snogerup 17548	Strid (1965)	2n=30
M. nervosa (Desf.) Benth.	Folegandros, Greece	LD, Runemark & Snogerup 14655	Strid (1965)	2n=30
M. nervosa (Desf.) Benth.	Kalamos, Anafi, Greece	LD, Runemark & Snogerup 14879	Strid (1965)	2n=30
M. nervosa (Desf.) Benth.	Naxos, Greece	LD, Runemark & Snogerup 4683	Strid (1965)	2n=30
M. nervosa (Desf.) Benth.	Sifnos, Greece	LD, Runemark & Snogerup 8797	Strid (1965)	2n=30
M. nervosa (Desf.) Benth.	Antimilos, Greece	LD, Runemark & Snogerup 8769	Strid (1965)	2n=30
M. nervosa (Desf.) Benth.	Amorgos, Greece	LD, Runemark & Snogerup 20273	Strid (1965)	2n=30
M. punctata R. Br. ex Benth.	Cameroon Mt., Cameroon	GC, Morton K522	Morton (1962)	2n=30, diploid
M. teneriffae (Poir.) Benth.	Bco. San Antonio, Teneriffe, Canary Is.	O, cult. 68-927	Borgen (1970)	2n=30
M. terebinthinacea W. & B.	See Micromeria teneriffae (Poir.) Benth.		Borgen (1970)	
M. thymifolia (Scop.) Fritsch	Orjen, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=20
M. tragothymus W. & B.	See Micromeria varia Benth.		Borgen (1970)	
M. varia Benth.	Bco. San Andres, Teneriffe, Canary Is.	O, cult. 67-1140	Borgen (1970)	2n=30
M. varia Benth.	Famara Mt., Lanzarote, Canary Is.	U, Loon 14064	Loon (1974)	2n=30

Brenaniella

B.robusta (Hook. f.) Doroszenko	Cameroon Mt., Cameroon	GC, Morton K525	Morton (1962)	2n=42, hexaploid

Satureja

S. acinos (L.) Scheele	See Acinos arvensis (Lam.) Dandy		Löve & Löve (1944) Gadella & Kliphuis (1966) Gill (1981)	
S. alpina L. var. granatensis Briq.	See Acinos alpinus ssp. meridionalis		Favarger & Kupfer (1968)	

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
S. biflora (Buch.-Ham.) Briq.	See Micromeria biflora (Buch.-Ham.) Benth.		Hedberg (1957)	
S. calamintha ssp. nepeta var. glandulosa	See Calamintha nepeta ssp. glandulosa		Contandriopoulos (1964)	
S. coerulea Janka	Sazlagjol, Bulgaria	SOM, L538	Markova (1983)	2n=30
S. douglasii (Benth.) Briq.	See Hesperothymus douglasii (Benth.) Doroszenko		Gill (1981)	
S. glabella (Michx.) Briq. var. angustifolia (Torr.) Svenson	See Diodeilis arkansana (Nutt.) Doroszenko		Gill (1981)	
S. hortensis L.	Seed from seedsmen Bjorklund, Helsinki	HHC, cult.	Vaarama (1949)	2n=45
S. hortensis L.	Cult. Bot. Gard. Kiel, Germany		Reese (1953)	2n=46-48
S. hortensis L.	Kiel, cult.	Hb. Mechelke, Germany	Mechelke (1954)	2n=48
S. hortensis L.	Dobra Voda, Czechoslovakia	SLO, Ferakova s.n.	Majovsky (1974)	2n=48
S. hortensis L.	Park Seed Co., North Carolina, USA	WLU, Gill Can. 334	Gill (1981)	n=24, tetraploid
S. horvatii Šilic	Orjen, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=30
S. kitaibelii Wierzb.	See Satureja montana ssp. kitaibelii		Borsos (1970)	
S. macedonica Form.	See S. montana L. ssp. montana		Strid (1981)	
S. montana L.	Seed from Bot. Gard. Basle, Switzerland	HHC, cult.	Vaarama (1949)	2n=30
S. montana L. ssp. illyrica Nyman	Gabrk, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=30
S. montana L. ssp. illyrica Nyman	Bilece Lake, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=30
S. montana L. ssp. kitaibelii (Wierzb.) P.W.Ball	Southern Roumania	BUC, cult.	Borsos (1970)	2n=12
S. montana L. ssp. kitaibelii (Wierzb.) P.W.Ball	Orjen, Yugoslavia	LJU 76896	Lovka, Susnik, Löve & Löve (1971)	2n=30
S. montana L. ssp. kitaibelii (Wierzb.) P.W.Ball	Predbalkan, Bulgaria	SOM, L607	Markova (1983)	2n=30
S. montana L. ssp. montana	Mt. Olympus, Greece	C, Strid 675-01-03	Strid (1981)	2n=30
S. montana L. ssp. montana	Biokovo, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=30
S. montana L. ssp. variegata (Host) P.W.Ball	Kras, Gabrk, Yugoslavia	SARA, Šilic s.n.	Papes & Šilic (1981)	2n=30
S. obovata Lag.	Sierra del Pozo, Spain	LIV, LD, N.0111	Love & Kjellqvist (1974)	2n=30

Species name	Place collected	Herbarium & Voucher	Reference	Chr. No.
S. pilosa Vel. var. pilosa	Taza, Bulgaria	SOM, L1321	Markova (1983)	2n=30
S. pilosa Vel. var. skorpilii (Vel.) Hayek	Momcilgrad, Bulgaria	SOM, L1322	Markova (1983)	2n=30
S. pseudosimensis Brenan	See Acinos pseudosimensis (Brenan) Doroszenko		Morton (1962)	
S. punctata (R.Br. ex Benth.) Briq.	See Micromeria puncata R. Br. ex Benth.		Morton (1962)	
S. robusta (Hook. f.) Brenan	See Brenaniella robusta (Hook. f.) Doroszenko		Morton (1962)	
S. silvatica (Broom.) Maly [sic]	See Calamintha sylvatica Broom.		Baksay (1958)	
S. subspicata Bartl. ex Vis. ssp. liburnica Šilic	See Satureja montana L. ssp. illyrica Nyman		Papes & Šilic (1981)	
S. subspicata Bartl. ex Vis. ssp. subspicata	See Satureja montana L. ssp. illyrica Nyman		Papes & Šilic (1981)	
S. thymbra L.	Anafi, Greece	LD, Runemark & Snogerup 14983	Bothmer (1970)	2n=30
S. vulgaris (L.) Fritsch	See Clinopodium vulgare L.		Löve & Löve (1944) Gill (1981)	
Xenopoma				
X. fasciculata (Benth.) Doroszenko	Ecuador	K, Hart 1707a	Harley & Heywood (in press)	2n=46

Chromosome Reports Bibliography

Baksay, L. (1958). Ann. Hist.-Nat. Mus. Nat. Hung. 50:123.
Bir, S. S. & Saggoo, M. I. (1981). J. Palynology 17:97.
Bjorkqvist, I., et al. (1969). Bot. Not. 122:274-275.
Borgen, L. (1969). Nytt. Mag. Bot. 16:97.
----- (1970). Nytt. Mag. Bot. 17:155.
Borsos, o. (1970). Acta Bot. Acad. Sci. Hung. 16:259.
Bothmer, R. von (1967). Bot. Not. 120:204.
----- (1970). Bot. Not. 123:52-59.
Cardona, M. A. (1973). Acta Phytotax. Barcinonensia 14:1-20.
----- & Contandriopoulos, J. (1980). Lagascalia 9:275-276.
----- & ----- (1983). Taxon 32:324.
Cenci, C. A. (1968). Ann. Fac. Ag. Univ. Perugia 23:1-7 [quoted in Webbia 34:347 (1979)].
Contandriopoulos, M. (1964). Rev. Gen. Bot. 71:374.
Dahlgren, R., et al. (1971). Bot. Not. 124:257.
Delay (1947). Rev. Cytol. Cytophysiol. Veg. 9:169-222.
Favarger, C. (1969). Neuchateloise des Sc. Nat. 92:18.
----- & Kupfer, P. (1968). Collect. Bot. 7:355.
Gadella, T. & Kliphuis, E. (1966). Proc. Roy. Neth. Acad. Sci. 69:550.
Gill. L. S. (1968). Caryologia 24:203-207.
Giordani, A., Miceli, P., & Monti, G. (1980). Inform. Bot. Ital. 12:329-330.
Hedberg, O. (1957). Symb. Bot. Upsal. 15:162.
Holub, J., Mesicek, J. & Javurkova, V. (1970). Folia Geobot. Phytotax. 5:346.
Hsu, C. (1968). Taiwania no. 14:18.
Kliphuis, E. & Wieffering, J. H. (1979). Taxon 28:399-400.
Krishnappa, D. G. & Indiramma, B. (1982). Taxon 31:361.
Loon, J. C. (1974). Acta Bot. Neerl. 23:117.
----- (1980). Taxon 29:719.
----- & de Jong, H. (1978). Taxon 27:59.
----- & Setten, A. K. (1982). Taxon 31:591.
----- & Snelders, H. C. M. (1979). Taxon 28:633.
Löve, A. & Kjellquist, E. (1974). Lagascalia 4(2):181.
Löve, A. & Löve, D. (1944). Ark. Bot. 31A(12):17-18.
----- & ----- (1982). Taxon 31:585-591.
Lovka, M., Susnik, F., Löve, A. & Löve, D. (1971). Taxon 20:791.
Majovsky, J. (1974). Acta Fac. Rerum. Nat. Univ. Comenianae 22:3.
Majovsky, J., et al. (1970). Acta Fac. Rerum. Nat. Univ. Comenianae 16:6.
----- (1974). Acta Fac. Rerum. Nat. Univ. Comenianae 23:18.
Markova, M. L. (1983). Taxon 32:510.
----- & Ivanova, P. (1972). Izv. Bot. Inst. (Sofia) 22:153-154.
----- & Nguen Thi Thu (1974). Taxon 23:194.
Mechelke, F. (1954). Die Kulturpflanzen 2:143-144.
Mehra, P. N. & Gill, L. S. (1971). Taxon 17:420-421.
Morton, J. K. (1962). J. Linn. Soc. Bot. 58:280.
----- (1973). Watsonia 9:240.
Papes, D. & Šilic, C. (1981). Taxon 30:70.
Reese, G. (1953). Ber. Deutsch. Bot. Ges. 64:70.
Saggoo, M. I. S. & Bir, S. S. (1981). Taxon 30:515.
Scheerer, H. (1939). Planta 29:639.
----- (1940). Planta 30:720.
Sopova, M. & Sekovski, Z. (1983). Ann. Fac. Biol. Univ. Skopje 35:145-160.
Strid, A. (1965). Bot. Not. 118:108-110.
----- (1971). Bot. Not. 124:274, 492-493.
----- (1980). Taxon 29:710.
----- (1981). Taxon 30:838.
----- & Franzen, R. (1983). Taxon 32:139.
----- & ----- (1983). Willdenowia 13:331.
Ubera, J. L. (1979). Lagascalia 9(1):123-124.
Vaarama, A. (1949). Arch. Soc. Zoo.-Bot. Fennicae, Vanamo 2:57.
Vij, S. P. & Kashyap, S. K. (1976). Cytologia (Japan) 41:714-715.
Wieffering, G. H. (1969). Taxon 18:442.

2.6. Gross Floral Morphology.

2.6.1. Corolla lips.

Throughout the Satureja s.l. complex the corolla is bilabiate with the upper lip emarginate or retuse, rarely entire, and the lower lip divided into three lobes, sometimes with the middle lobe divided into two lobules. The upper lip is most frequently slightly hooded or projecting straight out from the corolla tube. The lower lip is usually bent downwards; only rarely is it more or less straight. Of the 204 species for which accurate measurements of both upper and lower lips are available, 139 species have the lower lip longer than the upper, 42 species have more or less equal upper and lower lips, and only 23 species have the upper longer than the lower. It is interesting to note in which genera this latter condition occurs: six of the seven species of Brenaniella have the upper lip longer, only B. rungwensis has lips more or less equal in length; Gardoquia has its species more or less evenly divided amongst the three conditions; and Calamintha and Micromeria sect. Pseudomelissa also have a few species with the upper lip longer.

2.6.2. Corolla tube.

The corolla tube is always straight or curving slightly in one complete arc, i.e. never geniculate, widening gradually from the base. Very rarely the tube suddenly widens somewhere along its length, e.g. Gardoquia macrostema (see fig. 1A in McVaugh & Schmid, 1967). Rarely the tube hardly widens until near the throat, e.g. Satureja macrantha. The tube is never saccate or gibbous. Apart from Calamintha micrantha which has cleistogamous corollas, all the species are chasmogamous with a wide open throat.

The corolla tube is resupinate in all species of Cyclotrichium and also Micromeria cymuligera. This is easily seen by flattening a corolla and holding it up to the light. The veins cross over one another in a spiral fashion. Amongst the Labiatae, this type of resupination is shared with Ajuga orientalis L., Teucrium spinosum L., Teucrium resupinatum Desf., and species of Lophanthus Adans. and Hymenocrater Fisch. & Mey.

2.6.3. Corolla tube vasculature.

In fertile flowers there are always 9 vascular traces more or less equally spaced around the tube. Four of these traces enter the stamens, one for each stamen, and the other five are antipetalous. Even when the corolla is partially or completely sterile the 9 traces are present. I have only once seen vascular traces missing due to stamen sterility in a specimen of Micromeria cymuligera.

2.6.4. Stamens.

Fertile flowers have four stamens of which the anterior are always the longer though only marginally so in Cyclotrichium. If a flower is partially sterile it is always the posterior stamens which are reduced to staminodes. When the stamens are included in the corolla tube or are about equal to the upper lip in length they are held on the upper side of the tube or under the upper lip. The stamens are long exserted in all Cyclotrichium species and Satureja spicigera. The stamens are nearly always directly inserted into the corolla tube tissue. Rarely the base of the filament is adnate to the corolla tissue before complete insertion, e.g. in Micromeria nepalensis. The anthers have two thecae which are mostly divergent, with an angle never exceeding 180° between the two. The thecae are always parallel in Cyclotrichium and in a few species in other genera as well, e.g. Micromeria abyssinica. The anthers dehisce introrsely, i.e. the outer, anterior pair first (Knuth, 1899).

2.6.5. Style.

The length of the style relative to the position of the anthers is dependent on the age of the flower after anthesis. The style is usually shorter than the stamens initially with the stigmatic surfaces not receptive to pollen. Some time after anther dehiscence has begun the style grows out to usually exceed the anthers, sometimes very markedly so. The lower of the two stylar branches is frequently longer and/or broader.

2.6.6. Corolla hairs.

Every species has hairs on the inside of the tube which tend to point inwards especially those around the corolla throat. Cyclotrichium is unique in possessing a thick annulus of hairs toward the upper half of the tube. The majority of Gardoquia species and a few others are very densely hairy on the inside lower half of the corolla tube. This is associated with the protection of the ovary and nectaries and the conservation of nectar in bird and long-tongued insect pollinated flowers. The annulus of Cyclotrichium may also serve this function. The outside of the tube is usually sparsely hairy. The indumentum is always of simple hairs except in Cyclotrichium niveum which has dendritic hairs.

2.7 Pollination syndromes.

A pollination "syndrome" is so called because it is often noticed that certain combinations of floral features are commonly found associated with a specific pollinator. For example, red corollas and long corolla tubes tend to be found in bird pollinated flowers, and this can be called a bird pollination syndrome. The

Satureja complex is an excellent group to study such syndromes since there is great variation in floral structure and a wide range of known pollinators. The following is an account of how the different parts of the flower promote or otherwise modify pollination.

2.7.1. Corolla tube length and colour.

The corolla tube is an effective means of nectar concealment. It is reasonable to conclude that the length of the corolla tube modifies the kind of visitor to the flower since only those organisms with long enough tongues can fully benefit from a visit. However, a number of powerful insects, notably bees, can cut holes at the base of the corolla tube and consume the nectar "illegally". Since different organisms have different sensitivities to colour the colour of the corolla is also important.

The relationship between corolla tube length and colour is most clearly seen in the Americas, and here Gardoquia is an interesting case. Nearly all the species have very long, red corolla tubes. However, a few species have purple or white corollas, and these are all shorter tubed species. So there seems to be a correlation between tube colour and length. This correlation is further born out by Diodeilis. Seven of the eight species have purple corollas with tubes varying between 5.0 mm and 14.0 mm in length, and the only species with bright crimson flowers, D. coccinea, has a corolla tube 28.0–50.0 mm long.

There are very few confirmed, published records of the pollinators of American Satureja s.l. so species with long, red corolla tubes are usually only assumed to be bird pollinated. Grant & Grant (1968) list Montereya (Satureja) mimuloides as a plant with typical bird pollination features but they do not explicitly mention personal observations or cite literature records of birds visiting this plant. Moldenke (1977) notes that Gardoquia gilliesii, one of the short-tubed, purple-flowered species (see Moldenke's fig.1) is visited by solitary and semisocial bees and, in later opening flowers, by beeflies.

The Old World species are all relatively short tubed; practically all are under 12 mm in length. The predominant colours are white and purple. Published pollinator records show that there is a wide variety of insect visitors but are mainly longer-tongued bees, wasps and lepidoptera, rarely flies.

2.7.2. Flower alighting places.

Most insect visitors to flowers have to alight to partake of the nectar or the pollen. In the Labiatae it is mostly the lower corolla lip which fulfills the function of an alighting place. The length of the lower lip varies markedly in Satureja s.l., with the great majority of species having the lower lip longer than the upper. Obviously, as the flower gets smaller the advantage of a longer lower lip diminishes simply because it becomes more difficult for the insect to find the flower, but there may be a compensating aggregation of the flowers.

2.7.3 Guide marks.

Sprengel, in his classic work on pollination entitled Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen (1793), fully recognised the importance of guide marks, devoting a whole chapter to these marks; indeed he may have coined the term "nectar guide" ("Saftmaal" - literally "nectar mark"). His labiate examples of guide marks include Glechoma which has "white stripes which point the way to the nectar", and Ajuga pyrimidalis also has white lines. Two species of _Satureja_ s.l. are included: _Satureja hortensis_ L. has "the lower lip adorned with dark red spots ... which are the nectar guides", and _Thymus acinos_ L. (_Acinos arvensis_) also "has a nectar guide" (_Acinos arvensis_ has similar dark purple or white blotches on the lower corolla lip.)

2.7.4. _Corolla texture_.

It is difficult to judge accurately from dried specimens the texture of the flowers. However, as far as can be ascertained from rehydration and dissection of flowers, the corolla in nearly all Old World species and in all the smaller flowered species of the Americas is thin and rather delicate. Most of the longer-tubed _Gardoquia_ species seem somewhat tougher, especially toward the base of the tube where often a thick indumentum assists in strengthening the tube. Whilst dissecting _Diodeilis ashei_, which is probably a bee pollinated plant, the toughness of the corolla tube was very noticable.

2.7.5. _Corolla resupination_.

The resupination of the corolla in _Cyclotrichium_ and _Micromeria cymuligera_ has the effect of revolving the usual insect landing site, the lower corolla lip, to the normal position of the upper lip. One could suggest that this is a device to prevent insects landing on the corolla and to restrict pollination to hovering insects such as hawkmoths. However, the upper and lower corolla lips are very similar in length in most species. The hypothesis makes even less sense with _Micromeria cymuligera_; this species has very small-flowered, compact inflorescences which do not seem suited at all to pollination by hovering insects. It is possible that there has been a change of pollinator of these plants, rendering resupination of the corolla redundant as a specialised pollination device.

2.7.6 Zygomorphy

Zygomorphic flowers force pollinators to approach the flower one way, especially when the pollinator is about the same size as the flower. All species of Satureja s.l. have zygomorphic flowers. However, it tends to be true that insect pollinated flowers are more zygomorphic than bird pollinated flowers. The mainly bird-pollinated genus Gardoquia clearly shows a tendency away from differentiation of upper and lower corolla lips.

The study of van der Pijl (1972) showed the advantages of the bilabiate flower in Labiatae and other families. Coordination of various flower parts lead to improved precision of visits, more accurate deposition of pollen on pollinators, and better reception of pollen from the pollinator.

2.8. Gynodioecy

2.8.1. Genetic basis.

A gynodioecious species is one in which there are both hermaphrodite and male-sterile (female) plants in a population. This type of breeding system is particularly common in the Labiatae (Ross, 1978).

Male-sterile flowers occur frequently on hermaphrodite plants, even in gynodioecious species (Correns, 1904), but these are sporadic and clearly not under general genetic control. In other words, gynodioecious labiates are not, as far as I know, also consistently gynomonecious. In any case, male-sterile flowers of entirely male-sterile plants or as individuals on generally hermaphrodite plants have a similar morphological structure.

There are three main genetic bases for gynodioecy: recessive, dominant and cytoplasmic genetic control (Lewis, 1941; Lewis & Crowe, 1956; Lloyd, 1974). Male sterility is most usually a rare recessive mutant in higher plants (Lewis & Crowe, 1956) but this is not the case with gynodioecism. Monogenic recessive male sterility is unknown in gynodioecious species (Ross, 1978). In the Labiatae monogenic dominant gynodioecism has been reported in Salvia pratensis (Ross, 1978). Correns (1904), who was the first to suggest a genetic basis for gynodioecy, showed experimentally that cytoplasmic control was involved in Satureja hortensis L. He grew 897 plants and found 180 "gynomonoecious" (meaning hermaphrodite with sporadic female flowers) and hermaphrodite plants, and 717 female (male-sterile) plants; and a race sent to Correns by Haage & Schmidt had only 1 hermaphrodite plant out of 150. A similar preponderance of female plants was noted by Darwin (1877) in the same species. Correns therefore concluded that gynodioecy is governed by the female cytoplasm. He later showed (Correns, 1928) that both hermaphrodite and females bred true. Ross (1978) lists various other combinations of genetic control, including digenic control with a cytoplasmic effect in Origanum vulgare (see also Lewis & Crowe, 1956).

Lewis & Crowe (1956) showed that for both recessive and dominant genetic control, females would have to be twice as fertile as hermaphrodites to survive in the population, whereas if cytoplasmic control was involved then the females needed only a slight reproductive advantage to survive. In the latter case, equilibrium of females to hermaphrodites would be achieved when maximum utilisation of pollen is reached. Various authors have suggested mathematical models of how gynodioecy might arise, including Valdeyron, Dommée & Valdeyron (1973), Lloyd (1974 a, b), Charlesworth & Charlesworth (1978), Ross (1978) and Gregorius, Ross & Gillet (1982). The important factors they highlight in the development of gynodioecy included high levels of selfing, strong inbreeding depression, increased ovule production by females, high pollination rates, viability differences and overdominance, i.e. when heterozygotes have greater fitness than homozygotes.

Ross (1978) proposes two types of gynodioecy: stable and unstable. Stable gynodioecy, as found in many Labiatae, will not evolve to dioecy, whereas unstable gynodioecy might. This second possibility is discussed by Lloyd (1974 a), Charlesworth & Charlesworth (1978), Ross (1978; 1982) and Bawa (1980).

2.8.2. Morphological effects.

Since the information available is so extensive, the following account draws together selected literature reports of gynodioecy and anther sterility or dimorphism, and some of my own observations based upon boiled up corollas from herbarium specimens.

2.8.2.1. Satureja s.s.

A male-sterile specimen, identified provisionally as aff. S. macrantha (Lamond & Termé 4385), had pale mauve corollas only 5-7 mm long instead of the more usual dark mauve, 10-15 mm long corollas. The stamens were entirely absent, with only 5 vascular traces in the corolla tube rather than the usual 9. The flowers are also sessile in the axils of the floral leaves; usually the flowers are clearly pedunculate.

Semi-sterility, apparently of a sporadic nature, was seen in S. mutica. One of the thecae of the posterior stamen in Sintenis 947 had aborted entirely while in the other posterior stamen one theca was 0.6 mm long and the other only 0.3 mm long. The anterior anthers had 0.5 mm long thecae. A similar reduction in size of the posterior anther thecae was noted in S. intermedia (Wendelbo & Assadi 18508; posterior thecae 0.4 mm, anterior 0.6-0.7 mm). The semi-sterile stamens in another specimen of S. intermedia (Wendelbo & Assadi 18507) were white, while fertile stamens were purple.

The type specimen of S. bzybica has apparently fertile stamens but the thecae on each stamen are clearly dimorphic. One theca is about 0.7 mm long, and the other about 1.0 mm long.

2.8.2.2. Euhesperida

The flowers on the isotype of E. thymbrifolia are mostly female. Measurements of typical flowers are as follows: fertile corolla 9.4 mm long (sterile 3.8 mm); calyx (fertile flower) 2.8 mm long (sterile flower 2.0 mm); fertile stamens, 4.0 mm (posterior), 4.5 mm (anterior); sterile stamens, 0.3 mm (posterior and anterior).

2.8.2.3. *Micromeria*

Sporadic male-sterile flowers have been noted on mainly hermaphrodite plants in *M. marginata* (female corolla 10 mm, hermaphrodite 12-16 mm long), *M. taygetea* (female 4.5 mm, hermaphrodite c. 6 mm), *M. debilis* (female 2.4 mm, hermaphrodite 3.7 mm) and *densiflora*. Entirely female plants were noted in *M. congesta* (female corollas 2.5-3.0 mm, hermaphrodite 6 mm) and *M. hyssopifolia* (female flower calyx 5.0-5.7 mm, hermaphrodite flower calyx 4.0-4.5 mm) (for further details see Perez de Paz, 1978). In *M. debilis*, the stigma is longer and the stigmatic lobes much broader in female flowers than hermaphrodite flowers. Stamen dimorphism, mainly differences in dimensions, were noted in *M. elliptica* and *M. tenuis*.

Female flowers of *M. congesta* have slightly longer posterior stamens than the anterior. Since this is a key character of the Nepetoid genera, it may explain why Post (1888) originally placed a synonym of this species [*M. shepardii* (Post) Post] under *Nepeta*. McNeil 796 has entirely female flowers, all 2.5-3.0 mm long (fertile flowers c. 6 mm).

The posterior stamen anthers of the type specimen of *M. cymuligera* are much smaller than the anterior, and in the only other known specimen (Davis 45643) the posterior stamens, including the vascular traces, are entirely absent.

2.8.2.4. *Brenaniella*

Brenan (1951) reported that *B. masukuensis*, *B. wellmannii* and *B. myriantha* were gynodioecious, while only hermaphrodite flowers were known for *B. vernayana* and *B. cacondensis*. However, I have seen sporadic female flowers on a mainly female plant of *B. vernayana* (Wild 6193). Measurements for the sterile flower (fertile flower measurements in parenthesis) were: calyx 5.5 mm (6.5 mm); corolla 7.8 mm (9.5 mm); posterior stamen filaments 0.6 mm (3.0 mm); anterior stamen filaments 0.7 mm (4.0 mm); and style 7.0 mm (9.0 mm).

2.8.25. Killickia

In a note to L. E. Codd (Pretoria, S. Africa), Mr. I. C. Hedge (Edinburgh) reports that Hilliard & Burtt 7876 (K. compacta) and 8033 (K. pilosa) are male sterile. The former specimen had flowers with 5(-6) stamens instead of the usual 4, and although thecae were formed none produced pollen.

2.8.2.6. Discussion

Since partial or full sterility is common in Satureja s.l., it seems only a small step for a tetrandrous species to become genetically fixed in the diandrous state. In fact this has happened a number of times in Satureja s.l., with Acinos simensis from Africa, the three closely related species Calamintha gracilis, C. confinis and C. ussuriensis from the Far East, and the Mexican Gardoquia jaliscana. Diandry here must be of recent origin since there are closely related tetrandrous species (A. pseudosimensis, C. debilis and G. macrostema).

The diandrous American Hedeoma complex has many similarities to the generally tetrandrous Gardoquia and Acinos. Many Hedeoma s.s. have a gibbous calyx very similar to Acinos, and Hesperozygis marifolia has an uncanny similarity in habit to Gardoquia; also Irving (1972) related Poliomintha of the Hedeoma complex to Gardoquia. Irving (1980) noted that in Hedeoma the posterior staminodes are very variable in length, without or rarely with thecae (*H. pulegioides*). Therefore, a recent tetrandrous ancestry for *Hedeoma* seems probable.

Links between the Old and New World *Satureja* s.l. are, in my opinion, not at all close. For example, the similarities of the American *Montereya* and *Diodeilis* to the Mediterranean *Calamintha* and *Micromeria* are really superficial. However, the *Hedeoma* group seems to provide for this "missing link".

Chapter 3

Taxonomic Account

3.1. Generic key

1. Leaves conduplicate, at least in all small leaves, rarely only channelled in larger leaves 2

\+ Leaves flat or revolute 3

2. Leaves linear, elliptic or oblanceolate to spathulate (Old World) Satureja s.s.

\+ Leaves broadly ovate (South America) Gardoquia

3. Leaf with a more or less thickened marginal vein, entire 4

\+ Leaf without a thickened marginal vein, mostly crenulate to more or less toothed, rarely entire 5

4. Calyx tube sigmoid, slightly or strongly gibbous at base Acinos

\+ Calyx tube straight, not gibbous at base Micromeria

5. Calyx broadly obconical, actinomorphic; peduncles very long, (1.5–)5–22 mm; prostrate herbs (South Africa) Killickia

\+ Calyx tubular, zygomorphic or sometimes almost actinomorphic, but tube not broadly obconical; peduncles absent or short, up to 5 mm (occasionally longer); erect shrubs or herbs, rarely prostrate 6

6. Calyx sigmoid, gibbous at base and constricted near middle Acinos

\+ Calyx straight or curved, not gibbous at base or constricted near middle 7

7. Corolla resupinate 8

\+ Corolla not resupinate 9

8. Perennial; corolla annulate within; stamens long-exserted, anthers parallel Cyclotrichium

+ Annual; corolla not annulate; stamens just exserted from tube, anthers divergent *Micromeria cymuligera*

9. Plant entirely white-lanate, hairs all simple; leaves linear-oblong, not revolute; (calyx, though only 1.6-1.8 mm, clearly curved, 15-veined) *Euhesperida*

+ Plant not white lanate (except *Calamintha candidissima*, but hairs clearly dendroid); leaves various, if linear then margins revolute 10

10. Leaves elliptic to linear-oblong, entire, flat, glabrous, with numerous sunken punctate glands *Gontscharovia*

+ Leaves usually ovate and toothed, if linear then margins revolute, without numerous sunken glands, usually hairy 11

11. Inflorescence dense, spike-like, not interrupted or only shortly so at base; verticillasters sessile, multi-flowered; calyx lips straight, upper and lower ± equal in length; corolla white or purple 12

+ Inflorescence interrupted, not spike-like; verticillasters shortly pedunculate to sub-sessile, solitary to multi-flowered; upper calyx lip curving upward or both lips straight, equal or not; corolla red, yellow, white or purple 16

12. Leaves 7-47 mm long, flat 13

+ Leaves 2-9 mm long, margins revolute 15

13. Calyx tube curved; veins on lower side of leaf very prominent, white (South America) *Xenopoma*

+ Calyx tube straight; veins on lower side of leaf not white and prominent (African) 14

14. All calyx teeth similar, narrowly triangular or subulate; corolla white *Brenaniella*

\+ Upper calyx teeth broadly triangular, the lower narrowly triangular; corolla purple (*C. paradoxa*) *Calamintha*

15\. Inflorescence an ovoid, woolly head 2-3 cm long; leaves linear-lanceolate, 5-9 mm *Piloblephis*

\+ Inflorescence a narrow spike, not woolly, usually longer than 3 cm; leaves acicular-lanceolate, 2-4 mm, or orbicular-ovate, 3-6 mm *Xenopoma*

16\. Bracteoles longer than pedicel and peduncle, reaching at least to middle of calyx; calyx clearly curved *Clinopodium*

\+ Bracteoles, if present, shorter or as long as pedicel and peduncle, reaching only up to base of calyx; calyx straight or only slightly curved 17

17\. Plant entirely white-lanate with dendroid hairs (North Africa) (*C. candidissima*) *Calamintha*

\+ Plant not white-lanate, with simple or robust dendritic hairs, if any 18

18\. Leaf hairs robust dendritic; calyx tube 1.5-4.2 mm *Xenopoma*

\+ Leaf hairs, if any, simple; calyx tube 1.0-13.5 mm 19

19\. Leaves linear-oblong, so tightly revolute as to completely hide the lower side *Obtegomeria*

\+ Leaves not linear-oblong, flat or revolute but still with part of lower side visible 20

20\. Calyx 16-18 mm; corollas red, 34-50 mm; leaves camptodromous *Montereya*

\+ Calyx up to 14.5 mm; corollas red, yellow, purple or white, mostly less than 34 mm; leaves camptodromous or craspedromous 21

21. Prostrate sprawling or repent herbs, with long-petiolate (3-10 mm) leaves; flowers always solitary in axils of leaves, with long peduncles (3-5 mm) and pedicels (5-10 mm) <u>Hesperothymus</u>

\+ Erect or ascending shrubs or herbs, rarely prostrate, if so with shorter petioled leaves and flowers usually not solitary, with shorter peduncles and pedicels 22

22. Upper calyx lip curving upward and erect, truncate or upper teeth very short, up to 1/6 of the lower in length <u>Diodeilis</u>

\+ Upper calyx lobe straight, ± parallel with lower or if curving upward never erect, upper teeth [illegible] 1/5 or more the length of lower teeth 23

23. Leaves often with revolute margins; calyx tube curved, rarely straight; corolla 15-42 mm, red or yellow, rarely blue-purple, the lobes short, 1/16-1/4 the tube in length, upper and lower ± equal, tube strongly hairy in lower half (Central and South America) <u>Gardoquia</u>

\+ Leaves nearly always flat, rarely slightly revolute at margin; calyx tube straight, rarely curved; corolla purple or white, rarely red, mostly less than 15 mm, but if longer then lobes usually long, often more than 1/4 the tube, the lower c. 2 x the upper in length; tube not or a little hairy in the lower half (Widespread) 24

24. Leaves narrowly ovate or elliptic to linear-oblong, at least 3 x as long as broad, cuneate at base, entire or with very small acute teeth; lateral veins not visible or very narrow and faint 25

\+ Leaves ovate to orbicular, usually less than 3 x as long as broad, cuneate at base or not, entire, crenulate to dentate (small teeth being always rather rounded, not sharp); lateral veins usually quite strongly visible 28

25\. Calyx tube 3.5–4.0 mm; lower teeth as long as tube; leaves 3–6 cm *Gardoquia* sect. *Anomales*

\+ Calyx tube 1.0–3.5 mm; lower teeth much shorter than tube; leaves 1–3(–4.5) cm 26

26\. Leaves narrowly oval, usually rounded at apex, often somewhat revolute; calyx teeth all equal; corolla cream-yellow, 9.0–11.3 mm (*M. nepalensis*) *Micromeria* sect. *Pseudomelissa*

\+ Leaves usually ovate, acute or obtuse at apex, rarely rounded, not revolute; upper calyx teeth shorter than lower; corolla white or purple, 2.0–9.0 mm 27

27\. Calyx pedicels 3–10 mm; calyx tube 2.0–3.5 mm, throat with a dense fringe of hairs; teeth all very narrowly triangular *Diodeilis*

\+ Calyx pedicels 0–1.5 mm; calyx tube 1.0–2.5 mm, throat glabrous or with a sparse fringe of hairs; teeth all broadly triangular to lanceolate-subulate, rarely narrowly triangular *Xenopoma* sect. *Ceratominthe*

28\. Annual, 7–20 cm tall; leaves 8–20 mm, pedicels 2–10 mm 29

\+ Perennial, 3–200 cm tall; leaves various 30

29\. Leaves ovate to orbicular, lower side sparsely glandular-hispid; calyx tube c. 2 mm (*D. amissa*) *Diodeilis*

\+ Leaves narrowly ovate to obovate, lower side glabrous or rarely eglandular hairy; calyx tube 2.7–3.6 mm (*C. debilis*) *Calamintha*

30. Leaves elliptic-oblanceolate, 2-6 x 0.7-2.8 mm (_M. barosma_) _Micromeria_ sect. _Pseudomelissa_

\+ Leaves ovate-lanceolate to orbicular, usually larger than 6 x 2.8 mm 31

31. Upper calyx teeth 1/5-2/3 (rarely 3/4) the length of the lower teeth, sometimes curving upwards somewhat; tube broadly cylindrical; calyx (3-)4.5-14.5 mm _Calamintha_

\+ Upper calyx teeth 2/3 to as long as lower teeth, always ± straight and parallel with the lower teeth; tube narrowly cylindrical; calyx 1.9-4.5(-8.2) mm 32

32. Prostrate or sometimes erect shrubs, sometimes prostrate herbs; leaves 2-14 mm, numerous on stems, broadly ovate to orbicular; flowers 1-3(-6) in a leaf axil; calyx teeth short, never more than 1.3 mm (Central & South America) _Xenopoma_

\+ Erect shrubs or herbs, rarely prostrate shrubs; leaves (5-)10-35 mm, rather few on stems, ovate-elliptic to lanceolate, rarely orbicular; flowers (1-4-)5-40 in axil of a leaf; calyx teeth often longer than 1.3 mm (Old World) _Micromeria_ sect. _Pseudomelissa_

3.2. The Satureioid genera

The Satureioid genera include Satureja L. s.s., Gontscharovia ~~Popov~~ Boiss and Euhesperida Brullo & Furnari. The single species of Saccocalyx Coss. is similar in fascies to Satureja s.s., but is usually not considered to belong to Satureja s.l. on account of its inflating calices and channelled leaves. These diferences do not seem sufficient to exclude Saccocalyx from the Satureja complex, since both Gontscharovia and Euhesperida have channelled leaves and also have differences in calyx structure, though not so marked. Nevertheless, Saccocalyx has been omitted from this taxonomic account until its affinities are more clearly determined. To provide additional information for these studies Saccocalyx has been included in the investigation on leaf anatomy (see Chapter 2). It was shown that Saccocalyx has a very similar leaf anatomy to the Satureioid genera.

The three genera in this group may be distinguished by their campanulate, 10-13-nerved bilabiate calyx (sometimes the calyx is distinctly bilabiate, e.g. S. mutica, S. boissieri, S. macrantha, S. macrosiphonia), and conduplicate or channelled, usually narrowly oblanceolate, elliptic or linear leaves with isolateral palisade parenchyma. The marked differences in leaf structure between the suprageneric groups of Satureja s.l. are discussed fully in Chapter 2.

The Satureioid genera are closest in affinity to the Micromerioid genera (Micromeria, Killickia, Brenaniella), with the clearest similarities in floral structure. Species now in Satureja s.s. and Micromeria Benth. sect. Micromeria were included in one genus by Linnaeus (1753) in his treatment of Satureja. However, other than Briquet (1896) who combined Satureja s.s. and Micromeria sect. *Micromeria* in *Satureja* sect. *Sabbatia* Briq., no major author since the beginning of the nineteenth century has so closely linked *Satureja* and *Micromeria*. But even Briquet arranged the species within sect. *Sabbatia* Briq. so that the species belonging to *Satureja* s.s. are all listed before those of *Micromeria* sect. *Micromeria*. The two genera are easily distinguished by the characters described above.

3.3. *Satureja* L., Sp. Pl. 567 (1753).

Syn: *S.* sect. *Tragoriganum* Benth., Lab. Gen. Sp. 354 (1834); *S.* sect. *Annuae* Boiss., Fl. Or. 4:... (1879); *S.* sect. *Subbilabiatae* Boiss., Fl. Or. 4:... (1879); *S.* sect. *Sabbatia* Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:298 (1896), p.p.

Low shrubs, suffruticose herbs, or annuals, with a thick tap root branching just below, at or just above ground level; stems erect or ascending, rarely prostrate, simple or branched, glandular-punctate. Leaves narrowly oblanceolate, spathulate, obovate, elliptic, or linear, rarely lanceolate, usually cuneate below, entire or rarely minutely toothed, subsessile, conduplicate at least when young; veins camptodromous, lateral veins usually scarcely visible, margins rarely with cilia; hairs, if any, simple, eglandular; both sides densely sunken punctate glandular; palisade mesophyll isolateral. Verticillasters with flowers subsessile or in lax cymes, solitary or with up to c. 20 flowers; floral leaves sometimes much reduced; bracteoles small, elliptic, oblanceolate, or leaf-like. Calyx bilabiate, with 3 upper teeth clearly shorter than the lower two, rarely ± actinomorphic with equal teeth; all teeth most often of similar shape, usually narrowly triangular, ciliate or not; tube slightly or clearly ampliate, never gibbous at base, 10-13-veined, sutural veins sometimes obscure; throat usually with a sparse fringe of hairs, sometimes glabrous; glabrous inside below the throat. Corolla 5-15 mm long, 2-lipped, usually white, sometimes purple or mauve; tube straight, not annulate inside; glabrous inside in lower half of tube, very rarely with a few sparse hairs; lips (1/5-)1/3-1/2 x tube length. Stamens 4, inserted half-way up tube; filaments convergent, included or shortly, rarely longly, exserted from corolla; anthers divergent. Style shortly exserted from corolla; stigma lobes mostly equal, sometimes unequal, always narrowly subulate.

Type species: S. montana L.

Gen. distrib.: Mediterranean region, SE Asia, Near East; S. hortensis is widely cultivated.

Nomenclaturally incorrect variants in spelling of Satureja L. include: Satureia Miller, Gard. Dict. 4th. abridged ed. (1754); and Saturegia Leers, Fl. Herborn. 135 (1775).

The original Linnaean genus (Linnaeus, 1753) included not only Satureja s.s. but also species now placed in Micromeria sect. Micromeria, Pycnanthemum, Thymus and Cunila. Species belonging to these last three genera were gradually removed in the following editions of Species Plantarum and Systema Vegetabilum; and finally Bentham (1834) separated Satureja s.s. from Micromeria. It has already been discussed how Satureja s.s. may be clearly distinguished from Micromeria (see "Satureioid genera").

Satureja was not divided into subgeneric groups until Bentham's Labiatarum (1834). He described three sections: Sect. Tragoriganum for the single species S. thymbra; Sect. Pycnothymus for the American S. rigida [Piloblephis rigida]; and Sect. Satureia [sic] for the remainder of the genus. Boissier (1879) further divided the genus into 5 sections as follows: Sect. *Annuae* for the annual *S. hortensis*; the mainly Mediterranean Sect. *Eusatureiae* for *S. montana*, *S. parnassica*, *S. spinosa*, *S. cuneifolia* and *S. intermedia*, which are suffrutescent with regular calices [the first 4 species belong to the *montana* complex described by Ball (1970)]; Sect. *Subbilabiatae* for *S. boissieri*, *S. subdentata*, *S. mutica*, *S. spicigera*, *S. macrantha*, *S. longiflora* and *S. atropatana* which are suffrutescent with sub-bilabiate calices and are from a region bounded by E Turkey, Iraq, Iran and S USSR; Sect. *Zataroideae* for *S. bachtiarica*, a suffruticose Iranian species with 5 very prominent calyx sutural veins (actually 13-veined); and Sect. *Tragoriganum* for *S. thymbra*, a suffruticose species with a regular calyx, but particularly distinguished by the numerous, relatively large bracteoles surrounding the calices. *Satureja* sensu Briquet (1896) has an arrangement of species rather similar to that of Boissier (1879). Briquet recognised Sect. *Tragoriganum* for *S. thymbra*, and the rest of the species were included in Sect. *Sabbatia* (species *hortensis* to *bachtiarica* inclusive). An informal group (A) is described for *S. hortensis* within Sect. *Sabbatia*, and the remainder (group B) first lists the *montana* complex, then the Iranian/Iraqi/Turkish/USSR group, then the very distinct *S. inodora* from Morocco and S Spain, and finally *S. bachtiarica*.

The present arrangement is quite similar to that of both Boissier and Briquet. However, I do not believe the recognition of sections is justified. Boissier's sections were based mainly on calyx structure, particularly the extent of bilabiation. Other than *S. thymbra*, all *Satureja* species are more or less bilabiate, and it is impossible to draw a satisfactory line between what is "regular" and what is "bilabiate" in Boissier's sense. Reference to the Data

Tables for *Satureja* in the Appendix confirms this. Nevertheless, based on habit, vegetative and floral characters Boissier's groups are recognisable though without definite boundaries. I have therefore arranged the species into an order similar to that of Boissier and Briquet. There is something to be said for distinguishing *S. thymbra* from the rest of the genus because of its unusual verticillaster arrangement. However, to do so would bring in a certain inconsistency within the genus. Recognition of Sect. *Tragoriganum* would imply that the rest of the genus forms a close-knit, relatively invariable group; this, of course, is not true. The informal groupings recognised here are as follows:

A) species 1-11 which includes the *montana* complex and related species;

and B) species 12-25 which includes the group centred around Iran, Iraq and Turkey;

The remaining species *S. coerulea*, *S. thymbra*, *S. salzmannii* and *S. hortensis* are all distinct and could be put on their own in separate groups. However, *S. coerulea* and *S. hortensis* have affinities with group (A).

3.3.1. Satureja

1. Annual; with one widely branched stem 29. *hortensis*

\+ Perennial herbs or shrubs 2

2. Bracteoles numerous, ovate acuminate, long ciliate on margin; verticillasters subglobose 27. *thymbra*

\+ Bracteoles inconspicuous, linear-lanceolate, not ciliate; verticillasters never globose 3

3. Stamens long-exserted; inflorescence secund 25. *spicigera*

\+ Stamens included or only shortly exserted; inflorescence usually not secund 4

4. Calyx teeth obtuse; dwarf shrubs with linear-spathulate glabrous leaves (except for ciliate margin) 28. *salzmannii*

\+ Calyx teeth usually acute or acuminate; dwarf shrubs or erect herbs; leaves various, usually hairy 5

5. Leaves linear-oblong to lanceolate, glabrous except for ciliate margin; calyx teeth glabrous, as long as tube; flowers violet-blue 26. *coerulea*

\+ Not as above 6

6. Leaves narrowly to broadly elliptic or linear; flowers violet or mauve 7

\+ Leaves narrowly to broadly oblanceolate or spathulate; flowers most often white (sometimes mauve) 10

7. Corolla up to 2 x calyx, tube widely flared; calyx teeth sub-equal or calyx sub-bilabiate 8

\+ Corolla 2-5 x calyx, tube very narrow; calyx distinctly bilabiate 9

8. Leaves broadly elliptic, slightly toothed 22. *bzybica*

\+ Leaves narrowly linear-elliptic, entire 23. *aintabensis*

Satureja

9. Hairs on outside of calyx long; calyx teeth all very narrowly triangular 21. *macrantha*

\+ Hairs on outside of calyx minute; upper calyx teeth mostly lanceolate-subulate, lower teeth narrowly triangular to deltoid 17. *edmondii*

10. Leaves spathulate, very obscurely toothed; flowers purple 20. *intermedia*

\+ Leaves narrowly oblanceolate to broadly obovate, entire; flowers white (occasionally very faint purple) 11

11. Dwarf shrub with spiny branches 11. *spinosa*

\+ Dwarf shrubs or herbs with espinose branches 12

12. Dwarf shrubs, the leafy part 5–15 cm; verticillasters approximate 13

\+ Erect or accending suffruticose herbs, usually 20–60 cm; verticillasters ± distant 20

13. Stem hairs mostly more than 1.2 mm; stems ± erect 14

\+ Stems with few or no hairs more than 0.2 mm; stems ± procumbent 17

14. Calyx 4.2–5.0 mm (corolla 8–12 mm) 8. *pilosa*

\+ Calyx 3.0–4.0 mm 15

15. Suffruticose herb with simple stems; corolla 6–10 mm; lateral vein of leaf clearly visible beneath 5. *wiedemanniana*

\+ Small much-branched shrubs; corolla 6–7 mm; lateral veins of leaf inconspicuous 16

16. Calyx teeth half as long as tube; leaves sparsely glandular 7. *athoa*

\+ Calyx teeth at least 3/4 x tube; leaves densely glandular 6. *parnassica*

Satureja

17. Calyx 5-6 mm, upper teeth half as long as lower; lower teeth setaceous — 19. rumelica

\+ Calyx 3-4 mm, upper teeth 2/3-3/4 x lower teeth; lower teeth broader — 18

18. All leaves ± equal in length; lateral veins clearly visible, minutely hairy above and below; calyx minutely and densely hispidulous — 18. isophylla

\+ Leaves becoming smaller toward top of plant; lateral veins invisible, long-haired above and below; calyx sparsely pubescent — 19

19. Floral leaves 1 1/2-4 x calyces; corolla 8-9 mm — 10. amani

\+ Floral leaves as long as calyces; corolla 5-7 mm — 9. icarica

20. Floral leaves 10-20 mm, exceeding verticillasters; verticillasters usually crowded (very variable) — 1. montana

\+ Floral leaves 3-10(-11) mm, shorter than or about equalling verticillasters; verticillasters usually distant — 21

21. Verticillasters sessile or sub-sessile (peduncles less than 1.5 mm) — 22

\+ Verticillasters (at least lower ones) distinctly pedunculate (longer than 1.5 mm) — 25

22. Leaves obovate, spathulate, obtuse, 4-10 mm (Spain) — 3. obovata

\+ Leaves oblanceolate, acute, 4-20 mm — 23

23. Calyx sparsely punctate-glandular, glands usually yellow; teeth sub-equal — 2. cuneifolia

\+ Calyx densely punctate-glandular, glands red; upper teeth half as long as lower teeth — 24

24. Leaves 4-9 mm, mostly less than 1.5 mm broad 14. bachtiarica

\+ Leaves 8-15 mm, most leaves more than 2 mm broad 15. sahendica

25. Calyx teeth equal or slightly unequal; calyx 2.5-4 mm 26

\+ Calyx teeth very unequal, the upper three c. 1/2 as long as lower 2; calyx 4-6 mm 27

26. Stems glabrous; calyx with few obsolescent hairs 24. azerbaijanica

\+ Stems minutely puberulent; calyx clearly hairy 4. cilicica

27. Calyx tube 1-2 mm, lower teeth 0.9-1.7 mm, not ciliate 16. metastasiantha

\+ Calyx tube 2.0-2.4 mm, lower teeth 2-3 mm, ciliate 28

28. Leaves glabrous; verticillasters mostly 6-flowered; corolla c. 7 mm 12. mutica

\+ Leaves scabridulous; verticillsters (2-)6-17-flowered; corolla c. 9 mm 13. boissieri

3.3.2. 1. S. montana L., Sp. Pl. 568 (1753).

Syn: Thymus montanus (L.) Dum.-Cours., Bot. Cult. ed.2, 3:32 (1811), non Crantz (1769); Satureja hyssopifolia Bert., Ann. Stor. Nat. 3:406 (1829); Micromeria montana (L.) Reichenb., Fl. Germ. Exc. 311 (1831); Satureja ciliata Avé-Lall. in Ind. Sem. Hort. Petrop. 11 Suppl., 66 (1846); Saturiastrum montanum (L.) Fourr. in Ann. Soc. Linn. Lyon n.s. 17:133 (1869); Saturiastrum petraeum (Jord. & Fourr.) Fourr., loc. cit. (1869); Clinopodium montanum (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja dolzii Sennen in Bol. Soc. Iber. Cienc. Nat. 1933, 32:64 (1934), nomen.

Satureja

Ball (1972) concisely describes the *S. montana* group. He tabulates the characters which distinguish the 5 subspecies of *S. montana*, which are the same subspecies recognised in the present revision. A number of local variants, especially from the Balkans, have been seen which do not fit well into Ball's scheme, but lack of material frustrates proper assessment of these forms. Ball also realised that other variants could have been described at subspecific rank, but he declined to describe them because the species' variation was not fully known to him. The subspecies recognised are rather broadly circumscribed, and intermediate specimens are common. Nevertheless, this scheme is a useful and practical compromise between attempting to deal with every local form and not giving recognition to any variants.

1.	Stem puberulent on all four sides of stem	2
+	Stem glabrous, or hairy on 2 sides only, alternating up stem	3
2.	Calyx (3.5-)4-7 mm; verticillasters dense, peduncles and pedicels less than 5 mm	(a) ssp. *montana*
+	Calyx 2-4(-4.5) mm; verticillasters lax, at least lower pedicels and peduncles more than 5 mm	(b) ssp. *variegata*
3.	Maximum leaf width 5-10 mm	(d) ssp. *kitaibelii*
+	Maximum leaf width 1.5-4.5 mm	4
4.	Calyx 3.5-4.0 mm, verticillasters ± distant; corolla 6-8 mm	(e) ssp. *taurica*
+	Calyx 4-9 mm; verticillasters crowded; corolla (6-)8-15 mm	(c) ssp. *illyrica*

(a) ssp. montana

Syn: Satureja brevis Jord. & Fourr., Brev. Pl. Nov. 1:44 (1866); S. flexuosa Jord. & Fourr., loc. cit. 45 (1866); S. petraea Jord. & Fourr., loc. cit. 45 (1866); S. provincialis Jord. & Fourr., loc. cit. 45 (1866); S. rigidula Jord. & Fourr., loc. cit. 46 (1866); S. pyrenaica Jord. & Fourr., Brev. Pl. Nov. 2:89 (1868); S. x karstiana Justin in Mitt. Mus. Krain 17:182 (1904); S. ovalifolia Huter, Porta, & Rigo in Oest. Bot. Zeitschr. 57:402 (1907); S. pollinonis Huter, Porta, & Rigo, loc. cit. (1907).

Ic: Hegi, Fl. Mittel-Eur. 5, 4:2285, f.3191 (1927).

Fl. 7-10. Stony places, calcareous rocks, stony turf, dry rock crevices in gravelly clay, 55-2500 m.

Type: Described from Hetruria, Narbona (Hb. Linn. 723/5, microfiche!).

Gen. distrib.: Austria, S France, N Spain, N Greece, mostly W and N Italy, N Yugoslavia.

Specimens from Greece often have features characteristic of other species in the montana complex. Archibald 441 has the stature and sparsely hispid leaf surfaces of S. pilosa but has the short stem indumentum, long calyx teeth, and short (2-4 mm) peduncles typical of S. montana ssp. montana.

(b) ssp. variegata (Host) P.W. Ball in Bot. J. Linn. Soc. 65:352 (1972).

Syn: Satureja variegata Host, Fl. Austr. 2:134 (1832); Micromeria variegata (Host) Reichenb., Fl. Germ. Exc. 859 (1832).

Ic: Reichenb., Ic. Fl. Germ. 18: t.1273 (1857).

Fl. 7-11. Rocky places, calcareous rocks, road side, s.l.-1525 m.

Type: Described from Croatia; specimen unknown.

Gen. distrib.: N Italy, Yugoslavia.

Feoli & Poldini (1979) have made a detailed study of S. montana in Italy and Yugoslavia and established the distinctness of ssp. variegata from ssp. montana.

(c) ssp. illyrica (Host) Nyman, Consp. 591 (1881).

Syn: Satureja illyrica Host, Fl. Austr. 2:133 (1831); S. subspicata Bartl. ex Vis., Stirp. Dalm. 11 (1826); S. pygmaea Sieb. ex Vis., loc. cit. (1826) (K!); Micromeria pygmaea (Sieb. ex Vis.) Reichenb., Fl. Germ. Exc. 311 (1831); S. montana L. var. subspicata (Bartl. ex Vis.) Vis., Fl. Dalm. 2:194 (1847); S. macedonica Form. in Verh. Naturf. Ver. Brünn 37:186 (1899).

Ic: Reichenb., Ic. Fl. Germ. 18: t.1273 (1857).

Fl. 7-10. Rocky places, calcareous rocks, 200-1525 m.

Syntypes: Dalmatia, Petter 329; Sieber 1812; Fiume, Reichenbach Fl. Germ. Exs. 741; Trieste, Schultz Herb. Norm. Pl. Gall. et Germ. 540.

Gen. distrib.: N Italy, Austria, Yugoslavia, Bulgaria.

(d) ssp. kitaibelii (Wierz.) P.W. Ball in Bot. J. Linn. Soc. 65:352 (1972).

Syn: Satureja kitaibelii Wierz. ex Heuffel in Verh. Zool.-Bot. Ges. Wien 8:177 (1858); S. montana L. var. blavii Ascherson, Reisen in Bosnien (1877); S. montana L. var. kitaibelii (Wierz.) Briq., Lab. Alp. Mar. 400 (1895); S. subspicata Vis. var. blavii (Ascherson) Maly in Herb. Norm. no. 4930.

Ic: Savulescu, Fl. Rep. Pop. Romine 8: t.48, f.2 (1961).

Fl. 8-11. Rocky places, calcareous rocks, pasture, 50-365 m.

Type: In rupestribus montanis ad Szaszka et in toto Danubii tractu. Aug.-Sept., Wierzbicki (holo. W, iso. K!).

Gen. distrib.: Yugoslavia, Hungary, Roumania.

Briquet (1896) and Ball & Getliffe (1972) contradict each other on the description of ssp. kitaibelii (var. kitaibelii in Briquet). Ball & Getliffe describe it as having stems puberulent on 2 sides only or glabrous, the leaves mostly 4-7 mm wide, whereas Briquet in the key says "stems covered in a short fine pubescence, the adult leaves 1-3 x 0.2-0.3 cm". Heuffel (1858) in the original description of S. kitaibelii says "lower leaves obovate-cuneiform, broadly lanceolate", which would agree with Ball & Getliffe. Briquet's description is based on Wierzbicki, in Reichenbach Fl. Germ. Exs. no. 2545 (unfortunately not at E or B). This specimen is probably not, therefore, ssp. kitaibelii.

(e) ssp. taurica (Velen.) P. W. Ball in Bot. J. Linn. Soc. 65:352 (1972).

Syn: Satureja taurica Velen. in Sitz.-Ber. Böhm. Ges. Wiss. 1903, 28:9 (1904).

Fl. 9. Rocky places, chalk slopes, c. 300 m.

Type: [Crimea]: in calcareis ad Simferopol, Kaspar (holo. in Prague?).

Gen. distrib.: Crimea.

This subspecies is on the periphery of the species' range.

3.3.3. 2. S. cuneifolia Ten., Fl. Nap. 1, Prodr. 33 (1811).

Syn: Micromeria spicata Vis. ex Reichenb., Fl. Germ. Exc. 311

(1831); Satureja hirta Host, Fl. Austr. 2:134 (1831); S. virgata Vis. ex Benth., Lab. Gen. Sp. 353 (1834) (K!); S. spicata Vis., Fl. Dalm. 2:195 (1847), nomen ex herb. Pl. Sicc., non Garsault (1764), non Crantz (1766); S. hyssopifolia Duffour in Bull. Soc. Bot. Fr. 7:428 (1860) (K!), non Bert. (1829), non Briq. (1898); S. intricata Lange in Vid. Meddel. Dansk Naturh. Foren. Kjøbenhavn 1881:96 (1882); S. pisidica Wettst. in Sitz.-Ber. Akad. Wiss. Wien 98:374, t.3, f.13-15 (1889) (W!); S. olympica Hal. in Oest. Bot. Zeitschr. 40:40 (1890), nomen; Clinopodium cuneifolium (Ten.) O.Kuntze, Rev. Gen. Pl. 2:515 (1891); S. valentina Tourn., in herb. Tourn. no. 1354, nom. nud.

Ic: Ten., Fl. Nap., Atlas 4: t.155 (1811-38); Fiori & Paol., Ic. Fl. Ital. 375 (1902).

Fl. 7-9. Dry calcareous rocks, limestone banks, schistose slopes, rocky slopes, cliffs, 170-2100 m.

Type: Described from the vicinity of Naples (holo. NAP).

Gen. distrib.: Italy, Greece, Lebanon, Spain, Turkey, Yugoslavia, Albania.

The length of the leaf is distinctly greater in the eastern part of the range than in Europe. However, the length of the calyx is clearly greater in Europe than in oriental parts. Details of these differences and a discussion on the separation of this species from S. obovata Lag. is given after the taxonomic account of Satureja on page 206.

S. intricata Lange, considered as possibly a high altitude ecotype of S. obovata by Ball & Getliffe (1972), is more likely a form of S. cuneifolia. Three specimens identified by their collectors as S. intricata (Huter 1000; Boissier viii 1837, 2 specimens) have the oblanceolate leaf shape, acute leaf apex, and the calyx with very few, small, yellow, punctate glands that are characteristic of S. cuneifolia. Ball & Getliffe say that S. intricata has ciliate leaf margins like S. montana, however none of the specimens cited above have such cilia.

3.3.4. 3. S. obovata Lag., Gen. Sp. Nov. 18 (1816).

Syn: Satureja cuneifolia Ten. var. obovata (Lag.) Boiss., Voy. Bot. Esp. 2:495 (1839-45); S. hieronymi Sennen in Bol. Soc. Iber. Cienc. Nat. 1933, 32:63 (1934) (E!).

Ic: Willcomm, Ill. Fl. Hispan. Balear. 2: t.128, f. A (1889); Pau in Mem. Mus. Cienc. Nat. Barcelona 1(1):62 (1922).

Fl. 7-10. Sandy, rocky slopes above sea, steep rocky places in mountains, s.l.-?.

Type: Venit ad saxorum calcareorum rimas in australiori Hispania. Orcelitani et Murcitani appellant. Valentinis. (holo. ?).

Gen. distrib.: SE Spain.

Closely related to S. cuneifolia, but distinguished by its usually smaller, broadly obovate-spathulate leaves, relatively shorter calyx teeth, and distinctly glandular-punctate calyx tube. Further details are presented after the account of Satureja.

3.3.5. 4. S. cilicica P. H. Davis in Notes R.B.G. Edinb. 38:51 (1980).

Syn: Satureja cuneifolia Ten. var. tenuis Boiss., Fl. Or. 4:564 (1879) (E!).

Fl. 7-8. Rocky and grassy slopes, scree, limestone slopes, 1470-2150 m.

Type: Turkey C5 Nigde: valley W of Maden running S towards peak of

Bolkar Dag, 30 vii 1969, J. Darrah 335 (holo. E!).

Gen. distrib.: S Turkey.

Similar to S. cuneifolia but with a more slender habit, laxer verticillasters, and smaller, distinctly bilabiate calices with broader upper teeth.

3.3.6. 5. S. wiedemanniana (Lallem.) Vel. in Sitz. Böhm. Ges. Wiss. 29:24 (1894).

Syn: Satureja cuneifolia Ten. var. wiedemanniana Lallem., Ind. Sem. Hort. Petrop. 11, Suppl. 64 (1845).

Fl. 7-8. Limestone crevices, calcareous rocks and stony places, 400-1750 m.

Syntypes: In Natolia monte pus Mahmudagh et Kiskischdagh (K!), prope Kaisareh, ann. 1835, Wiedemann.

Gen. distrib.: N & SW Turkey.

Similar to S. cuneifolia but lower in stature, the whole plant densely white patent-pubescent, and the verticillasters much more compact with the floral leaves clearly exceeding the corollas.

3.3.7. 6. S. parnassica Heldr. & Sart. ex Boiss., Fl. Or. 4:563 (1879).

Syn: Satureja spinosa L. var. stygia Orph., Fl. Graec. Exs. no. 622; S. parnassica var. stygia (Orph.) Hal., Consp. Fl. Graec. 2:552 (1902); S. parnassica Heldr. & Sart. ex Boiss. ssp. sipylea P. H. Davis in Notes R.B.G. Edinb. 38:52 (1980) (E!).

Fl. 7-10. Crevices of calcareous rocks, 400-1950 m.

Syntypes: Greece: In monte Parnassi, rupibus, 7000 ped., vii 1848, Heldreich. (E!); in rupibus regionis mediae montis Parnassi (Karkaria), 4500 ped., 24 viii 1856, Heldreich 80 (Satureja spinosa var. parnassica Heldr. & Sart., nomen in schaed., E!).

Turkey: Partie superieure du Mont Sipyle, au-dessus de Magnesie, dans les feutes des rochers, 16 viii 1854, B. Balansa 309 (ssp. sipylea, holo. E!).

Gen. distrib.: Greece, W Turkey.

Ssp. sipylea is distinguished by its more erect divaricately branched habit, and narrower cuneate more pointed leaves. However, in view of the scanty material available for study, and the variability of the specimens, subspecific rank does not seem to be justified.

Davis 1004 is a rather anomalous specimen. It is nearest to S. parnassica but is rather sparsely hairy (tending toward S. montana), only sparsely yellow punctate-glandular (aff. S. athoa), has corollas up to 10 mm (as in S. pilosa), and rather prominent lateral veins on the leaves (similar to S. wiedemanniana). However, features characteristic of S. parnassica include: calyx c. 4 mm, the lower teeth as long as the tube, lower leaves spathulate, apex obtuse. Its collection locality (near the monastry of Megaspelieon, Peloponesus) corresponds to that of S. parnassica.

3.3.8. 7. S. athoa K. Maly in Glasn. Muz. Bosni Herzeg. 22:690 (1910).

Syn: Satureja approximata Friv. in Flora 14:438 (1836), non Biv. (1816); S. spinosa Heldr. ex Nym., Consp. 591 (1881).

Type: Described from Athos, Greece.

Distinguished from S. parnassica, to which it is very similar, by its sparsely glandular leaves and calyx teeth half as long as the calyx tube. I have not yet seen a specimen of this species but from its description it may only be a form of S. parnassica.

3.3.9. 8. S. pilosa Velen. in Sitz.-Ber. Bohm. Ges. Wiss. 40:6 (1899).

Syn: Satureja parnassica Heldr. & Sart. ex Boiss. var. macrophylla Hal. in Verh. Zool.-Bot. Ges. Wien 49:191 (1899).

Fl. 8. Rocky places, 900-1800 m.

Type: [Bulgaria]: in rupestribus m. Elensky Balkan et supra Karlovo, Urumov (holo. in Prague?).

Gen. distrib.: Balkans, N Italy.

This species is closest to S. parnassica. It is distinguished by its sparsely hispid pubescence, greater height (to 23 cm), obovate-oblanceolate leaves with acute to sub-obtuse apices twice as long (to 21 mm), and larger calices and corollas.

3.3.10. 9. S. icarica P. H. Davis in Notes R.B.G. Edinb. 38:51 (1980).

Syn: Satureja hellenica Heldr. ex Hal. in Verh. Zool.-Bot. Ges. Wien 49:192 (1899), nomen; Satureja montana L. var. hellenica Heldr. ex Hal., Consp. Fl. Graeca 2:551 (1902).

Fl. 6-8. On hard schists in open heath, cliffs, 100-1040 m.

Type: Greece: Ikaria, Mt. Atheras, 900-1040 m, hard schists, in open heath, 12 vii 1958, Runemark & Snogerup 12460 (holo. LD!).

Gen. distrib.: Greece (Ikaria, Euboea).

S. icarica was thought to be only a variety of S. montana, to which it is certainly closely related. It merits specific rank on account of its low cushion-forming habit, small oblanceolate, patently scabrid-pubescent leaves with mucronate apices, very short inflorescence with verticillasters of solitary, sessile flowers, with the floral leaves not exceeding the flowers, and smaller calices and corollas.

Satureja

3.3.11. 10. *S. amani* P. H. Davis in Notes R.B.G. Edinb. 38:50 (1980).

Type: Turkey C6 Adana: Kusliji Dagh (Kislici Da.), 1520–1980 m, viii 1908, *Haradjian* 2507 (holo. E!).

Gen. distrib.: S Turkey.

A local species belonging to the *montana* complex identified by its low habit, narrow, mucronate leaves, dense inflorescence of sessile, 2-flowered verticillasters, with floral leaves 1.5–4 x the flowers, and small calices with the lower teeth as long as the tube.

3.3.12. 11. *S. spinosa* L., Cent. Pl. 2:19 (1756).

Syn: *Satureja spinosa* L. var. *glabra* Barbey & Major, Samos 54 (1891).

Ic: Sibth. & Sm., Fl. Graeca 6: t.541 (1827).

Fl. 5–10. Exposed limestone rocks, crevices, and screes, 650–2200 m.

Type: Described from Crete (*Hb. Linn.*).

Gen. distrib.: Crete, E Aegaean islands, W Turkey.

Easily identified by the spinose branches.

3.3.13. 12. *S. mutica* Fisch. & Mey., Ind. Sem. Hort. Petrop. 2:49 (1836).

Syn: *Satureja intermedia* sensu Benth. p.p., in DC., Prodr. 12:210 (1848).

Ic: Rech. f., Fl. Iranica 150: t. 393 (1982).

Fl. 7–8. Rocky and stony places, limestone mountain slopes, c. 1830 m.

Type: [USSR]: in altioribus montibus Talusch, *C.A. Meyer* (holo. G-BOISS, iso. LE, photo!).

Gen. distrib.: N Iran, S USSR (Caucasus).

This is the first of fourteen species belonging to a group centred around Iran and Iraq, which includes most of the species of Sect. Subbilabiatae Boiss. (1879). Of these 14 species S. mutica, S. boissieri, S. bachtiarica, S. sahendica, S. metastasiantha and S. edmondii (nos. 12-17) have a similarly tall, slender, virgate or erect-ascending habit. Most have widely spaced, at least below, few-flowered verticillasters.

3.3.14. 13. S. boissieri Hausskn. ex Boiss., Fl. Or. 4:565 (1879).

Ic: Rech. f., Fl. Iranica 150: t.559 (1982).

Fl. 7-9. Crevices of limestone cliffs, rocky volcanic slopes, Quercus scrub, 1100-1480 m.

Type: [Turkey]: in monte Akdagh Cataonia inter Malatya et Adiaman, 13 ix 1865, Haussknecht (holo. G!).

Gen. distrib.: N Iran, E Turkey.

This species is very closely related to S. mutica, but is distinguished by the scabridulous leaves, verticillasters with more flowers, and longer corollas.

3.3.15. 14. S. bachtiarica Bunge in Mem. Acad. Scienc. Petersb. ser. 7, 21:37 (1873).

Ic: Rech. f., Fl. Iranica 150: t.397 (1982).

Fl. (5-)7-11. Limestone cliffs, rocky places, 1700-2740 m.

Type: [Iran] in Persiae australis districtus Bachtiarici montosis supra Abergun, Haussknecht (lecto. G-BOISS, W).

Gen. distrib.: Iran.

The species is unusual in its dense verticillasters, distinct below, confluent above, and the calyx with 5 prominent veins. The calyx is actually 13-veined (all Satureja s.s. are 10-13-veined), but the 5 intercostal veins are strongly developed. The prominence of these veins is similar to that of Euhesperida thymbrifolia (Hedge & Feinbrun) A. Doroszenko (S. thymbrifolia). However, E. thymbrifolia has flat or channelled, linear-oblong, uninervate leaves, actinomorphic, slightly curved, 15-nerved (though only 5 strongly developed) calices with similar upper and lower teeth, while S. bachtiarica has oblanceolate, conduplicate leaves with visible lateral veins, and straight calices with much broader upper teeth, half as long as the lower teeth.

3.3.16. 15. S. sahendica Bornm. in Verh. Zool.-Bot. Ges. Wien 60:160 (1910).

Ic: Rech. f., Fl. Iranica 150: t.396 (1982).

Fl. 7-9. Stony places, [1850-2600 m].

Type: Persia: Isperechan, in declivibus borealibus montis Sahend, 30 vii 1884, Knapp (holo. WU).

Gen. distrib.: Iran.

Closest to S. bachtiarica but distinguished by the generally longer leaves, distant though similarly crowded verticillasters, longer calyx tube and teeth, and longer corollas.

3.3.17. 16. S. metastasiantha Rech. f., Fl. Iranica 150:497 (1982).

Ic: Rech. f., Fl. Iranica 150: t.390 (1982).

Fl. 8-10. Calcareous rocky slopes, crevices of cliffs, 1220-3200 m.

Type: Iraq: distr. Erbil, montes Qandil ad confines Persiae, in saxosis calc. supra lacum Goam-e Kirmosoran, c. 3200 m, 1 viii 1957, K. H. Rechinger 11142 (holo. W, iso. E!).

Gen. distrib.: Iraq.

Similar to S. boissieri (no. 13) but distinguished by the dense, white, patent pubescence, the minutely puberulent calyx tube only half as long, glabrous in the throat, and much shorter calyx teeth.

3.3.18. 17. S. edmondii Briq. in Ann. Cons. Jard. Bot. Genéve 2:186 (1898).

Syn: Satureja longiflora Boiss. & Hausskn. ex Boiss., Fl. Or. 4:566 (1879), non Presl (1826); Satureja boissieri Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:298 (1897).

Ic: Rech. f., Fl. Iranica 150: t. 395 (1982).

Fl. 8-9. Rocky places, c. 1500 m.

Type: Iran: in rup. in Parrow supra Kermanschah, 1525 m, 6 ix 1867, Haussknecht (holo. G-BOISS, iso. K!, W).

Gen. distrib.: Iran.

3.3.19. 18. S. isophylla Rech. f. in Pl. Syst. Evol. 133:107 (1979).

Ic: Rech. f., Fl. Iranica 150: t.392 (1982).

Fl. 9-10, 1000-2000 m.

Type: N Persia, Prov. Mazanderan, Firuzabad in ditione fl. Chalus, 1000-2000 m, 12-16 x 1956, F. Schmid 6676 (holo. G, iso. W).

Gen. distrib.: Iran.

Close to S. intermedia (no. 20) but distinguished by the low-growing, multi-branched habit, numerous conferted narrowly oblanceolate leaves, all of similar size, and the few-flowered, condensed verticillasters.

3.3.20. 19. S. rumelica Velen., Fl. Bulg. 466 (1891).

Type: [Bulgaria]: in rupestribus calidis prope Philippopolin et Belova, ann. 1890, Stribrny. (holo ?).

Gen. distrib.: SC Bulgaria.

No specimens have been seen of this species. The markedly bilabiate calyx (e. descr.) with the lower setaceous calyx teeth as long as the calyx tube, with the upper teeth only half as long, is diagnostic for the species. Such bilabiate calices are similar to many of the Near East group of species. However, on vegetative characters and geographic distribution, S. rumelica may be better placed with the montana complex.

3.3.21. 20. S. intermedia C.A. Mey., Verz. Pfl. Cauc. 91 (1831).

Syn: Satureja subdentata Boiss., Fl. Or. 4:565 (1879); Clinopodium intermedium (C.A. Mey.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); S. gunibica Woronow, Acta Inst. Bot. Acad. Sc. URSS ser. 1, 1:222 (1933).

Ic: Schischkin (ed.), Fl. URSS 21: t.22, f.1 (1954); Rech. f., Fl. Iranica 150: t.391 (1982).

Fl. 7. Rocky slopes, 1900-2400 m.

Type: Talysch, pr. Swant, C.A. Meyer 775 (holo. LE, photo!).

Gen. distrib.: Iran, S USSR (Caucasus).

Easily distinguished by the spathulate, minutely serrulate leaves, condensed inflorescence, and verticillasters with solitary, subsessile flowers in the floral leaf axils.

3.3.22. 21. S. macrantha C.A. Meyer in Ind. Sem. Hort. Petrop. 11, Suppl. 67 (1845).

Syn: Satureja macrosiphonia Bornm. in Fedde, Repert. Sp. Nov. Beih. 6:114 (1908); Satureja macrantha C.A. Meyer var. macrosiphonia (Bornm.) Blakelock in Kew Bull. 1949:548 (1950).

Ic: Rech. f., Fl. Iranica 150: t.394 (1982).

Fl. 7-10. Limestone cliff ledges and crevices, clay stony soil, 680-2600 m.

Syntypes: [Iran]: in provincia Karabagh prope Schuscha, Hohenacker;

et prope loca Ghierus, Akartschai et Pachlutschinari, Szovits (holo. LE, photo.!, iso. G).

Gen. distrib.: Iraq, Iran, USSR (Armenia).

Closest to S. aintabensis and S. azerbaijanica which share the slender stemmed habit and narrowly linear-elliptic leaves. All of the other species of the Near East group, except S. bzybica, tend to have oblanceolate or spathulate leaves. S. macrantha is easily distinguished by the long, narrowly tubular corollas, 2-5 x as long as the markedly bilabiate calyx, and short upper and lower lips. The inflorescence is lax, with long pedicels and peduncles. The floral leaves are distinctly shorter than the flowers.

3.3.23. 22. S. bzybica Woron. in Trud. Bot. Inst. AN SSSR 1:222 (1933).

Fl. 10. Calcareous rocks.

Type: [USSR]: Abchazia. Fauces fl. Zhove-kvara prope Gagry, in detriticis calcareis, 20 x 1915, A. Grossheim (holo. LE, iso. K!).

Gen. distrib.: USSR, southern Caspian Sea area.

Related to S. azerbaijanica but distinguished by the broadly elliptic, serrulate leaves, the inflorescence rather less dense with more flowers in each verticillaster, the calyx teeth clearly longer than the calyx tube, and longer corollas.

3.3.24. 23. S. aintabensis P. H. Davis in Notes R.B.G. Edinb. 38:50 (1980).

Fl. 6. Dry calcareous places, c. 600 m.

Type: Turkey C6 Gaziantep: in apricis calcareis circa Aintab, 610 m, 25 vi 1865, Haussknecht (holo. W!), as Micromeria velutina.

Gen. distrib.: S Turkey (C6).

This distinct, low-growing, shortly and densely patent-pubescent species is only known from two specimens, the Type and another rather scrappy specimen (Kotschy 409). It probably comes closest to S. macrantha.

3.3.25. 24. S. azerbaijanica A. Doroszenko, nom. nov.

Syn: Satureja confinis Boriss. in Not. Syst. (Leningrad) 15:325 (1953), non Kudo in Mem. Fac. Sci. Ag. Taihoku Imp. Univ. 2(2):100 (1929).

Fl. 5. In rocky places, c. 1500 m.

Type: [USSR]: Caucasus, Talysch, distr. Lenkoran prope opp. Dyman, 20 v 1898, fl., B. Levandovsky (holo. LE, photo.!).

Gen. distrib.: USSR (Caucasus).

This species has been confused with S. montana ssp. taurica from the Crimea which also has glabrous stems and leaves of similar size. However, S. azerbaijanica has much more elliptic leaves, deeply punctate glandular on both sides, longer pedunculate verticillasters, the calyx teeth only half as long as the calyx tube (not as long as the tube) and the corolla tube much narrower and less ampliate. In these respects S. azerbaijanica is much closer to S. macrantha than to S. montana.

3.3.26. 25. S. spicigera (C. Koch) Boiss., Fl. Or. 4:566 (1879).

Syn: Micromeria spicigera C. Koch in Linnaea 17:295 (1843), non (C. Koch) Walp. (1852); Micromeria alternipilosa C. Koch in Linnaea 19:25 (1846); Satureja intermedia C. A. Meyer var. laxior Benth. in DC., Prodr. 12:210 (1848); Satureja alternipilosa (C. Koch) C. Koch in Linnaea 21:668 (1849); Satureja diffusa Benth. ex Boiss., Fl. Or. 4:566 (1879), nomen; Clinoodium alternipilosum (C. Koch) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Clinopodium spicigerum (C. Koch) O. Kuntze, Rev. Gen. Pl. 2:516 (1891).

Ic: Schischkin (ed.), Fl. URSS 21: t.22, f.3 (1954).

Fl. 7-9(-11). Dry rock ledges, banks, screes, 25-1500 m.

Type: [USSR?]: in Radscha, Ruprecht (holo. G-BOISS).

Gen. distrib.: Turkey, USSR (Caucasus).

The species is unusual in its spike-like, secund inflorescence, and corolla with long-exserted stamens. It is related to the Near East group of species (nos. 12-25).

3.3.27. 26. S. coerulea Janka ex Velen., Fl. Bulg. 465 (1891).

Syn: Satureja coerulea Janka ex Kanitz, Pl. Roumania 2(2):94 (1880), nomen; S. skorpilii Velen., Sitz. Bohm. Ges. Wiss. 1899:6 (1899)?

Fl. 7-10. Dry calcareous rocks, stony places, c. 60 m.

Syntypes: [Bulgaria]: Razgrad, Velenovsky; Trnova, Velenovsky; m. Balkan, Janka; m. Trojan-Balkan, Skorpil; Sliven, Aitos, Camdere, Kotel, Skorpil; m. Rhodope ad Bela Cerkva, Lukas.

Gen. distrib.: Bulgaria, W Turkey.

Shrublets with linear-lanceolate leaves, glabrous except for the ciliate margin, 2-4-flowered sub-sessile verticillasters, small actinomorphic calices, and small violet-blue corollas. It probably comes closest to the montana complex.

3.3.28. 27. S. thymbra L., Sp. Pl. 567 (1753).

Syn: Thymus tragoriganum L., Mant. 1:84 (1767); S. collina Salisb., Prod. Stirp. Hort. Chapel Allerton Vig. 77 (1796), nomen; Thymus hirsutissimus Poir., Encycl. Meth. 7:650a (1806); Thymbra hirsuta Pers., Syn. Pl. 2:114 (1807); Thymbra hirsutissima Vent. ex Pers., Syn. Pl. 2:114 (1807); S. tragoriganum (L.) Tausch, Syll. Pl. Ratisb. 2:248 (1828); Micromeria thymbra (L.) Kostel., Allg. Med.-Pharm. Fl. 3:763 (1834); Clinopodium thymbra (L.) O. Kuntze, Rev. Gen. Pl. 2:516 (1891); S. biroi Jav. in Magyar Bot. Lap. 1922, 21:25 (1923); *S. thymbra* L. var. *hirsutissima* Rech. f., Denkschr. Akad. Wiss. Math.-Nat. Wien 105:121 (1943).

Ic: Sibth. & Sm., Fl. Graeca 6: t.541 (1827); Reichenb., Ic. Fl. Germ. 18: t.270 (1857); Feinbrun, Fl. Palaestina 3: t.243 (1977).

Fl. 3-9. Calcareous rocks, scree, cliffs, rocky places by the sea, stony waste ground, macchie, phrygana, s.l.-760 m.

Type: Described from Crete (*Hb. Linn*. 723/2, microfiche!).

Gen. distrib.: Greece, Crete, Turkey, Israel, Lebanon, Syria, Libya, Algeria.

A common plant of the east Mediterranean. The species has been placed in its own section (*Tragoriganum* Benth.) on account of the dense, globose verticillasters, with numerous conspicuous oblong-lanceolate bracteoles hiding most of the actinomorphic calices. Apart from the bracteoles there is nothing particularly unusual about these features, so I do not believe recognising a section for this species is necessary.

3.3.29. 28. *S. salzmannii* (O. Kuntze) A. Doroszenko, comb. nov.

Syn: *Satureja inodora* Salzmann ex Benth., Lab. Gen. Sp. 354 (1834), non Host (1831); *S. glomerata* Schousb. ex Ball, J. Linn. Soc. 16:613 (1878), nomen; *Clinopodium salzmannii* O. Kuntze, Rev. Gen. Pl. 2:515 (1891); *Satureja salzmannii* P. W. Ball in Bot. J. Linn. Soc. 65:356 (1972), nom. nov. superfl.

Ic: Rouy, Illustr. Pl. Eur. Rar. 9: t.219 (1898), as *S. inodora* Salzm.

Fl. 6-8. Stony slopes, c. 200 m.

Type: Morocco: Tanger, ann. 1825, *Salzmann* (holo. K!, iso. E!).

Gen. distrib.: Morocco, S Spain.

Some comment is required on the correct citation for this species. When Ball (1972) published *S. salzmannii* P. W. Ball as a new name for S. inodora Salzmann ex Benth. (1834), it appears that he was not aware of Clinopodium salzmannii O. Kuntze. Kuntze took a very broad view of the Satureioid group of genera similar in concept to Briquet's (1896) but considered Clinopodium to have nomenclatural priority. He therefore made numerous new combinations, transferring species of Satureja s.s., Micromeria, etc. into Clinopodium. In doing this S. inodora Salzmann ex Benth. (1834) required a new name because of the clash with Micromeria inodora (Desf.) Benth. (1834) [based on Thymus inodorus Desf. (1798)]. S. inodora Host (1831) had been made a synonym of Micromeria parviflora (Vis.) Reichenb. in 1832 [basionym S. parviflora Vis. (1829)] which became Clinopodium parviflorum (Vis.) O. Kuntze in Kuntze (1891). Both C. salzmannii O. Kuntze and S. salzmannii P. W. Ball are based on the same species and the same type, although the name change was for different reasons. If Kuntze had chosen an epithet other than "salzmannii", a new combination using Kuntze's epithet would have to be made in Satureja since Ball's name is superfluous. Although both Ball and Kuntze chose the name "salzmannii", Ball does not refer to Kuntze as the source of the name. Therefore, Ball's use of the epithet as a nomen novum is illegal. This however does not invalidate the nomen novum of Kuntze. Therefore it was necessary to make a new combination here.

3.3.30. 29. S. hortensis L., Sp. Pl. 568 (1753).

Syn: S. officinarum Crantz, Inst. Rei Herb. 1:526 (1766); S. brachiata Stokes, Bot. Mat. Med. 3:300 (1812); S. pachyphylla C. Koch in Linnaea 17:295 (1843); S. laxiflora C. Koch in Linnaea 21:668 (1848); S. hortensis L. var. includens Schur, Enum. Pl. Transs. 531 (1866); S. hortensis L. var. exserens Schur, loc. cit. (1866); S. filicaulis Schott ex Boiss., Fl. Or. 4:562 (1879), nomen; *S. hortensis* L. var. *grandiflora* Boiss., Fl. Or. 4:562 (1879); *Clinopodium hortense* (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); *C. pachyphyllum* (C. Koch) O. Kuntze, loc. cit. 515 (1891); *S. litwinowii* Schmalh. ex Lipsky, Fl. Kavk. 108 (1899); *Thymus cunila* E. H. L. Krause in Sturm, Fl. Deutschland, ed. 2, 11:172 (1903); *Calamintha hortensis* (L.) Hort. ex F. T. Hubbard in L. H. Bailey, Standard Cycl. Hort. 3082 (1917), nomen; *S. hortensis* L. var. *speciosa* Nab., Iter Turc.-Pers. 3:44 (1926); *S. hortensis* L. var. *laxiflora* (C. Koch) Grossh., Fl. Kavk. 3:327 (1932); *S. hortensis* L. var. *depauperata* Thieb., Fl. Libano-Syrienne 3:49 (1953); *S. altaica* Boriss., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 15:326 (1953); *S. densiflora* Zeinal., Izv. Akad. Nauk Azerbaid. SSR (Ser. Biol.) 1969:15 (1969), nom. nud.

Ic: Reichenb., Ic. Fl. Germ. 18: t. 1272 (1857); Fiori & Paol., Ic. Fl. Ital. 375 (1902).

Type: Described from S France and Italy (*Hb. Linn.* 723/9, microfiche!)

Gen. distrib.: France, Italy, Spain, Switzerland, Turkey, Albania, Yugoslavia, Greece, USSR; widely introduced.

The only annual species in the genus. It is very variable which accounts for the many synonyms cited above. The species is cultivated, particularly in the USSR, for its essential oils and as a culinary herb.

3.3.31. *Addendum*

The following names were omitted from the synonymy of the above *Satureja* s.s. species. The number following the = is the species number in the text.

S. cuneata Reichenb., Ic. Fl. Germ. 18: t.1272 (1856-58) = 2

S. fasciculata Tausch, Syll. Pl. Ratisb. 2:248 (1828) = 2?

S. horvatii Silic, Glasnik Zemal. Muz. Bosne Herceg. 13:108 (1975) = 8?

S. innota Pau, Sennen Pl. d'Espagne no. 627 (1908), in schaed. = 2

S. montana L. ssp. cuneifolia (Ten.) Bolos & Vigo, Coll. Bot. 14:94 (1983) = 2

S. montana L. ssp. obovata (Lag.) Bolos & Vigo, Coll. Bot. 14:94 (1983) = 3

S. montana L. ssp. pisidica (Wettst.) Šilic, Glasnik Zemal. Muz. Bosne Herceg. 13:108 (1974) = 2

S. montana L. var. prostrata Boiss., Voy. Bot. Esp. 2:495 (1839-45) = 3

S. mucronifolia Stokes, Bot. Mat. Med. 3:300 (1812) = 1

S. nevadensis Huter, Porta & Rigo, in schaed. (1879)! = 2

S. subspicata Bartl. ex Vis. ssp. liburnica Šilic, Glasnik Zemal. Muz. Bosne Herceg. 13:110 (1974) = 1 (c)

S. tenuis Form., Verh. Naturf. Ver. Brunn 37:185 (1899) = 1 (c)?

S. trifida Moench., Meth. Pl. 386 (1794) = 1

3.3.32. Nomina dubia

S. x amoena Sunderm., Allg. Bot. Zeitschr. 12:92 (1906).

S. amplifoliata Pau, Cavanillesia 3:77 (1930), nomen.

S. arganietorum Emberger, Bull. Soc. Sc. Nat. Maroc 15:182 (1935).

S. atropatana Bunge, Mem. Acad. Imp. Sc. Petersb. ser. 7, 21:36 (1873).

S. bellardi Colla, Herb. Pedem. 4:421 (1835).

S. bianoris Sennen, Bul. Soc. Iber. Cienc. Nat. 1933, 32:54 (1934), nomen.

S. borissovae Zeinal., Izv. Akad. Nauk Azerb. SSR (Ser. Biol.) 1969:14 (1969), nom. nud.

S. campanella Ehrenb., Naturg. Reise Nord-Afrika 13 (1828).

S. filiformis Ces Pas. & Gibelli, Comp. Fl. Ital. 2:302 (1886).

S. hispida Ehrh., Beitr. Naturk. 7:147 (1792).

S. monantha Font Quer, Mem. Acad. Cienc. Barcelona ser. 3, 25 (14):15 (1936).

S. nemorosa Tardent, Ess. Hist. Nat. Bessarab. 54 (1841), nomen.

S. olla Ehrenb., Naturg. Reise 13 (1828).

S. scabra (Presl) Presl, Fl. Sic. 36 (1826), nomen; basionym Thymus scaber Presl.

S. secondaireana Sennen, Bol. Soc. Iber. Cienc. Nat. 1933, 32:54 (1934), nomen.

3.3.33. Nomina rejecienda

S. americana Poir. in Lam., Encycl. 6:571 (1804) = Hyptis americana (Poir.) Briq. fide Epling in Rev. Mus. La Plata 7 (1949).

S. argaea (Boiss. & Bal.) Fisch. & Mey., Ann. Sc. Nat. ser. 4, 1:33 (1854) = Thymus serpyllum L.

S. bonariensis (Fisch. & Mey.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:300 (1896) = Hedeoma multiflorum Benth. fide Irving (1980).

S. camphorata Bornm., Mitt. Thur. Bot. Ver. 30:80 t.1, f.2 (1913) = Origanum dayi Post.

S. capitata L., Sp. Pl. 568 (1753) = Thymbra capitata (L.) Cav.

S. condea Juss. ex Poir., Encycl. 6:571 (1804), nomen = Hyptis americana (Poir.) Briq. fide Epling, Rev. Mus. La Plata 7 (1949).

S. globulifera Desf., Tabl. Ecole Bot., ed. 1, 58 (1804) may be a

Hyptis sp. or a *Pycnanthemum* sp.

S. japonica Matsum. & Kudo, Bot. Mag., Tokyo 26:299 (1912) = *Mentha japonica* (Miq.) Makino

S. mastichina L., Sp. Pl. 567 (1753) = *Thymus mastichina* (L.) L.

S. origanoides L., Sp. Pl. 568 (1753) = *Cunila origanoides* (L.) Britton (see Taxon 29:332-334 (1980).

S. palmeri (A. Gray) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:303 (1896) is probably a *Hedeoma* species.

S. sintenisii Bornm. in schaed. Published later as *Thymbra sintenisii* Bornm. & Aznavour.

S. spicata (L.) Garsault, Fig. Pl. Anim. Med. t.518 (1764) = *Thymbra spicata* L.

S. spinosa sensu Gaudry, Recherches 195 (1855) non L. = *Thymus capitatus* (L.) Hoffm. & Link.

S. stricta Banks & Solander in Russ., Nat. Hist. Aleppo ed.2, 2:255 (1794) (see Eig & Zohary in J. Bot. 75:185-192 (1937).

S. subdentata Fisch. & Mey. ex Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:298 (1896), typ. err. = *S. mutica* Fisch. & Mey. For retraction see Ann. Conserv. Jard. Bot. Genéve 2:186 (1898).

S. virginiana L., Sp. Pl. 567 (1753) = *Pycnanthemum* sp.

3.3.34. The separation of S. cuneifolia Ten. and S. obovata Lag.

S. cuneifolia and S. obovata are closely related species. Boissier (1839-45) thought S. obovata to be only a variety of S. cuneifolia. However, Ball & Getliffe (1972) showed that the Spanish endemic S. obovata is clearly separable from the more widely ranging S. cuneifolia by its leaves only up to 10 mm (not up to 19 mm), spathulate to obovate (not oblanceolate), apex obtuse (not acute), the calyx distinctly glandular-punctate (not sparsely punctate-glandular), and the corolla only 6-7 mm (not 5-10 mm). On the other hand, Ball & Getliffe refer to specimens from Anatolia similar to S. obovata, and intermediates between the two species from Spain, Italy and the Balkans. To investigate this problem, 17 specimens of S. obovata (by Ball & Getliffe's criteria), and 41 specimens from Europe and 26 specimens from the Orient of S. cuneifolia were measured for leaf length, leaf apex shape, number and colour of punctate glands on the calyx, and the length of the calyx tube and teeth.

3.3.34.1. Maximum leaf length

The length of the largest leaves on the specimens were measured to test Ball & Getliffe's first point of distinction between the two species. The results are presented in Table 6.1. The differences in leaf length between S. obovata and S. cuneifolia, and between the two populations of S. cuneifolia are statistically highly significant.

3.3.34.2. Leaf apex shape

The leaf shape fell into one of three possible categories: all leaves acute, some leaves acute and some obtuse, and all leaves obtuse at the apex. The results, presented in Table 6.2, show a marked difference in leaf apex shape between the two species but not between the two populations of S. cuneifolia.

3.3.34.3. Calyx punctate glands

The difficulty of making a quantitative assessment of the numbers of glands on the calyx has led to subjective comparisons between species, such as "few" compared with "distinctly punctate-glandular" (Ball & Getliffe, 1972). My own assessment of calyx glands is also admittedly subjective. Nevertheless, a general trend may be discerned from the results.

The number of glands was estimated and divided into four groups: 1) none, or rarely very few; 2) at least a few glands always present; 3) a moderate number of glands; and 4) glands very numerous. These categories are denoted by -+, +, ++, and +++, respectively, in Table 6.3 which summarizes the observations. The results show that S. obovata has a much denser covering of punctate glands on the calyx than S. cuneifolia, which confirms Ball & Getliffe's observation. Table 6.4 shows that the glands tend to be red in S. obovata and yellow in S. cuneifolia. Since there is no correlation between specimen collection date and gland colour, and it is unlikely that the specimens of one species were dried in a different manner from the other, this difference in gland colour is probably not an artifact of age or drying. However, it is interesting to note, as Table 6.5 shows, that as the number of glands decline, the proportion of yellow glands increase. The data of both species are combined in Table 6.5.

3.3.34.4. Calyx tube and teeth length

Measurements were made of the length of the calyx, and the ratio of the lower teeth to the whole calyx length was calculated. Table 6.6 shows that there is a distinct difference in calyx length between S. obovata and the European population of S. cuneifolia. Statistically this is significant at the 0.1% level. However there is no statistically significant difference between the Anatolian population of S. cuneifolia and S. obovata. Interestingly there is a marked, and obviously significant, difference in calyx length between the European and Anatolian populations of S. cuneifolia. A more important measurement, as far as this species is concerned, rather than the calyx length, is the ratio between the calyx teeth to the length of the whole calyx.

Table 6.7 clearly shows a marked difference in the calyx teeth:calyx length ratio between the two species, but not between the two populations of S. cuneifolia. The tight clustering of the ratios about the mean implies a reasonably good linear correlation between the length of the teeth and the length of the calyx. This is in fact the case. The relationship between calyx length (X) and the teeth (Y) in S. obovata is $Y = 0.42 X - 0.31$ (correlation coefficient $r=0.77$), and for the combined data of both populations of S. cuneifolia is $Y = 0.55 X - 0.31$ ($r=0.90$). A similar linear correlation between calyx and teeth was found in S. montana L. by Feoli & Poldini (1979).

Table 6.1

Max. leaf length (mm)	S. obovata (Spain)	S. cuneifolia (Europe)	S. cuneifolia (Anatolia)
4 - 5	6	3	0
6 - 7	8	7	0
8 - 9	1	12	4
10 - 11	2	10	4
12 - 13	0	3	6
14 - 15	0	4	7
16 - 17	0	1	2
18 - 19	0	1	2
Mean	6.53	9.82	12.77
Standard deviation	1.65	3.10	3.08

Table 6.2

Leaf apex shape	S. obovata (Spain)	S. cuneifolia (Europe)	S. cuneifolia (Anatolia)
Acute	0	34	21
Acute-Obtuse	4	6	4
Obtuse	13	1	0

Table 6.3

No. of calyx glands	S. obovata (Spain)	S. cuneifolia (Europe)	S. cuneifolia (Anatolia)
-+	0	4	5
+	2	26	13
++	7	9	5
+++	7	2	0

Table 6.4

Calyx punctate gland colour	S. obovata (Spain)	S. cuneifolia (Europe)	S. cuneifolia (Anatolia)
Yellow	2	30	15
Yellow, few reddish	1	6	5
Yellow with red	1	2	1
Red, few yellowish	2	1	0
Red	9	0	0

Table 6.5

Number of glands	Yellow	Y, few R	Y and R	R, few Y	Red
-+	8	0	0	0	0
+	21	5	0	0	1
++	5	2	2	3	3
+++	0	0	1	2	4

Table 6.6

Length of calyx (mm)	S. obovata (Spain)	S. cuneifolia (Europe)	S. cuneifolia (Anatolia)
1.1 - 1.5	0	0	1
1.6 - 2.0	3	0	1
2.1 - 2.5	5	2	12
2.6 - 3.0	6	9	9
3.1 - 3.5	1	10	1
3.6 - 4.0	0	10	0
4.1 - 4.5	0	3	0
4.6 - 5.0	0	3	0
5.1 - 5.5	0	3	0

Table 6.7

Calyx teeth length Total calyx length	S. obovata (Spain)	S. cuneifolia (Europe)	S. cuneifolia (Anatolia)
0.11 - 0.2	1	0	0
0.21 - 0.3	8	2	2
0.31 - 0.4	6	7	5
0.41 - 0.5	0	26	15
0.51 - 0.6	0	5	2
Mean	0.297	0.452	0.446
Standard deviation	0.0597	0.0727	0.0691

3.4. Gontscharovia Boriss., Not. Syst. (Leningrad) 15:321 (1953).

Low shrubs, stems with slender, shortly hirsute branches. Leaves elliptic to linear-oblong, base cuneate, apex acute, entire, subsessile, flat; veins camptodromous, primary vein distinct, lateral veins weak; lower side densely punctate-glandular, upper side with few punctate glands, both sides glabrous; palisade mesophyll isolateral. Inflorescence a narrow, lax, terminal spike. Verticillasters 1-6-flowered, with short pedicels and peduncles. Bracteoles small, linear, subulate. Calyx sub-actinomorphic, all teeth similar, triangular; tube ampliate, not gibbous, 15-veined, throat glabrous or with a sparse fringe of hairs. Corolla 5-6 mm, 2-lipped; tube straight, not annulate inside; lips 1/3-1/2 x tube length. Stamens 4, inserted near top of tube; filaments straight, anterior pair shortly exserted from tube, posterior pair included; anthers divergent. Style shortly exserted from corolla tube; stigma lobes equal, narrowly subulate. Monotypic.

One of the Satureioid genera. It is distinguished from Satureja s.s by the flat, not conduplicate, leaves, 15-veined calyx, and straight, not convergent, stamen filaments. Euhesperida differs by the linear, channelled, densely hairy leaves, dense spike-like inflorescence, and 15-veined (5 sutural veins especially prominent), curved calyx tube.

3.4.1. G. popovii (B. Fedtsch. & Gontsch.) Boriss., Not. Syst. (Leningrad) 15:322 (1953).

Syn: Satureja popovii B. Fedtsch. & Gontsch., Acta Hort. Petrop. 41:117 (1929); Micromeria gontscharovii Vved., Not. Syst. Herb. Inst. Bot. Acad. Sci. Uzbekistan 16:17 (1961); Micromeria popovii (B. Fedtsch. & Gontsch.) Vved., Fl. Uzbekistan 5:404 (1961); Micromeria afghanica Freitag, Notes R.B.G. Edinb. 31:353 (1972).

Ic: Borissova, Not. Syst. (Leningrad) 15:323 (1953).

Fl. 12. Stony slopes, calcareous rocks, 500-2500 m.

Type: Several syntypes from W Tadzhikistan, Regel (LE).

Gen. distrib.: USSR (Pamir-Alai), E Afghanistan, Pakistan (Chitral, Kashmir).

Freitag (1972) distinguished Micromeria afghanica from Satureja popovii by differences in leaf shape, slightly shorter calyx teeth, and the lack of hairs in the calyx throat. The few specimens collected with affinities to Gontscharovia reveal a great diversity in leaf shape, from broadly elliptic to linear-oblong to lanceolate. With such scanty material available, however, it seems prudent not to make any judgement whether more than one taxon is involved here or not. However, placement of M. afghanica in Micromeria cannot be supported; the structure of the leaves, calyx and corolla are markedly different. Having seen the type of M. afghanica [Freitag 7405, holo. E! iso. GOET] the affinity is with the Satureioid genera. Comparison with the description of Gontscharovia and the illustration cited above suggests that M. afghanica is synonymous with G. popovii.

3.5. Euhesperida Brullo & Furnari, Webbia 34:433 (1979).

Dwarf, much-branched shrubs, with a thick woody root stock, stems 10-40 cm tall, erect-ascending, densely white hairy. Leaves linear-oblong, entire, apex obtuse, sessile, flat or channelled, uninervate, lateral veins entirely absent, margins not ciliate, lamina densely white, simple, eglandular hairy, punctate glandular; palisade mesophyll isolateral. Verticillasters approximate, with few, sessile flowers, subtended by floral leaves shorter than or equalling flowers, and bracteoles in pairs. Calyx actinomorphic, upper and lower teeth of similar shape, not ciliate; tube slightly ampliate, curved, never gibbous at base, 15-veined, sutural veins very obscure, throat glabrous or hairy, glabrous inside below throat. Corolla small, 9-10 mm, 2-lipped, white or pinkish, tube straight, not annulate inside, lower half of inside of tube glabrous; lips 2/5-1/2 x tube length, upper lip emarginate. Stamens 4, ± straight, parallel, excluded from corolla tube, anthers divergent. Style reaching apex of upper corolla lip; stigma lobes unequal, both narrow subulate.

Type species: E. linearifolia.

A Saharo-Sindian? genus with two species.

The genus is closely related to Satureja s.s. but distinguished by its linear-oblong, flat or slightly channelled, uninervate leaves (not conduplicate, oblanceolate or elliptic to linear, multinervate leaves), slightly curved, actinomorphic, 15-nerved calyx, the tube only 1.6-1.9 mm and teeth 1.0-1.3 mm long (not straight, sub-bilabiate, 10-13-nerved and of much larger dimensions), parallel stamen filaments (not convergent), and unequal stigma lobes.

3.5.1. Calyx throat with a dense fringe of hairs; leaves 5.0-8.0 mm long; bracteoles linear [Cyrenaica] 1. linearifolia

Calyx throat glabrous; leaves 7.5-13.0 mm long; bracteoles elliptic to oblanceolate [Israel] 2. thymbrifolia

3.5.2. 1. E. linearifolia Brullo & Furnari, Webbia 34:434 (1979)!

Ic: Brullo & Furnari, Webbia 34:435 (1979).

Fl. 4-5. Rocky slopes, calcareous rocks.

Type: [Libya] Uadi el-Chresci, 7 v 1974, Brullo & Furnari (holo. CAT, iso. G!).

3.5.3. 2. E. thymbrifolia (Hedge & Feinbrun) A. Doroszenko, comb. nov.

Syn: Satureja thymbrifolia Hedge & Feinbrun, Israel J. Bot. (1968)17:213 (1969)!

Ic: Feinbrun, Fl. Palaestina 3:244 (1977).

Fl. 10. Limestone rocks.

Type: Israel, Judean Desert, Khirbet el Mird (Horkaniye), 3 km NE of the Mar Saba Monastery, 240 m a.s.l., hard limestone, N exposure, 27 x 1967, Danin (holo. HUJ, iso. E!).

3.6. Micromeria Benth., Bot. Reg. 15: no.1282 (1829).

Syn: Sabbatia Moench, Meth. 386 (1794), non Pursh.; Piperella Presl, Fl. Sic. 37 (1826); Micronema Schott, Oest. Bot. Wochenbl. 7:95 (1857); Tendana Reichenb. f., Oest. Bot. Wochenbl. 7:160 (1857).

Perennial, rarely annual, herbs or shrublets; stems erect or ascending, rarely prostrate; rarely stoloniferous. Leaves flat or revolute, entire or shortly toothed, veins camptodromous; hairs, if any, simple, often densely punctate-glandular, more densely so on the lower side; palisade mesophyll dorsiventral. Calyx tube straight or slightly curved, parallel-sided cylindrical or slightly ampliate, not gibbous, 13-15-veined, actinomorphic or slightly bilabiate, 3 upper and 2 lower teeth similar in shape, ciliate or not, glabrous or hairy in throat. Corolla small, 3-14(-20) mm, white, purple or lilac, rarely red or yellow; tube narrow, widening slowly from base, not annulate, glabrous or hairy in throat; upper lip emarginate, sometimes retuse, rarely entire, lower lip 3-lobed, lower central lobe entire or divided into 2 lobules. Stamens 4, straight or connivent, held under the upper corolla lip; anthers divergent, rarely parallel.

About 70 species of the Mediterranean region, N, E & S Africa, Macronesia, SE Asia, India, and east to China.

Micromeria is by far the largest genus in Satureja s.l. The genus, as treated here, has 5 sections which are divided into two groups: sect. Micromeria, the closely related sect. Pineolentia, and the somewhat more distantly related sections Cymularia and Madagascarenses in one group, and sect. Pseudomelissa in the other group. Outside of the Micromerioid genera (Micromeria, Killickia and Nanbrea), Calamintha is probably the nearest ally to sect. Pseudomelissa, and Satureja s.s. the nearest to Micromeria sect. Micromeria (Linnaeus, 1753; Briquet, 1897). Micromeria is clearly distinguished from Satureja s.s. by its leaves ovate to elliptic, flat or revolute, palisade dorsiventral, calyx narrowly tubular or slightly ampliate, 13-15-veined (not leaves oblanceolate to elliptic, conduplicate, palisade isolateral, calyx tube clearly ampliate, 10-13-veined as in Satureja), and from Calamintha by its parallel-sided cylindrical or only slightly ampliate, actinomorphic calyx with similar upper and lower teeth.

3.6.1. 1. Annual; bracteoles ovate-acuminate, long-ciliate; corolla resupinate (c) Sect. Cymularia

\+ Perennial; bracteoles oblong to linear, not long ciliate; corolla not resupinate 2

2. Flower solitary in leaf axils on very long pedicels and peduncles; bracteoles similar in shape to the leaves; style branches markedly different in length, one very narrow filiform only 1/4-1/3 as long as the other broad lanceolate branch (e) Sect. Madagascarenses

\+ Flowers numerous in leaf axils, rarely solitary, sessile or on very short pedicels and peduncles; bracteoles clearly different in shape to leaves; style branches equal or one up to 2 x the other in length, both branches either narrow subulate or broad lanceolate 3

3. Leaves without a marginal vein, ± flat, entire to weakly crenate-dentate (d) Sect. Pseudomelissa

\+ Leaves with a prominent marginal vein, often revolute, entire 4

4. Leaves (14-)16-30 mm long, at least some 20 mm; tall erect shrubs [Canary Isles] (b) Sect. Pineolentia

\+ Leaves 2-16 mm long; usually low ascending or erect shrublets (a) Sect. Micromeria

3.6.2. (a) Sect. Micromeria

Syn: Micromeria Benth. sect. Piperella Benth., Lab. Gen. Sp. 373 (1834); Satureja L. sect. Sabbatia Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:298 (1897), p.p.; Satureja L. sect. Piperella Briq., loc. cit. 299 (1897).

Perennial, suffruticose herbs or shrubs. Leaves 2-16 x 0.3-8.0 mm, ovate, elliptic, lanceolate, linear or oblong, flat or tightly revolute, entire, with a thick, conspicuous marginal vein; petiole 0-1.5(-2.0) mm. Flowers 1-10(-20) in floral leaf axils, rarely always solitary. Bracteoles narrowly linear-filiform, lanceolate or elliptic, 0.6-3.0(-6.0) mm, not distinctly ciliate. Calyx mostly hairy in throat, teeth ciliate or not. Corolla not resupinate. Stamens included, or anterior pair (rarely both pairs) exserted from tube but not beyond upper corolla lip; all anthers similar in size. Style branches equal, very rarely slightly unequal, either both narrowly subulate or both broadly lanceolate, very rarely both very short with blunt apices. Nutlets ovoid or obloid, nearly always glabrous, rarely minutely eglandular hairy at apex.

3.6.2.1. Micromeria in Macronesia.

Perez (1978) has produced a very detailed monograph of Micromeria in Macronesia, so the following discussion is no more than a summary of the relationships and distribution of the species.

All seventeen species of Micromeria in Macronesia are endemic to the region. Members of two sections are present: sect. Micromeria with 15 species and sect. Pineolentia with 2 species. The latter section, endemic to NW Gran Canaria, is dealt with separately from this discussion.

Section Micromeria may be divided into four species-groups. The smallest of these groups, with only M. teneriffae and M. forbesii, is the most similar to the Mediterranean species, especially to M. microphylla, M. filiformis, and the Grand Atlas endemics M. debilis, M. fontanesii, and M. hochreutineri. The second group comprises M. helianthemifolia, M. rivas-martinezii, and M. glomerata which have large oblong to lanceolate leaves, minutely glandular-papillose below. The third group, endemic to Gran Canaria, is easily recognised by its white lanate leaves and includes M. lanata, M. benthamii, and M. tenuis. The remainder of the species belong to the varia agg. As its name suggests this is a highly variable group of species but is recognised by its small, often imbricate and revolute, pubescent leaves, and small flowers in compact pedunculate cymes. The aggregate ranges over all the islands in Macronesia except the Cape Verde Islands. There is some similarity in habit to M. fruticulosa from S Italy, but probably the closest relative on the African continent is the Maroccan M. macrosiphon.

3.6.2.1.1. 1. Leaves, especially underside, densely white recurved-lanate, tightly revolute [Gran Canaria] 2

\+ Leaves not white lanate (only very rarely so), flat or tightly revolute 4

2. Calyx tube 1.6-1.8 mm, lips c. 0.7 mm, teeth broadly triangular; corolla tube 1.7-1.8 mm 6. lanata

\+ Calyx tube 2.5-3.7 mm, lips 1.3-2.5 mm, teeth narrowly triangular; corolla tube 4.0-7.2 mm 3

3. Cymes 1-3-flowered, pedicels and peduncles together only 1.0-1.5 mm long; upper teeth at least 3/4 x as long as lower; leaves held close to stem, often curved backwards longitudinally 7. *benthamii*

\+ Cymes 3-11-flowered, pedicels and peduncles together 3.8-8.8 mm long; upper teeth about 1/2 x as long as lower; leaves mostly at an angle of 45° or more from stem, straight 8. *tenuis*

4. Calyx tube 4.3-6.6 mm; corolla tube 8.5-12.0 mm; leaves broadly lanceolate, oblong, or oval-orbicular, mostly 10-15 mm long, flat or revolute just at margins, densely minutely patent-pilose and very densely minutely glandular-punctate below 5

\+ Calyx tube 1.3-3.6 mm; corolla tube 2.8-5.0 mm; leaves linear, linear-lanceolate, or elliptic, rarely ovate, mostly 5-10 mm long, tightly revolute, or if +- flat then sparsely hairy or glabrous, sparsely glandular-punctate below 7

5. Lower calyx teeth 3.0-3.7 mm, upper only 1/3 x as long; calyx tube 5.3-6.6 mm [Gran Canaria] 3. *helianthemifolia*

\+ Lower calyx teeth 2.0-2.6 mm; upper c. 3/4 x as long; calyx tube 4.3-5.5 mm [Teneriffe] 6

6. Leaves lanceolate-oblong; verticillasters rather lax; calyx 6-7 mm 4. *rivas-martinezii*

\+ Leaves oblong to oval-orbicular; vericillasters condensed into a head at stem apex; calyx 7-9 mm 5. *glomerata*

7. Leaves ovate-lanceolate or ovate, flat 8

\+ Leaves linear to narrowly elliptic, nearly always tightly revolute 9

8. Leaves glabrous [Teneriffe] 1. *teneriffae*

\+ Leaves sparsely pilose [Cape Verde Is.] 2. *forbesii*

9. Calyx tube 2.9-3.6 mm; leaves with minute glandular and larger eglandular hairs 9. *lepida*

\+ Calyx tube 1.4-2.6 mm; leaves eglandular hairy 10

10. Peduncles absent; calyx tube with a sparse fringe of hairs at throat [Gomera] 15. *densiflora*

\+ Peduncles 0.5-6.5 mm; calyx tube glabrous at throat 11

11. Corolla 1 1/2-2 x as long as calyx [Palma] 12. *herpyllomorpha*

\+ Corolla 1-1 1/2 x as long as calyx 12

12. Calyx tube ± 13-nerved, bilabiate, upper teeth 1/2-2/3 x the lower in length 13

\+ Calyx tube ± 15-nerved, ± actinomorphic, upper teeth more than 2/3 x the lower in length 14

13. Plant greyish hairy in aspect; leaves greyish-green; corolla white (rarely pinkish-purple); calyx greyish-tomentose, rarely becoming green 11. *hyssopifolia*

\+ Plant glabrescent or sparsely pilose, green; leaves frequently reddish-tinted; corolla purple or pink; calyx green, at times red-tinted 10. *varia*

14. Plant glabrescent or with very few sparse hairs; corolla white (at times very pale pink), limb 2.5-3(-3.5) mm diam., lip lobes flat 13. *lachnophylla*

\+ Plant densely pilose; corolla whitish or lilac with purple stripes, limb 3.5-4.0 mm diam., lip lobes revolute 14. *lasiophylla*

3.6.2.1.2. 1. *Micromeria teneriffae* (Poir.) Benth., Lab. Gen. Sp. 378 (1834).

Syn: *Thymus teneriffae* Poir. in Lamarck, Encycl. Meth. Bot. 7:650

(1785), non Hortul. ex Benth. (1834); T. terebinthinaceus Brouss., Cat. Hort. Monsp. 59 (1805); Micromeria terebinthinacea (Brouss.) Webb & Berth., Phyt. Canar. 3:80, t.164 (1844); Clinopodium terebinthinaceum (Brouss.) O. Kuntze, in Rev. Gen. Pl. 2:514 (1891); Satureja teneriffae (Poir.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Ref: Perez, P. Revision del Micromeria Bentham (Lamiaceae-Stachyoideae) en la Region Macaronesica, in Inst. Est. Canar. Univ. La Laguna, sect.4, 16 [henceforth Perez, Revis. Micromeria] 50 (1978).

Ic: Perez, Revis. Micromeria 66-70, fig. 9-13 (1978).

Fl. 1-5, 10-11, rarely 7-8. Coastal rock fissures, 20-500(-600) m.

Type: Teneriffa, collector unknown, in Herb. Lamarck (lecto. P, photo!).

Gen. distrib.: S side of E Teneriffe.

A variable species, especially in habit and leaves, apparently related to the dryness of the habitat. It is fairly common in its area of distribution.

3.6.2.1.3. 2. Micromeria forbesii Benth., Lab. Gen. Sp. 376 (1834).

Syn: Clinopodium forbesii (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja forbesii (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Ref: Perez, Revis. Micromeria 73 (1978).

Ic: Perez, Revis. Micromeria 79, fig. 17 (1978).

Fl. probably all year. Mountain slopes amongst rocks, 800-1800 m.

Type: Ins. Sancti Nicolai, ann. 1822, Forbes (holo. K!).

Gen. distrib.: Cape Verde Is.

Though about 1000 miles distant from Teneriffe on the Cape Verde Islands, this species is very similar to M. teneriffae. M.

forbesii is distinguished by its hirsute leaves and relatively shorter calyx teeth. Perez (1978) has distinguished three varieties based mainly on leaf shape and habit which are, as in M. teneriffae, very variable in the species.

3.6.2.1.4. 3. Micromeria helianthemifolia Webb & Berth., Phyt. Canar. 3:79, t.162 (1844).

Syn: Clinopodium helianthemifolium (Webb & Berth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja helianthemifolia (Webb & Berth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); Satureja despreauxii Briq. in Ann. Conserv. Bot. Jard. Genéve 2:186 (1898), syn. nov.

Ref: Perez, Revis. Micromeria 81 (1978).

Ic: Perez, Revis. Micromeria 92-93, fig. 21-22 (1978).

Fl. 3-7. Dry rocks and rock fissures, 500-1500 m.

Type: In fissuris rupium ad pylas vallis Tiraxanae, Degollada de Manzanilla dicta, in rupibus altissimis insulae Canariae, Webb (lecto. FI, photo!).

Gen. distrib.: S Central Gran Canaria.

This is a rare plant of the southern upper slopes of the central volcano. It is easily distinguished by its large, narrowly lanceolate leaves, and narowly tubular calyx and corolla. Var. mary-annae Perez is distinguished by its more slender stems, narrower leaves, and laxer inflorescence.

3.6.2.1.5. 4. Micromeria rivas-martinezii Wildpret in Vieraea 3(1973):72 (1974).

Ref: Perez, Revis. Micromeria 96 (1978).

Ic: Perez, Revis. Micromeria 102, 103, fig. 26, 27 (1978).

Fl. 4-6. Rock fissures.

Type: In fissuris rupium loco vulgo dicto, Roque de Juan Bay, insula Nivaria, Tenerife dicta, 7 iv 1973, W. Wildpret, TFC 1708 (holo. TFC; iso. MAF, herb. Rivas-Martinez).

Gen. distrib.: E Teneriffe.

This species, only known from the type locality, is most similar to M. glomerata.

3.6.2.1.6. 5. Micromeria glomerata P. L. Perez in Vieraea 3(1973):78 (1974).

Ref: Perez, Revis. Micromeria 105 (1978).

Ic: Perez, Revis. Micromeria 110, fig. 29 (1978).

Fl. 5-6. Rock fissures, 300-400 m.

Type: In fissuris rupis regione septentrionali Anagae, circa pago Taganana, 400 m, 27 v 1972, P. Perez de Paz, TFC 1710 (holo. TFC, photo!; iso. K!, MA).

Gen. distrib.: E Teneriffe.

Only known from the immediate vicinity of the type locality.

3.6.2.1.7. 6. Micromeria lanata (Chr. Sm. ex Link) Benth., Lab. Gen. Sp., Suppl. 731 (1835).

Syn: Satureja lanata Chr. Sm. ex Link in Buch, Beschr. Canar. Ins. 143 (1828); Clinopodium lanatum (Chr. Sm. ex Link) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); S. micrantha Webb, nom. in schaed. (FI).

Ref. Perez, Revis. Micromeria 112 (1978).

Ic: Perez, Revis. Micromeria 119, fig. 32 (1978).

Fl. 4-7. Common amongst rocks and on mountain slopes, 700-1900 m.

Type: In convalle Tejeda jugisque montium vicinis Magna Canaria rupibus aridis, Webb (neotype FI, photo!).

Gen. distrib.: Central Gran Canaria.

A very common plant everywhere on the upper slopes of Central Gran Canaria. It is most similar to M. benthamii but may be distinguished by its lower stature, verticillasters with long pedunculate cymes with more flowers, and smaller size of all its floral parts.

36.2.1.8. 7. Micromeria benthamii Webb & Berth., Phyt. Canar. 3:77 (1844).

Syn: Micromeria lanata sensu Benth., Lab. Gen. Sp. 374 (1834); M. tenuis Benth., Lab. Gen. Sp., Suppl. 731 (1835), non (Link) Webb & Berth. (1845); Satureja mollis Webb ex Steud., Nom. Bot. ed.2, 2:515 (1841), nomen; Clinopodium benthamii (Webb & Berth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); S. benthamii (Webb & Berth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Ref: Perez, Revis. Micromeria 121 (1978).

Ic: Perez, Revis. Micromeria 133, fig. 37 (1978).

Fl. 4-7(-8). Common amongst shrubs and pines on rocky soil, above 500 m.

Type: In rupibus altissimis Montis Saucillo dicto insulae Canariae, Webb (lecto. FI, photo!).

Gen. distrib.: Central Gran Canaria.

A common plant which occupies the same area as the last species, M. lanata. A hybrid between these two species has been described by Perez (1978).

36.2.1.9. 8. Micromeria tenuis (Link) Webb & Berth., Phyt. Canar. 3:75, t.158 A (1844).

Syn: Satureja tenuis Link in Buch, Phys. Beschr. Canar. Ins. 143 (1825); Micromeria polioides Webb & Berth., Phyt. Canar. 3:76, t.158 B (1844); M. linkii Webb & Berth., loc. cit. 79, t.161 (1844); M. buchii Webb in Webb & Berth., loc. cit. t.161 (1844); M. bourgaeana Webb ex Bolle in Bonplandia 8:283 (1860); Clinopodium bourgaeanum (Webb) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); C. tenue

(Link) O. Kuntze, loc. cit 516 (1891); Satureja bourgaeana (Webb) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); S. polioides (Webb & Berth.) Briq., loc. cit. (1897); S. buchii (Webb) Briq. in Ann. Conserv. Jard. Bot. Genéve 2:186 (1898).

Ref: Perez, Revis. Micromeria 134 (1978).

Ic: Perez, Revis. Micromeria 149, 150, fig. 41, 42.

Fl. 3-8. Rocky ravines, rock fissures, 200-800 m.

Type: Gran Canaria, 296, Despreaux, (neotype FI, photo!).

Gen. distrib.: N and W Gran Canaria.

This is a variable species and two subspecies have been described by Perez (1978), ssp. tenuis and ssp. linkii (Webb & Berth.) Perez, to distinguish plants of different habit, leaf shape, and pubescence.

3.6.2.1.10 9. Micromeria lepida Webb & Berth., Phyt. Canar. 3:74, t.157 A (1844).

Syn: Micromeria densiflora Bolle in Bonplandia 8:283 (1860), non Benth. (1834); Clinopodium lepidum (Webb & Berth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja lepida (Webb & Berth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); M. pitardii Bornm. in Fedde, Rep. Spec. Nov. 6:1 (1908); S. pitardii Bornm., loc. cit. (1908).

Ref: Perez, Revis. Micromeria 151 (1978).

Ic: Perez, Revis. Micromeria 169-172, fig. 48-51.

Fl. 1-7(-8). Rocks, fissures, amongst shrubs and in forest clearings, above 300 m (rarely below this altitude).

Type: In rupibus praeruptis montium Gomerae, Despreaux 316 (lecto. FI, photo!).

Gen. distrib.: Gomera.

A very variable species which Perez (1978) divided into two subspecies, ssp. lepida and ssp. bolleana Perez, based on habit and density of the inflorescence. It is a local plant, distributed mainly in central parts of Gomera.

3.6.2.1.11. 10. Micromeria varia Benth., Lab. Gen. Sp. 374 (1834).

Syn: ? Thymus ericaefolius Roth, Cat. Bot. 2:50 (1800); Micromeria thymoides Solander ex Lowe in Trans. Camb. Phil. Soc. 6:19 (1831); Satureja thymoides Solander ex Lowe, loc. cit. (1831), nomen, non (DeNot) Nym. (1854), non (Kunth) Briq. (1897); M. tragothymus Webb & Berth., Phyt. Canar. 3:73, t.155 (1844); Clinopodium ericaefolium (Roth) O. Kuntze, Rev. Gen. Pl. 2:514 (1891); S. varia Webb & Berth. ex Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); M. ericaefolia (Roth) Bornm. in Fedde, Rep. Sp. Nov. 19:198 (1924).

Ref: Perez, Revis. Micromeria 173 (1978).

Ic: Perez, Revis. Micromeria 205-206, 251, fig. 62-63, 77B.

Fl. all year. Mixed woodland, scrub, dry rocky slopes, 50-1800 m.

Type: Ins. Teneriffa (lecto. K!).

Gen. distrib.: N Teneriffe, Gomera, Gran Canaria, Lanzarote, Fuerteventura, El Hierro, Madeira.

This is the most widely distributed and most variable species in Macronesia. Seven subspecies have been described by Perez (1978); most are confined to certain islands, but ssp. varia is found on Teneriffe and Gomera, and ssp. rupestris is confined to areas above 500 m on Lanzarote and Fuerteventura. Ssp. thymoides is the only representative of Micromeria on the islands of Madeira. The other subspecies are ssp. gomerensis Perez [Gomera], ssp. canariensis Perez [Gran Canaria], ssp. meridialis Perez [Gran Canaria] and ssp. hierrensis Perez [El Hierro]. The following species (nos. 11-15) are all closely related to and probably all derived from *M. varia*. Perez (1978) presents a diagram of the possible relationships within the aggregate.

Perez (1978) has proposed to conserve the name *M. varia* Benth. (1834) against *M. ericaefolia* [basionym *Thymus ericaefolius* Roth. (1800)]. I have seen a microfiche of the Willdenow specimen upon which the latter name is based and the specimen definitely belongs to the *varia* agg., but without direct examination I cannot be more specific. Bentham (1834) had *T. ericaefolius* as a synonym of *M. varia*.

3.6.2.1.12 11. *Micromeria hyssopifolia* Webb & Berth., Phyt. Canar. 3:72, t.154, b1 (1844).

Syn: *Satureja hyssopifolia* (Webb & Berth.) Briq. in Ann. Conserv. Jard. Bot. Genéve 2:186 (1898), non Bert. (1829), non Duff. (1860); *Micromeria kuegleri* Bornm. in Fedde, Repert. Sp. Nov. 19:197 (1924).

Ref: Perez, Revis. Micromeria 208 (1978).

Ic: Perez, Revis. Micromeria 235, fig. 73 (1978).

Fl. all year. Dry, rocky, open situations, sometimes at forest margins, or in degraded forest scrub, 10-2000 m.

Type: In rupestribus siccis Ins. Canar. vulgatissima, *Webb* (lecto. FI, photo!).

Gen. distrib.: Teneriffe, El Hierro.

This species is most easily distinguished from *M. varia* by its dense indumentum. Perez (1978) described three varieties: var. *hyssopifolia* on both Teneriffe and El Hierro, and vars. *glabrescens* and *kuegleri* from Teneriffe. They are differentiated on pubescence and calyx features but the species as a whole is very variable also in habit, leaf size and inflorescence density. The species is very common on both Teneriffe and El Hierro.

3.6.2.1.13. 12. Micromeria herpyllomorpha Webb & Berth., Phyt. Canar. 3:72, t.155 A (1844).

Syn: Micromeria serpyllomorpha Webb ex Benth. in DC., Prodr. 12:217 (1848); M. perezii Bolle in Bonplandia 8:282 (1860); Satureja perezii (Bolle) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); S. herpyllomorpha (Webb & Berth.) Briq., loc. cit. (1897); M. palmensis [Bolle] Lid in Skr. Norske Vid.-Akad. Oslo, Mat. Nat. n.s. 23:152 (1968); M. albicoma Bourgeau, nom. in schaed. (FI).

Ref: Perez, Revis. Micromeria 237 (1978).

Ic: Perez, Revis. Micromeria 251, fig. 77A.

Fl. mainly 3-8, but individuals at any time. Rocks and cliffs in heath and pine forest, s.l.-1500 m.

Type: In rupestribus convallium insulae Palmae, Webb (lect. FI, photo!).

Gen. distrib.: Palma.

A common plant closely related to M. varia. Perez (1978) discusses the differences at length but this species is most easily distinguished from M. varia ssp. varia, a plant not found on Palma, by the large corollas, and less bilabiate, and usually 15-nerved calyx.

The source of the specific epithet of M. palmensis Lid is M. julianoides Webb & Berth. var. palmensis Bolle in Bonplandia 8:283 (1860). Perez (1978) has this variety as a synonym of M. lasiophylla.

3.6.2.1.14 13. Micromeria lachnophylla Webb & Berth., Phyt. Canar. 3:73, t.156 A (1844).

Syn: Micromeria julianoides Webb & Berth., Phyt. Canar. 3:78, t.160 B (1844); M. teydensis Bolle in Bonplandia 8:282 (1860);

Clinopodium julianoides (Webb & Berth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); C. teydense (Bolle) O. Kuntze, loc. cit. 516 (1891); Satureja lachnophylla (Webb & Berth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); S. julianoides (Webb & Berth.) Briq., loc. cit. (1897); S. teydensis (Bolle) Briq., loc. cit. (1897).

Ref: Perez, Revis. Micromeria 253 (1978).

Ic: Perez, Revis. Micromeria 262, fig. 79A (1978).

Fl. 4-8, rarely other times. Sub-alpine leguminous scrub on pumice, 2000-2700 m.

Type: In rupestribus elatis aridissimis ultra pagum Chasnam, non longe a monte Pico del Almendro dicto, Webb (lecto. FI, photo!).

Gen. distrib.: Central Teneriffe.

A common plant confined to the sub-alpine parts of the caldera, almost reaching the summit. It has a much more slender habit than M. varia, with simple stems, rarely with branches.

3.6.2.1.15 14. Micromeria lasiophylla Webb & Berth., Phyt. Canar. 3:74, t.156 B (1844).

Ref: Perez, Revis. Micromeria 263 (1978).

Ic: Perez, Revis. Micromeria 262, fig. 79B (1978).

Fl. 6-8, rarely other times. Rock fissures on upper part of caldera, 2000-2400 m.

Type: No locality, Webb (lecto. FI, photo!). This specimen is labelled Micromeria oreothymbra.

Gen. distrib.: Central Teneriffe, summit of caldera of Palma.

A locally common plant found close to the summit on the southern side of the calderas on both Teneriffe and Palma. The closest relatives are M. lachnophylla and M. hyssopifolia.

3.6.2.1.16. 15. *Micromeria densiflora* Benth., Lab. Gen. Sp. 375 (1834).

Syn: *Thymus floribundus* Willd. ex Benth. in Linnaea 11:341 (1837), nomen; *Clinopodium densiflorum* (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); *Satureja densiflora* (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Ref: Perez, Revis. Micromeria 156 (1978).

Ic: Perez, Revis. Micromeria 157, fig. 43 (1978), of a fragment only.

Robust shrub, stems 20-40 cm, densely shortly recurved-pubescent. Leaves linear-lanceolate, tightly revolute, 3.0-6.0 x 0.6-1.3 mm, both sides densely minutely hairy. Verticillasters with 1-4-flowered cymes, peduncles absent, pedicels 0.1-0.5 mm. Bracteoles linear, 0.8-1.5 mm. Calyx straight, parallel-sided tubular or slightly ampliate; tube 2.0-2.3 mm, densely minutely patent-pilose, throat sparsely hairy; lips 0.8-1.2 mm; upper teeth narrowly to broadly triangular, 0.5-0.8 mm; lower teeth narrowly triangular to lanceolate-triangular, 0.8-1.2 mm. Corolla purplish (?); tube 3.0-4.2 mm; upper lip 0.8-1.0 mm; lower lip 1.5-1.6 mm. Fl. 1. Steep west-exposed rocks, c. 800 m.

Type: In Ins. Canariensibus, *Broussonet* (K).

Gen. distrib.: Gomera.

Perez (1978) was doubtful about the status of this species and only described the type specimen and discussed the problem of its identity under his account of *M. lepida*. The type specimen is only a fragment, apparently a short lateral shoot, but the essential features of this species are discernable: densely aggregated inflorescence with few flowered cymes without peduncles, small, shortly patent-pilose calyx, hairy in the throat, and small revolute leaves. Only two species, other than this one, are found on Gomera, *M. lepida* and *M. varia* ssp. *varia*. The features outlined above clearly associates *M. densiflora* Benth. with the *varia* aggregate rather than *M. lepida*. I have seen a specimen (at E) collected by the Aarhus University Expedition to Gomera in 1971 (AAU 71-7706) which almost certainly belongs to *M. densiflora* Benth. The specimen almost exactly matches Bentham's description of his species, and confirms its association with, but its distinctness from, *M. varia*.

3.6.2.1.17 The following hybrids have been described:

Micromeria x angosturae Perez, Revis. Micromeria 146 (1978) = *M. tenuis* (Link) Webb & Berth. ssp. *linkii* (Webb & Berth.) Perez x *M. varia* Benth. ssp. *canariensis* Perez.
Type: [Gran] Canaria, Baranco de Langostura, iii 1846, *Bourgeau* 914 (holo. FI, photo!).

Micromeria x benthamineolens Svent., Ind. Sem. Hort. Acclim. Plant. Arautapae 1969, 4:48 (1969) = *M. benthamii* Webb & Berth. x *M. pineolens* Svent.
Ic: Perez, Revis. Micromeria 281, fig. 84 (1978).
Type: Gran Canaria: Tamadaba, in pineto, valde rara, 31 vii 1966, *Sventenius* (lecto. ORT 6503, photo!).

Micromeria x confusa Kunkel & Perez, Cuad. Bot. Canar. 26/27:21 (1976) = *M. benthamii* Webb & Berth. x *M. lanata* (Chr. Sm. ex Link) Benth.
Ic: Perez, Revis. Micromeria 94, fig. 23 B (1978).
Type: Gran Canaria: in montibus Goyedrae circa loco dicto Tamadaba, 1050 m.s.m., 14 vi 1974, *G. Kunkel* 17349 (holo. BM, photo!, iso.

herb. Kunkel).

Micromeria x intermedia Kunkel & Perez, Cuad. Bot. Canar. 26/27:23 (1976) = M. benthamii Webb & Berth. x M. helianthemifolia Webb & Berth.

Ic: Perez, Revis. Micromeria 94, fig. 23 A (1978).

Type: Gran Canaria: Degollada de la Manzanilla ca. S. Bartolome de Tirajana, 1000 m.s.m., 1 xi 1973, G. Kunkel 15944 (holo. BM, photo!, iso. herb. Kunkel).

Micromeria x nogalesii Kunkel & Perez, Cuad. Bot. Canar. 26/27:25 (1976) = M. lanata (Chr. Sm. ex Link) Benth. x M. varia Benth. ssp. canariensis Perez.

Ic: Perez, Revis. Micromeria 120, fig. 33 (1978).

Type: Gran Canaria: in montibus Goyedrae circa Tamadaba, 950 m.s.m., 3 vii 1974, G. Kunkel 17384 (holo. BM, photo!, iso. herb. Kunkel).

Micromeria x perez-pazii Kunkel, Vieraea 8:360 (1980) = M. benthamii Webb & Berth. x M. tenuis (Link) Webb & Berth.

Micromeria x preauxii (Webb & Berth.) Perez, Revis. Micromeria 127 (1978) = M. benthamii Webb & Berth. x M. varia Benth. ssp. canariensis Perez

Syn: Micromeria preauxii Webb & Berth., Phyt. Canar. 3:75, t.157 B (1844).

Type: [Gran Canaria]: inter rupes Goyavrae-Guayedra dicta, v 1839, Despreaux 30 (lecto. FI, photo!).

Micromeria x tagananensis Perez, Revis. Micromeria 108 (1978) = M.

glomerata Perez x *M. varia* Benth. ssp. *varia*.

Ic: Perez, Revis. Micromeria 111, fig. 30 (1978).

Type: Tenerife: in rupis semiumbrosis in loco vulgo dicto, Roque de Enmedio, ca. Taganana, 25 v 1972, *Perez* 19 (holo. herb. Perez, photo!).

Micromeria x wildpretii Perez, Revis. Micromeria 99 (1978) = *M. rivas-martinezii* Wildpret x *M. varia* Benth. ssp. *varia*.

Ic: Perez, Revis. Micromeria 104, fig. 28 (1978).

Type: Tenerife: in fissuris rupium loco vulgo dicto, Roque de Juan Bay regione meridionalis Anagae, 12 v 1974, *J. R. Acebes & Perez* 20 (holo. herb. Perez, photo!, iso. TFC 1748).

3.6.2.2. *Micromeria sect. Micromeria, excluding Macronesian species.*

3.6.2.2.1. 1. Ericoid dwarf shrub with acicular leaves, 1.5-3.5 x 0.3-0.5(-1.2) mm ... 28. *inodora*

\+ Shrubs to 50 cm, at least some leaves larger, never acicular ... 2

2. Calyx tube 3.5-5.2 mm; corolla 11.5-19.0 mm ... 3

\+ Calyx tube 1.4-3.5 mm; corolla 3.0-11.5 mm ... 7

3. The upper, or at least the floral, leaves linear-lanceolate or linear ... 4

\+ Upper leaves, including the floral, broadly ovate ... 6

4. Leaf mid-vein prominent, others not visible; upper calyx teeth narrowly triangular, 0.7-1.0 mm; flowers solitary in leaf axils 8. <u>macrosiphon</u>

\+ Leaf mid-vein and lateral veins ± prominent; upper calyx teeth narrowly triangular or subulate, 1.3-2.0 mm; cymes with usually more than one flower 5

5. Leaves elliptic, 10-16 x 2.0-3.6 mm, very densely recurved-pubescent, the petiole 1.0-2.0 mm; lower calyx teeth not ciliate 30. <u>longiflora</u>

\+ Leaves ovate-elliptic to linear-lanceolate, 6-14 x 2-7 mm, sparsely hairy, petiole 0.5-1.0 mm; lower calyx teeth ciliate 26. <u>graeca</u>

6. Puberulent or sparsely pubescent; leaves up to 5 mm broad, obtuse; calyx teeth c. 1/2 as long as tube 5. <u>marginata</u>

\+ Densely patent-pubescent; leaves up to 8 mm broad, sub-acute; calyx teeth c. 2/3 as long as tube 6. <u>croatica</u>

7. Leaves linear, strongly revolute, ± erect, markedly overlapping on nearly all shoots, the internodes half the leaf length or less 8

\+ Leaves broadly ovate-elliptic to linear-lanceolate, strongly revolute or not, usually not erect, not overlapping or only slightly so, the internodes at least 3/4 leaf length (sometimes less in young axillary shoots) 10

8. Flowering stems bearing short, hairy, imbricate-leaved resting buds at base 17. <u>cristata</u>

\+ Flowering stems without imbricate-leaved resting buds at base (but axillary fascicles of leaves may be present) 9

9. Stems with conspicuous axillary fascicles of leaves; calyx 3.8-5.4 mm; corolla 4-6 mm longer than calyx tube [S Italy, Sicily] 27. *fruticulosa*

\+ Stems without axillary fascicles of leaves; calyx 2.4-2.7 mm; corolla 2.5-4.0 mm longer than calyx tube [Libya] 14. *conferta*

(Very depauperate forms of *juliana* may key out as far as here)

10. All middle stem leaves 2.0-4.0 mm 11

\+ All middle stem leaves 4.0-15.5 mm 17

11. Calyx minutely retrorse-pubescent; lower calyx teeth 1.5-2.0 mm 1. *filiformis*

\+ Calyx hispid or shortly patent-pubescent; lower calyx teeth 0.7-1.5 mm 12

12. Stems brittle, decumbent, 2-5 cm tall; leaves cordate at base; flowers solitary 33. *contardoi*

\+ Stems ascending, usually more than 5 cm; leaves rounded or cuneate at base; flowers 1-10 per cyme 13

13. Calyx long-hispid; upper calyx teeth 1/2-1/3 x the lower [Central Mediterranean] 14

\+ Calyx shortly patent-pubescent; upper calyx teeth 3/4-5/6 x the lower [Sinai, Jordan, W Arabia] 15

14. Plant densely hairy; stem hairs patent 4. *hispida*

\+ Plant sparsely hairy; stem hairs retrorse 2. *microphylla*

15. Habit loose, ascending; leafy stem diameter 0.5-1.0 mm; stem hairs retrorse 24. *sinaica*

\+ Habit cushion-forming; leafy stem diameter 0.2-0.3 mm; stem hairs patent 16

16. Leaves dark grey-green in aspect, densely patent-villous, with hairs 0.4-0.7 mm long; lower calyx teeth 0.9-1.4 mm 29. cinerea

\+ Leaves light green in aspect, densely white hispid to scabrous, with hairs 0.2-0.3(-0.5) mm; lower calyx teeth 0.5-0.9 mm 31. serbaliana

17. Flowers ± sessile, crowded in tight verticillasters, often 10-20-flowered; pedicels up to 0.5 mm 18

\+ Flowers in lax verticillasters, usually less than 10-flowered (sometimes more); pedicels (0.3-)0.5-3.5 mm 20

18. Calyx throat glabrous 16. juliana

\+ Calyx throat bearded 19

19. Stem hairs patent; verticillaster peduncles 2.0-6.5 mm; calyx tube 1.5-1.7 mm, lower calyx teeth 0.6-1.0 mm; corolla c. 3.5 mm; nutlets acute 10. weilleri

\+ Stem hairs recurved; verticillaster peduncles 0.5-2.6 mm; calyx tube 1.8-2.5 mm, lower teeth 1.0-1.3 mm; corolla 4.0-5.0 mm; nutlets obtuse 15. myrtifolia

20. Verticillasters sessile, peduncles less than 0.3 mm 21

\+ Verticillasters clearly pedunculate, peduncles (0.4-)0.7-6.0 mm 22

21. Leaves revolute, apex obtuse, lateral veins not visible; bracteoles ovate-lanceolate; calyx tube c. 3.4 mm, upper teeth broadly triangular, lower teeth not ciliate 13. brivesii

\+ Leaves flat, apex ± acute, lateral veins clearly visible; bracteoles narrowly linear; calyx tube 2.0-2.7 mm, upper teeth narrowly triangular, lower teeth ciliate 32. imbricata

22. Calyx densely villous-plumose, with patent hairs more than 0.5 mm 7. *nervosa*

\+ Calyx densely or sparsely pubescent, hairs patent or recurved, less than 0.5 mm 23

23. Corolla 3.0-5.5 mm; lower calyx teeth not ciliate (except in kerneri) 24

\+ Corolla (5.0-)5.5-11.5(-15.0) mm; lower calyx teeth ciliate (except in elliptica) 31

24. Upper part of stem with patent hairs 25

\+ Upper part of stem with recurved hairs 28

25. Lower calyx teeth 1.2-1.6 mm, ciliate 18. *kerneri*

\+ Lower calyx teeth 0.6-1.2 mm, not ciliate 26

26. Leaves ovate-elliptic to lanceolate, 2.3-7.0 mm broad [NW Africa] 9. *fontanesii*

\+ Leaves ovate-elliptic to oblong, 0.5-3.0 mm broad [E Mediterranean] 27

27. Stems densely patent-pubescent; leaves mostly overlapping; resting buds at base of stem 17. *cristata*

\+ Stems puberulent; leaves mostly not overlapping; no resting buds at base of stem 19. *cremnophila*

28. Calyx shortly recurved-puberulent; lower part of stem long-patent-pubescent, hairs mostly 0.5 mm or more 11. *debilis*

\+ Calyx hispidulous or shortly patent-pubescent; lower part of stems shortly patent or recurved-pubescent, hairs up to 0.5 mm 29

29. Upper leaf surface hairs minute, 1/20 mm, very few longer; calyx throat densely bearded; upper calyx teeth broadly triangular, about 4/5 x as long as lower teeth; pedicels 0.3-0.6 mm 12. *hochreutineri*

\+ Upper leaf surface shortly hispidulous or pubescent, many hairs 0.2 mm or more; calyx throat sparsely bearded; upper calyx teeth narrowly triangular, 1/2-3/4 x the lower in length; pedicels 0.7-2.9 mm 30

30. Stems very numerous from a woody stock, stiffly erect; corolla 4.6-5.5 mm 22. *persica*

\+ Stems few from a woody stock, arctuate-ascending; corolla 3.0-4.7 mm 19. *cremnophila*

31. The upper, or at least the floral, leaves linear-lanceolate or linear; stems recurved-pubescent 32

\+ Upper leaves (including the floral ones) ovate or triangular (rarely oblong-lanceolate); stems long-patent or shortly recurved pubescent 35

32. Calyces not exceeding subtending leaves; verticillasters (2-)6-18-flowered; lower leaves 6-14 x 2-7 mm 26. *graeca*

\+ Calyces distinctly exceeding subtending leaves; verticillasters 2-6 (rarely to 16)-flowered; lower leaves 3.5-10.0 x 0.5-5.0 mm 33

33. Lowest floral leaf 3-4 mm, lanceolate 24. *sinaica*

\+ Lowest floral leaf (5.0-)6.5-11.0 mm, elliptic or linear 34

34. Corolla 8.0-9.5 mm; floral leaves mostly elliptic (sometimes ± linear at top) 21. *elliptica*

\+ Corolla 5.5-6.5 mm; floral leaves linear 20. *parviflora*

35. Peduncles or pedicels as long as subtending leaves (leaves c. 5 mm, oblong-lanceolate) 3. *acropolitana*

\+ Peduncles or pedicels not nearly as long as subtending leaves 36

36. Stem hairs patent 37

\+ Stem hairs recurved 38

37. Stem hairs sparse, very long, 0.5-1.0 mm; lower calyx teeth 1.5-1.7 mm — 23. cypria

\+ Stem hairs densely hispidulous or pubescent, less than 0.5 mm long; lower calyx teeth 2.4-2.7 mm — 6. croatica

38. Calyx tube 2.8-3.0 mm, lower teeth 1.2-1.5 mm, not ciliate; corolla 8.0-9.5 mm — 21. elliptica

\+ Calyx tube 1.7-2.2 mm, lower teeth 0.8-1.2 mm, ciliate; corolla 5.3-6.3 mm — 39

39. Plant 10-30 cm tall; leaves up to 7 mm long — 24. sinaica

\+ Plant 40-50 cm tall; leaves up to 11 mm long — 25. hedgei

3.6.2.2.2. 1. M. filiformis (Ait.) Benth., Lab. Gen. Sp. 378 (1834).

Syn: Thymus filiformis Ait., Hort. Kew. ed.1, 2:313 (1789); Piperella filiformis (Ait.) Presl, Fl. Sic. 37 (1826); Cunila thymoides Gouan ex Benth., Lab. Gen. Sp. 378 (1834), nomen; Micromeria rodriguezii Freyn & Janka in Oest. Bot. Zeitschr. 24:16 (1874); Micromeria nervosa (Desf.) Benth. ssp. rodriguezii (Freyn & Janka) Nyman, Consp. Fl. Eur. 520 (1881); Clinopodium filiforme (Ait.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja cordata Moris ex Bertol. ssp. rodriguezii (Freyn & Janka) Bolos & Vigo, Collect. Bot. 14:94 (1983).

Fl. 4-7. On walls, calcareous rocks, cliffs, 30-50 m.

Type: ?

Gen. distrib.: Balearic Is., Corsica.

Easily recognised by its slender, ascending stems to 25 cm, apparently glabrous, small leaves, 1-2-flowered cymes without peduncles and small corollas (to 5 mm).

Sennen described the hybrid M. x knochei Sennen & Bianor in Sennen, Fl. Catal. 139 (1917), supposedly M. nervosa x rodriguezii, from Palma (Balearic Is.)

3.6.2.2.3. 2. M. microphylla (D'Urv.) Benth., Lab. Gen. Sp. 377 (1834).

Syn: Thymus microphyllus D'Urv. in Mem. Soc. Linn. Par. 1:327 (1822); Satureja microphylla (D'Urv.) Guss., Fl. Sic. Prodr. 2:120 (1828), non Briq. (1897); Thymus teneriffae Hortül. ex Benth., Lab. Gen. Sp. 377 (1834), nomen; Micromeria sphaciotica Boiss. & Heldr. ex Benth. in DC., Prodr. 12:220 (1848); Satureja cordata Moris ex Bertol., Fl. Ital. 10:519 (1854)! Micromeria cordata (Moris ex Bertol.) Moris, Diag. Stirp. Sard. Nov. 3 (1857)! Clinopodium cordatum (Moris ex Bertol.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! non Vell. (1825); Clinopodium microphyllum (D'Urv.) O. Kuntze, loc. cit. (1891); Satureja microphylla (D'Urv.) Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897); Satureja filiformis (Ait.) Nym. var. cordata Bég. in Fiori & Paol., Fl. Anal. Ital. 3:58 (1903); Micromeria carpatha Rech. f. in Phyton 1:208 (1949).

Fl. 4-10. Arid calcareous rocks, rocks by the sea, s.l.-20 m.

Type: ?

Gen. distrib.: S Italy, Balearic Is., Malta, Crete.

3.6.2.2.4. 3. M. acropolitana Hal., Consp. Fl. Graec., Suppl. 87 (1908).

Fl. 5. Rocks.

Type: In Acropoli Athenarum, Aug. 1906, Maire, in Maire & Petitmengin, Miss. Bot. Or. exsicc. no. 1073.

Gen. distrib.: Greece.

Shrubs with slender virgate stems to 30 cm tall, recurved pubescent. Leaves and floral leaves oblong-lanceolate, c. 5 x 1.0-2.0 mm, flat, apex obtuse, both sides pubescent. Verticillasters with 2-5-flowered cymes on pedicels as long as subtending leaf. Calyx and corolla like M. microphylla its closest relative.

3.6.2.2.5. 4. M. hispida Boiss. & Heldr. ex Benth. in DC., Prodr. 12:215 (1848).

Syn: Satureja hispida (Boiss. & Heldr. ex Benth.) Nym., Syll. Fl. Eur. 1:102 (1855)! Clinopodium hispidum (Boiss. & Heldr. ex Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)!

Fl. 4-7. Fissures of calcareous rocks, mountain summit, in grass and sparse mountain meadows, 300-2000 m.

Type: [Crete] in rupestribus, Epaschiae Mirabello, iv 1846, Heldreich (K!, MANCH!).

Gen. distrib.: Crete.

Very similar to M. microphylla.

3.6.2.2.6. 5. M. marginata (J.E.Sm.) Chater in Bot. J. Linn. Soc. 64:381 (1971).

Syn: Thymus marginatus J. E. Smith ex Dickson, Coll. Dried Pl. fasc. 3, t.71 (1791); Thymus piperella All., Fl. Pedem. 1:21, t.37, f.3 (1785), non L. (1753); Calamintha piperella Reichenb., Fl. Germ. Excurs. 328 (1830), non sensu Schloss & Vukot (1857); Micromeria piperella (All.) Benth., Lab. Gen. Sp. 379 (1834); Satureja piperella (All.) Bert., Fl. Ital. 6:50 (1847); Micronema piperella (All.) Schott. in Oest. Bot. Wochenbl. 7:95 (1857); Tendana piperella (All.) Reichenb. f. in Oest. Bot. Wochenbl. 7:160 (1857).

Fl. 7-9. Rock fissures, stony places, cliffs, open dolomitic rocks, 1000-1600 m.

Type: ?

Gen. distrib.: N Italy, SE France (Maritime Alps).

Most closely related to M. croatica.

3.6.2.2.7. 6. M. croatica (Pers.) Schott. in Oest. Bot. Wochenbl. 7:93 (1857).

Syn: Thymus croaticus Pers., Syn. Pl. 2:130 (1806); Calamintha croatica (Pers.) Host, Fl. Austr. 2:132 (1831); Micromeria subcordata Vis. ex Benth., Lab. Gen. Sp. 379 (1834); Thymus subcordatus (Vis.) Vis., Fl. Dalm. 2:197, t.19 (1847); Micromeria serpyllifolia Scheele in Linnaea 22:593 (1849), non (M. Bieb.) Boiss. (1859); Calamintha piperella sensu Schloss. & Vukot., Syll. Fl. Croat. 80 (1857), non Reichenb. (1830); Satureja croatica (Pers.) Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897).

Fl. 7-8. Stony places, Quercus woods amongst rocks, calcareous rock fissures, 300-1900 m.

Type: Dalmatia, ann. 1832, Visiani (lecto. K!).

Gen. distrib.: Yugoslavia.

Similar to M. marginata but whole plant densely long patent-pubescent; leaves 5.0-10.0 x (2.5-)4.0-8.0 mm; verticillasters with up to 9-flowered cymes, peduncles 0.5-6.0 mm, pedicels 1.5-3.0 mm; calyx tube 2.5-3.0 mm, throat very densely hairy, upper lip straight, 1.8-2.2 mm, lower lip slightly curving upward, 2.4-2.7 mm, teeth all very narrowly triangular to almost setaceous, upper 1.8-2.2 mm, lower 2.4-2.7 mm; corolla tube 6.5-10.0 mm, upper lip 1.5-2.0 mm, lower lip 2.0-4.0 mm.

3.6.2.2.8. 7. M. nervosa (Desf.) Benth., Lab. Gen. Sp. 376 (1834).

Syn: Satureja nervosa Desf., Fl. Atl. 2:9, t.121 f.2 (1798); Satureja capitata Desf., loc. cit. (1798), non L. (1753); Satureja filiformis Ten., Prodr. Fl. Nap. (1811); Thymus filiformis Sieb. ex Benth., Lab. Gen. Sp. 376 (1834), nomen; Satureja plumosa Hampe in Flora (Regensburg) 25(1):127 (1842); Micromeria plumosa (Hampe)

Buek, Cand. Ind. 3:297 (1858); *Micromeria hirsuta* Mazziar. ex Nym., Consp. Fl. Eur. 590 (1881), nomen; *Clinopodium nervosum* (Desf.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); *Satureja graeca* L. ssp. *nervosa* (Desf.) Bolos & Vigo, Collect. Bot. 14:94 (1983).

Fl. 2-7, rarely 12. Limestone slopes, in macchie, calcareous or serpentine rocks, pine woods, roadsides, s.l.-800 m.

Type: [Morocco] in fissuris rupium Atlantis, *Desfontaines* (holo. P).

Gen. distrib.: Greece, Aegaean Is., Crete, Balearic Is., Cyprus, SW Turkey, Syria, Israel, Jordan, Egypt, Libya, Algeria, Tunisia.

3.6.2.2.9. 8. *M. macrosiphon* Coss. in Bull. Soc. Bot. Fr. 27:72 (1880).

Syn: *Satureja peltieri* Maire in Bull. Soc. Hist. Nat. Afr. Nord 20:34 (1929); *Satureja macrosiphon* (Coss.) Maire in Jahandiez & Maire, Cat. Pl. Maroc 3:647 (1934)!

Fl. 3-6. Rocky limestone slopes, dense macchie, cliffs and steep slopes, 20-1300 m.

Type: Morocco: Gorge D'Amsemmez, vers b. cap. Guir, Agadir, 16 v 1877, *Ibrahim* (holo. K!).

Gen. distrib.: Morocco.

A shrub to 1 m with many short spreading branches, narrowly linear-elliptic leaves, verticillasters of solitary flowers on short pedicels and peduncles, and distinctive narrowly parallel-sided tubular calyces and very narrowly tubular corollas 11-15 mm long. There is some similarity in habit to *M. varia* of the Canary Is., but it probably comes closest to the Moroccan/Algerian group of *M. fontanesii*, *M. debilis* and *M. hochreutineri*.

3.6.2.2.10. 9. *M. fontanesii* Pomel, Nouv. Mat. Fl. Atlant. 123 (1874).

Syn: *Satureja filiformis* Desf., Fl. Atlant. 2:8 (1798); *Satureja* battandieri Briq. in Ann. Conserv. Bot. Jard. Genéve 2:186 (1898).

Fl. 4-5. Shady limestone rocks, crevices of limestone and volcanic rocks, 20-800 m.

Type: Morocco, Desfontaines (holo. P); illustrated in Desf., Fl. Atlant. 2, t.121 (1798).

Gen. distrib.: Morocco, Algeria.

Closely related to M. debilis and M. hochreutineri, but distinguished by the hispid pubescence in all parts of the plant, and longer, slightly divergent calyx teeth, ciliate on the margins. These apparently trivial differences hold even where the distributions of these species overlap in Morocco.

Some specimens collected near Oran, Algeria [Munby 79; 10 viii 1930, A. Faure; 30 vi 1880, E. Cosson] have a strong similarity to M. cremnophila of the eastern Mediterranean, but also have a clear affinity to M. fontanesii. A hybrid between these species seems unlikely and an outlying population of M. cremnophila also seems improbable. Further study is required.

Micromeria bourlieri Maire & Lievre in Bull. Soc. Hist. Nat. Afr. Nord 1921, 12:173 (1921) [syn. Satureja x bourlieri (Maire & Lievre) Maire in Bull. Soc. Bot. Hist. Nat. Afr. Nord 32:60 (1931)] is supposedly a hybrid between M. fontanesii and M. graeca; it was found with the presumptive parents.

36.22.11 10. M. weilleri (Maire) A. Doroszenko, comb. nov.

Syn: Satureja weilleri Maire, Bull. Soc. Hist. Nat. Afr. Nord 19:62 (1928).

Fl. 4-5. Quartz and silicious rock crevices, 600-630 m.

Type: Morocco: secus amnem Ksiksou prope Oulmes, ad rupes vulcanicas, 800 m, fl. Apr. Mai., Jahandiez & Weiller s.n. (holo. AL).

Gen. distrib.: Morocco.

Closely related to M. fontanesii and possibly not specifically distinct. It has more revolute leaves, 8-36-flowered verticillasters on peduncles 2.0-6.5 mm long, pedicels only 0.2-0.5 mm, calyx tube 1.5-1.7 mm, throat more strongly hairy, and teeth more narrowly triangular.

3.6.2.2.12 11. M. debilis Pomel, Nouv. Mat. Fl. Atlant. 122 (1874).

Syn: Satureja debilis (Pomel) Briq. in Ann. Conserv. Jard. Bot. Genéve 7-8:203 (1904), non (Bunge ex Ledeb.) Briq. (1897); Micromeria microphylla Cosson, in schaed? [see Conserv. Jard. Bot. Gard. Genéve 7-8:201 (1904)] non. Benth. (1834); Satureja briquetii Maire in Jahandiez & Maire, Cat. Pl. Maroc 3:646 (1934).

Fl. 4-6, rarely 9. Limestone rocks, 650-1500 m.

Type: Morocco: escarpments et rochers des montagnes, Zouia pres Garrouban. (Collector?).

Gen. distrib.: Morocco, Algeria.

Similar to M. fontanesii but distinguished by short, tightly recurved pubescence on upper part of stem, long patent pilose at base of stem; calyx tube 1.6-1.9 mm, densely recurved-puberulent, lips 0.5-0.7 mm; teeth more broadly triangular, upper 0.3-0.4 mm, lower 0.5-0.7 mm; corolla tube 2.3-2.4 mm.

3.6.2.2.13. 12. M. hochreutineri (Briq.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 7:273 (1916).

Syn: Satureja hochreutineri Briq., Ann. Conserv. Jard. Bot. Genéve 7-8:201 (1904); Micromeria microphylla sensu Ball, J. Linn. Soc. Bot. 16:613 (1878); ?Satureja guichardii Quetzel & Zaffran, Bull. Soc. Hist. Nat. Afr. Nord 52:219 (1961); ?Micromeria guichardii (Quetzel & Zaffran) Brullo & Furnari, Webbia 34:168 (1979).

Fl. 3-7. Rocks, dry limestone slopes, in gulleys amongst pines, 200-2100 m.

Type: Morocco: Oran, oasis de Tiout, chaine rocheuse au S. de l'oasis, 1050 m, 31 v, Collector? no. 549; id. rochers arides au N. de l'oasis de Mograr Foukani, 950 m, 4 vi, Collector? no. 644.

Gen. distrib.: Morocco, Algeria.

Similar to *M. fontanesii* but distinguished by very short tightly recurved pubescent on all parts of stem; leaves only minutely hairy on upper side; calyx tube 1.4-1.9 mm, densely, very shortly hispidulous, throat densely hairy; calyx lips 0.5-0.7 mm, upper teeth 0.4-0.6 mm, lower teeth 0.5-0.7 mm.

3.6.2.2.14. 13. *M. brivesii* Batt. in Bull. Hist. Nat. Afr. Nord 13:69 (1922).

Syn: *Satureja brivesii* (Batt.) Murbeck in Lunds Univ. Arssk. 2:30 (1923).

Fl. 5. Alluvial soil, 1000 m.

Type: ?

Gen. Distrib.: Morocco.

Near to *M. fontanesii* but with strongly revolute, softly hirsute-pubescent leaves, verticillasters usually of solitary flowers, and the corollas twice as long as the calyx.

3.6.2.2.15. 14. *M. conferta* (Coss.) De Stefani in Bol. Orto Bot. Giard. Palermo 11:148 (1912).

Syn: *Micromeria juliana* (L.) Benth. ex Reichenb. var. *conferta* Coss ex Dur. & Bar., Fl. Lib. Prodr. 186 (....); *Satureja conferta* (Coss.) Beg. & Vacc., Spec. Nov. Rar. Fl. Libia 2 (1912).

Fl. 3-5, rarely 9. Limestone rocks, gulleys, in macchie, 100-800 m.

Type: ?

Gen. distrib.: N Libya.

Related to M. juliana. It is distinguished by the densely recurved puberulent indumentum on all parts of the plant, verticillasters of only 1-2 sub-sessile flowers, and shorter calyx teeth (0.5-0.8 mm).

3.6.2.2.16 15. M. myrtifolia Boiss. & Hohen in Boiss., Diagn. ser. 1, 5:19 (1844).

Syn: Micromeria juliana (L.) Benth. ex Reichenb. var. myrtifolia (Boiss. & Hohen) Boiss., Fl. Or. 4:569 (1879); Micromeria lycia Stapf in Denkschr. Akad. Wiss. Wien, Math. Nat. Kl. 50(2):94 (1885).

Fl. mainly 4-8, but a few at any time. Rock crevices, shady banks, Pinus brutia woods, Quercus coccifera scrub on limestone, screes, boulder clay and serpentine, stony grassland, s.l.-1900 m.

Type: [Iraq] in rupestribus montis Gara Kurdistaniae, Kotschy (holo. G).

Gen. distrib.: Greece, Crete, Aegaean Is., Turkey (mainly Turkey-in-Europe and S & E Anatolia), Cyprus, Syria, N Iraq, W Iran, Israel, Lebanon.

Similar to M. juliana, and frequently confused with it, but distinguished by the calyx always villous in the throat and the relatively shorter calyx teeth. A common species of the eastern Mediterranean.

3.6.2.2.17 16. M. juliana (L.) Benth. ex Reichenb., Fl. Germ. Excurs. 311 (1831).

Syn: Satureja juliana L., Sp. Pl. 567 (1753); Satureja spicata Crantz, Inst. Rei Herb. 1:525 (1766), non Garsault (1764), non Vis. (1847); Sabbatia corymbosa Moench, Meth. 386 (1794); Satureja virgata Stokes, Bot. Mat. Med. 3:299 (1812); Satureja sophia Hort.

ex Steud., Nom. Bot. ed.1, 733 (1821), nomen; Satureja hirsuta J. & K. Presl, Delic. Prag. 79 (1822); Satureja parviflora Presl, Fl. Sic. 36 (1826); Micromeria reinholdii Heldr. ex Boiss., Fl. Or. 4:570 (1879); Micromeria hirsuta (J. & K. Presl) Nym., Consp. Fl. Eur. 590 (1881); Clinopodium julianum (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Micromeria obtusiflora Gandoger, Fl. Crete 80 (1916); Micromeria minoa Coust. & Gandog. in Bull. Soc. Bot. Fr. 1916, 58:12 (1917); Micromeria juliana (L.) Benth. ex Reichenb. var. minoa (Coust. & Gandog.) Rech. f. in Oest. Bot. Zeitschr. 84:177 (1934).

Fl. 4-10. Calcareous rocks, rocky slopes in macchie, roadsides, limestone cliffs, schistose rocks, s.l.-1700 m.

Type: Described from Italy: in Hetruria, in Tyrrheni maris asperis, Florentinae. (Hb. Linn. 723/1?).

Gen. distrib.: Greece, Crete, Italy, Yugoslavia, Albania, Spain, Portugal, Bulgaria, W Turkey, Aegaean Is.

3.6.2.2.18. 17. M. cristata (Hampe) Griseb., Spicil. Fl. Rumel. 2:122 (1844).

Syn: Thymus cristatus Hampe in Flora (Regensburg) 20(1):233 (1837)! Thymus inodorus Friv. ex Griseb., Spicil. Fl. Rumel. 2:122 (1814), nomen, non Desf. (1798); Satureja cristata (Hampe) Nym., Syll. Fl. Eur. 1:102 (1855)! Clinopodium cristatum (Hampe) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)!

The species is easily identified by the imbricate-leaved resting buds at the base of the stems. A key to the subspecies is provided by Davis, Fl. Turkey vol. 7 (1982).

ssp. cristata

Type: [Bulgaria] in Rumelien, Frivaldsky (iso. K!).

Fl. 6-9. Dry calcareous rocks, gravelly clay, rock fissures, 200-1900 m.

Gen. distrib.: N & C Balkans, N Turkey.

spp. xyllorhiza (Boiss. & Heldr.) P. H. Davis in Notes R. B. G. Edinb. 21:64 (1952).

Syn: Micromeria xyllorhiza Boiss. & Heldr. in Boiss., Diagn. ser. 1, 12:49 (1853).

Fl. 7-8. Rock fissures, limestone cliffs, 1500-1900 m.

Type: [Turkey] in fissuris rupium Tauri Lycaonici, 1520 m, in monte Anemas, Heldreich (lecto. G).

Gen. distrib.: SW Anatolia.

ssp. phrygia P. H. Davis, Notes R. B. G. Edinb. 38:40 (1980).

Fl. 7-8. Limestone rocks, 1000-2000 m.

Type: Turkey B2 Kutahya: d. Gediz, Saphane Da., 1900-2000 m, sunny rocks, flowers white with mauve spotting on lip, 27 viii 1950, Davis 18457 (holo. E!, iso. K).

Gen. distrib.: Western C & SW Anatolia.

Intermediate between ssp. xylorrhiza and ssp. carminea.

ssp. orientalis P. H. Davis, Notes R. B. G. Edinb. 38:41 (1980).

Syn: Micromeria elliptica C. Koch var. pubescens Boiss. & Kotschy ex Boiss., Fl. Or. 4:571 (1879)!

Fl. 8-9. Cliff ledges, amongst rocks, 1400-2100 m.

Type: Turkey B6 Malatya: Gurun to Malatya, 40 km from Malatya, c. 1400 m, cliff ledges, cracks, flowers pale lilac, 7 viii 1956, McNeill 461 (holo. E!).

Gen. distrib.: E Anatolia.

ssp. *carminea* (P. H. Davis) P. H. Davis, Notes R. B. G. Edinb. 21:65 (1952).

Syn: *Micromeria carminea* P. H. Davis, Kew Bull. 1949:400 (1949).

Fl. 7. Rock crevices, 1800-1900 m.

Type: [Turkey] Denizli: d. Acipayam, Boz Da. above Geyran yayla, 1800-1900 m, crevices of limestone rock with *Globularia dumulosa*, flowers almost pure carmine, 16 vii 1947, *Davis* 13403 (holo. K, iso. E!).

Gen. distrib.: SW Anatolia.

3.6.2.2.19 18. *M. kerneri* Murb., Lunds Univ. Arsskr. 27(5):53 (1892).

Syn: *Satureja kerneri* (Murb.) Fritsch, Exkursionsfl. ed.3, 449 (1922).

Type: [Yugoslavia] Mostar, 29 vi 1889, *S. Murbeck* (holo. LD?).

Gen. distrib.: Yugoslavia.

Similar to *M. juliana* but distinguished by the very dense, shortly patent-pubescent indumentum, 2-6-flowered cymes, the pedicels and peduncles longer than the calyx, with lower calyx teeth more than half the calyx tube length and clearly longer than the upper teeth, and very small corollas (3.5-5.5 mm).

3.6.2.2.20 19. *M. cremnophila* Boiss. & Heldr., Fl. Or. 4:570 (1879).

Syn: *Clinopodium cremnophilum* (Boiss. & Heldr.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! *Satureja cremnophila* (Boiss. & Heldr.) Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897)!

The subspecies are distinguished on indumentum and slight differences in leaf shape.

ssp. *cremnophila*

Fl. 6-8. Calcareous rocks, amongst *Pinus* and *Abies*, 250-1900 m.

Type: Greece: in m. Oeta (nunc m. Katavothra) Phthiotides. In regione abietina, alt. 4500-6000 ped., 14 vii 1879, Heldreich (K!).

Gen. distrib.: C & NW Greece, Albania.

ssp. amana (Rech. f.) P. H. Davis, Notes R. B. G. Edinb. 38:40 (1980).

Syn: Micromeria amana Rech. f., Svensk. Bot. Tidsskr. 43:42 (1949)!

Fl. 6-9. Gorges, rocky calcareous slopes, 700-2200 m.

Type: [Turkey] Mons Amanus, mont de Düldül, 1500-2000 m, viii 1911, Haradjian 3887 (holo. S, iso. E! W).

Gen. distrib.: S Anatolia.

ssp. anatolica

Fl. 5-8. Limestone rocks, crevices of boulders, pinewood with scree and rock faces, 750-1800 m.

Type: Turkey B9 Van: 5 km N of Çertak, in crevices of boulders, 25 vii 1954, P. H. Davis & O. Polunin (D. 23258) (holo. E!, iso. K).

Gen. distrib.: S & E Anatolia.

Similar to ssp. amana but stems patent pubescent-hispidulous, upper side of leaves hispidulous to scabridulous.

3.6.2.221 20. M. parviflora (Vis.) Reichenb., Fl. Germ. Excurs. 859 (1832).

Syn: Satureja parviflora Vis., Flora 12(1):13 (1829), non Presl (1826); Satureja inodora Host, Fl. Austr. 2:135 (1831); Clinopodium parvifolium [sic] O. Kuntze, Rev. Gen. Pl. 2:515 (1891).

Fl. 5-7. Limestone rocks, 250-1100 m.

Type: In montibus Pastrovich in extremo Dalmatiae confinio prope Albaniam, Aug., Visiani.

Gen. distrib.: S Yugoslavia, Albania.

3.6.2.2.22. 21. M. elliptica C. Koch, Linnaea 21:669 (1849).

Syn: Micromeria calvertii Boiss., Fl. Or. 4:571 (1879), nomen; Clinopodium ellipticum (C. Koch) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja elliptica (C. Koch) Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897)! non Briq., loc. cit. 300 (1897); Satureja kochii Popov ex Grossheim, Fl. Kavkaza 3:330 (1932), nomen; Micromeria elegans Boriss., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 15:330 (1953).

Fl. 7-8. Crevices of dry igneous outcrops, open Abies woods amongst rocks, 1180-2000 m.

Type: [Turkey] in Hochgebirge des Gaues Pertakrek (Peterek) auf Urgestein, c. 1520-1830 m, C. Koch (holo. B! iso G).

Gen. distrib.: NE Anatolia.

3.6.2.2.23 22. M. persica Boiss., Diagn. ser.1, 12:48 (1853).

Syn: Satureja persica (Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897)!

Fl. 4-7. Limestone hillsides, in fissures or on ledges of cliffs, 670-2650 m.

Syntypes: [Iran] Persia australis, Aucher-Eloy 5190; Prope ruinas u. Persepolis, pr. monumentum Nakschi Rustam, iv 1842, T. Kotschy 882 (K!).

Gen. distrib.: Iran, Iraq.

Easily identified by the numerous stiffly erect slender, simple or little branched stems arising from a stout rootstock, verticillasters of 1-3-flowered cymes, with pedicels and peduncles usually longer than the 2-3 mm calyx. Closely related to M. elliptica and M. sinaica.

3.6.2.2.24 23. M. cypria Kotschy in Unger, Ins. Cypern 270 (1865).

Syn: Satureja graeca L. ssp. cypria (Kotschy) Holmboe, Veg. Cyprus 159 (1914); Satureja cypria (Kotschy) Holmboe, loc. cit. (1914), nomen.

Fl. (1-)3-5(-7). Limestone or igneous rocks, in crevices, 300-1300 m.

Type: ?

Gen. distrib.: Cyprus.

3.6.2.2.25 24. M. sinaica Benth., Lab. Gen. Sp. 380 (1834).

Syn: Clinopodium sinaicum (Benth.) O. Kuntze, Rev. Gen. Pl. 2:516 (1891); Satureja sinaica (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897).

Fl. 4-6, 8-10. Mountain slopes, in Juniper woods, sandstone rock crevices, 1000-1900 m.

Type: Silesle Arab. Rochers du Sinai, vi 1832, N. Bové 61 (holo. K!)

Gen. distrib.: Sinai, Jordan, Oman.

A very variable species, particularly in indumentum and leaf size. Closely related to M. persica and M. elliptica.

3.6.2.2.26 25. M. hedgei Rech. f., Fl. Iranica 150:276 (1983).

Fl. 2, 6. Steppe on stony slopes, 1000-1700 m.

Type: Iran: Bashagerd, Gariche, 1000 m, 20 ii 1973, Iranshahr & Moussavi 15436 (E!, W), Iranshahr & Moussavi 35809 (E!).

Gen. distrib.: S Iran.

Very similar to M. sinaica, but taller, with sessile cymes usually with more flowers, larger leaves, and smaller calyx.

3.6.2.2.27 26. M. graeca (L.) Benth. ex Reichenb., Fl. Germ. Excurs. 311 (1831).

Syn: Satureja graeca L., Sp. Pl. 568 (1753); Satureja congesta

Hornem., Hort. Bot. Hafn. 2:541 (1815), non (Boiss. & Hausskn.) Briq. (1897); *Satureja sessiliflora* Presl, Fl. Sic. 36 (1826); *Satureja sicula* Guss., Fl. Sic. 2:89 (1844); *Micromeria sicula* (Guss.) Nym., Consp. Fl. Eur. 590 (1881); *Clinopodium graecum* (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); *Satureja deserti* J. Thieb., Bull. Soc. Bot. Fr. 96:211 (1950).

A very variable species, particularly in Italy. A key to the subspecies is provided in Flora Europaea 3:169 (1972).

ssp. *graeca*

Syn: *Thymus hirtus* Banks & Soland. in Russ., Nat. Hist. Aleppo ed.2, 2:256 (1794); *Thymus micranthus* Brot., Fl. Lusit. 1:176 (1804); *Satureja micrantha* (Brot.) Hoffm. & Link., Fl. Port. 1(5):142 (1810).

Fl. 3-8. Sandstone, shaley, limestone and mica-schist slopes, rock crevices, roadsides, macchie, garrigue, 20-1300 m.

Type: [Greece] in Archipelagum.

Gen. distrib.: Spain, Italy, Tunisia, Algeria, Corsica, W & S Turkey, Lebanon, Syria, Balearic Is., Portugal, Sardinia, Greece, Yugoslavia, Crete.

ssp. *imperica* Chater, Bot. J. Linn. Soc. 64:381 (1971).

Syn: *Micromeria thymoides* DeNot, Repert. Fl. Ligust. 54 (1844), non Webb & Berth. (1844); *Thymus notarisii* Zumag., Fl. Pedem. 1:226 (1849); *Satureja thymoides* (DeNot) Nym., Syll. Fl. Eur. 1:102 (1854); *Clinopodium thymoides* (DeNot) O. Kuntze, Rev. Gen. Pl. 2:516 (1891); *Satureja graeca* L. ssp. *graeca* var. *thymoides* (DeNot.) Briq., Lab. Alp. Mar. 418 (1895); *Micromeria notarisii* (Zumag.) Gandoger, Nov. Consp. Fl. Eur. 367 (1910).

Fl. 5-10. Calcareous rocks, lowlands.

Gen. distrib: N Italy.

ssp. *garganica* (Briq.) Guinea, Bot. J. Linn. Soc. 64:381 (1971).
Syn: *Satureja graeca* L. ssp. *garganica* Briq., Lab. Alp. Mar. 421 (1895); *Satureja garganica* (Briq.) Briq., loc. cit. (1895), nomen.
Fl. 4-6. Dry calcareous rocks, steep schistose slopes, 200-650 m.
Gen. distrib.: SE Italy.

ssp. *longiflora* (C. Presl) Nym., Consp. Fl. Eur. 590 (1881).
Syn: *Satureja longiflora* C. Presl, Fl. Sic. 36 (1826), non Boiss. & Hausskn. (1879); *Satureja canescens* Guss., Pl. Rar. 228, t.42 (1826); *Micromeria canescens* (Guss.) Benth., Lab. Gen. Sp. 376 (1834); *Micromeria longiflora* (C. Presl) Tod. ex Nym., Consp. Fl. Eur. 590 (1881), nomen.
Fl. 4-6. Rocky places, lowlands.
Gen. distrib.: C & S Italy, Corfu.

ssp. *tenuifolia* (Ten.) Nym., Consp. Fl. Eur. 590 (1881).
Syn: *Satureja tenuifolia* Ten., Prodr. Fl. Nap. 33 (1826); *Thymus virgatus* Ten., loc. cit. 35 (1826); *Micromeria tenuifolia* (Ten.) Reichenb., Fl. Germ. Excurs. 311 (1831); *Micromeria longifolia* Scheele, Linnaea 22:593 (1849); *Clinopodium tenuifolium* (Ten.) O. Kuntze, Rev. Gen. Pl. 2:216 (1891).
Fl. 4-8(-10). Limestone rocks and banks, walls, 20-275 m.
Lectotypes: in regno Neapolitano, ann. 1845, *R. C. Alexander*; in nostris montibus, v 1830, *Tenore* (K!).
Gen. distrib.: S Italy, Sardinia.

ssp. *consentina* (Ten.) Guinea, Bot. J. Linn. Soc. 64:381 (1971).
Syn: *Satureja consentina* Ten., Fl. Neap. Prodr. App. 5:17 (1826);

Satureja angustifolia C. Presl, Fl. Sic. 36 (1826); Micromeria consentina (Ten.) N. Terracc., Nuov. Giorn. Bot. 5:227 (1873); Satureja graeca L. ssp. consentina (Ten.) Arcangeli, Comp. Fl. Ital. 540 (1882); Clinopodium consentinum (Ten.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891).

Type: [Italy] Nicolosi pr. Catane, 19 ix 1834, A. Richard (lecto. K!).

Gen. distrib.: S Italy.

ssp. laxiflora (Post) Mout., Fl. Liban Syrie 3:176 (1979).

Syn: Micromeria graeca (L.) Benth. ex Reichenb. ssp. graeca var. laxiflora Post, Fl. Syr. Palest. Sinai 621 (1896).

Type: ?

Gen. distrib.: Lebanon, Syria.

3.6.2.2.28 27. M. fruticulosa (Bertol.) A. Doroszenko, comb. nov.

Syn: Thymus fruticulosus Bertol., Jour. Bot. Appl. 4:76 (1814); Satureja fasciculata Rafin., Prec. Decouv. 39 (1814); Satureja approximata Biv., Stirp. Rar. Sic. 4:13 (1816), non Friv. (1836); Micromeria approximata (Biv.) Reichenb., Fl. Germ. Exsurs. 859 (1832); Thymus punctatus Tineo ex Benth. in DC., Prodr. 12:217 (1848), nomen, non Vis. (1843); Clinopodium approximatum (Biv.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja fruticulosa (Bertol.) Grande in Nuov. Giorn. Bot. Ital. n.s. 32:91 (1925); Micromeria graeca (L.) Benth. ex Reichenb. ssp. fruticulosa (Bertol.) Guinea, Bot. J. Linn. Soc. 64:381 (1971).

Type: ?

Gen. distrib.: S Italy.

Clearly distinguished from M. graeca, to which it was subordinated in Flora Europaea (1972), by its robust shrubby habit (not suffruticose as in M. graeca), numerous small linear leaves and axillary fascicles of leaves, and pubescent-hirsute indumentum.

3.6.2.2.29 28. M. inodora (Desf.) Benth., Lab. Gen. Sp. 375 (1834).

Syn: Thymus inodorus Desf., Fl. Atlant. 2:30 (1798); Thymus hispanicus Hort. ex Poir., Encycl. 7:646 (1806); Micromeria barceloi Willk., Oest. Bot. Zeitschr. 25:111 (1875)! Clinopodium inodorum (Desf.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja fontanesii Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897); Thymus mutisii Caball., Mem. Soc. Esp. Hist. Nat. 8:279 (1915); Satureja barceloi (Willk.) Pau, Bol. Soc. Esp. Hist. Nat. 21:202 (1921)! Satureja inodora (Desf.) Pau, loc. cit. (1921), non Host (1831), non Salzm. ex Benth. (1834).

Fl. 1-4, 11-12, rarely other times. Limestone scree, dry calcareous rocks, sand hills, s.l.-200 m.

Type: ?

Gen. distrib.: Algeria, rare in Morocco, S Spain and Balearic Is.

A dwarf, much-branched shrub easily recognised by the numerous very small acicular leaves.

3.6.2.2.30 The "biflora" complex.

This complex is named after Micromeria biflora (Buch.-Ham. ex D. Don) Benth. Its range is from the Himalayas eastward to China, India (Nilgiris), Pakistan, Afghanistan, S and W Arabia, and E African mountains to S Africa. The complex is extremely variable in habit, inflorescence density (from 1 to many flowers in the floral leaf axils), leaf shape, indumentum, and nutlet shape.

Few authors have attempted a scheme encompassing the whole complex. The earliest arrangements (Bentham 1834, 1848) relied upon very scanty material and in consequence were very much easier to deal with. Bentham's first arrangement included four species: M. ovata, M. punctata, M. biflora, and M. forskahlei; they were not placed consecutively. These four species were described from 1 specimen from Abyssinia, 1 specimen from Abyssinia, 3 specimens from India, and 1 specimen from Arabia, respectively; based upon this material each species was quite distinct. Bentham's second revision (1848) included the same four species. The only major change was to place M. punctata, M. biflora and M. forskahlei consecutively; S. ovata was related to M. microphylla rather than to these "biflora" complex species.

Briquet's arrangement in Natürlichen Pflanzenfamilien was similar to that of Bentham (1848), including Satureja punctata for Abyssinian material, S. biflora for plants from India, Abyssinia and the Cape Province, and S. imbricata for plants from Arabia. The very broad view of S. biflora was taken up by various Flora writers, which was appropriate since their restricted view of Micromeria usually only included one of the "biflora" complex taxa. However, there have been attempts in recent years to delimit the taxa within the "biflora" complex more satisfactorily, notably Walther & Walther (1957) who dealt mainly with African material.

Walther & Walther (1957) adopted a narrow view of the taxa within the complex, describing five species. What follows is a translation of their key.

1. Cymes 1-2-flowered; pedicels mostly much longer than the bracts; calyx distinctly 2-lipped, teeth long M. biflora

\+ Calyx mostly 3 or more flowered; pedicels shorter or about as long as the bracts; calyx campanulate or cylindrical, seldom weakly 2-lipped; calyx teeth short 2

2. Cymes elongate or intermixed with foliage leaves; branches mostly erect; nutlets beaked M. purtschelleri

\+ Cymes neither conspicuously elongate nor intermixed with foliage leaves; branches ascending; nutlets rounded to pointed 3

3. Middle and upper stem leaves lanceolate, at the base gradually narrowing; stem hairs only shortly recurved M. schimperi

\+ Middle and upper stem leaves ovate, at the base cordate or rounded 4

4. Leaf margins strongly revolute or bent back; underside of lamina strongly bristly or villous M. ovata

\+ Leaf margins not or weakly revolute; underside of lamina sparsely hairy; punctate glands distinctly visible M. punctata

Examining a large number of African specimens, I found this key rather difficult to use. There were many instances when one could have gone to either branch of a couplet.

A number of taxa were not considered by Walther & Walther (1957), some of which are listed in Cufodontis, Enum. Pl. Aeth. Sperm. 1:821-824 (1974) [M. neumannii, Satureja ellenbeckii, S. contardoi, S. quartiniana and S. unguentaria]. In addition there is Micromeria remota from Socotra in Vierhapper, Flora von Südarabien und Sokotra 117-118 (1907).

Having spent a great deal of time trying to put the complex into some reasonable order, I cannot claim to have succeeded.

However, it would seem that the complex is too variable to comprise just one species. As a compromise I have keyed out the most distinctive species within the complex (*M. cinerea*, *M. longiflora*, *M. imbricata* and *M. contardoi*) and list the remainder below with their synonymy.

3.6.22.31. 29. *M. cinerea* A. Doroszenko, sp. nov.

Cushion-forming shrub, 3-10(-25) cm; leafy stems filiform; whole plant densely greyish long patent-pubescent. Leaves ovate, rounded at base, apex obtuse, 3.0-6.5 x 1.2-3.3 mm, flat or tightly revolute. Verticillasters crowded, each 2-10-flowered, peduncles 0.5-0.7 mm, pedicels 0.5-1.0 mm. Calyx cylindrical; tube 1.6-2.0 mm, sparsely hairy in throat; upper lip 0.8-1.0 mm; lower lip 0.9-1.4 mm; teeth narrowly triangular-acuminate, upper 0.7-0.8 mm, lower 0.9-1.4 mm. Corolla rosy to pale lilac; tube 3.0-4.5 mm; upper lip 1.0-1.5 mm, emarginate; lower lip 1.5-2.5 mm.

Fl. 3-4, Rock crevices, red granite, ravines, roadsides, 1600-2600 m.

Type: Saudi Arabia: Tanoumah, 12 km S of An Numas, on the Taif-Abha road, pink granite, watered valley, 6500 ft., 17 iii 1980, *J. S. Collenette* 2136 (holo. E!).

Specimens seen: Saudi Arabia: Asir Prov. 122 km N of Abha, in crevices in rocky area, 4 iv 1980, *A. K. Nasher* IH32; S of Taif, 5-7000 ft., iv 1968, *H. Leach*; Tanoumah basin, S of An Nimas, ± 200 km N of Abha, in rock crevices, 2600 m, 17 iii 1980, *J. J. Lavranos* 18387 & *J. S. Collenette*; 5 km S of Biljurshi, Grande Lavori road, near edge of scarp, 7000 ft., exposed crevices, Fl. pink, non-aromatic, 30 iv 1981, *J. S. Collenette* 2575.

Gen. distrib.: W Saudi Arabia.

Easily recognised by the low, cushion-forming habit, numerous small, revolute, round-tipped leaves, with very dense, greyish indumentum. It comes closest to M. serbaliana.

3.6.2.2.32 30. M. longiflora Hochst. in Schimp., Pl. Abyss. Exsicc. no. 2192 (1850).

Syn: Micromeria unguentaria Schweinf., Beitr. Fl. Aethiop. 124 (1867); Satureja unguentaria (Schweinf.) Cufodontis, Bull. Jard. Bot. Brux. 32 (Suppl.):824 (1962).

Type: [Ethiopia] in montibus prope Dschadscha, 5700 ped., 30 ix 1854, Schimper 2192 (holo. K!).

Gen. distrib.: Ethiopia.

Identified by the long, narrow leaves and dense recurved pubescence. I have only seen the type.

3.6.2.2.33 31. M. serbaliana Danin & Hedge, Notes R. B. G. Edinb. 32:261 (1973).

Fl. 8-9. Granite cliffs, rocky places, 1700-1850 m.

Type: Sinai, Gebel Serbal, cliffs of smooth red granite, NW exposure, 6 viii 1968, A. Danin (iso. E!).

Gen. distrib.: Sinai, W Saudi Arabia.

Not usually placed in the "biflora" complex, but there are similarities to M. cinerea and M. imbricata. It is distinguished by its low, cushion-forming habit, very slender stems (0.2-0.3 mm diameter), densely hispid to scabrous leaves (2-4 x 1-2 mm) also with glandular hairs.

3.6.2.2.34. 32. M. imbricata (Forssk.) Christensen, Dansk Bot. Arkiv 4(3):21 (1922).

Syn: Thymus imbricatus Forssk., Fl. Aegypt.-Arab. 108 (1775)! Thymus piperella Vahl, Symb. Bot. 2:65 (1791), non L. (17..), non

All. (1785); *Thymus biflorus* Buch.-Ham. ex D. Don, Prodr. Fl. Nepal. 112 (1825); *Micromeria biflora* (Buch.-Ham. ex D. Don) Benth., Lab. Gen. Sp. 378 (1834); *Micromeria forskahlei* Benth., loc. cit. 379 (1834); *Micromeria microphylla* (D'Urv.) Benth. var. *imbricata* Balf. f., Trans. Roy. Soc. Edinb. 31:241 (1888); *Clinopodium imbricatum* (Forssk.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! non Vell. (1825); *Clinopodium biflorum* (Buch.-Ham. ex D. Don) O. Kuntze, loc. cit. (1891); *Satureja imbricata* (Forssk.) Briq. in Engler & Prantl, Nat. Pflanzenfam 4,3a:299 (1897); *Satureja biflora* (Buch.-Ham. ex D. Don) Briq., loc. cit. (1897); *Thymus cavaleriei* Levl., Fedde, Repert. Sp. Nov. 11:298 (1912)! *Micromeria perrottetii* Gandoger, Bull. Soc. Bot. France 65:67 (1918).

Type: Kurmae, *Forskål* (holo. C!).

Gen. distrib.: China, Himilayas, S Arabia, Ethiopia; possibly elsewhere.

The type specimen is apparently procumbent, with few slender branches, not cushion-forming, stems recurved puberulent, leaves broadly ovate, flat, cordate or rounded at base, 3.0-5.5 x 2.0-3.3 mm, glabrous or extremely minutely hairy, cymes 1-3-flowered, calyx tube 2.5-3.0 mm, calyx teeth half as long as the tube. The type has no corollas, but on other similar specimens is 5.0-10.0 mm long.

3.6.2.2.35 33. *M. contardoi* (Pichli-Sermolli) A. Doroszenko, comb. nov.

Syn: *Satureja contardoi* Pichli-Sermolli, Miss. Stud. Lago Tana 7, Ricerche Bot., pt.1, 218 (1951).

Type: Ethiopia: M. Bauhit in Semien, *Pichli-Sermolli* 2689.

Gen. distrib.: Ethiopia.

Identified by the numerous, slender stems and tiny leaves (1-2 mm).

3.6.2.2.36 M. ellenbeckii (Gürke) Chiovenda [Cufodontis (1974) cites this combination; it is not in IK].

Syn: Satureja ellenbeckii Gürke, Bot. Jahrb. 36:129 (1905).

Gen. distrib.: Ethiopia.

3.6.2.2.37 M. ovata Benth., Lab. Gen. Sp. 377 (1834).

Syn: Satureja ovata R.Br. in Salt, Voy. Abyss. App. 64 (1814), nom. nud.; S. ovata R.Br. ex Pichli-Sermolli, Miss. Stud. Lago Tana 7, Ricerche Bot., pt.1:124 (1951).

Type: Hab. in Abyssinia, R. Browne (holo. BM).

Gen. distrib.: Ethiopia.

3.6.2.2.38 M. punctata Benth., Lab. Gen. Sp. 378 (1834).

Syn: Satureja punctata R.Br. in Salt, Voy. Abyss. App. 64 (1814), nom. nud.; Micromeria biflora sensu Bak. in Thiselton-Dyer, Fl. Trop. Afr. 5:452 (1900).

Type: Hab. in Abyssinia, R. Browne (holo. BM).

Gen. distrib.: Ethiopia, Somali, Uganda.

A tall, erect plant, with broad ovate leaves, 7-10 mm long, cordate at the base.

3.6.2.2.39 M. purtschelleri Gürke ex Engler, Abh. Preuss. Acad. Wiss. [Engler, Hochgebirgsfl. Trop. Afr.] 1891:365 (1892).

Gen. distrib.: Sudan, Uganda, Kenya, Tanzania, Cameroon, Congo, Zimbabwe (fide Walther & Walther, 1957).

According to Walther & Walther (1957), a variable species.

3.6.2.2.40 M. quartiniana A. Rich., Tent. Fl. Abyss. 2:190 (1850).

Syn: Satureja quartiniana (A. Rich) Cufod., Bull. Jard. Bot. Brux. 32 (Suppl.):823 (1962).

Gen. distrib.: Ethiopia.

3.6.2.2.41 M. remota (Balf. f.) Vierhapper, Fl. Südarabien und Sokotra 117 (1907).

Syn: Micromeria microphylla (D'Urv.) Benth. var. remota Balf. f., Trans. Roy. Soc. Edinb. 31:241 (1888); Satureja remota (Balf. f.) Vierhapper, Denkschr. Akad. Wiss. Wien 71:437 (1907).

Gen. distrib.: Socotra, Yemen.

Differing from M. imbricata by its robust shrubby habit, narrower, more strongly ribbed calyx up to 5 mm long, shorter calyx teeth (2/5 of tube length), and mostly solitary corollas 2-2.5 x calyx in length.

3.6.2.2.42 M. schimperi Vatke, Linnaea 37:326 (1872).

Syn: Satureja schimperi (Vatke) Cufodontis, Bull. Jard. Bot. Brux. 32 (Suppl.):824 (1962).

Gen. distrib.: Ethiopia, Sudan, Somali (fide Walther & Walther, 1957).

3.6.2.2.43 M. biflora (Buch.-Ham. ex D. Don) Benth. var. hispida Kitamura & Murata, Faun. Fl. Nepal Himal. 1:212 (1955).

Erect-ascending, densely white-hispid plants from Nepal [Polunin, Sykes & Williams 2480, 4146; Stainton, Sykes & Williams 5688, 7470] with affinities to the "biflora" complex may be this variety of Kitamura & Murata. Specific rank may be appropriate.

3.6.3. (b) Sect. Pineolentia P. Perez, Inst. Est. Canar. Univ. La Laguna, sect.4, 16:32 (1978).

Perennial, robust shrubs. Leaves 14-30 x 3.3-7.0 mm, narrowly ovate-lanceolate, petiole 1.5-2.0 mm, revolute or tightly revolute, entire, with a narrow but distinct marginal vein. Inflorescence a dense, leafy spike; flowers 1-10 per floral leaf. Bracteoles linear or narrowly lanceolate, 3.5-8.0 mm, not ciliate. Calyx throat glabrous or sparsely hairy, teeth not ciliate. Corolla not resupinate. Posterior stamens included, anterior stamens + exserted from corolla tube; all anthers of similar size. Style branches equal, both broadly lanceolate. Nutlets ovoid, glabrous.

Type species: M. pineolens Svent.

Gen. distrib.: Gran Canaria, Canary Is.

Close to sect. Micromeria, but much more robust shrubs, with larger, narrowly lanceolate leaves, and the inflorescences in dense, leafy spikes.

3.6.3.1. Calyx tube 4.0-5.0 mm, upper teeth broadly triangular, 0.5-0.6 mm, lower teeth lanceolate, 0.8-1.0 mm; [pine woods] 1. pineolens

Calyx tube c. 7.5 mm, all teeth narrowly triangular, upper c. 2.5 mm, lower c. 4.0 mm; [rock fissures] 2. leucantha

3.6.3.2. 1. M. pineolens Svent., Addit. Fl. Canar. 1:55 (1960).

Ic: P. Perez, Inst. Est. Canar. Univ. La Laguna, sect.4, 16:280, fig. 83 (1978).

Fl. 4-9. In damp Pinus canariensis woods, 850-1300 m.

Type: [Gran Canaria] Tamadaba, 21 iv 1958, Sventenius s.n. [Perez (1978) designated ORT 6504, with the same collection details cited by Sventenius (1960), as the lectotype.]

3.6.3.3. 2. M. leucantha Svent. ex Perez, Vieraea 5:82 (1975).

Ic: P. Perez, Inst. Est. Canar. Univ. La Laguna, sect.4, 16:287, fig. 85 (1978).

Fl. 7-11. In crevices of cliffs, 200-800 m.

Type: In fissuris rupis regione SW Canaria Magna, 200-800 m, circa San Nicolas de Tolentino, 28 vii 1974, P. Perez (holo. TFC 1730, iso. FI, MA, O).

3.6.4. (c) Sect. Cymularia Boiss., Fl. Or. 4:569 (1879).

Syn: Satureja L. sect. Cymularia (Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Annual herbs. Leaves 7-11 x 2-6 mm, ovate; petiole 1.0-3.5 mm, flat or slightly revolute at margins, margins entire, marginal vein absent. Flowers 4-10 in leaf axils. Bracteoles ovate, long acuminate, 3-4 mm, ciliate on margins. Calyx throat sparsely hairy, teeth long ciliate. Corolla resupinate. Stamens all just exserted from tube but not beyond upper corolla lip, posterior stamen anthers only half the size of anterior stamen anthers, posterior stamens sometimes entirely absent. Style branches equal, narrowly subulate. Nutlets sub-globose, glabrous. Monotypic.

3.6.4.1. M. cymuligera Boiss. & Hausskn. in Boiss., Fl. Or. 4:569 (1879).

Syn: Clinopodium cymuligerum (Boiss. & Hausskn.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja cymuligera (Boiss. & Hausskn.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Fl. 6-8. Stony torrent beds and damp alpine slopes, 900-2150 m.

Type: [Turkey C6 Maras] in glareosis torrentium ad radices montis Berytdagh (Berit Da.) Cataoniae, 915 m, 16 viii 1865, Haussknecht (holo. G!, iso. W).

Gen. distrib.: E Turkey.

This species is very isolated in the genus on account of the annual habit, globose verticillasters, floral leaves twice the flowers in length, slightly ampliate calyx with the narrowly triangular-subulate teeth almost as long as the tube, and particularly the small (2.5-3.0 mm), resupinate corolla. However, in facies there is more similarity to sect. Micromeria than any other section.

3.6.5. (d) Sect. Pseudomelissa Benth., Lab. Gen. Sp. 382 (1834).

Syn: Melissa L. sect. Orthomeria Griseb., Spic. Fl. Rum. 2:124 (1844); Satureja L. sect. Pseudomelissa (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897).

Perennial herbs or suffruticose herbs. Leaves 5-35 x 2-22 mm, broadly ovate, lanceolate or almost orbicular, flat or scarcely revolute at margin, crenate to ± entire, marginal vein absent, petiole 0.5-7.0(-11.0) mm. Flowers 1-30(-40) in floral leaf axils, never always solitary. Bracteoles linear to narrowly elliptic or lanceolate, 0.4-3.0(-5.5) mm, not conspicuously ciliate. Calyx mostly hairy in throat, teeth nearly always without cilia. Corolla not resupinate. Stamens mostly exserted from tube with anterior pair longer than upper lip, rarely included; all anthers similar in size. Style branches mostly unequal, sometimes ± equal, nearly always narrowly subulate, rarely both broadly lanceolate or very short with blunt apices. Nutlets ovoid or obloid, minutely glandular or eglandular hairy, or with minute sessile glands at apex, rarely glabrous.

3.6.5.1. 1. Lower calyx teeth 4/5-1 1/2 x the calyx tube 2

\+ Lower calyx teeth mostly under 1/2 x tube length, rarely to 3/5 5

2. All calyx teeth 3.0-3.7 mm, 1 1/2 x the calyx tube, narrowly triangular 6. nummularifolia

\+ Lower calyx teeth 1.2-1.8 mm, longer than the upper teeth, 4/5 to as long as the calyx tube, very narrowly subulate 3

3. Leaves entire to scarcely toothed, dense and subadpressed velvety-tomentose [Turkey] 11. dolichodonta

\+ Leaves serrulate to serrate, sparsely to more or less densely recurved-pubescent [Balkans, Roumania] 4

4. Calyx 2.5-3.0 mm, lower teeth 1.2-1.3 mm; stem hairs very minute, recurved-puberulent 10. dalmatica

\+ Calyx 3.0-4.0 mm, lower teeth 1.3-1.8 mm; stem hairs longer, recurved-pubescent 12. pulegium

5. Leaves 2.0-6.0 x 0.7-2.8 mm, very numerous on stems; corolla rose-red [China] 17. barosma

\+ Leaves much larger; corollas not rose-red [Widespread] 6

6. Calyx 6.2-7.3 mm, very narrowly tubular; corolla tube narrow, abruptly widening at throat; anthers parallel [E Africa, N Yemen] 14. abyssinica

\+ Calyx less than 6.2 mm, mostly ± broadly tubular; corolla tube widening from lower part of tube; anthers divergent (very rarely parallel) 7

7. Leaves numerous on stems, all narrowly elliptic to linear-elliptic, apex rounded; upper and lower calyx teeth equal (1.2-1.7 mm); corolla creamy yellow (9.0-13.4 mm) 19. nepalensis

\+ Leaves usually few on stems, broadly ovate, sometimes elliptic, apex obtuse to rounded; lower calyx teeth slightly to clearly longer than upper ones; corolla white or purple 8

8. Calyx tube 3.7-5.2 mm; corolla 10.4-14.5 mm [China, Himilayas] 9

\+ Calyx tube 1.4-3.6 mm; corolla 3.7-10.0 mm 11

9. Calyx tube very narrowly tubular, lower teeth 0.7–0.9 mm — 18. wardii

\+ Calyx tube broadly tubular, lower teeth 1.4–3.0 mm — 10

10. Calyx sparsely pubescent, hairy in throat; lower teeth ciliate; stigma lobes short, obtuse [China] — 16. euosma

\+ Calyx with few minute hairs only; glabrous in throat; lower teeth not ciliate; stigma lobes long, narrowly subulate [Kashmir] — 15. hydaspidis

11. Leaves glabrous on both sides; lower calyx teeth 0.4–0.5 mm (calyx glabrous in throat) — 4. thymifolia

\+ Leaves hairy, sometimes only minutely so, at least on one side; lower calyx teeth longer than 0.5 mm — 12

12. Calyx glabrous in throat (plants erect) — 13

\+ Calyx sparsely to densely hairy in throat (rarely glabrous but then plants decumbent) — 14

13. Calyx teeth narrowly triangular; stem hairs recurved; leaves 10–20 x 5–10 mm; calyx pedicels 0.3–0.6 mm — 3. cilicica

\+ Calyx teeth triangular-deltoid; stem hairs ± patent; leaves 5–10 x 2.5–6.5 mm; calyx pedicels 1.5–3.6 mm — 8. carica

14. Stems and leaves adpressed-velutinous (individual hairs not usually discernable) — 1. fruticosa

\+ Stem and leaves patent or recurved-pubescent (individual hairs usually easily discernable) — 15

15. Cymes globular, usually many-flowered, pedicels very short but peduncles often long, 1.0–13.0 mm; verticillasters distant; corollas 3.0–4.0 mm [India] — 20. capitellata

\+ Cymes not globular though sometimes congested, peduncles short or long; verticillasters usually not distant; corollas 4.0-10.0 mm [Mediterranean region, Near East] 16

16. Calyx tube 3.4-3.6 mm, lower calyx teeth 1.6-1.7 mm; leaves often broader than long (low ascending herb) 13. frivaldskyana

\+ Calyx 1.5-3.0 mm, lower teeth 0.5-1.4 mm; leaves longer than broad 17

17. Stems 20-35 cm, robust from a large woody stock; inflorescences strongly congested at stem apex, 6-60 flowers per verticillaster 2. congesta

\+ Stems mostly less than 20 cm, very thin, brittle from a small woody stock; inflorescence lax, 2-16 flowers per verticillaster 18

18. Peduncles 4.0-13.0 mm; pedicels 2.5-3.5 mm [Turkey, Iraq] 9. mollis

\+ Peduncles 1.0-4.7 mm; pedicels 0.4-1.5 mm 19

19. Calyx tube 2.4-3.0 mm, lower teeth 0.9-1.1 mm, upper teeth lanceolate-subulate [Lebanon, Syria] 5. libanotica

\+ Calyx tube 1.5-2.2 mm, lower teeth 0.5-0.7 mm, upper teeth broadly triangular [S Greece] 7. taygetea

3.652. 1. M. fruticosa (L.) Druce, Rep. Bot. Exch. Club Brit. Is. 3:421 (1914).

Syn: Melissa fruticosa L., Sp. Pl. 593 (1753)! Thymus creticus DC. in Lam. & DC., Fl. Fr. 3:564 (1779), non L. (17..); Melissa rupestris Salisb., Prod. Stirp. Chapel Allerton Vig. 86 (1796), nomen; Melissa cretica Desr. in Lam., Encycl. Meth. 4:79 (1797), non L. (1753); Nepeta marifolia Cav., Anal. Cienc. Nat. 2:192 (1800); N. cretica F. G. Dietr., Vollst. Lexik. Gaertn. 6:348 (1806); Melissa marifolia (Cav.) Pers., Syn. Pl. 2:132 (1807); Thymus marifolius (Cav.) Willd., Enum. Hort. Berol. 2:624 (1809); Thymus fruticosus (L.) Link, Enum. Hort. Berol. Alt. 2:116 (1822)! Thymus barrelieri Spreng., Syst. Veg. 2:698 (1825); Micromeria marifolia (Cav.) Benth., Lab. Gen. Sp. 382 (1834); N. parvifolia Hortul. ex Benth., loc. cit. 383 (1834), nomen; Bystropogon marifolius (Cav.) Juss. ex Steud., Nom. Bot., ed.2, 1:243 (1841); Calamintha fruticosa (L.) Steud., loc. cit. 251 (1841)! Calamintha marifolia (Cav.) Steud., loc. cit. 251 (1841); Satureja marifolia (Cav.) Car. in Parl., Fl. Ital. 6:125 (1884); Clinopodium fruticosum (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! non. Forssk. (1775); Satureja fruticosa (L.) Briq., Ann. Conserv. Jard. Bot. Geneve 2:192 (1898)!

1. Upper verticillasters much-branched, forming an ovate-oblong head (2.5-)3.5 cm broad; calyx throat strongly and very conspicuously bearded [Turkey, S Amanus] ssp. davisii

\+ Verticillasters distant, forming an elongated, interrupted inflorescence 1.5-3.0 cm broad; calyx throat less distinctly bearded to almost naked 2

2. Calyx not visibly bearded at throat, obconical-cylindrical, c. 2.5 mm [USSR, Crimea, SW Yugoslavia, NE Turkey] ssp. serpyllifolia

\+ Calyx clearly hairy at throat, 1.5-2.5 mm 3

3. Calyx 1.5-2.0 mm, teeth very broadly triangular, apex obtuse [S Turkey] ssp. brachycalyx

\+ Calyx 2.0-2.5 mm, teeth narrowly triangular, apex acute 4

4. Stems procumbent, thin, brittle, up to 30 cm tall; inflorescence broad, lax [NE Turkey] ssp. giresunica

\+ Stems erect, thicker and more robust, up to 60 cm tall; inflorescence narrow, spike-like, compact [Spain, Italy] ssp. fruticosa

ssp. fruticosa

Fl. 7-10. On dry rocks, rock crevices, garrique, c. 1500 m.

Ic: Fiori, Ic. Fl. Ital. f.3188 (1902).

Type: Described from Spain (Hb. Linn. 745/9, microfiche!).

Gen. distrib.: Spain, Italy.

ssp. giresunica P. H. Davis, Notes R.B.G. Edinb. 38:39 (1980).

Type: Turkey A7 Giresun: Tamdere to Yavuzkemal, nr. Karinca, 1500 m, crevices of granite rocks, near road tunnel, 13 viii 1952, P. H. Davis 20750, Dodds & Cetik (holo. E!, iso. K).

Only known from the type.

ssp. serpyllifolia (M. Bieb.) P. H. Davis, Kew Bull. 1951:77 (1951).

Syn: Nepeta serpyllifolia M. Bieb., Fl. Taur.-Cauc. 2:40 (1808); Calamintha spicigera C. Koch, Linnaea 21:671 (1848)! Micromeria spicigera (C. Koch) Walp., Ann. Bot. Syst. 3:251 (1852)! non C. Koch (1843); Micromeria serpyllifolia (M. Bieb.) Boiss., Diag. Ser. 2, 4:13 (1859), only those plants collected in Crimea; Melissa serpyllifolia (M. Bieb.) Nym., Syll. Fl. Eur. Suppl. 20 (1865); Clinopodium serpyllifolium (M. Bieb.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja serpyllifolia (M. Bieb.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897); Micromeria insularis Candargy, Bull. Soc. Bot. Fr. 44:149 (1897); ?Satureja albanica

(Griseb. ex K. Maly) K. Maly, Glaznik Muz. Bosne Herceg. 22:690 (1910).

Fl. 5-9. On limestone and granite rocks, cliff crevices, 5-2100 m.

Type: [USSR, Crimea] in Tauriae rupestribus, circa ruinas castelli Inkiermen (holo. LE).

Gen. distrib.: Albania, Israel, Italy, Turkey.

ssp. brachycalyx P. H. Davis, Kew Bull. 1951:77 (1951).

Fl. 6-8. On cliffs, limestone slopes and stony places, 90-2100 m.

Type: Turkey C5 Icel, Portes Ciliciennes Gulek Bogazi, viii 1855, Balansa 538 (holo. K, iso. E!, W).

Gen. distrib.: Italy (Sicily), Turkey.

ssp. davisii A. Doroszenko, nom. nov.

Syn: Micromeria barbata Boiss. & Kotschy in Boiss., Diagn. ser. 2, 4:14 (1859), non C. A. Mey. in Fisch. & Mey., Ind. Sem. Hort. Petrop. 8:67 (1842); Micromeria fruticosa (L.) Druce ssp. barbata (Boiss. & Kotschy) P. H. Davis, Kew Bull. 1951:77 (1951).

Fl. 5-12. Rocky slopes, 200-800 m.

Type: [Lebanon] in jugis inferioribus Danie Antilibani, 1680 m, Kotschy (holo. G).

Gen. distrib.: Israel, Lebanon, Syria, Turkey.

3.6.5.3. 2. M. congesta Boiss. & Hausskn. ex Boiss., Fl. Or. 4:575 (1879).

Syn: Nepeta shepardi Post, J. Linn. Soc. (Bot.) 24:439 (1888); Clinopodium congestum (Boiss. & Hausskn. ex Boiss.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Micromeria shepardi (Post) Post, Bull. Herb. Boiss. ser.1, 1:405 (1893); Satureja congesta (Boiss. & Hausskn. ex Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897)!

Ic: Post, Fl. Syria, Palestine & Sinai 622 (1896), as M. shepardi.

Fl. 8-11. Calcareous stony slopes, cliffs, 700-1830 m.

Type: [Turkey C7 Adiyaman] in rupestribus calcareis montis Akdagh inter Adiyaman et Malatia [6000 ped., 12 ix 1865], Haussknecht (holo. G!, iso. BM! G!).

Gen. distrib.: SE Turkey, Iraq.

Very similar to M. fruticosa but somewhat shorter in stature, densely white-tomentose (rather than adpressed-velutinous) on all parts, and with a denser, columnar inflorescence, the peduncles 0.1-0.3 mm (not 2.0-6.0 mm).

3.6.5.4. 3. M. cilicica Hausskn. ex P. H. Davis, Kew Bull. 1949:109 (1949).

Fl. 8. On rocks, 1200-1300 m.

Type: [Turkey C5 Icel] Cilicia, 1895, Siehe 315 (holo. K).

Gen. distrib.: S Turkey.

Close to M. fruticosa and M. thymifolia, but differing in its dense and minutely adpressed-pubescent indumentum, leaves clearly veined beneath, smaller calyx tube and narrower calyx teeth.

3.6.5.5. 4. M. thymifolia (Scop.) Fritsch in A. Kerner, Sched. Fl. Exsicc. Austro-Hung. 8:119 (1899).

Syn: Satureja thymifolia Scop., Fl. Carn. ed.2, 1:428, t.29 (1772); Satureja rupestris Wulf. ex Jacq., Coll. 2:130 (1789); Melissa alba Waldst. & Kit., Pl. Rar. Hung. 3:227 (1807); Nepeta pumila Spreng., Cent. Sp. Cogn. 29 (1813); Thymus albus (Waldst. & Kit.) Link, Enum. Hort. Berol. 2:116 (1822); Nepeta croatica Spreng., Syst. 2:727 (1825); ?Mentha croatica Weld, Flora 8(1):218 (1830), nomen; Calamintha alba (Waldst. & Kit.) Reichenb., Fl. Germ. Exc. 328 (1831); Calamintha thymifolia (Scop.) Reichenb., loc. cit. (1831); Calamintha rupestris (Wulf. ex Jacq.) Host, Fl. Austr. 2:131

(1832); Thymus duinensis Moretti ex Reichenb., Fl. Germ. Exc. 2(2):860 (1832), nomen; Melissa thymifolia (Scop.) Benth., Lab. Gen. Sp. 386 (1834); Cuspidocarpus rupestris (Wulf. ex Jacq.) Spenn. in T. Nees, Gen. Fl. Germ. Gamop. 2, n.18 (1843); Micromeria rupestris (Wulf. ex Jacq.) Benth. in DC., Prodr. 12:225 (1848); Cuspidocarpus thymifolius (Scop.) O. Kuntze, Rev. Gen. Pl. 2:514 (1891).

Fl. 6-9. Calcareous rocks, cliffs, waste places, road-sides, 210-700 m.

Type: Habitat in muris, Idriae.

Gen. distrib.: Greece, Italy, Yugoslavia.

3.6.5.6. 5. M. libanotica Boiss., Diagn., ser.1(12):50 (1853).

Syn: Clinopodium libanoticum (Boiss.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja libanotica (Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897).

Ic: Boul., Fl. Liban & Syrie t.337 (1930).

Fl. 6-8. Calcareous rocks, rock crevices, 1830-2590 m.

Syntypes: hab. in Libano supra Cedros, Labillardier; hab. in Libano supra Cedros in fissuris rupium, Boissier (G).

Gen. distrib.: Lebanon, Syria.

Related to M. fruticosa and M. thymifolia but distinguished by the distant, 2-16-flowered verticillasters, narrowly tubular calyx, tube 2.4-3.0 mm, and lanceolate calyx teeth 0.6-1.1 mm long.

3.6.5.7. 6. M. nummularifolia Boiss., Diagn. ser. 1(12):49 (1853).

Syn: Clinopodium nummularifolium (Boiss.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja nummularifolia (Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897)!

Ic: Boul., Fl. Liban & Syrie t.337 (1930).

Fl. 6-9. Fissures of calcareous rocks.

Type: Syria libanus supra Eden [Ehden], vi 1846, Boissier (holo. K!, iso. E!).

Gen. distrib.: Syria.

A very distinct species, recognised by the prostrate habit, broadly ovate to orbicular, entire leaves 4.5-9.0 mm long, usually solitary flowers, densely long, soft hispid calyx, tube 2.0-2.3 mm, teeth all similarly narrowly triangular 3.0-3.7 mm. It possibly comes closest to M. taygetea.

3.6.5.8 7. M. taygetea P. H. Davis, Kew Bull. 1949:110 (1949).

Fl. 10. Calcareous rocks, c. 1530 m.

Type: Greece, Peloponnesi, in rupium calcar. fissuris montis Taygeti supra pagum Trypi, c. 1530 m, 2 x 1938, P. H. Davis (holo. E!).

Gen. distrib.: Greece.

Only known from the type.

3.6.5.9. 8. M. carica P. H. Davis, Kew Bull. 1949:109 (1949).

Fl. 7. Limestone rocks, 1520-1670 m.

Type: Turkey, Prov. Denizli, distr. Acipayam, Boz dag above Geyram yayla. In limestone rocks, 1520-1670 m, 16 vii 1947, P. H. Davis 13422 (holo. K!, iso. E!).

Gen. distrib.: Turkey.

Closely related to M. taygetea. Only known from the type.

3.6.5.10. 9. M. mollis Benth. in DC., Prodr. 12:225 (1848).

Syn: Clinopodium molle (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja flacca Nab., Publ. Fac. Sci. Univ. Masaryk (Brno) 70:44 (1926); Micromeria flacca (Nab.) I. C. Hedge, Notes R.B.G.

Edinb. 25:51 (1965).

Ic: Rech. f., Fl. Iranica 150, t.398 (1982), as M. flacca.

Fl. 6-8. Limestone rocks and cliffs, 600-1830 m.

Type: Pl. Mesopot., Kurdistan et Mossul, ann. 1841, Kotschy 552a (holo. K!).

Gen. distrib.: Iraq, Turkey.

A variable species easily recognised by the sub-orbicular leaves 5-15 mm long, verticillasters with 2-6-flowered cymes on 4-13 mm peduncles and 2.5-3.5 mm pedicels, and tubular-obconical calyx with subequal teeth half as long as the calyx tube. It is in many ways similar to M. nummularifolia.

3.6.5.11. 10. M. dalmatica Benth. in DC., Prodr. 12:225 (1848)!

Syn: Thymus origanifolius Vis., Flora 13(1):132 (1830), non G. Don (1825); Calamintha thymifolia Host, Fl. Austr. 2:132 (1831), non (Scop.) Reichenb. (1831); Calamintha origanifolia (Vis.) Vis., Fl. Dalm. 2:199 (1847), non Host (1832), non (Labill.) Boiss. (1853); Satureja dalmatica (Benth.) Nym., Syll. Fl. Eur. 1:102 (1854)! Micromeria origanifolia Boiss., Fl. Or. 4:575 (1879), non (Labill.) Benth. (1848); Clinopodium thymifolium (Host) O. Kuntze, Rev. Gen. Pl. 2:516 (1891); Satureja thymifolia (Host) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897); Zygis origanifolia (Vis.) Deg., Bull. Herb. Boiss. 4:521 (1896); Micromeria origanifolia Boiss. ssp. bulgarica Vel., Oest. Bot. Zeitschr. 49:292 (1899); Satureja bulgarica (Vel.) Maly in Dorfler, Herb. Norm. no. 4931 (1908); Micromeria bulgarica (Vel.) Hayek, Fedde Repert. Beih. 30(2):323 (1929); Micromeria dalmatica Benth. ssp. bulgarica (Vel.) Guinea, Bot. J. Linn. Soc. 64:381 (1971).

Fl. 6-8. Calcareous rocks.

Syntypes: In saxosis prope Cataro in Dalm., ann. 1837, Visiani

(K!); Montenegro ad Nepeg, Visiani (K!).

Gen. distrib.: Bulgaria, Yugoslavia.

A very variable species in stature, leaf size, verticillaster density, and indumentum. It is most closely related to M. pulegium.

3.6.5.12 11. M. dolichodonta P. H. Davis, Kew Bull. 1951:75 (1951).

Fl. 8. Limestone rocks.

Type: Turkey C4 Icel, distr. Gulnar, Kizilyokus De. near Bozagas (near Gulnar), flat and sloping limestone rocks, 500 m, 20 viii 1949, P. H. Davis 16356 (holo. K!, iso. E!).

Gen. distrib.: S Turkey.

Only known from the type gathering. A distinct species recognised by the distant, lax, 10-30-flowered verticillasters, slightly ampliate tubular calyces, calyx tube 1.4-1.6 mm, the narrowly triangular upper teeth (0.7-1.0 mm) distinctly shorter than the lower teeth (1.4-1.8 mm). M. dalmatica is probably the nearest relative.

3.6.5.13. 12. M. pulegium (Rochel) Benth., Lab. Gen. Sp. 382 (1834).

Syn: Melissa pulegium Rochel, Pl. Banat. Rar. 6 (1828); Calamintha origanifolia Host, Fl. Austr. 2:130 (1832); Melissa nova Portenschl. ex Steud., Nom. Bot. ed.2, 122 (1841), nomen; Calamintha pulegium (Rochel) Reichenb. f., Ic. Fl. Germ. 18:45, f.1278 (1858); Satureja pulegium (Rochel) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897).

Ic: Savulescu, Fl. Rep. Pop. Romine 8: t.48, f.1 (1961).

Type: [Romania] hab. in Banatu ad rupes thermarum Herculis, Rochel.

Gen. distrib.: Romania, Hungary.

Closely related to M. dalmatica but distinguished by leaves adpressed pubescent, verticillasters approximating and more dense, and longer calyx tube and calyx teeth.

3.6.5.14 13. M. frivaldszkyana (Deg.) Vel., Oest. Bot. Zeitschr. 49:291 (1899)!

Syn: Zygis frivaldszkyana Deg., Bull. Herb. Boiss. 4:523 (1896)! Satureja frivaldszkyana (Deg.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897)! Micromeria balcanica Vel., Fl. Bulg. Suppl. 1:235 (1898); Satureja balcanica (Vel.) Stoyanoff & Steffanoff, Fl. Bulg. ed.2, 878 (1933).

Fl. 7-8. Cliffs, rocky places, c. 1800 m.

Type: [Bulgaria] Rumelica, ann. 1837, Frivaldszky (holo. K!).

Gen. distrib: Bulgaria.

Similar to M. pulegium but with shorter stems, flexuous ascending (not erect), leaves glabrous, fewer flowered, lax verticillasters, and longer, subglabrous calyx tube (3.4-3.6 mm).

3.6.5.15 14. M. abyssinica Hochst. ex Benth. in DC., Prodr. 12:224 (1848)!

Syn: Melissa abyssinica Hochst., Flora 24(1), Intell. 2:23 (1841), nomen [based on Schimper 326!]; Calamintha abyssinica (Hochst. ex Benth.) A. Rich., Tent. Fl. Abyss. 2:191 (1847)! Clinopodium abyssinicum (Hochst. ex Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja abyssinica (Hochst. ex Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897)! Satureja abyssinica (Hochst. ex Benth.) Briq. var. condensata Hedberg, Symb. Bot. Upsal. 15(1):164 (1957).

Fl. all year. In thick bush, dry banks, steep grassy slopes, 900-2900 m.

Type: Ethiopia in regione septentrionali superioris partis et inferioris montis Scholoda, 3 x 1837, Schimper 326 (holo. K!).

Gen. distrib.: Ethiopia, Kenya, Somali, Sudan, Tanzania, Uganda, Yemen.

A distinct species identified by the slender ascending stems, ovate to lanceolate, distinctly petiolate, thin leaves, 2-14-flowered, lax verticillasters, very narrowly tubular calyx, slightly narrower at throat than base, the corolla tube narrowly tubular, lips widely flaring, the stamen anthers parallel.

3.6.5.16 15. M. hydaspidis Falc. ex Benth. in DC., Prodr. 12:224 (1848)!

Syn: Clinopodium hydaspidis (Falc. ex Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja hydaspidis (Falc. ex Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897)!

Fl. 8-9. Rocky banks, c. 2440 m.

Type: Kashmir, from Patlee to Magha valley of the Gheleena, ix 1837, Falconer 1250 (holo. K!).

Gen. distrib.: India (Kashmir), Pakistan.

3.6.5.17 16. M. capitellata Benth. in DC., Prodr. 12:218 (1848)!

Syn: Marrubium malcolmianum Dalz. in Hook., J. Bot. Kew Misc. 4:109 (1852); Micromeria malcolmiana (Dalz.) Benth. ex Hook. f., Fl. Brit. Ind. 4:650 (1885), nomen; Clinopodium capitellatum (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja capitellata (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897)!

Fl. 1-5, 12. Damp open ground, river and stream banks, 760-2150 m.

Type: India, Mont. Nilagiri, incoltis, Kodangu, prope Kaderu, April. M. malcolmiana Benth. m.s. on label. Pl. Ind. or. no. 1402 (holo. K!).

Gen. distrib.: India.

Easily recognised by the distant verticillasters with dense, almost spherical cymes on usually long peduncles, small calyces (2.1-2.6 mm) and small corollas c. 3.0 mm long.

3.6.5.18 17. M. euosma (W. W. Sm.) C. Y. Wu, Act. Phytotax. Sin. 10:229 (1965)!

Syn: Calamintha euosma W. W. Sm., Notes R.B.G. Edinb. 9:89 (1916)! Satureja euosma (W. W. Sm.) Kudo, Mem. Fac. Sci. Ag. Taihoku Univ. 2(2):100 (1929)!

Ic: Fl. Reip. Pop. Sin. 66:221, t.51, f.6-10 (1977).

Fl. 7. Open calcareous pasture, c. 3300 m.

Type: China: Yunnan: Mountains NE of the Yangtze bend, 11000 ft., open limy pastures. Lat. 27 45 N, vii 1913, G. Forrest 10574 (holo. E!).

Gen. distrib.: China, Yunnan.

The following four species (nos. 17-20) are closely related to each other. M. euosma and its nearest relative M. barosma are very distinct species, and Kudo (1929) described a section under Satureja [sect. Barosma Kudo, Mem. Fac. Sci. Taihoku 2(2):99 (1929)] to accommodate them. The description of his section reads: "Multi-stemmed, suffruticose, much-branched, stems slender or filiform, verticillasters few- to sometimes 1-flowered, in lax spikes arranged dorsiventrally at the stem apex, bracteoles narrow, calyx tubular, throat between the teeth densely hairy, corolla twice as long as the calyx." However, excepting the unusual habit, the characters mentioned are not uncommon in other species of sect. Pseudomelissa.

3.6.5.19 18. M. barosma (W. W. Sm.) Hand.-Mazz., Symb. Sin. 7:932 (1936)!

Syn: Calamintha barosma W. W. Sm., Notes R.B.G. Edinb. 9:88 (1916)!

Satureja barosma (W. W. Sm.) Kudo, Mem. Fac. Sci. Ag. Taihoku Univ. 2(2):99 (1929)!

Ic: Fl. Reip. Pop. Sin. 66:221, t.51, f.1-5 (1977).

Fl. 7-10. Open rocky slopes, calcareous cliff ledges, 2130-3660 m.

Type: China: Yunnan: mountains in the NE of the Yangtze bend, lat. 27 45 N, 12000 ft., vii 1913, G. Forrest 10371 (holo. E!).

Gen. distrib.: China, Yunnan.

A distinct species identified by the numerous elliptic to oblanceolate, glabrous leaves, 2.0-6.0 x 0.7-2.8 mm, approximating verticillasters of 2-6-flowered cymes, calyx tube narrowly tubular, slightly curved, tube 4.5-6.8 mm, with narrowly triangular-subulate teeth, and red corollas 15-20 mm long.

3.6.5.20. 19. M. wardii Marquand & Shaw, J. Linn. Soc. 48:216 (1929)!

Fl. 7-11. Amongst bracken in moorland, river banks, dry rocks in pine forest, shade of boulders, 2130-3050 m.

Type: Tibet: Tsangpo Gorge, 7000 ft., 28 xi 1924, F. Kingdon Ward 6324 (holo. K!, iso. E!).

Gen. distrib.: Tibet.

This species shares with M. barosma the slightly curved, narrowly tubular calyx, but is distinguished from that species by the ovate, much larger leaves, broader and shorter calyx teeth, and purplish corolla.

3.6.5.21. 20. M. nepalensis Kitamura & Murata, Acta Phytotax. Geobot., Kyoto 16:3 (1955).

Fl. 7-10. Dry rocky slopes, 2440-3660 m.

Type: Nepal: Bangu Khola, 3400 m, 11 vi 1953, S. Nakao s.n. (holo. KYO).

Gen. distrib.: Nepal.

Close to M. barosma, but the similarly shaped leaves 10.0-21.0 x 2.5-8.4 mm, verticillasters laxer, calyces smaller (tube 2.7-3.1 mm) and corolla smaller and yellow.

3.6.6. (e) Sect. Madagascarenses A. Doroszenko, sect. nov.

Perennial herbs. Leaves 1.5-11.5 x 0.7-7.2 mm, broadly ovate-orbicular, narrowly ovate, or linear-oblong, petiole 0.2-0.6 mm, flat or tightly revolute, entire or with few small teeth, marginal veins absent. Flowers always solitary on very long pedicels and peduncles. Bracteoles leaf-like, 1.0-3.8 mm, not ciliate. Calyx 13-15-nerved, throat glabrous, teeth not ciliate. Corolla not resupinate. Posterior stamens included, anterior stamens just excluded from tube but not beyond upper lip; all anthers similar in size. Style branches very unequal, one very narrow filiform only 1/4-1/3 as long as the other broad lanceolate branch.

Gen. distrib.: Madagascar.

The three species of this section are the only Madagascaran members of Satureja s.l. In floral structure there is a clear similarity to other Micromeria, with the closest overall affinity apparently with the E African representatives of sect. Pseudomelissa.

3.6.6.1. 1. Leaves linear-oblong, entire, glabrous, 4.0-11.5
x 0.7-3.2 mm; calyx teeth broadly triangular,
rather less than 1/3 x tube length 1. madagascarensis

\+ Leaves narrowly ovate to almost orbicular, entire
or with 1-2 small teeth per side, hairy, 1.5-6.8 x
1.0-7.2 mm; calyx teeth narrowly triangular,
1/2-3/5 x tube length 2

2. Leaves narrowly ovate, upper entire, lower with 1-2 distinct teeth, minutely puberulent; calyx tube 2.2-2.8 mm, lower teeth 1.0-1.6 mm; lower central corolla lobe entire 2. flagellaris

\+ Leaves broadly ovate to orbicular, all entire, with long, weak hairs; calyx tube 3.0-3.6 mm, lower teeth 1.8-2.3 mm; lower entire lobe divided into 2 lobules 3. sphaerophylla

3.6.6.2. 1. M. madagascarensis Baker, Journ. Bot. 20:244 (1882).

Fl. 11. Margin of marshy places, c. 1600 m.

Type: Central Madagascar, Parker (holo. K!).

Gen. distrib.: Madagascar.

3.6.6.3. 2. M. flagellaris Baker, J. Linn. Soc. 20:232 (1883).

Syn: Micromeria rutenbergiana Vatke, Abh. Naturw. Ver. Bremen 9:135 (1885); Satureja flagellaris (Baker) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Fl. 11-12, 1-7. Margins of marshy places, banks of torrents, humid depressions, 1400-2550 m.

Syntypes: Central Madagascar, Baron 2062 (K!), Baron 2065 (K!).

Gen. distrib.: Madagascar.

Closest to M. sphaerophylla.

3.6.6.4. 3. M. sphaerophylla Baker, J. Linn. Soc. 20:232 (1883).

Syn: Satureja sphaerophylla (Baker) Briq., Bull. Herb. Boiss. 2:134 (1894).

Fl. 1, 12.

Type: Central Madagascar, Baron 2141 (holo. K!).

Gen. distrib.: Madagascar.

3.6.7. Nom. dubia

M. calaminthoides Lojac., Fl. Sic. 2(2):212 (1907).

M. diffusa Lojac., Fl. Sic. 2(2):216 (1907).

M. echioides Lacaita ex Lojac., Fl. Sic. 2(2):215 (1907).

M. falcata Nab., Publ. Fac. Sc. Masaryk, Brno No. 70 (1926).

M. fenzlii Regel, Ind. Sem. Hort. Petrop. 93 (1866).

This is described as "Affinis M.[icromeria] rupestri, caule incano; foliis longius petiolatis; inferioribus ovatis profundinque dentatis dignosticur."

M. filicaulis Schott. & Kotschy, Tchihat. Asie Min. Bot. 2:131 (Date?), nomen.

M. formosana Marquand, Hook. Ic. Pl. 33, t.3230 (1934).

This species was described from a living specimen grown from seed sent to Kew from Formosa by Yashiroda (no. 31). I know the plant only from the illustration cited; it appears to be distinct.

M. grandis Lojac., Fl. Sic. 2(2):213 (1907).

M. hybrida Zagan., Actes Inst. Bot. Univ. Athenes 1:250 (1940).

M. lacaita Lojac, Fl. Sic. 2(2):214 (1907).

M. x meteorica Hausskn., Mittheil. Thuring. Bot. Ver. 11:48 (1897).

M. neumannii O. Hoffm. ex Engler, Sitz. Preuss. Akad. Wiss. 1906:744 (1906).

A tropical African species.

M. parvula Chiov., Racc. Bot. Miss. Consol. Kenya 103 (1935).

M. purpurea (Kellogg) A Gray, Bot. Calif. 1:595 (18..).

Syn: Satureja purpurea (Kellogg) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:300 (1897).

M. tapeinantha Rech. f., Denkschr. Akad. Wiss. Wien Math.-Nat. Kl. 105(2,1):123 (1943).

3.6.8. Nom. exclud.

M. affinis Hook. f., Hook. Lond. Journ. Bot. 6:274 (1847) = Mentha affinis (Hook. f.) Druce

M. australis (R. Br.) Benth., Lab. Gen. Sp. 380 (1834) = Mentha australis R. Br.

M. bonariensis (Ten.) Fisch. & Mey., Ind. Sem. Hort. Petrop. 10:56 (1845) = Hedeoma multiflorum Benth. fide Irving (1980).

M. bracteolata (Roem. & Schult.) Benth., Lab. Gen. Sp. 371 (1834) = possibly a Conradina sp. fide Epling & Stewart, Fedde Rep. Beih. 115:46 (1939).

M. calostachya Rech. f., Denkschr. Akad. Wiss. Wien Math.-Nat. Kl. 105(2,1):122 (1943) = Thymbra calostachya (Rech. f.) Rech. f.

M. cunninghamii Benth., Lab. Gen. Sp. 730 (1835) = Mentha cunninghamii (Benth.) Benth.

M. gracilis (R. Br.) Benth., Lab. Gen. Sp. 380 (1834) = Mentha diemenica Spreng.

M. japonica Miq., ann. Mus. Bot. Lugd. Bat. 2:106 (1865) = Mentha japonica (Miq.) Makino.

M. perforata Miq., Ann. Mus. Bot. Lugd. Bat. 2:106 (1865) = Mosla japonica (Benth.) Maxim.

M. pulchella (Clos.) Wedd., Chlor. And. 2:151 (1857) = Kurzamra pulchella (Clos.) O. Kuntze

M. repens Hook. f., Hook. Lond. Journ. Bot. 6:274 (1847) = Mentha diemenica Spreng.

M. satureioides (R. Br.) Benth., Lab. Gen. Sp. 380 (1834) = Mentha satureioides R. Br.

M. sessilis Benth., Hook. Lond. Journ. Bot. 6:274 (1847) = Mentha diemenica Spreng.

M. subulifolia Rech. f., Danske Vid. Selsk. Biol. Skrift. 8(1):74

(1955) = Hyssopus subulifolius (Rech. f.) Rech. f.

M. yezoensis Miyabe & Tatew., Trans. Sapporo Nat. Hist. Soc. 14:8 (1935) = Mentha japonica (Miq.) Makino.

3.7. *Brenaniella* A. Doroszenko, gen. nov.

Tall, erect, perennial herbs or shrubs. Leaves ovate to lanceolate, flat, toothed, sometimes entire, lower side densely punctate-glandular, glands few on upper side, veins usually prominent, camptodromous, palisade mesophyll dorsiventral. Inflorescence a dense leafless spike, uninterrupted or interrupted only at base. Verticillasters many-flowered, ± sessile. Bracteoles narrowly elliptic to broadly ovate. Calyx tube straight, 13-nerved, somewhat ampliate, throat glabrous, lips ± equal, all 5 teeth similar in shape, straight, upper teeth slightly to clearly shorter than lower teeth, teeth ciliate. Corolla small, 5-11 mm, white, tube not annulate inside, glabrous in lower half, lips 1/4-1/2 tube length, upper galeate, lower bent downwards at 90 to tube, upper longer than or equalling lower; stamens 4, shortly exserted from tube but not or scarcely beyond upper lip; anther filaments ± parallel. Style branches slightly unequal, rarely ± equal.

Type species: *B. robusta*, designated here.

Seven species on tropical African mountains.

Brenan (1954) described, but did not name, this group of tropical African species as a probable section of *Micromeria*, i.e. should Benthams classification be followed (Bentham, 1848). However, Brenan rightly points out there is only "a certain resemblance in foliage, habit, and to a lesser extent inflorescence" to *Micromeria* sect. *Pseudomelissa*, and that "the African plants remain a very distinct group". The species of *Brenaniella* are much taller and robust plants than *Micromeria*, with a dense spicate inflorescence of sessile verticillasters, small, somewhat ampliate calyces, small white corollas with galeate upper lip and lower lip sharply bent downwards. Together these characters give *Brenaniella* a quite unmistakable facies.

3.7.1. 1. Leaf apex rounded or broadly obtuse 2

\+ Leaf apex acute 3

2\. Leaf margin clearly crenulate-serrulate, venation plainly reticulate; lower leaf surface pubescent; lower calyx teeth 1.3-1.7 mm 1. *robusta*

\+ Leaf margin entire to scarcely denticulate, venation inconspicuous; lower leaf surface ± glabrous; lower calyx teeth 2.1-2.8 mm 4. *verneyana*

3\. Leaves on lower part of main stem broadly ovate, up to 1 1/2 x as long as broad, abruptly apiculate; leaves clearly pubescent on both sides 4

\+ Leaves on lower part of main stem narrowly lanceolate, at least 2 x as long as broad, apically attenuate, narrowly acute; leaves glabrous or minutely puberulent on both sides 5

4\. Most leaves distinctly shorter than 20 mm, densely pubescent beneath 2. *masukuensis*

\+ Most leaves much longer than 25 mm, less pubescent beneath 3. *myriantha*

5\. Leaves densely but minutely puberulent; stem hairs extremely minute and dense, impossible to separate individual hairs; calyx tube 3.6-4.0 mm, teeth clearly less than half tube length 7. *rungwensis*

\+ Leaves glabrous (rarely with a few long hairs); stems with short to long hairs, individual hairs clearly discernable; calyx tube 2.5-3.5 mm, teeth more than half to as long as tube 6

6\. Calyx minutely puberulous with few hairs 5. *cacondensis*

\+ Calyx clearly pubescent with numerous long hairs 6. *wellmannii*

3.7.2. 1. B. robusta (Hook. f.) A. Doroszenko, comb. nov.

Syn. Nepeta robusta Hook. f., Journ. Linn. Soc. 7:212 (1864)! Satureja robusta (Hook. f.) Brenan, Mem. N.Y. Bot. Gard. 9:48 (1954)!

Fl. 1-6, 11-12. Montane grassland, margins of woods, wet hollows, stream beds, 1590-2900 m.

Type: Cameroon Mt., 2130-2440 m, xii 1861, Mann (holo. K!).

Gen. distrib.: Cameroon, Nigeria.

Much the tallest species in the genus, reaching up to 300 cm, recognised by the broadly ovate leaves, with obtuse apex, closely spaced, small serrations, and reticulate venation.

3.7.3. 2. B. masukuensis (Baker) A. Doroszenko, comb. nov.

Syn: Leucas masukuensis Baker, Kew Bull. 1898:162 (1898)! Nepeta usafuensis Gurke, Bot. Jahrb. 30:394 (1901)! Calamintha masukuensis (Baker) S. Moore, J. Linn. Soc. Bot. 40:179 (1911)! Satureja masukuensis (Baker) Eyles, Trans. Roy. Soc. S. Africa 5:462 (1916)!

Fl. 3-10. Montane grassland and bracken scrub, 1060-2370 m.

Type: Malawi, Masuku plateau, 1980-2140 m, vii 1896, Whyte (holo. K!).

Gen. distrib.: Malawi, Tanzania, Zambia, Zimbabwe.

Closely related to B. myriantha.

3.7.4. 3. B. myriantha (Baker) A. Doroszenko, comb. nov.

Syn: Leucas myriantha Baker, Kew Bull. 1898:163 (1898)! Satureja myriantha (Baker) Brenan, Mem. N.Y. Bot. Gard. 9:49 (1954)!

Fl. 5-10. Montane grassland, grassland by riverside, savanna woodland, 1500-2250 m.

Syntypes: Nyika plateau, 1830-2140 m, vi 1896, Whyte 178; idem, Whyte 214; between Impala and commencement of [Nyasa-]Tanganyika plateau, vii 1896, Whyte s.n. (all at K!).

Gen. distrib.: Malawi, Tanzania, Zambia.

3.7.5. 4. B. vernayana (Brenan) A. Doroszenko, comb. nov.

Syn: Satureja vernayana Brenan, Mem. N.Y. Bot. Gard. 9:46 (1954)!

Fl. 5-9. Montane grassland, woodland, rocky slopes, damp situations in shrubberies, 1370-2150 m.

Type: [Malawi] Tuchila plateau, Mlanje, 1830 m, v 1901, J. M. Purves 13 (holo. K!).

Gen. distrib.: Malawi.

A distinct species easily recognised by the broadly elliptic to obovate, ± glabrous, entire leaves, with rounded apices, 7-18 x 3.0-11.5 mm.

3.7.6. 5. B. cacondensis (G. Taylor) A. Doroszenko, comb. nov.

Syn: Calamintha cacondensis G. Taylor, Journ. Bot. 69, suppl. 2:167 (1931)! Satureja cacondensis (G. Taylor) Brenan, Mem. N.Y. Bot. Gard. 9:49 (1954)!

Fl. 2. Along watercourses.

Type: Angola, Benguella, country of the Ganguellas and Ambuellas, along the watercourses of Caputi near Caconda, February, J. Gossweiller 2861 (holo. K!).

Gen. distrib.: Angola.

3.7.7 6. B. wellmannii (C. H. Wright) A. Doroszenko, comb. nov.

Syn: Nepeta wellmannii C. H. Wright, Kew Bull. 1909:380 (1909)! Nepeta huillensis Gurke, Bot. Jahrb. 36:121 (1905).

Fl. 5-6. Mountain slopes and woodland, 1520-1900 m.

Stems with spreading flexuous hairs	var. wellmannii
Stems minutely recurved-puberulent	var. brachytricha

var. *wellmannii*

Syn: *Satureja myriantha* (Baker) Brenan var. *wellmannii* (C. H. Wright) Brenan, Mem. N.Y. Bot. Gard. 9:49 (1954)!

Type: Angola, Benguella, Bailundo distr., 1520 m, *F. C. Wellmann* s.n. (holo. K!).

Gen. distrib.: Angola, Zambia (rare).

var. *brachytricha* (Brenan) A. Doroszenko, comb. nov.

Syn: *Satureja myriantha* (Baker) Brenan var. *brachytricha* Brenan, Mem. N.Y. Bot. Gard. 9:49 (1954)!

Type: Angola, Benguella, Bailundo distr., 1520 m, *F. C. Wellmann* s.n. (holo. K!).

Gen. distrib.: Angola.

37.8. 7. *B. rungwensis* A. Doroszenko, sp. nov.

Stems slender, erect, 100-150 cm, much-branched above, densely and extremely minutely-hairy. Leaves lanceolate, 14-23 x 6-11 mm, broadly cuneate at base, petiole 2.0-4.5 mm, apex acute, margins serrulate, teeth closely spaced, lateral veins prominent below, minor veins usually clearly visible, both sides very densely minute-pubescent. Inflorescence 4-10 x c. 1.0 cm. Calyx tube 3.6-4.0 mm, densely minute-hairy on veins, teeth lanceolate-subulate, upper lip 2.7-3.8 mm, entire or retuse, lower lip 2.8-4.0 mm, lobes oblong, entire. Nutlets unknown.

Fl. 8. Among shrubs in semi-shade, c. 1830 m.

Type: Tanzania, Rungwe distr., Lower Fishing Camp, Kiwara River, 1830 m, 9 viii 1949, locally common in secondary bush in semi-shade and on a yellow-brown volcanic soil, *P. J. Greenway* 8385 (holo. K!).

Gen. distrib.: Tanzania.

This new species is closely related to B. cacondensis and B. wellmannii. These three species form a distinct group distinguished by their slender stems, narrowly ovate to lanceolate leaves, glabrous or very minute-hairy on both sides, and margins with many closely spaced teeth. B. rungwensis is clearly separated from these two species by its very dense, minute patent pubescence, giving a greyish-green aspect, narrower, more lanceolate leaves, more cuneate at base, longer calyx tube, lanceolate-subulate teeth clearly less than half length of tube (not narrowly triangular teeth longer than half to as long as tube), upper corolla lip entire or scarcely notched (not clearly emarginate), and the lower corolla lip twice as long as the other species.

38. Killickia A. Doroszenko, gen. nov.

Prostrate perennial herbs; stoloniferous or not. Leaves broadly ovate to sub-orbicular, flat, serrate to serrulate, simple hairy, marginal veins absent, lateral veins distinct, camptodromous; clearly petiolate; palisade mesophyll dorsiventral. Inflorescence of solitary- to few-flowered verticillasters, with very long pedicels and peduncles. Bracteoles foliose or minute, linear. Calyx obconical, straight, 13-15-veined, actinomorphic or sub-bilabiate, all teeth similar in shape, half to as long as tube, not ciliate, throat glabrous. Corolla cobalt-violet, yellow or white, not resupinate, tube wide at throat, not annulate inside; upper lip emarginate or retuse, lower lip 3-lobed, longer than upper. Stamens 4, convergent; filaments short, anterior pair longer, posterior included in tube, anterior exserted but not beyond upper lip; anthers divergent.

Type species: K. pilosa, designated here.

Three species, locally distributed in Natal, South Africa.

When Killick (1961) placed these S. African species under Satureja s.l. it was to maintain uniformity of treatment with Thonner, Flowering Plants of Africa 479 (1915), Brenan in Mem. N.Y. Bot. Gard. 9:317-318 (1954) and Hedberg, Afroalpine Vascular Plants 160-164, 317-318 (1954), who all followed Briquet (1897). Killick originally described one of his species under Micromeria (M. grandiflora) as had Bentham for M. pilosa (1886). However, Killick was not really happy with these species' placement in either Satureja or Micromeria.

Killickia has similarities to Micromeria, particularly to sect. Pseudomelissa, in habit and leaf shape. However, it is distinguished from Micromeria by the solitary- or few-flowered verticillasters, on very long peduncles (up to 22 mm) and pedicels (to 7 mm), obconical, actinomorphic to sub-bilabiate calyx, with similar upper and lower teeth, and corollas wide at the throat.

3.8.1. 1. Bracteoles foliose, 7-11 mm long; calyx lips 4.0-5.0 mm, teeth narrowly triangular 3. grandiflora

\+ Bracteoles linear, 1-2 mm; calyx lips 0.9-2.0 mm, teeth broadly triangular or lanceolate 2

2. Calyx tube 2.0-3.5 mm, teeth 0.9-1.7 mm; corolla tube 5.0-12.0 mm, upper lip less than half as long as lower lip 1. pilosa

\+ Calyx tube 1.3-2.0 mm, teeth 1.4-2.0 mm; corolla tube 3.0-5.0 mm, upper lip as long as lower lip 2. compacta

3.8.2. 1. K. pilosa (Benth.) A. Doroszenko, comb. nov.

Syn: Micromeria pilosa Benth., Hook. Icon. Pl. 15: t.1522 (1886)!

Satureja reptans Killick, Bothalia 7:436 (1961)!

Fl. 1-4, 12. In tall grass, grassy hillsides, damp earth cliffs, amongst rocks, 1300-2100 m.

Type: [Natal] Faku's Territory, Sutherland (holo. K!).

Gen. distrib.: Natal, S. Africa.

3.8.3. 2. K. compacta (Killick) A. Doroszenko, comb. nov.

Syn: Satureja compacta Killick, Bothalia 7:437 (1961)!

Fl. 1, 11-12. Amongst grass tussocks, damp grass slopes on sandstone, steep banks, 2200-2350 m.

Type: Natal, locally frequent on side of bridle path in Festuca costata grassveld. Flowers deep cobalt violet. Below Amphletts, Cathkin Peak Area, 12 xii 1952, Killick 1866 (holo. PRE, iso. B! K!).

Gen. distrib.: Natal, S. Africa.

3.84. 3. K. grandiflora (Killick) A. Doroszenko, comb. nov.

Syn: *Micromeria grandiflora* Killick, Bothalia 6:439 (1954)! *Satureja grandibracteata* Killick, Bothalia 7:435 (1961)!

Fl. 1-2, 11-12. Grassveld, mountain slopes, 1800-2000 m.

Type: Natal, Cathedral Peak Forest Influences Research Station, locally frequent in *Themeda triandra* grassveld, 6400 ft., 19 ii 1952, Killick 1684 (holo. PRE, iso K!).

Gen. distrib.: Natal, S. Africa.

3.9. Calamintha Miller, Gard. Dict., Abr. ed. 4 (1754).

Syn: Melissa Sect. Calamintha Benth., Lab. Gen. Sp. 384 (1834); Melissa Sect. Macromelissa Benth., loc. cit. 385 (1834) p.p.; Melissa Sect. Heteromelissa Benth., loc. cit. 386 (1834); Calamintha Sect. Calamintha Benth. in DC., Prodr. 12:226 (1848); Calamintha Sect. Heteromelysson (Benth.) Benth., loc. cit. 234 (1848); Satureja Sect. Calamintha Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897).

Perennial herbs, rarely annual. Leaves broadly ovate to orbicular or lanceolate, crenate to serrate or dentate, rarely entire, flat, veins usually prominent, camptodromous or craspedromous; palisade mesophyll dorsiventral; distinctly petiolate. Inflorescence bracteate or ebracteate. Verticillasters few- to many-flowered, cymes dense or lax. Bracteoles linear-lanceolate or -elliptic, not or just reaching base of calyx. Calyx broad, straight, + parallel-sided tubular, 11-13-veined, throat usually hairy, sometimes glabrous, distinctly bilabiate, upper teeth usually broader than lower and mostly only 1/4-1/2 as long as lower teeth, rarely to 5/6 as long, lower teeth nearly always ciliate. Corolla white, violet to pink or red, tube not annulate inside, glabrous or hairy on inside lower half, lips 1/6-1/2 x tube length, upper usually shorter, emarginate, lower 3-lobed, central lobe sometimes bifid. Stamens 4, convergent, inserted half way up tube, posterior pair 1/4-1/2 as long as anterior pair, inserted below or at same level as anterior, all fertile or anterior pair fertile and posterior pair infertile and staminodial, included to shortly exserted from tube but not beyond upper lip; thecae divergent, very rarely parallel. Style branches unequal, sometimes markedly so, rarely equal, mostly the longer broad lanceolate and the shorter narrowly subulate, rarely both narrowly subulate.

Nutlets suborbicular to broadly ovoid, glabrous, apex rounded or obtuse.

20 species from Europe, the Mediterranean region, E Africa, Turkey and eastwards to India, China and Japan.

Calamintha is the largest of the four Calaminthoid genera. These genera are distinguished mainly on floral characteristics: Cyclotrichium by the resupinate corollas and longly exserted stamens; and Acinos by the sigmoid, usually glabrous calyces. However, the differences between Calamintha and Clinopodium are less marked. Some species, particularly the Chinese ones, have been shuffled between Calamintha and Clinopodium. The most recent treatment of Calamintha/Clinopodium in Fl. Reip. Pop. Sin. (1977) favoured Clinopodium, whereas earlier treatments favoured Calamintha (Bentham, 1848; Franchet & Savatier, 1875) or Satureja s.l. (Kudo, 1929). Notwithstanding this confusion, Calamintha and Clinopodium as treated here are clearly distinguishable on floral characteristics. The calyx of Calamintha is straight, usually broadly tubular, the lower teeth straight, and the upper calyx teeth slightly curving. In Clinopodium the calyx is curved, the lower teeth are also curved, and the upper teeth curve upward and become + erect. The bracteoles of Calamintha are always short and never exceed the base of the calyx, while in Clinopodium the bracteoles always exceed the calyx base, usually reaching the calyx teeth and forming a distinct involucre. The verticills of Clinopodium tend to be denser and more spherical.

3.9.1. 1. Whole plant densely white, dendroid hairy
[N Africa] 9. candidissima
\+ Plant not densely white hairy; hairs, if any, simple 2

2. Annual [S Central Asia] 19. debilis

\+ Perennial 3

3. Inflorescence condensed into a short dense head, 2-3 cm long, 1.5-2.0 cm wide [Ethiopia] 14. paradoxa

\+ Inflorescence not condensed into a short spike-like head, internodes clearly discernable between verticillasters 4

4. Calyx 11-nerved; corolla 16-45 mm; leaf veins tending to run directly into teeth 5

\+ Calyx 13-nerved; corolla 2.5-16 mm (to 20 mm in sylvatica); leaf veins curving away from the margin, not running directly into teeth (except uhligii which has craspedromous veins) 9

5. Stems 5-10 cm; leaves 4.5-9.0 x 4.0-8.0 mm, with 2-4 very obscure serrulations on each side, minutely puberulent; flowers solitary in leaf axils 5. piperelloides

\+ Stems 10-60 cm; leaves 9-40(-85) x 6-30(-49) mm, with 3-10 distinct teeth per side, usually pilose, pubescent or villous; flowers usually not solitary in leaf axils 6

6. Lower calyx teeth 2.5-4.5 mm; median leaves with 7-12 teeth per side (if fewer then very large teeth); corolla 20-44 mm (as short as 17 mm in N. African material) 1. grandiflora

\+ Lower calyx teeth 1.3-2.5 mm; median leaves with 5-8(-10) small teeth per side; corolla 16-26 mm 7

7. Median leaves 17-37 mm, with 6-8 short, distinct, acute to obtuse teeth on each side 2. betulifolia

\+ Median leaves 9-25 mm, with 3-6 scarcely discernable or very short, sharply pointed and outcurving teeth on each side 8

8. Leaves prominently veined beneath; leaf hairs both glandular and eglandular; calyx peduncles 1.0-1.5 mm, pedicels 0.4-0.5 mm 3. tauricola

\+ Leaves not very prominently veined beneath; leaf hairs all eglandular; calyx peduncles 1.6-2.7 mm, pedicels 3.5-4.5 mm 4. pamphylica

9. Leaves entire or scarcely notched, densely, short-haired, white tomentose (leaves 3.0-10.0(-14) mm) [E. Mediterranean region] 10

\+ Leaves + toothed, pubescent, grey or greenish 11

10. Calyx with long, patent hairs, throat with a sparse fringe of hairs, upper teeth 0.5-0.9 mm; corolla white 10. cretica

\+ Calyx with short adpressed or crispate hairs, throat with a dense fringe of hairs, upper teeth 0.4-0.6 mm; corolla mauve to pink 11. incana

11. Calyx tube 4.0-7.6 mm, lower teeth 2.0-4.0 mm; corolla tube 8.0-17.0 mm 12

\+ Calyx tube 1.7-3.8 mm, lower teeth 1.0-2.0(-2.5) mm; corolla tube 1.7-8.0(-10.5) mm 14

12. Leaves narrow elliptic to lanceolate, cuneate at base; upper and lower calyx teeth all similar, narrow triangular [Nepal] 20. piperita

\+ Leaves broadly ovate, base rounded, truncate, or broad triangular; upper and lower calyx teeth dissimilar, upper teeth broadly triangular-deltoid 13

13. Leaves + sessile, petiole 0.5-2.0 mm; distance between verticillasters 1 or less than 1 length of the subtending leaf; corolla tube widely flaring [E. African mountains] 13. uhligii

+ Leaves clearly stalked, petioles 4.0-16.0 mm; verticillasters well separated, more than 1 length of the subtending leaf apart; corolla tube narrow [Mediterranean region, S. Europe] 6. sylvatica

14. Leaves 2.7-8.0 x 1.5-7.5 mm; flowers solitary in leaf axils 15

+ Leaves 8.0-45.0 x 5.5-30.0 mm; flowers usually not solitary in leaf axils 16

15. Calyx shortly retrorse hairy, without minute glandular hairs between them, lower teeth 1.0-1.3 mm [Balearic Islands] 8. rouyana

+ Calyx shortly patent hairy with minute glandular hairs between them, lower teeth 1.5-1.9 mm [High E. African mountains] 12. kilimandschari

16. Anterior and posterior thecae similar in size; peduncles at least 1 mm and usually very much longer; corolla tube 6.0-10.5 mm [Mediterranean region] 7. nepeta

+ Anterior thecae much larger than posterior thecae; peduncles 0-0.5 mm; corolla tube 1.7-5.4 mm [Far East] 17

17. Calyx glabrous or very rarely minutely puberulent on the nerves; inflorescence bracteate 17. confinis

+ Calyx shortly and sparsely hairy; inflorescence terminal, ebracteate 18

18. Leaves narrowly ovate, often cuneate at base, (12-)20-57 x (7-)10-29 mm, teeth deep, mostly acute 18. ussuriensis

+ Leaves broadly ovate, mostly rounded at base, 8.0-30.0 x 6.0-19.0 mm, shallowly toothed, rather rounded, obtuse 19

19. Corolla cleistogamous, c. 2.5 mm; under-side of leaf minutely punctate-glandular 16. micrantha

\+ Corolla open, 3.5-5.5 mm; under-side of leaf without punctate glands 15. gracilis

C. grandiflora, C. betulifolia, C. tauricola, C. pamphylica and C. piperelloides (sp. nos. 1-5) are closely related. They share an 11-nerved calyx, large corollas, and craspedromous leaf venation. All other species have a 13-nerved calyx, smaller corollas, and nearly always camptodromous leaf venation.

3.9.2. 1. C. grandiflora (L.) Moench, Meth. 408 (1794).

Syn: Melissa grandiflora L., Sp. Pl. 592 (1753)! Calamintha montana Garsault, Fig. Pl. Anim. Med. t.189 (1764); Thymus grandiflora (L.) Scop., Fl. Carn. ed. 2, 1:424 (1772)! Satureja grandiflora (L.) Scheele, Flora 26:577 (1843); Faucibarba grandiflora (L.) Dulac, Fl. Hautes-Pyr. 402 (1867)! Clinopodium grandiflorum (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! non (Willd.) Gueldenst. ex M. Bieb. (1819).

Ic: Fl. URSS 21: t.23 f.1 (1954).

Calyx tube 6.5-10.0 mm; lower teeth 3.5-4.5 mm; corolla 25-42 mm [S & C Europe, Caucasus, Crimea, Anatolia, Iran] ssp. grandiflora

Calyx tube 5.0-6.5 mm; lower teeth 2.5-3.5 mm; corolla 18-22 mm [Morocco, Algeria] ssp. baborensis

ssp. grandiflora

Fl. 5-10. Damp banks, in forests and scrub, limestone slopes, 200-2500 m.

Type: Described from Hetruriae (Tuscany, N Italy) (Hb. Linn. 745/3, microfiche!).

Gen. distrib.: S & S C Europe, Anatolia, Caucasus, Crimea, NW Iran.

ssp. baborensis (Batt.) A. Doroszenko, comb. nov.

Syn: Calamintha baborensis Batt., Bull. Soc. Bot. Fr. 36:64 (1889); Calamintha grandiflora (L.) Moench var. parviflora Coss., Bull. Soc. Bot. Fr. 9:176 (1862); Calamintha atlantica Coss., loc. cit. (1862), nomen; Satureja baborensis (Batt.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897); Satureja grandiflora (L.) Scheele ssp. baborensis (Batt.) Maire, Cat. Pl. Maroc 3:647 (1934).

Fl. 6-7. Calcareous rocks in cedar forest, 1900-2000 m.

Type: In silvaticis regionis montanae, hucusque tantum in Kabyliae orientalis montibus Tababor, et Babor, 1200-1500 m, an. 1861, H. Perraudiere (type of Calamintha grandiflora var. parviflora).

Gen. distrib.: Morocco, Algeria.

C. baborensis is distinguished from C. grandiflora only in the size of the floral parts. Therefore, subspecific rank for C. baborensis under C. grandiflora seems appropriate.

3.9.3. 2. C. betulifolia Boiss. & Bal. in Boiss., Diagn. ser. 2(4):14 (1859)!

Syn: Clinopodium betulifolium (Boiss. & Bal. ex Boiss.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja betulifolia (Boiss. & Bal. ex Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897)! Calamintha betulifolia Boiss. & Bal. ex Boiss. ssp. cilicica Quezel & Contandr., Bull. Soc. Bot. Fr. 123:428 (1976).

Ic: Post, Fl. Syria, Palestine & Sinai 623 (1896).

Type: [Turkey C5 Icel] in rupestribus vallis Guzel Dere supra Sedichig, in regione calida Ciliciae littoralis, 12 iv 1855, Balansa 496 (holo. G!, iso. E!, K).

Gen. distrib.: S Anatolia.

3.9.4. 3. C. tauricola P. H. Davis, Kew Bull. 1951:68 (1951)!

Fl. 5-8. Calcareous rocks, 940-1700 m.

Type: [Turkey C4 Konya] d. Ermenek, Hamitseydi Bogazi between Sarivadi and Beskoyu, 1500-1700 m, 16 viii 1949, P. H. Davis 16225 (holo. K, iso. E!).

Gen. distrib.: S Anatolia.

3.9.5. 4. C. pamphylica Boiss. & Heldr. in Boiss., Diagn. ser. 1(12):52 (1853)!

Syn: Satureja pamphylica (Boiss. & Heldr.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897)!

Fl. 4-8. Limestone rocks, Cedrus libani, Pinus brutia or Cupressus sempervirens forest, 50-1500 m.

Stems and petioles shortly villous, with hairs 0.5-1.0 mm; median leaves triangular, 6-12 x 6-12 mm, shallowly crenate-denticulate, base truncate to sub-cordate ssp. pamphylica

Stems and petioles pubescent, eglandular hairs very minute; median leaves broadly ovate, up to 24 x 21 mm, distinctly crenate-dentate, base widely cuneate to truncate ssp. davisii

ssp. pamphylica

Type: [Turkey C4 Antalya] ad rupes calcareis montium Pamphyliae orientalis regio superior montis Ghibelleis (Cebireis Da.) prope Alaya (Alanya), Heldreich (holo. G!, iso. G!, K, WU!).

Gen. distrib.: SW Anatolia.

ssp. davisii (Quezel & Contandr.) P. H. Davis, Fl. Turk. 7:326 (1982).

Syn: Calamintha davisii Quezel & Contandr., Bull. Soc. Bot. Fr. 123:427 (1976).

Type: [Turkey C3 Antalya] rochers calcaires a l'ouest de Kmer (Kemer), 200-300 m, 23 vii 1973, P. Quezel & J. Contandriopoulos 73-436 (Hb. Marseille St. Jerome).

Gen. distrib.: SW Anatolia.

3.9.6. 5. C. piperelloides Stapf, Denksch. Akad. Wiss. Wien, Math. Nat. Kl. 50:123 (1885)!

Fl. 5.

Type: [Turkey C2 Antalya] Lycia, ad Golbaschi, 4 v 1882, Luschan (holo. W!).

The species is only known from the type. It is related most closely to C. pamphylica and distinguished by its lower, more suffruticose habit, smaller leaves, flowers always solitary in leaf axils, and calyx teeth half as long as tube (not only about 1/4 as long as tube).

3.9.7 6. C. sylvatica Bromf., Phytologist 2:49 (1845).

Syn: Melissa sylvatica (Bromf.) Nym., Syll. Fl. Eur. 1:100 (1855); Satureja rhombifolia Maly in Dorfler, in syn. Herb. Norm. no. 4482 (1903).

Closely related to C. nepeta. Both C. sylvatica and C. nepeta are very variable, especially in habit, indumentum, and density of the inflorescence. Hence the large number of synonyms for these species.

Leaves up to 70 x 45 mm, ovate, coarsely dentate
  or serrate, 6-10 teeth per side; peduncles
  up to 15 mm; lower calyx teeth 2.5-4.0 mm;
  corolla 13-22 mm ssp. sylvatica
Leaves up to 40 x 35 mm, rarely longer, ovate-
  orbicular to ovate, scarcely notched or shallow
  crenate-dentate, 5-8 teeth per side; peduncles
  up to 5 mm, sometimes to 10 mm; lower calyx teeth
  1.3-3.0(-3.5) mm; corolla 9-16 mm ssp. ascendens

ssp. sylvatica

Syn: Calamintha montana Lam., Fl. Fr. 2:396 (1778), non Garsault (1764); Calamintha menthaefolia Host, Fl. Austr. 2:129 (1832); Satureja calamintha (L.) Scheele ssp. sylvatica (Bromf.) Briq. var. sylvatica Briq., Lab. Alp. Mar. 3:434 (1895); Satureja menthaefolia (Host) Fritsch, Exkurs. Fl. Austr. 478 (1897); Satureja calamintha (L.) Scheele ssp. officinalis sensu Gams in Hegi, Ill. Fl. Mitteleur. 5:2294 (1928); Calamintha montana Lam. ssp. officinalis (Moench) Dostal, Kvetena CSR 1240 (1950); Calamintha montana Lam. ssp. menthaefolia (Host) Dostal, loc. cit. (1950).

Ic: Sowerby & Sm., Engl. Bot. Suppl. 7, t.1052 (1867).

Type: Described from Isle of Wight, England.

Gen. distrib.: Europe as far N as S England, eastward to Turkey.

ssp. ascendens (Jord.) P. W. Ball, Bot. Jour. Linn. Soc. 65:346 (1972).

Syn: Calamintha ascendens Jord., Obs. Pl. Crit. 4:8 (1846); Melissa intermedia Baumg., Enum. Stirp. Transs. 2:184 (1816); Thymus calaminthoides Reichenb., Fl. Germ. Exc. 1:329 (1831), nomen; Melissa rotundifolia Soland. ex Lowe, Trans. Camb. Phil. Soc. 6:14 (1838), non Benth. (1834); Calamintha baetica Boiss. & Reut., Pugillus 92 (1852); Calamintha heterotricha Boiss. & Reut., Pugillus 93 (1852); Calamintha nervosa Pomel, Nouv. Mat. Fl. Atl. 2:307 (1875); Calamintha intermedia (Baumg.) H. Braun, Verh. Zool.-Bot. Ges. Wien 39:220 (1889); Clinopodium pomelianum O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja calamintha (L.) Scheele ssp. ascendens (Jord.) Briq., Lab. Alp. Mar. 3:435 (1895); Satureja pomelii Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897); Satureja ascendens (Jord.) Maly, Oest. Bot. Zeit. 57:159 (1907); Clinopodium ascendens (Jord.) Sampaio, Herb. Portug. 119 (1913); Calamintha sennenii Cad., Bull. Geogr. Bot. 24:228 (1914); Calamintha catalaunica Sennen & Pau, Fl. Catal. 142 (1917); Calamintha x bonanovae Sennen & Pau, loc. cit. 143 (1917); Satureja baetica (Boiss. & Reut.) Pau, Mem. Soc. Esp. Hist. Nat. 12:374 (1924); Satureja calamintha (L.) Scheele ssp. menthifolia sensu Gams in Hegi, Ill. Fl. Mitteleur. 5:2294 (1928); Calamintha hirta (Briq.) Hayek, Fedde, Repert. Beih. 30:326 (1929); Satureja heterotricha (Boiss. & Reut.) Sennen & Mauricio, Cat. Fl. Rif Or. 89 (1933); Calamintha ferreri Sennen, Bol Soc. Iber. Cien. Nat. 1933, 32:27 (1934); Satureja ferreri Sennen, loc. cit. (1934), nomen; Calamintha peniciliata Sennen, loc. cit. 31 (1934); Satureja peniciliata Sennen, loc. cit. 31 (1934), nomen; Calamintha bonanovae Sennen, loc. cit. 49 (1934); Satureja bonanovae Sennen, loc. cit. 49 (1934), nomen; Calamintha eriocaulis Sennen, loc. cit. 50 (1934); Satureja eriocaulis Sennen, loc. cit. 50 (1934), nomen; Calamintha brevisepala Sennen, loc. cit. 51 (1934); Satureja brevisepala Sennen, loc. cit. 51 (1934), nomen; Calamintha longeracemosa Sennen, loc. cit. 53 (1934); Satureja longeracemosa Sennen, loc. cit. 53 (1934), nomen; Calamintha mairei Sennen, loc. cit. 53 (1934); Satureja mairei Sennen, loc. cit. 53 (1934), nomen.

Ic: Jordan, Obs. Pl. Crit. 4: t.1 f.B (1846), as Calamintha ascendens.

Fl. 6-12. Dry calcareous rocks, scrub, banks, s.l.-1800 m.

Type: Described from France [figure in Jordan, Obs. Pl. Crit. 4: t.1 f.B (1846)].

Gen. distrib.: W, S and SC Europe, eastward to Turkey and Iran, N Africa.

There is considerable morphological overlap between the two subspecies throughout their range. It is often difficult to assign specimens to one subspecies or the other. The range of ssp. sylvatica is entirely within the range of ssp. ascendens but tends to be mostly in the northern part of the species' distribution.

3.9.8 7. C. nepeta (L.) Savi, Fl. Pis. 2:63 (1798)!

Syn: ?Clinopodium carolinianum Miller, Gard. Dict. ed.8 (1768); Melissa parviflora Salisb., Prodr. Stirp. Chapel Allerton Vig. 86 (1796), nomen; Thymus nepeta (L.) Sm., Fl. Brit. 2:642 (1800)! Melissa obtusifolia Pers., Syn. Pl. 2:132 (1807); ?Thymus minor Trev., Ind. Sem. Hort. Vratisl., App. 1:4 (1819); Calamintha canescens Presl, Fl. Sic. 37 (1826); Calamintha rotundifolia Host, Fl. Austr. 2:131 (1832); Melissa aethos Hort. ex Benth., Lab. Gen. Sp. 387 (1834); Calamintha dilitata Schrad., Ann. Sci. Nat. 6:100 (1836); Satureja nepeta (L.) Scheele, Flora 26:577 (1843); Calamintha canescens C. Koch, Linnaea 21:672 (1848), non Presl (1826), non Torr. & A. Gray ex Benth. (1848); Clinopodium nepeta (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja x narentana K.

Maly, Herb. Norm. no. 4931 (1908).

Leaves 20-45 mm long, clearly 5-9-toothed on each side; verticillasters very lax, cymes (5-)10-20-flowered; peduncles 8-18 mm; pedicels 5-10 mm ssp. nepeta

Leaves 8.5-20(-25) mm long; sub-entire or with up to 5 shallow teeth; verticillasters crowded, cymes 5-10(-15)-flowered; peduncles 0-5(-10) mm; pedicels 0-5 mm ssp. glandulosa

ssp. nepeta

Syn: Melissa nepeta L., Sp. Pl. 593 (1753)! Calamintha trichotoma Moench, Meth. 409 (1794); Thymus diffusus Hortul. ex Benth., Lab. Gen. Sp. 387 (1834), nomen in syn., non Bluff & Fingerh. (1826); Calamintha nepetoides Jord., Obs. Pl. Crit. 4:16 (1846); Calamintha mollis Jord. ex Lamotte, Prod. Fl. Plat. Centr. 2:599 (1881); Calamintha thessala Hausskn., Mitt. Thur. Bot. Verh. 9:46 (1890); Satureja nepetoides (Jord.) Fritsch, Exk. Fl. Austr. 478 (1897); Satureja varbossiana Maly, Wiss. Mitt. Bosn. Herzeg. 8:444 (1901); Satureja calamintha (L.) Scheele ssp. nepetoides (Jord.) Br.-Bl., Jahresb. Naturf. Ges. Graubundens 1923, 24:203 (1924); Satureja mollis (Jord. ex Lamotte) E. Perrier, Mem. Acad. Sci. Savoie, ser. 5, 5:201 (1928); Calamintha largiflora Klokov, Fl. RSS Ucr. 9:660 (1960).

Ic: Jordan, Obs. Pl. Crit. 4: t.2 f.B (1846), as Calamintha nepetoides.

Fl. 7-10. Calcareous rocks, cliffs, scree, open areas, dry river bed bank, grassland, gullies, 300-1520 m.

Type: Described from Italy (Hb. Linn. 745/5, microfiche!).

Gen. distrib.: S & SC Europe, eastwards to Turkey.

ssp. glandulosa (Req.) P. W. Ball, Bot. J. Linn. Soc. 65:347 (1972).

Syn: Thymus glandulosus Req., Ann. Sci. Nat., ser.1, 5:386 (1828); Melissa calamintha L., Sp. Pl. 593 (1753); Calamintha vulgaris Garsault, Fig. Pl. Anim. Med. t.187 (1764); Thymus calamintha (L.) Scop., Fl. Carn. ed.2, 1:425 (1771); Calamintha parviflora Lam., Fl. Fr. 2:396 (1778); Calamintha officinalis Moench, Meth. 409 (1794); Melissa subnuda Waldst. & Kit., Desc. Ic. Pl. Rar. Hung. 3:291, t.262 (1810); Thymus moschatella Poll., Brugnat. Giorn. Fis. 9:33 (1816); Thymus umbrosus Spreng., Nov. Prov. 41 (1819); Thymus subnudus (Waldst. & Kit.) Spreng., Syst. Veg. 2:698 (1825); Thymus athonicus Bernh. ex Reichenb., Fl. Germ. Exc. 1:329 (1831); Calamintha subnuda (Waldst. & Kit.) Host, Fl. Austr. 2:130 (1832); Calamintha obliqua Host, loc. cit. 131 (1832); Melissa glandulosa (Req.) Benth., Lab. Gen. Sp. 387 (1834); Thymus clandestinus Salzm. ex Mutel, Fl. Fr. 3:18 (1836), nomen; Satureja calamintha (L.) Scheele, Flora (Regensburg) 26:577 (1843); Calamintha glandulosa (Req.) Benth. in DC., Prodr. 12:227 (1848); Calamintha byzantina C. Koch, Linnaea 21:672 (1848); Micromeria dalmatica Fenzl, Cat. Sem. Vind. (1851); Micromeria byzantina (C. Koch) Walp., Ann. Bot. Syst. 3:251 (1852); Calamintha spruneri Boiss., Diagn. ser. 1(12):53 (1853); Calamintha fenzlii Vis., Revis. Pl. Min. Cogn. 7 (1855); Calamintha stricta Reichenb., Ic. Fl. Germ. 18:44 (1858), nomen; Satureja fenzlii (Vis.) Nym., Syll. Fl. Eur., Suppl. 1:20 (1865); Faucibarba officinalis (Moench) Dulac, Fl. Hautes-Pyr. 402 (1867); Faucibarba umbrosa Dulac, loc. cit. (1867); Faucibarba parviflora (Lam.) Dulac, loc. cit. 403 (1867); Calamintha gussonei Tod. ex Nym., Consp. 588 (1881), nomen; Calamintha calamintha (L.) H. Karst, Deutsche Fl. Pharm. Med. Bot. 1002 (1882), nomen illeg.; Satureja glandulosa (Req.) Car. in Parl., Fl. Ital. 6:125 (1884);

Clinopodium glandulosum (Req.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Clinopodium calamintha (L.) O. Kuntze, loc. cit. 515 (1891); Clinopodium subnudum (Waldst. & Kit.) O. Kuntze, loc. cit. 516 (1891); Satureja bosniaca Maly, Glasn. Zem. Muz. Bosn. Herzeg. 11:138 (1899); Satureja subnuda (Waldst. & Kit.) Dorfler, Herb. Norm. no. 4289 (1902); Calamintha enriquei Sennen & Pau in Sennen, Fl. Catal. 141 (1917); Satureja calamintha (L.) Scheele ssp. glandulosa (Req.) Gams in Hegi, Ill. Fl Mitteleur. 5:2292 (1928); Satureja calamintha (L.) Scheele ssp. subnuda (Waldst. & Kit.) Gams in Hegi, loc. cit. 2293 (1928); Calamintha nepeta (L.) Savi var. spruneri (Boiss.) Hayek, Prodr. Fl. Balc. 2:326 (1929); Satureja villosa (Boiss.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 1928, 8:873 (1929), non (Pers.) Dorfler (1898); Calamintha cantabrica Sennen & Elias, Bol. Soc. Iber. Cien. Nat. 1933, 32:26 (1934); Satureja cantabrica Sennen & Elias, loc. cit. (1934), nomen; Calamintha josephi Sennen, Bol. Soc. Iber. Ciec. Nat. 1933, 32:30 (1934); Satureja josephi Sennen, loc. cit. (1934), nomen; Calamintha caballeroi Sennen ex Sennen & Pau, Bol. Soc. Iber. Cien. Nat. 1933, 32:55 (1934); Satureja caballeroi Sennen & Pau, loc. cit. (1934), nomen; Calamintha litardieri Sennen, loc. cit. 56 (1934); Satureja litardieri Sennen, loc. cit. 56 (1934), nomen; Calamintha macra Klokov, Fl. RSS Ucr. 9:660 (1960).

Ic: Jordan, Obs. Pl. Crit. 4: t.2 f.A (1846), as Calamintha nepeta.

Fl. (4-)6-11. Road banks, granitic or calcareous rocks, river valley alluvium, river and stream banks, fields, sandy beach, s.l.-2000 m.

Type: [Corsica] sur les bords de la riviere de Calarima, dans le Niolo en Corse, M. Requien.

Gen. distrib.: E England, S Europe, eastwards to Turkey, rare in NW

Africa.

The following taxa correspond with intermediates between C. nepeta ssp. nepeta and ssp. glandulosa.

Thymus brauneanus Hoppe ex Reichenb., Fl. Germ. Exc. 1:329 (1831); Calamintha einseliana F. Schultz, Arch. Fl. Fr. Allem. 178 (1850); Calamintha subisodonta Borbas, Oest. Bot. Zeit. 32:219 (1892); Satureja einseliana (F. Schultz) Hayek in Wettstein, Sched. Fl. Exsicc. Austro-Hung. 10:46 (1913); Calamintha fontii Sennen & Pau, Fl. Catal. 143 (1917); Satureja brauneana (Hoppe ex Reichenb.) Jav., Magy. Bot. Lap. 17:50 (1918); Satureja brauneana (Hoppe ex Reichenb.) Jav. ssp. transsilvanica (Jav.) Borza, Bul. Grad. Bot. Cluj 5:100 (1925); Calamintha nepeta (L.) Savi ssp. subisodonta (Borbaş) Hayek, Prod. Fl. Balc. 926 (1931); Calamintha brauneana (Hoppe ex Reichenb.) O. Schwarz, Mitt. Thur. Bot. Ges. 1:113 (1949); Satureja subisodonta (Borbas) Soo, Bot. Kozl. 49:157 (1961).

The following are probably synonyms of either C. sylvatica or C. nepeta.

Calamintha cacuminiglabra Sennen, Bol. Soc. Iber. Cien. Nat. 1933, 32:52 (1934); Satureja cacuminiglabra Sennen, loc. cit. (1934), nomen; Calamintha dufourii Sennen, loc. cit. 59 (1934); Satureja dufourii Sennen, loc. cit. (1934), nomen.

3.9.9. 8. C. rouyana (Briq.) Rouy in Rouy & Foucaud, Fl. Fr. 11:336 (1909).

Syn: Satureja rouyana Briq., Lab. Alp. Mar. 442 (1895).

Ic: Knoche, Fl. Balearica 4: t.13 (1923).

Fl. 8. Fissures of calcareous rocks, 1200-1300 m.

Type: ?

Gen. distrib.: Balearic Islands, Corsica.

Closely related to C. nepeta but distinguished from it by its very low suffruticose habit, very slender stems, much smaller, more narrowly ovate leaves, flowers always solitary in leaf axils, smaller calyx and smaller corolla.

3.9.10. 9. C. candidissima (Munby) Benth. in DC., Prodr. 12:226 (1848).

Syn: Melissa candidissima Munby, Fl. Alger. 61 (1847); Clinopodium candidissimum (Munby) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja candidissima (Munby) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897); ?Satureja x alboviridis Faure & Maire, Bull. Soc. Hist. Nat. Afr. Nord 20:195 (1929).

Fl. 8-11. In waste and rocky places, c. 450 m.

Type: ?

Gen. distrib.: Algeria.

This species is easily identifiable on account of the dense, dendroid indumentum. It comes closest to C. nepeta and C. sylvatica.

3.9.11. 10. C. cretica (L.) Lam., Fl. Fr. 2:395 (1778)!

Syn: Melissa cretica L., Sp. Pl. 593 (1753)! Nepeta incana Sieber ex Reichenb., Fl. Germ. Exc. 328 (1831), nomen; Thymus hirtus Sieber ex Benth., Lab. Gen. Sp. 386 (1834), nomen; Clinopodium creticum (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja cretica (L.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897)!

Fl. 6-10. Calcareous rocks, stony places, gorges, 150-650 m.

Type: Described from Monspelia (Hb. Linn. 745/6, microfiche!).

Gen. distrib.: Crete.

3.9.12. 11. C. incana (Sm.) Boiss., Fl. Atticae Heldr. 1844 (1845).

Syn: Thymus incanus Sm. in Sibth. & Sm., Prod. Fl. Graec. 1:421 (1809); Melissa cretica sensu Banks & Sol. in Russ., Nat. Hist. Aleppo, ed.2, 2:256 (1794); Melissa incana (Sm.) Benth., Lab. Gen. Sp. 386 (1834); Clinopodium incanum (Sm.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja incana (Sm.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:301 (1897), non (Ruiz & Pav.) Spreng. (1825); Satureja boissieri Briq., loc. cit. 302 (1897) [supposedly S. incana x S. calamintha ssp. nepeta var. nepeta] = S. x atheniensis Briq., Ann. Conserv. Jard. Bot. Geneve 2:192 (1898); ?Satureja pallaryi Thiebaut, Bull. Soc. Bot. Fr. 1937, 84:699 (1938).

Ic: Sibth. & Sm., Fl. Graec. 6:62, t.577 (1827).

Fl. 1, 5-11. Dry stony ground, roadside, fields, 30-910 m.

Type: ?

Gen. distrib.: Cyprus, Greece, Aegean Islands, Turkey, W Syria, Israel, Lebanon, Libya.

C. incana has been confused with C. cretica. However, the dense, grey crispate-tomentose indumentum of C. incana contrasts quite clearly from the sparser, patent pubescence of C. cretica.

3.9.13. 12. C. kilimandschari Gurke ex Engler, Abh. Preuss. Akad. Wiss. 1891, 2:366 (1892).

Syn: Satureja kilimandschari (Gurke) Hedberg, Symb. Bot. Upsal. 15:162 (1957).

Fl. 2-11. Dry rock slopes, rock crevices, bare ground, alpine grasslands, 3350-4420 m.

Type: Tanganyika Tanzania, Kilimanjaro, between Mue River and vegetation limit, 2800-4000 m, Meyer 234 (holo. B - lost). Kilimanjaro, on dry ground near Peter's Hut, 3800 m, Hedberg 1245 (neotype BR, EA, K, LD, S, UPS).

Gen. distrib.: Kenya, Tanzania, Uganda.

There is a facies similarity of some of the more luxurient specimens to Killickia compacta. However, closer inspection reveals a wide divergence in inflorescence, calyx and corolla structure.

3.9.14. 13. C. uhligii (Gurke) Verdcourt, Kew Bull. 1956:447 (1957)!

Syn: Satureja uhligii Gurke, Bot. Jahrb. 36:128 (1905); Calamintha elgonensis Bullock, Kew Bull. 1932:502 (1932)!

Fl. 1-4, 6-7, 9, 12. Grassland, open banks, crater of volcano, in shade of Junipers, thickets, 2280-3960 m.

Type: Kenya, Kilimandscharo Gebiet uber Arusha, 2800 m, Uhlig 517.

Gen. distrib.: Kenya, Tanzania, Uganda.

3.9.15. 14. C. paradoxa Vatke, Linnaea 37:327 (1872)!

Fl. 1-2, 5, 8-12. Moist grassy places, margins of evergreen forest, near stream banks, 1520-3360 m.

Type: [Ethiopia] ex Tigre v. Begemder, ann. 1863-8, Schimper 1546 (holo. K!).

Gen. distrib.: Ethiopia.

The ovate leaves with rounded apices, subcordate bases and numerous, regularly-spaced crenations, the condensed head-like inflorescence with sessile verticillasters, and the parallel thecae are together unusual in the genus. However, the shape of the calyx and corolla has close similarities to other African Calamintha species.

3.9.16 15. C. gracilis Benth. in DC., Prodr. 12:232 (1848).

Syn: Melissa cretica sensu Thunb., Fl Jap. 247 (1784), non L. (1753); Cunila moluccana Zipp. nomen in herb. Lugd. Bat.; Calamintha moluccana Zip. ex Miq., Fl. Ind. Bat. 2:968 (1859);

Clinopodium gracile (Benth.) O. Kuntze, Rev. Gen. Pl. 2:514 (1891); Calamintha radicans Van., Bull. Acad. Int. Geog. Bot. 14:182 (1904), p.p. [Bodinier 1131!]; Satureja gracilis (Benth.) Nakai, Journ. Coll. Sc. Univ. Tokyo 31:149 (1911); Clinopodium longipes C. Y. Wu & Hsuan ex H. W. Li, Acta Phytotax. Sin. 12(2):217 (1974).

Ic: Fl. Reip. Pop. Sin. 66:237 t.54 f.1-6 (1977).

Fl. 3-9. Ploughed field, grassy banks, path-sides, sub-tropical hill jungle, 100-1830 m.

Syntypes: Java, Zolling 332, 1841 (G).

Gen. distrib.: SE China, Hong Kong, S Japan, Burma, Malaya, Java, Lesser Sunda Islands, Celebes, Moluccas.

Much confusion has arisen over the C. gracilis-confinis-ussuriensis complex. These species are particularly variable in habit, leaf shape and verticillaster density. Also numerous errors of identification have added to the difficulties. However, a detailed study of these species revealed that they are easily identified on leaf, inflorescence and calyx characters, as follows:

1. Inflorescence bracteate; calyx glabrous or very rarely minutely puberulent on nerves — C. confinis
\+ Inflorescence terminal, ebracteate; calyx shortly and sparsely hairy — 2
2. Leaves broadly ovate, mostly rounded at base, 11-30(-40) x 8.5-18(-25) mm; shallowly toothed, teeth 0.3-1.2 mm, rather rounded, obtuse — C. gracilis
\+ Leaves narrowly ovate, often cuneate at base, (10-)20-57 x (6.5-)10-29 mm; deeply toothed, teeth 1.0-2.6 mm, apex mostly acute — C. ussuriensis

Kudo (1929) reduced Melissa cretica sensu Thunb. to a synonym of S. confinis (Hance) Kudo, but from Thunberg's description, "Melissa racemis terminalibus, pedunculis solitariis brevissimis", it is more likely to refer to C. gracilis.

3.9.17 16. C. micrantha (Regel) A. Doroszenko, comb. nov.

Syn: Hedeoma micrantha Regel, Gartenfl. 1864:357 (1864); Calamintha gracilis Benth. var. densiflora Hance, Ann. Sci. Nat., ser. 5, 5:236 (1866); Clinopodium micranthum (Regel) Hara, Journ. Jap. Bot. 16:156 (1940); Clinopodium omuranum Honda, Bot. Mag., Tokyo 54:223 (1940); Satureja micrantha (Regel) Nakai, Bull. Nat. Sci. Mus. Tokyo n.s. 31:99 (1952).

Ic: Somoku Dzusetsu ed.2, 11: t.21 (1874).

Roadsides, open places.

Type: A cultivated specimen raised from seed collected by C. Maximovicz near Yokohama, Japan (holo. LE).

Gen. distrib.: Japan.

Very similar to C. gracilis but distinguished by its more cuneate leaf base, lower leaf lamina densely punctate-glandular, and the cleistogamous flowers with a tube only c. 1.7 mm long. Further study may show that C. micrantha is merely a cleistogamous form of C. gracilis.

3.9.18 17. C. confinis Hance, Journ. Bot. 6:331 (1868).

Syn: Clinopodium confine (Hance) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Calamintha radicans Van., Bull. Acad. Int. Geog. Bot. 14:182 (1904), p.p. [Kouy-Tcheou, Hoang Ko, 1 vi 1898, Leguin s.n.!]; Calamintha argyi Levl., Fedde, Rep. Sp. Nov. 8:423 (1910)! Satureja confinis (Hance) Kudo, Mem. Fac. Sci. Agric. Taihoku Imp. Univ. 2:100 (1929).

Ic: Fl. Reip. Pop. Sin.66:237 t.54 f.7-9 (1977).

Fl. 4-6. Margin of river, among rocks in shade, thickets, c. 40 m.
Type: [China] ad Sai-chii-shan, Prov. Cantoniensis, iv 1866, T. Sampson 13045.
Gen. distrib.: E & SE China.

3.9.19. 18. C. ussuriensis Regel & Maack ex Regel, Mem. Acad. Imp. Sci. St. Petersb. ser. 7, 4(4):116 (1861).
Syn: Calamintha umbrosa sensu Miq., [Prol. Fl. Jap. 38] Ann. Mus. Lugd. Bat. 2(4):38 (1865); Calamintha umbrosa (M. Bieb.) Fisch. & C. A. Mey. var. sachalinensis Fr. Schm., Fl. Sachal. 164 (1868); Calamintha umbrosa (M. Bieb.) Fisch. & C. A. Mey. var. japonica Fr. & Sav., Enum. Pl. Jap. 1:368 (1875); Calamintha multicaulis Maxim., Mel. Biol. 9:444 (1875); Clinopodium multicaule (Maxim.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Clinopodium ussuriensis (Regel & Maack) O. Kuntze, loc. cit. 2:516 (1891); Calamintha fauriei Levl. & Van., Fedde Repert. Beih. 8:259 (1910)! Calamintha taquetii Levl. & Van., loc. cit. 8:423 (1910), p.p. [Taquet 1254, 1255, 3093, non Taquet 1240]; Satureja umbrosa Matsum & Kudo, Bot. Mag., Tokyo 26:299 (1912); Satureja multicaulis (Maxim.) Nakai, Rep. Veg. Quelpaert 78 (1914); Satureja multicaulis (Makim.) Nakai var. fauriei (Levl. & Van.) Nakai, Bot. Mag., Tokyo 35:194 (1921)! Satureja ussuriensis (Regel & Maack) Kudo, Journ. Coll. Sci. Imp. Univ. Tokyo 43(8):36 (1921); Satureja sachalinensis (Fr. Schm.) Kudo, loc. cit. 34 (1921); Clinopodium sachalinense (Fr. Schm.) Koidzumi, Bot. Mag., Tokyo 43:387 (1929); Clinopodium fauriei (Levl. & Van.) Hara, Journ. Jap. Bot. 11:106 (1935)! ?Clinopodium minimum Hara, loc. cit. 109 (1935); Satureja fauriei (Levl. & Van.) Nakai, Bull. Nat. Sci. Mus., Tokyo no. 31:99 (1952)!
Ic: Regel & Maack, loc. cit. t.9, f. 10-11 (1861); Hara, Journ. Jap. Bot. 11:103 f.15 (1935), as Clinopodium multicaule.

Fl. 7-10. In forest and grassy places, sandy banks.

Type: [USSR] an der Ussuri-Mundung and am obern Ussuri bei Tschomborko. Wachst auf sandigen Ufern and Inseln. Maack (holo. LE?).

Gen. distrib.: NE China, USSR (Ussuri & Sakhalin), Korea, Japan.

3.9.20. 19. C. debilis (Bunge) Benth. in DC., Prodr. 12:232 (1848).

Syn: Thymus debilis Bunge in Ledeb., Fl. Alt. 2:391 (1830); Melissa debilis (Bunge) Benth., Lab. Gen. Sp. 391 (1834); Calamintha annua Schrenk, Bull. Acad. Sci. St. Petersb. 10:353 (1842)! Clinopodium annuum (Schrenk) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Clinopodium debile (Bunge) O. Kuntze, loc. cit. (1891); Satureja debilis (Bunge) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897); Satureja annua (Schrenk) Briq., loc. cit. (1897)! Calamintha caucasica Somm. & Lev., Nuov. Giorn. Ital. 1897:207 (1897).

Ic: Ledebour, Ic. Pl. Ross. 5: t.438 (1834); Fl. Reip. Pop. Sin. 66:241, t. 55 (1977).

Fl. 8.

Type: ?

Gen. distrib.: S USSR, eastwards to China.

The affinities of C. debilis seem to be with the Mediterranean rather than Far East species, though in leaf shape it is similar to the Nepalese C. piperita.

3.9.21. 20. C. piperita (D. Don) A. Doroszenko, comb. nov.

Syn: Thymus piperitus D. Don, Prodr. Fl. Nep. 112 (1825); Thymus origanifolius D. Don, loc. cit. 113 (1825), non Vis. (1830); Clinopodium longicaule Benth. in Wall., Pl. As. Rar. 1:66 (1830); Melissa longicaulis (Benth.) Benth., Lab. Gen. Sp. 395 (1834);

Calamintha longicaulis (Benth.) Benth. in DC., Prodr. 12:234 (1848); Satureja piperita (D. Don) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897); Satureja longicaulis (Benth.) Benerji, Rec. Bot. Surv. Ind. 19(2):77 (1966); Clinopodium piperitum (D. Don) Murata, Acta Phytotax. Geobot. 28:30 (1977) [the comb. nov. by Press in Hara, Chater & Williams, Enum. Fl. Pl. Nepal 3:150 (1982) is superfluous].

Fl. 2-5. Beneath shrubs and trees, moist shady banks, 1430-2750 m.

Type: ?

Gen. distrib.: Nepal.

This species is isolated in the genus. However, the calyx and corolla are similar to C. grandiflora and C. betulifolia, though rather more narrowly tubular, and in leaf shape is similar to C. debilis.

39.22. Nom. dubia et rejec.

C. adriani Sennen & Teodoro, Treb. Mus. Cienc. Nat. Barcelona 15, ser. Bot., 1:30 (1931), nomen.

C. albiflora Van., Bull. Acad. Geog. Bot. 14:181 (1904) [holo. at Le Mans] = Nepeta cataria L.

C. arvensis (L.) Garsault, Fig. Pl. Anim. Med. t.190 (1764) = Mentha arvensis L.

C. x barolesii Sennen, Bol. Soc. Iber. Cien. Nat. 1933, 32:61 (1934) = possibly an Acinos sp.

C. bianoris Sennen, Bol. Soc. Iber. Cien. Nat. 1933, 32:54 (1934).

C. x cadevallii Sennen, Bol. Soc. Arag. 11:237 (1912) according to Sennen is Calamintha adscendens x clinopodium.

C. canescens Torr. & A. Gray ex Benth. in DC., Prodr. 12:229 (1848) = Conradina canescens (Torr. & A. Gray ex Benth.) A. Gray.

C. cavaleriei Levl. & Van., Fedde Rep. Sp. Nov. 8:424 (1910) = Melissa axillaris (Benth.) Bakh. f.

C. clipeata Van., Bull. Acad. Geog. Bot. 14:184 (1904) = Mosla chinensis Maxim.

C. conillii Sennen, Bol. Soc. Arag. 11:237 (1912).

C. x degenii Murr., Neue Ubersicht Farn & Blutenpfl. Vorarlb. 255 (1923).

C. elata Lojac., Fl. Sic. 2:221 (1907).

C. epilosa A. J. Wilmott, Journ. Bot. 56:145 (1918).

C. esquirolii Levl., Fedde Rep. Sp. Nov. 8:450 (1910) [type at Le Mans] = Coleus esquirolii (Levl.) Dunn.

C. foliosa Opiz, Natural. 3:20 (1823).

C. hederacea (L.) Scop., Fl. Carn. ed. 2, 1:423 (1772) = Glechoma hederacea L.

C. herba-barona (Loisel.) Heynh., Nom. 1:144 (1840) = Thymus herba-barona Loisel.

C. ilicifolia A. Gray, Proc. Amer. Acad. 8:368 (1873) = Acanthomintha ilicifolia (A. Gray) A. Gray.

C. intermedia Velen., Rel. Mrkvickanae 26 (1922).

C. x joffrei Sennen, Treb. Mus. Cienc. Nat. Barcelona 15, ser. Bot., 1:31 (1931), nomen.

C. microphylla Rafin., Herb. Rafin. 79 (1833), nomen.

C. minoae Lojac, Fl. Sic. 2:220 (1907).

C. neglecta Opiz, Natural. 3:20 (1823).

C. palmeri A. Gray, Proc. Amer. Acad. 11:100 (1876) has all the features of Hedeoma but has 4 fertile? stamens. It is rather similar in morphology to H. pulegioides (L.) Pers.

C. x planasii Sennen, Diagn. Nouv. Pl. Espagne & Maroc 40 (1936).

C. rotundifolius sensu Losc. & Pard., Ser. Inconf. 82 (1863) = Ziziphora acinoides L.

C. secondaireana Sennen, Bol. Soc. Iber. Cien. Nat. 1933, 32:54 (1934), nomen.

C. spicata Lojac., Fl. Sic. 2:222 (1907).

C. stenostoma Stapf, Denkschr. Acad. Wiss. Wien 1:95 (1885).

310. Clinopodium L., Sp. Pl. 587 (1753).

Syn: Melissa L. sect. Clinopodium (L.) Benth., Lab. Gen. Sp. 391 (1834); Calamintha Miller sect. Clinopodium (L.) Benth. in DC., Prodr. 12:232 (1848); Satureja L. sect. Clinopodium (L.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897).

Erect-ascending perennial herbs or prostrate and suffruticose. Leaves ovate to lanceolate, crenulate to serrate-dentate, flat, long-petiolate, veins usually prominent, camptodromous, palisade mesophyll dorsiventral. Inflorescence of usually distant, condensed, bracteate verticillasters. Verticillasters few- to many-flowered, cymes very dense. Floral leaves exceeding verticillasters. Bracteoles linear, reaching at least to middle of calyx, sometimes forming an involucre. Calyx curved, narrow, + parallel-sided tubular, 13-veined, distinctly bilabiate, throat sparsely hairy; upper lip, sometimes also lower lip, curving upward; upper teeth usually broader and 1/2-3/4 x as long as lower, teeth long-ciliate. Corolla pink to purple, red or white; tube not resupinate, not annulate inside, glabrous on inside lower half; lips 1/6-1/3 x tube length, upper emarginate, shorter or sometimes as long as lower, lower 3-lobed, central lobe entire or bifid. Stamens 4, convergent, all fertile, sometimes posterior only or all sterile, posterior pair included, anterior just exserted from tube, posterior filaments 1/3-1/2 x as long as anterior filaments, inserted in upper half of tube; anthers divergent. Style branches very unequal, the longer broad lanceolate, the shorter narrow filiform. Nutlets sub-orbicular to orbicular, glabrous.

Type species: C. vulgare L.

Clinopodium is most closely related to Calamintha, and rather more distantly to Acinos and Cyclotrichium. These are the four genera of the Calaminthoid group as I have called them. These genera differ mainly in floral characteristics. Clinopodium is clearly distinguished from Calamintha by its curved calyx tube, with the lower teeth often curving upward. The bracteoles are distinctly longer than the pedicels and peduncles, and the verticillasters as a whole are generally more globose and compact.

Kuntze (1891) and Briquet (1897) had very similar ideas; Clinopodium sensu Kuntze and Satureja sensu Briquet (i.e. Satureja s.l.) are more or less equivalent except that Kuntze thought that the name Clinopodium L. had priority over Satureja L. His argument, based on works published prior to Species Plantarum, ed.1 (1753), is invalid by the present rules of nomenclature. Nevertheless one could still argue in favour of Clinopodium rather than Satureja since both were published in Species Plantarum ed.1. However, from the start Satureja was more broadly circumscribed than Clinopodium by including what is now Micromeria sect. Micromeria. Clinopodium and Satureja were kept apart in all the following editions of Species Plantarum (Linnaeus, 2nd. ed. 1763, 3rd. ed. 1764; Willdenow, 4th. ed. 1800) and by various Floras (e.g. Moench, 1794; Lamarck & DeCandolle, 1805) until the first quarter of the nineteenth century. Bentham in Labiatarum Genera et Species (1834) maintained Satureja, removing Micromeria sect. Micromeria as a distinct genus, but sunk Clinopodium to sectional level in Melissa L. In Bentham's next revision of the Labiatae [in De Candolle's Prodromus (1848)] Satureja s.s. remains more or less unchanged but Clinopodium is transferred to Calamintha Miller again as a section (though this is nomenclaturally insupportable since Clinopodium was published before Calamintha). As far as I can ascertain no work before or since Kuntze (1891) places Satureja s.s. under Clinopodium. All either keep both as distinct genera or keep Satureja at generic level and Clinopodium at sectional level. Therefore if I were to unite the two genera I would chose the name Satureja just as Briquet (1897) has done.

Janchen (1943) seems to propose the conservation of Calamintha Lam., Fl. France 2:293 (1778), with type C. arvensis Lam., and the rejection of Clinopodium L., Sp. Pl. 587 (1753). His paper is rather vague about what he actually means. As I understand it Janchen is not actually proposing that Clinopodium L. should be rejected and Calamintha Lam. used in preference. What he does say is "if one, as in this systematic opinion, does not transfer all of the numerous Calamintha species to Clinopodium, only because this is the older name, one must then preserve Calamintha". This proposition is quite correct. The only comment that can be made is that Janchen missed the prior valid publication of the genus Calamintha by Miller in his 4th. abridged edition of the Gardener's Dictionary (1754). DeWolf (1955) discusses in detail the nomenclatural status of Clinopodium and Calamintha in the light of Janchen's paper and recommends "that the proposal for the conservation of the name Calamintha Lam. and the rejection of the name Clinopodium L. [should] not receive favourable action". As Janchen had already noted that Clinopodium L. "is the older name", it is no surprise that the Special Committee for Pteridophyta and Phanerogamae (1954) voted in favour of Clinopodium by 9 votes to 0 (with 2 abstentions).

There have been marked differences of opinion on the treatment of the Far East Calaminthoid species. Numerous errors of identification have also caused confusion. If one refers to a paper such as Hara (1935) it is seen how often a species' name is used "sensu" such and such an author but placed as a synonym of another species. The recent treatment of this group in Fl. Reip. Pop. Sin.

(1977) maintains a very narrow species concept but at least the treatment is taxonomically consistent. The synonyms also seem to be correctly assigned. However, if the order in which these species are presented is an indication of the author's opinion of relationships then even this treatment is hopelessly confused. The most unusual feature is that 11 species are included under Clinopodium and one species under Calamintha (the annual Calamintha debilis). Most previous arrangements have attempted to encompass all of the Calaminthoid species in one genus, either under Satureja sensu Briquet (1897) (e.g. Kudo, 1929), Clinopodium (e.g. Hara, 1935), or Calamintha (e.g. Franchet & Savatier, 1875). Nevertheless, in the Mediterranean region Calamintha and Clinopodium are quite distinct, and it is no less the case in the Far East.

3.10.1. 1. A procumbent plant, 8-20 cm tall; leaves 4.5-16 mm long; calyx tube 2.5-3.4 mm, lower teeth as long as tube . 2. atlanticum

\+ An erect plant (15-)20-80 cm tall; leaves 15-65(-80) mm long; calyx tube (2.8-)3.5-7.5 mm, lower teeth clearly shorter than tube 2

2. Verticillasters lax, pedicels 2.5-6.0 mm; leaves very deeply toothed, teeth apex sharply acute, apical side 2-4.5 mm long 5. macranthum

\+ Verticillasters ± dense, pedicels 0.8-2.5 mm (rarely to 4.0 mm); leaves shallowly toothed, teeth apex rather rounded or broadly acute, generally less than 2 mm on apical side 3

3. Leaves narrowly ovate-lanceolate, cuneate to rounded at base, regularly and clearly broadly acute-toothed [China, Korea, Japan] 3. chinense

\+ Leaves broadly ovate, nearly always rounded at the base, margins scarcely notched to small rounded-toothed (very rarely with acute teeth) 4

4. Bracteoles 5.5-12 mm, reaching at least to calyx teeth, forming an involucre; verticillasters compact [Mediterranean region, east to India] 1. vulgare

\+ Bracteoles (1-)3-7 mm, reaching to middle of calyx, not forming an involucre; verticillasters loose [Far East, west to NE Turkey] 4. umbrosum

3.10.2. 1. C. vulgare L., Sp. Pl. 587 (1753).

Syn: Clinopodium origanifacie Gilib., Fl. Lithuan. 2:76 (1782); Clinopodium aegypiacum Lam., Encycl. Meth. 2:50 (1786); Thymus sylvaticus Bernh., Syst. Verz. Erf. 77 (1800); Melissa glomerata Stokes, Bot. Mat. Med. 3:366 (1812); Clinopodium plumosum Sieb. in Bot. Zeit. 5:242 (1822); M. clinopodium Benth., Lab. Gen. Sp. 392 (1834)! Clinopodium atropurpureum Biroli ex Colla, Herb. Pedem. 4:471 (1835); Clinopodium variegatum Hort. ex Steud., Nom. Bot. ed.2, 1:386 (1840); M. vulgaris (L.) Trevis., Prosp. Fl. Eugan. 26 (1842)! Calamintha clinopodium (Benth.) Benth. in DC., Prodr. 12:233 (1848)! Calamintha aegypiaca Lam. ex Schur, Enum. Pl. Transs. 531 (1866), nomen; Faucibarba clinopodium (Benth.) Dulac, Fl. Hautes-Pyr. 403 (1867)! Calamintha vulgaris (L.) H. Karst, Deutsche Fl. Pharm. Med. Bot. 1002 (1882)! Satureja clinopodium Car. in Parl., Fl. Ital. 6:135 (1884)! S. vulgaris (L.) Fritsch, Excurs. Fl. Austr. 477 (1897)! T. clinopodium (Benth.) E. H. L. Krause in Sturm, Fl. Deutschl. ed.2, 11:176 (1903)! Clinopodium

clinopodium (Benth.) Degen in Magyar Bot. Lap. 4:131 (1905), nom. illeg.; Calamintha vulgaris (L.) Druce in Ann. Scot. Nat. Hist. 1906:224 (1906)! Clinopodium aegyptiacum L. ex Jackson, Index Linn. Herb. 59 (1912), nomen! Satureja vulgaris (L.) Fritsch var. neogaea Fernald, Rhodora 46:388 (1944).

Ic: Reichenb., Fl. Germ. 18: f.1274, I (1858).

Gen. distrib.: Europe, Mediterranean region, E to Afghanistan and NW India.

Bothmer (1967), in his detailed study of this species, concluded that three sub-species could be recognised: spp. vulgare, ssp. orientale, and ssp. villosum. Ball in Flora Europaea (1972) only recognised two sub-species, ssp. vulgare and ssp. arundanum. The present treatment recognises three: ssp. vulgare, ssp. arundanum, and ssp. villosum.

Ssp. orientale differs only in trivial indumentum and calyx teeth characters from ssp. arundanum, so Ball and this revision treat it as a synonym of ssp. arundanum. A map presented by Bothmer shows that ssp. villosum is mainly from the NW African Mediterranean coast and Andalucia (Spain) but a few scattered specimens from S Central Spain were attributed to this sub-species. Ball possibly saw these Spanish specimens and decided they were densely hairy forms of ssp. arundanum. To be fair, Bothmer does indicate the intermediate nature of the the Central Spanish specimens. I have not seen any Spanish material that is clearly identifiable with ssp. villosum but specimens with narrowly lanceolate leaves, similar to this subspecies and named and labelled as such by Bothmer, have been seen from Andalucia (at E). Very dense, long-plumose inflorescence indumentum and large lanceolate leaves clearly distinguish ssp. villosum in NW Africa.

Dunn (1913) and Doan (1936) took a very broad view of the species and also included C. umbrosum and C. chinense. However C. umbrosum is distinguished by much laxer verticillasters with sparsely ciliate bracteoles only reaching to the middle of the calyx, often smaller calyx teeth, and smaller, broader leaves. C. chinense has much more narrowly ovate and clearly broadly acute-toothed leaves, and much shorter calyx teeth. C. vulgare ranges from Europe, eastwards to the Caucasus, Iran, N India, Nepal, and NW African coastal mountains, while C. umbrosum extends to most of SE Asia westwards to NE Turkey. C. chinense is confined to E China, Korea, and Japan. Where there is an overlap in the ranges of C. vulgare and C. umbrosum there is generally no difficulty distinguishing them.

Gleason (1952) states that Satureja [Clinopodium] vulgaris is "certainly native" in northern parts of NE America but introduced in southern U.S.A. If this is so it would be the only species of Satureja s.l. to have a distribution which extended to both Old and New World. However, by its distribution in America (SE Canada, NE USA, south to N Carolina), I would not be surprised if in fact this species had been introduced by the early New England settlers. Study of pollen profiles may settle the issue.

1. Calyx 7-9.5 mm; lower teeth 2.5-4.0 mm ssp. vulgare
\+ Calyx 9.5-12.5 mm; lower teeth 4.0-6.0 mm 2
2. Calyx extremely densely white-plumose;
leaves 40-80 mm, narrowly lanceolate ssp. villosum
\+ Calyx sparsely pubescent; leaves usually
less than 45 mm, broadly ovate ssp. arundanum

ssp. vulgare

Syn: Clinopodium aegyptiacum Mill., Gard. Dict. ed.8, n.6 (1768); Calamintha x pillichiana J. Wagner in Magyar Bot. Lap. 23/1924:76 (1925); Clinopodium integerrimum Boriss. in Not. Syst. Herb. Inst. Acad. Sci. URSS 15:328 (1953); Clinopodium vulgare L. ssp. cimbricum Bocher in Vida, Symp. Biol. Hung. 12:29 (1972); x Calapodium pillichianum (J. Wagner) Holub in Folia Geobot. Phytotax. 11:82 (1976).

Type: Described from Europe and Canada (Hb. Linn. 742/1, microfiche!).

Gen. distrib.: Europe, N Turkey, Caucasus, S USSR, N Iraq, N Iran, Afghanistan, Kashmir, N India (introduced to SE Canada, NE USA, south to N Carolina).

I have not seen the type of the Danish C. vulgare L. ssp. cimbricum Bocher. However, one specimen from N Denmark near the type locality (Holm, et al 496) and two from Sweden (both Erikson ann. 1907) match very well the description and photograph presented by Bocher. These specimens are prostrate, short-stemmed, and with small (25-38 x 13-19 mm), shortly petiolate (3-7 mm) leaves. The solitary, terminal verticillaster has only 5-6 flowers with small calyces (tube 4-5 mm, upper teeth 1.5-2.0 mm, lower teeth 3.0-3.5 mm) and corollas (tube c. 11 mm) just as described by Bocher. Although specimens of spp. cimbricum keep their distinctive habit in cultivation (Bocher, 1972), this dwarf alpine variant cannot otherwise be separated from C. vulgare ssp. vulgare. Similarly depauperate alpine specimens have been found in Turkey (Davis, 1982).

The differences given in Flora URSS (1954) to distiguish C. integerrimum from C. vulgare (entire leaves, glandular hairs, stronger calyx curvature, smaller corollas, and different nutlet shape) do not hold. Entire leaves are common in C. vulgare. Glandular hairs have been seen sporadically in specimens from India, Pakistan, Cyprus, and Turkey. Calyx curvature varies a great deal in C. vulgare and the curvature in C. integerrimum is nothing out of the ordinary, neither is the small corolla completely without equal in C. vulgare. As for nutlet shape I can see no difference at all judging by a drawing presented in Flora URSS.

From the description of Calamintha x pillichiana this taxon appears to be a female sex-form of Clinopodium vulgare. The possibility of this being an inter-generic hybrid as suggested by Wagner (1925) [Calamintha nepeta (L.) Savi ssp. glandulosa (Req.) P.W. Ball x Clinopodium vulgare L.] seems highly unlikely.

ssp. arundanum (Boiss.) Nym., Consp. Fl. Eur. 587 (1881).

Syn: Melissa arundana Boiss., Voy. Bot. Esp. 2:498 (1841); Calamintha arundana (Boiss.) Benth. in DC., Prodr. 12:233 (1848); Clinopodium arundanum (Boiss.) Nym., Syll. Fl. Eur. 101 (1854-55); Clinopodium vulgare L. ssp. orientale Bothmer in Bot. Not. 120:206 (1967).

Type: In regione montana, in ditione Serrania de Ronda inter montem Sierra de la Nieve et pagum Igualeja, fl. Jul., Haenseler. (holo. G?).

Gen. distrib.: S Europe.

ssp. villosum (Noe) Bothmer in Bot. Not. 120:205 (1967).

Syn: Clinopodium villosum Noe in Bull. Soc. Bot. Fr. 2:580 (1855); Satureja vulgaris (L.) Fritsch ssp. villosa (Noe) Maire, Cat. Pl. Maroc 3:649 (1934).

Syntypes: Algeria: in sylva cedrorum Teniet-el-Haad; in rupestribus umbrosis montis Djebel Mouzaia; prope Medeah; Boghar ad saepes fere scandens; Blidah, in dumetis secus torrentem Oued Knis prope Alger; Alger; in Kabyliae montosis Tizi-Ouzou; in vallibus Sebaou; in montibus Aurasiis Djebel Cheliah; in convallibus montis Hedough prope Bone; La Calle. All collected by E. Cosson (P).

Gen. distrib.: NW Africa, S Spain.

3.10.3 2. C. atlanticum (Ball) A. Doroszenko, comb. nov.

Syn: Calamintha atlantica Ball in Jour. Bot. 13:175 (1875), non Coss. (1862), nomen; Satureja atlantica (Ball) Maire in Mem. Soc. Sc. Nat. Maroc. 7:193 (1924).

Fl. 6-8. Calcareous cliffs, dry ledges, rocky hillsides, 1800-2800 m.

Syntypes: Morocco: in regione media et subalpina Atlantis Majoris Ait Mesan, 1800-2800 m; Djebel Tezah; in convalle Ourika. All collected by J. Hooker & J. Ball in 1871 (K?).

Gen. distrib.: Morocco.

A distinct species restricted to the Grand Atlas of Morocco. It comes closest to C. vulgare in leaf shape and verticillaster arrangement, but differs in its procumbent ascending habit, slender, flexuous stems 8-20 cm long, generally smaller leaves, shorter bracteoles, smaller calyx with lower teeth as long as the tube, and smaller corollas.

3.10.4. 3. C. chinense (Benth.) O.Kuntze, Rev. Gen. Pl. 2:515 (1891).

Syn: Calamintha chinensis Benth. in DC., Prodr. 12:233 (1848)! Clinopodium vulgare sensu Thunb., Fl. Jap. 247 (1784), non L. (1753); Calamintha clinopodium (Benth.) Benth. var. chinensis (Benth.) Miq. in Ann. Mus. Bot. Lugd. Bat. 2:236 (1866)! Satureja chinensis (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897)!

Ic: Sugawara, Fl. Saghalien 4:1600, t.733 (1940); Fl. Reip. Pop.

Sin. 66:227, t.52 (1977).

A very variable species especially in stature, leaf size, depth of teeth and pubescence. It is closest to C. vulgare but differs in its usually narrower lanceolate, distinctly serrate leaves, shortly pubescent bracteoles (not plumose), and shorter calyx teeth. C. chinense is from China, Korea and Japan, whereas C. vulgare is from Europe eastward to NW India.

Calyx 5-7.5 mm; corolla 7-13 mm	var. chinense
Calyx 8-10 mm; corolla 17-21 mm	var. discolor

var. chinense

Syn: Calamintha clinopodium (Benth.) Benth. var. urticifolia Hance in Ann. Sc. Nat., ser.5, 5:235 (1866); Calamintha coreana Levl. in Fedde, Rep. Sp. Nov. 9:246 (1911)! Calamintha urticifolia (Hance) Hand.-Mazz. in Act. Hort. Gothoburg. 9:83 (1934); Clinopodium coreanum (Levl.) Hara in Journ. Jap. Bot. 12:40 (1936)! Satureja coreana (Levl.) Nakai in Bull. Nat. Sci. Mus. Tokyo 31:99 (1952)! Clinopodium urticifolium (Hance) C.Y.Wu & Hsuan ex H.W.Li in Acta Phytotax. Sin. 12:219 (1974).

Fl. 6-10. Roadside, open grassy slopes, calcareous meadows, 200-3400 m.

Syntypes: In China, Fortune A.90. Bonin Is.: Loo Choo, Beechey (iso. E!).

Gen. distrib.: E China, Korea, Japan, Bonin Is.

The Beechey type specimen is depauperate and atypical of the species.

var. discolor (Diels) A. Doroszenko, comb. nov.

Syn: Calamintha discolor Diels in Notes RBG Edinb. 5:232 (1912)!

Satureja chinensis (Benth.) Briq. var. discolor (Diels) Kudo in Mem. Fac. Sci. Ag. Taihoku 2(2):104 (1929)! Clinopodium discolor (Diels) C. Y. Wu & Hsuan ex H. W. Li in Acta Phytotax. Sin. 12:221 (1974)!

Fl. 6-9. Grassy openings in and on margins of pine and mixed forests, 1600-3050 m.

Type: Yunnan: Side valleys on the eastern flank of the Tali Range, 25° 40'N, 2750-3050 m, G. Forrest 4527 (holo. E!).

Gen. distrib.: Yunnan, China.

This variety is much larger in all its floral parts, and the corolla tends to be of a redder hue, but otherwise it is indistinguishable from the type variety. However, their distributions are distinct in China. Subspecific rank for these taxa may, therefore, be justified.

3.10.5. 4. C. umbrosum (M. Bieb.) C. Koch in Linnaea 11:673 (1848).

Syn: Melissa umbrosa M. Bieb., Fl. Taur.-Cauc. 2:63 (1808); Scutellaria repens Buch.-Ham. ex D. Don, Prod. Fl. Nep. 110 (1825); Thymus repens D. Don, loc. cit. 113 (1825); Ziziphora javanica Bl., Bijdr. 822 (1826); Clinopodium repens (D.Don) Wall. ex Benth., Pl. As. Rar. 1:66 (1830), non Vell. (1825); Scutellaria cana Wall. ex Benth., loc. cit. 67 (1830); Scutellaria wallichiana A. Ham., Esq. Monogr. Scutell. 28, t.2, f.1 (1832); Melissa repens (D.Don) Benth., Lab. Gen. Sp. 392 (1834); Calamintha umbrosa (M. Bieb.) Fisch. & Mey., Ind. Sem. Hort. Petrop. 6:6 (1839); Satureja umbrosa (M. Bieb.) Scheele, Flora 26:577 (1843); Calamintha repens (D. Don) Benth. in DC., Prodr. 12:233 (1848); Calamintha biebersteineri C. Koch ex Ledeb., Fl. Ross. 3:355 (1849), nomen; Acinos multiflora C. Koch ex Boiss., Fl. Or. 4:579 (1879), nomen; Clinopodium japonicum Makino, J. Jap. Bot. 3:30 (1926); Satureja chinensis (Benth.) Briq.

var. repens (D. Don) Kudo in Mem. Fac. Sci. Ag. Taihoku 2(2):104 (1929); Satureja makinoi Kudo, loc. cit. 105 (1929); Clinopodium umbrosum (M. Bieb.) C.Koch var. shibetchensis (Levl.) McKean, Notes R.B.G. Edinb. 40:161 (1982).

This plant is usually found in damp shady localities and by streamsides, often in forests, and, particularly in the eastern part of its range, is weedy and frequently found in disturbed or cultivated situations, especially if the soil is damp. It is very variable in habit, leaf size, number of flowers in the verticillaster, and calyx and corolla size.

Calyx 4-7(-8.5) mm; corolla 5-11 mm	var. umbrosum
Calyx (6.5-)7-10.5 mm; corolla 12-18 mm	var. souliei

var. umbrosum

Syn: Calamintha polycephala Van. in Bull. Acad. Geogr. Bot. 14:183 (1904)! Stachys rubisepala Elm., Leafl. Philip. Bot. 1:338 (1908)! Calamintha tsacapanensis Levl. in Fedde, Repert. Sp. Nov. 8:423 (1910)! Calamintha clinopodium (Benth.) Benth. var. polycephala (Van.) Dunn, Notes R.B.G. Edinb. 8:159 (1915)! Satureja chinensis (Benth.) Briq. var. parviflora Kudo, Jour. Coll. Sc. Imp. Univ. Tokyo 43(8):38 (1921); Satureja polycephala (Van.) Steward in Journ. Arnold Arb. 35:86 (1954)! Clinopodium polycephalum (Van.) C.Y.Wu & Hsuan ex H.W.Li in Acta Phytotax. Sin. 12:216 (1974)!

Ic: Fl. Taiwan 4:457, t.1068 (1978).

Fl. 3-11. Rocky slopes in scrub, woods and stream sides, margin of swamps, meadows, bank of paddy fields, beds of seasonal mountain torrents, weed of cultivation, arid rocks, granitic, schistose, limestone or clay substrate, 100-3970 m.

Type: USSR:Georgia: c. Ananur et Duschet, Sept., M. Bieberstein.

Gen. distrib.: China, S Korea, Taiwan, islands bounded by the Philipines, Papua, Java and Malaysia, Tibet, India, Sri Lanka, Afghanistan, N Iran, E Turkey and adjacent USSR.

var. souliei (Levl.) McKean in Notes R.B.G. Edinb. 40:161 (1982).
Syn: Calamintha chinensis Benth. var. souliei Levl. in Fedde, Rep. Sp. Nov. 9:246 (1911)! Calamintha nepalensis Fisch. & Mey., Ind. Sem. Hort. Petrop. 11:53 (1846); Calamintha chinensis Benth. var. megalantha Diels, Notes R.B.G. Edinb. 5:233 (1912)! Calamintha clinopodium (Benth.) Benth. var. megalantha (Diels) Dunn, Notes R.B.G. Edinb. 8:159 (1915)! Calamintha clinopodium (Benth.) Benth. var. nepalensis (Fisch. & Mey.) Dunn, loc. cit. 160 (1915); Satureja chinensis (Benth.) Briq. var. megalantha (Diels) Kudo, Jour. Coll. Sc. Imp. Univ. Tokyo 43(8):39 (1921)! Calamintha megalantha (Diels) Hand.-Mazz. in Acta Hort. Gothoburg. 1934, 9:84 (1934)! Clinopodium megalanthum (Diels) C.Y.Wu & Hsuan ex H.W.Li in Acta Phytotax. Sin. 12:220 (1974)!
Ic: Fl. Reip. Pop. Sin. 66:231, t.53 (1977), as C. megalanthum.
Fl. 2-9. Amongst grass in willow scrub, margins of streams, shady limestone screes, 1650-3350 m.
Type: China: Szechuan, Ta-Tsien-Lou, ann. 1893, Soulie 1063 (Calamintha chinensis var. souliei, holo. E!).
Gen. distrib.: China: Yunnan, Szechwan.

The calyx and corolla size are the best features to distinguish these varieties. However, var. souliei also tends to be much more densely long-yellowish-pilose.

3.10.6. 5. C. macranthum (Makino) Hara in Journ. Jap. Bot. 11:110 (1935).
Syn: Clinopodium chinense (Benth.) O.Kuntze var. macranthum Makino in Bot. Mag. (Tokyo) 20:3 (1906); Satureja macrantha (Makino) Kudo,

Jour. Coll. Sc. Tokyo 43(8):37 (1921).

Fl. 7-9. Grassy slope on mountain path, c. 2000 m.

Syntypes: Japan: Prov. Echigo: Mt. Shimidzu-toge, 19 vii 1886, R. Yatabe & S. Okubo (TI); Mt. Shimidzu-toge, ix 1888, T. Makino (TI); Mt. Godzu, 2 viii 1886, R. Yatabe & S. Okubo (TI). Prov. Iwashiro: Mt. Iide, 8-10 vii 1904, G. Nakahara (TI). Prov. Sado: Mt. Kimpoku, 26 vii 1886, R. Yatabe & S. Okubo (TI). Prov. Uzen: Mt. Gassan, vii 1903, G. Nakahara (TI).

Gen. distrib.: Japan.

3.10.7. Nomina exclud. et nom. dubia.

C. albidum Vell., Fl. Flum. 242, t.6a (1825).

O. Kuntze (1891) and Epling (1937) both equate this with Hyptis paludosum Benth., but Epling's later revision of Hyptis (Epling, 1949) makes no mention of this name.

C. angustifolium Roxb., Hort. Beng. 44 (1814), nomen.

C. arvense Vell., Fl. Flum. 243, t.9a (1825) = Hyptis sp. fide Epling (1937).

C. asiaticum (G. Don) Lour., Fl. Cochinch. 2:374 (1790).

Merrill (1935), in his commentary of Loureiro's Flora Cochinchinensis, suggests that this may belong to Plectranthus.

C. bracteolatum (Nutt.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891) = Conradina sp.?

C. bonariense (Ten.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891) = Hedeoma multiflorum Benth. fide Irving (1980).

C. brasilicum Vell., Fl. Flum. 241 t.3a (1825) = Hyptis sp. fide Epling (1937). O. Kuntze (1891) suggests Hyptis gaudichaudii Benth.

C. campanella (Ehrenb.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891).

C. capitatum Sw. Prodr. Veg. Ind. Occ. 88 (1788) = Hyptis capitata

(Sw.) Jacq.

C. chamaedrys Vahl, Symb. 3:77 (1794) = Marsypianthes chamaedrys (Vahl) O. Kuntze. See Fl. Panama in Ann. Missouri Bot. Gard. 56:97 (1969).

C. cordatum Vell., Fl. Flum. 6:243, t. 8a (1825).

Kuntze (1891) equated this with Mesosphaerum spicigerum (Lam.) O. Kuntze. Epling (1937) included Mesophaerum within Hyptis but does not indicate a species with which this taxon may be synonymous or associated with.

C. fruticosum Forssk., Fl. Aegypt.-Arabia 107 (1775) = Otostegia fruticosa (Forssk.) Briq.

C. glabrescens Pomel, Nouv. Mat. Fl. Atlantique 122 (1874).

C. grandiflorum (Willd.) Gueldenst. ex M. Bieb., Fl. Taur.-Cauc. 3:399 (1819), nomen.

This name was placed in the synonymy of Betonica grandiflora Willd. by M. Bieberstein (1819) and quoted as "Clinopodium grandiflorum Guldenst. it. 1 p.424, 426, 429". I have not been able to see Reisen durch Russland und im Caucasischen Gebirge (1787), the work refered to by Bieberstein, but if C. grandiflorum is validly published here, the citation of Betonica grandiflora (published in 1800) must be changed.

C. humile Mill., Gard. Dict. ed.8, n.4 (1767)

This 20-25 cm tall, perennial N. American species is described as having long side branches, few flowered verticillasters, and small, rugose leaves. It has been placed in Melissa [M. humilis (Mill.) G.Don] but from the very brief description I cannot tell if it belongs to this genus or not. As far as I am aware there are no North American Satureja s.l. species with rugose leaves except for Xenopoma schusteri but this plant is 300-500 cm tall.

C. imbricatum Vell., Fl. Flum. 6:242, t.5a (1825).

Epling (1937) has this as a doubtful name under Hyptis and does not suggest a species to which it may be related. Kuntze (1891) has this taxon as a synonym of Mesosphaerum pectinatum (L.) O. Kuntze.

C. incanum L., Sp. Pl. 588 (1753) = Pycnanthemum incanum. Grant & Epling (1943) provide a note on the typification of this plant.

C. kudoi (Hosokawa) Nemoto, Fl. Jap. Suppl. 632 (1936).

Syn: Satureja kudoi Hosokawa, Trans. Nat. Hist. Soc. Formosa 22:225 (1932).

C. laxiflorum (Hayata) Shimizu, Journ. Fac. Text. Sci. Techn. Shinshu Univ. no.30, Biol. no.11:96 (1962).

Syn: Calamintha laxiflora Hayata, Journ. Coll. Sc. Univ. Tokyo 30:228 (1911); Satureja laxiflora (Hayata) Matsum. & Kudo, Bot. Mag. (Tokyo) 26:299 (1912); Satureja yakusimensis Matsamune, Journ. Soc. Trop. Agric., Taiwan, 2:35 (1930).

C. martinicense Jacq., Enum. Pl. Carib. 25 (1760) = Leucas martinicensis (Jacq.) R. Br.

C. olla (Ehrenb.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891).

C. omeiense C.Y.Wu & Hsuan ex H.W.Li, Acta Phytotax. Sin. 12:223 (1974).

C. palmeri (A. Gray) O. Kuntze, Rev. Gen. Pl. 2:515 (1891).

Possibly a Hedeoma sp.

C. parvifolium O. Kuntze, Rev. Gen. Pl. 2:515 (1891) (sphalm.) = parviflora = Micromeria parviflora (Vis.) Reichenb. (c.v.).

C. purpurea (Kellogg) O. Kuntze, Rev. Gen. Pl. 2:515 (1891).

The basionym of this taxon is Hedeoma purpurea Kellogg. Irving (1980) in his revision of Hedeoma makes no mention of the name so it may or may not belong here.

C. repens Vell., Fl. Flum. 242, t.7a (1825) = Peltodon repens (Vell.) O. Kuntze

C. rugosum L., Sp. Pl. 588 (1753). = Hyptis alata (Raf.) Shinners fide Harley (1983), Kew Bull. 38:47-52.

C. verticillatum Vell., Fl. Flum. 6:242, t. 4a (1825).

Kuntze (1891) has this as a synonym of Mesosphaerum fasciculatum (Benth.) O. Kuntze, but Epling (1937) thinks this may belong to Stachys.

C. walterianum O. Kuntze = Macbridea caroliniana (Walter) Blake.

3.11. Acinos Miller, Gard. Dict., abr.ed. 4 (1754).

Syn: Acynos Pers., Syn. 2:131 (1806); Melissa L. sect. Acinos Benth., Lab. Gen. Sp. 389 (1834); Calamintha Miller sect. Acinos Benth. in DC., Prod. 12:230 (1848); Satureja sect. Acinos Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897).

Annual or perennial herbs, or suffruticose, prostrate or ascending. Leaves ovate-orbicular to narrowly ovate, sometimes broadly spathulate, serrulate, crenulate or entire, flat, clearly petiolate, lateral veins usually prominent, sometimes only distally so, craspedromous, a thick marginal vein sometimes present; palisade mesophyll dorsiventral. Inflorescence of distant or approximate, few-flowered verticillasters; cymes sessile; pedicels dorsiventrally compressed or terete. Bracts shorter than or exceeding flowers. Bracteoles linear or linear-elliptic, nearly always shorter than pedicels. Calyx tube sigmoid, gibbous or not at base, usually constricted at middle, 13-veined, throat densely, rarely sparsely, hairy, distinctly bilabiate, upper and lower lip usually curving upwards; upper teeth broader and only 1/4-2/3 as long as lower teeth; lower teeth narrowly triangular-subulate, ciliate. Corolla purple, violet or mauve; tube not resupinate, not annulate inside, glabrous or hairy on inside lower half; lips 1/6-1/2 x tube length; upper emarginate, half as long as to a little shorter than lower lip, lower lip 3-lobed, central lobe entire or bifid. Stamens 4, convergent, all fertile or posterior reduced to staminodes, posterior usually included in, anterior + exserted from tube, filaments of fertile posterior stamens 1/2-3/4 x anterior filaments, inserted in upper half of tube; anthers divergent, sometimes widely so. Stylar branches unequal, the longer broad lanceolate, the shorter narrow-filiform, rarely both narrow-filiform. Nutlets obovoid, glabrous.

Type species: A. alpinus, designated here.

3.11.1. 1. Pedicels round in section [High tropical African mountains] 2

\+ Pedicel clearly dorsi-ventrally compressed [Mediterranean region] 3

2. Leaves distinctly petiolate, petioles 2-5(-9) mm; calyx tube 2-4.2 mm, throat sparsely hairy; posterior stamens reduced to staminodes, 0.4-0.8 mm long 8. simensis

\+ Leaves shortly petiolate, petioles 0.5-1.5 (-4.0) mm; calyx tube 3.6-4.8 mm, throat densely hairy; all 4 stamens fertile, posterior 1.5-4.0 mm long 9. pseudosimensis

3. Leaves with a thick marginal vein distinct from the lateral veins, entire 4

\+ Leaves without a marginal vein distinct from lateral veins, toothed or scarcely lobed 5

4. Minute annual herbs, 1-4 cm tall; leaves 2-4.5 mm long; calyx strongly gibbous; corolla c. 6 mm 5. nanus

\+ Perennial procumbent shrublets, 2-10 cm tall; leaves 3-10 mm long; calyx weakly gibbous; corolla 12.5-14.5 mm 7. corsicus

5. Calyx sigmoid but not gibbous at base; leaves orbicular to ovate-lanceolate, entire or scarcely lobed, hairs dense and very minute; lateral veins very prominent 6. troodii

\+ Calyx distinctly sigmoid and gibbous at base; leaves distinctly toothed even if orbicular, hairs mostly long, sparse; lateral veins scarcely prominent 6

6. Leaf lamina not more than 1 1/2 x as long as wide, abruptly acuminate to mucronate at apex 4. rotundifolia

+ Leaf lamina usually at least 1 1/2 x as long as broad; apex obtuse or acute 7

7. Leaves narrowly elliptic-lanceolate, 2-3 x as long as wide, narrowly cuneate at base; whole plant usually yellowish-green when dry, usually densely hairy; calyx tube 4.3-5.5 mm, markedly gibbous at base, teeth strongly converging, almost closing calyx mouth 2. suaveolens

+ Leaves broadly elliptic, mostly under 2 x as long as broad, cuneate or rounded at base; plant light green when dry, usually puberulous or sparsely hairy; calyx tube 3-4.5 mm, not markedly gibbous, throat + open 8

8. Annual or short-lived perennial; corolla 7-10 (-13) mm, not exceeding the subtending bract; upper and lower calyx lips + equal 3. arvensis

+ Perennials with woody root stock; corolla 10-18 mm, usually distinctly exceeding subtending bract; lower calyx lips + equal 1. alpinus

3.11.2. 1. A. alpinus (L.) Moench, Meth. 407 (1794).

Syn: Thymus alpinus L., Sp. Pl. 591 (1753); Thymus montanus Crantz, Stirp. Austr. ed.2, fasc.4:278 (1769), non Dum. Cours. (1811); Calamintha alpina (L.) Lam., Fl. Fr. 2:394 (1779); Thymus nummularifolius Loisel., Fl. Gall. ed.1, t.9, f.2 (1807); Thymus villosissimus Tausch, Syll. Ratisb. 2:248 (1828); Melissa alpina (L.) Benth., Lab. Gen. et Sp. 390 (1834); Calamintha alba Lam. ex Steud., Nom. Bot. ed.2, 1:251 (1841); Satureja alpina (L.) Scheele in Flora 26:577 (1843); A. acutifolius Schur, Enum. Pl. Transs. 530 (1866); Faucibarba alpina (L.) Dulac, Fl. Hautes-Pyr. 403 (1867); Melissa x jahniana Simonk. in Termesz. Fuzetek. 9:25 (1885); Calamintha x mixta Ausserd. ex H. Braun & G. Sennholz in Oest. Bot. Zeitschr. 40:158 (1890); Clinopodium alpinum (L.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); M. montana Bub., Fl. Pyr. 1:412 (1897), non Noronha (1790); S. mixta (Ausserd. ex H. Braun & G. Sennholz) Dalla Torre & Sarnth., Fl. Tirol 6(3):199 (1912); Calamintha pseudacinos Lac. in Bull. Ort. Bot. Napoli 3:301 (1913); S. orontia K. Maly in Glasnik Mus. Bos. Herceg. 32:148 (1921); Calamintha suavis Sennen in Bol. Soc. Iber. Cienc. Nat. 1933, 32:57 (1934); S. suavis Sennen, loc. cit. (1934), nomen; Calamintha alpina (L.) Lam. var. orontia (K.Maly) Hayek in Bot. Mag. 160, sub. t.9508 (1938); A. x jahnianus (Simonk.) Sojak, Cas. Nar. Muz. Prague 140:129 (1972); A. pseudacinos (Lacaita) Fenaroli in Webbia 28(2):373 (1973); A. orontius (K. Maly) Silic, Glasn. Zem. Muz. Bosne Herceg. 13:118 (1975); A. x mixtus (Ausserd. ex H. Braun & Sennholz) Bassler in Feddes Repert. 8:417 (1977); A. alpinus (L.) Moench var. pseudacinos (Lac.) Pign. in Giorn. Bot. Ital. 111:52 (1977).

A detailed discussion on the variation in A. alpinus is given by Ball (1972). His general conclusion was that although the species is highly variable, only 3 broad taxa can be easily distinguished, and that even though there are distinctive local variants, based on habit, leaf-size and indumentum density, too many intermediates occur to make further sub-division meaningful. Examination of hundreds of specimens leads me to the same conclusion.

1. Upper calyx teeth 0.5-1.0 mm; calyx tube
hairs crispate; corolla 10-14 mm (c) ssp. meridionalis

\+ Upper calyx teeth 1.0-2.0 mm; calyx tube
hairs usually straight; corolla 12-20 mm 2

2. Leaves up to 15 x 11 mm, veins not prominent
beneath (a) ssp. alpinus

\+ Leaves up to 20 x 16 mm, veins prominent
below, especially near margins (b) ssp. majoranifolius

(a) ssp. alpinus

Syn: Melissa x bolnokensis Simk., Enum. Fl. Transs. 445 (1886); M. baumgartenii Simk. in Term. Fuz. 10:182 (1886); Calamintha baumgartenii (Simk.) Nym., Consp. Fl. Eur., Suppl. 2(1):255 (1889); Calamintha alpina (L.) Lam. ssp. baumgartenii (Simk.) Borza in Bul. Grad. Bot. Cluj 5:101 (1925); Calamintha hybrida Kerner ex Hegi, Ill. Fl. Mittel-Eur. 5:2301 (1928), ex nomen in schaed.; Calamintha bolnokensis (Simonk.) Domin, Veroff. Geobot. Inst. Rubel 10:110 (1933); Calamintha x alboi Sennen, Bol. Soc. Iber. Cien. Nat. 1933, 32:32 (1934); S. x alboi Sennen, loc. cit. (1934), nomen; S. alpina (L.) Scheele ssp. pyrenaea Br.-Bl., Comm. S.I.G.M.A. 87:228 (1945); Acinos baumgartenii (Simk.) Klokov, Fl. RSS Ucr. 9:273 (1960); A. alpinus (L.) Moench ssp. pyrenaeus (Br.-Bl.) M. Lainz in Bol. Inst. Estud. Astur. Supl. Cienc. 22:29 (1976); S. alpina (L.) Scheele var. pyrenaea (Br.-Bl.) Bolos & Vigo, Collect. Bot. 14:95 (1983); Calamintha villosula Jord., in schaed.

Ic: Hegi, Ill. Fl. Mittel-Eur. 5(4):2300, f.3203, a-d (1927), as Satureja alpina.

Fl. 4-9. Calcareous cliffs, rocky places, grassy banks, 700-2000 m.

Type: Described from Swiss Alps, Austria, Montpellier, D. Rathgeb (Hb. Linn. 744/16, microfiche!).

Gen. distrib.: Pyrenees, C Europe, eastwards to Greece.

(b) ssp. majoranifolius (Miller) P. W. Ball in Bot. J. Linn. Soc. 65:344 (1972).

Syn: Melissa majoranifolia Miller, Gard. Dict. ed.8, no.7 (1768); Thymus patavinus Jaquin, Obs. Bot. 4:7, t.87 (1771); T. verecundus Salisb., Prod. Stirp. Hort. Chap. Allerton Vig. 86 (1796), nomen; Acinos adscendens Moench, Meth. Suppl. 138 (1802); A. patavinus (Jacq.) Pers., Syn. 2:131 (1806); Calamintha patavina (Jacq.) Host, Fl. Austr. 2:133 (1832); M. patavina (Jacq.) Benth, Lab. Gen. Sp. 389 (1834); T. rotundifolius Rochel ex Nym, Consp. Fl. Eur. 588 (1881), nomen; M. x hungarica Simk. in Termesz. Fuzet. 10:182 (1886); Calamintha hungarica Simk., loc. cit. (1886); Calamintha commutata Willk., Ost. Bot. Zeit. 39:90 (1889); Clinopodium patavinum (Jacq.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja patavina (Jacq.) Degen, Ost. Bot. Zeitschr. 58:303 (1908); S. majoranifolia (Miller) K. Maly, Glasnik Mus. Bos. Herceg. 22:690 (1910); S. hungarica (Simk.) Hayek in Wettst., Sched. Fl. Exsicc. Austro-Hung. 10:47 (1913); S. elatior (Griseb.) Borza, Bul. Grad. Muz. Bot. Univ. Cluj 1925, 5:99 (1926); Calamintha alpina (L.) Lam. ssp. majoranifolia (Miller) Hayek, Prodr. Fl. Penins. Balcan. 2:328 (1929); Calamintha alpina (L.) Lam. ssp. hungarica (Simk.) Hayek, loc. cit. (1929); Calamintha alpina (L.) Lam. ssp. elatior (Griseb.) Rech. f., Denkschr. Akad. Wiss. Wien 105:529 (1943); Calamintha alpina (L.) Lam. ssp. nomismophylla Rech. f., loc. cit. (1943); A. alpinus (L.) Moench ssp. patavinus (Jacq.) Sojak in Cas. Nar. Muz. (Prague) 140(3-4):129 (1972); A. alpinus (L.) Moench ssp. hungaricus (Simk.) Sojak, loc. cit. (1972); A. alpinus (L.) Moench. ssp. nomismophyllus (Rech. f.) Leblebici, Bitki 1:405 (1974); A. majoranifolius (Miller) Silic in Glasn. Muz. Bosne

Herceg. 13:119 (1975); A. majoranifolius (Mill.) Silic ssp. elatior (Griseb.) Holub, Folia Geobot. Phytotax. 12:428 (1977).

Fl. 4-9. Calcareous rocky and stony places, 300-600 m.

Type: Described from Italy. No specimen cited.

Gen. distrib.: N Balkans, (?)Spain.

A number of specimens on the fringes of the distribution of typical ssp. majoranifolius and one rather surprisingly from Spain, though closest in aspect to this subspecies, have some features typical of ssp. alpinus and ssp. meridionalis. The intermediates are often from higher altitudes than the typical form.

(c) ssp. meridionalis (Nyman) P. W. Ball in Bot. J. Linn. Soc. 65:344 (1972).

Syn: Calamintha alpina (L.) Lam. ssp. meridionalis Nyman, Consp. Fl. Eur. 589 (1881); Calamintha granatensis Boiss. & Reut., Pugillus 94 (1852); Melissa granatensis (Boiss. & Reut.) Nym., Syll. Fl. Eur. 101 (1855); Calamintha aetnensis Strobl in Oest. Bot. Zeitschr. 24:29 (1874), nomen; Calamintha nebrodensis Strobl ex A. Kerner, Oest. Bot. Zeitschr. 24:171 (1874), nomen; Calamintha alpina (L.) Lam. ssp. granatensis (Boiss. & Reut.) Arcangeli, Comp. Fl. Ital. 543 (1882); Calamintha alpina (L.) Lam. ssp. nebrodensis (Strobl ex A. Kerner) Arcangeli, loc. cit. (1882); Calamintha aetnensis Lojac., Fl. Sic. 2:219 (1907); Calamintha gillesii Sennen, Bol. Soc. Iber. Cienc. Nat. 1933,32:58 (1934); Satureja gillesii Sennen, loc. cit. (1934), nomen; S. granatensis (Boiss. & Reut.) Sennen, Diag. Nouv. Pl. Esp. & Maroc 204 (1936); Calamintha alpina (L.) Lam. ssp. aetnensis (Strobl) Rech. f., Fl. Aegaea 528 (1943); Acinos granatensis (Boiss. & Reut.) Pereda Saez, Comp. Cat. Florist. Prov. Satander 5 [in Altamira 1-3:289] (1960); S. acinos (L.) Scheele ssp. meridionalis (Nym.) Bolos & Vigo, Collect. Bot.

11:77 (1979).

Fl. 4-9. Road margins, open oak and pine woods, calcareous, schistose or volcanic rocks, grassy slopes, 1000-2750 m.

Syntypes: Spain, Bourgeau hisp. 390, 1418a. Sicily, Todaro exs. sic. 208.

Gen. distrib.: S Europe.

A broad view has been taken of ssp. meridionalis. At first it was thought that a fourth subspecies could be recognised (ssp. aetnensis) confined to the volcanic slopes of Sicily, which has a very low, prostrate habit, small leaves not exceeding 7 x 5 mm, stem densely minute patent-puberulent, calyx only 5 mm long, and corolla 10 mm long. However, specimens very similar in facies have been seen from Spain which have the indumentum characters typical of ssp. meridionalis, and small calyces and corollas have been found in individual specimens throughout the range of ssp. meridionalis. In any case, specimens from Sicily do not retain all of the characters of ssp. aetnensis consistently.

3.11.3. 2. A. suaveolens (Sibth. & Sm.) G.Don f. in Loudon, Hort. Brit. 239 (1830).

Syn: Thymus suaveolens Sibth. & Sm., Fl. Graec Prod. 1:420 (1809); T. acinoides Ten., Prod. Fl. Nap. 35 (1826); Acinos heterophyllus (Poir.) G.Don in Loud., loc. cit. (1830); A. acuminatus Friv. in Flora 18:332 (1835); Calamintha suaveolens (Sibth. & Sm.) Boiss., Diagn. 1(12):54 (1853); Melissa acinoides (Ten.) Nym., Syll. Fl. Eur. 101 (1855); M. suaveolens (Sibth. & Sm.) Nym., Syll. Fl. Eur. Suppl. 20 (1865); Calamintha acinoides (Ten.) Nym., Consp. Fl. Eur. 589 (1879); Calamintha patavina Heldr. ex Nym., Consp. Fl. Eur. 588 (1881), nomen; Calamintha langei Nym, loc. cit. 589 (1881), nomen; Clinopodium suaveolens (Sibth. & Sm.) O.Kuntze, Rev. Gen. Pl. 2:516

(1891); Calamintha montenegrina Sagorski in Oest. Bot. Zeitschr. 53:20 (1903); Satureja montenegrina (Sagorski) Druce in Rep. Bot. Exch. Cl. Brit. Is. 1916:644 (1917); A. montenegrinus (Sagorski) Silic, Glasn. Zem. Muz. Bosne Herceg. 13:122 (1975).

Fl. 5-8. Dry calcareous rocks, roadsides, s.l.-1160 m.

Type: In monte Parnasso. Sibth. & Sm. (1809) also refer to an illustration in Bocc. Mus. vol. 1, t.45, A. In the Smith herbarium the following species are listed under T. suaveolens: 1. H. L. fil [=Linnaeus f.]; 2. Hort. C. A. L. Bellardi, Taurinae, [ann.] 1787.

Gen. distrib.: Balkans, S Italy, W Turkey.

3.11.4. 3. A. arvensis (Lam.) Dandy in Jour. Ecol. 33:326 (1946).

Syn: Thymus acinos L., Sp. Pl. 591 (1753); Calamintha arvensis Lam., Fl. Fr. 2:394 (1778); Acinos clinopodiifacie Gilib., Fl. Lithuan. 2:75 (1782); A. thymoides Moench, Meth. 407 (1794); T. concinnus Salisb., Prod. Stirp. Hort. Chap. Allerton Vig. 86 (1796), nomen; T. heterophyllus Poir., Encycl. 7:648 (1806); A. villosus Pers., Syn. 2:131 (1807); A. vulgaris Pers., loc. cit. (1807); Calamintha acinos (L.) Clairv., Man. Herb. 197 (1811); T. gibbosus Stokes, Bot. Mat. Med. 3:360 (1812); T. diffusus Bluff & Fingerh., Comp. Fl. Germ., ed.1, 2:41 (1826); T. canescens Dum., Fl. Belg. 48 (1827); Melissa acinos (Lam.) Benth, Lab. Gen. Sp. 389 (1834); Satureja acinos (L.) Scheele in Flora 26:577 (1843); Calamintha hispidula Boiss. & Reut., Pug. Pl. Nov. 93 (1852); A. aestivalis Kit. in Linnaea 32:432 (1863); T. arvensis (Lam.) Schur, Enum. Pl. Transs. 972 (1866); Faucibarba acinos (L.) Dulac, Fl. Haute-Pyr. 403 (1867); Calamintha thymoides (Moench) Schloss. & Vuk., Fl. Croat. 560 (1869); Clinopodium acinos (L.) O.Kuntze, Rev. Gen. Pl. 2:513 (1891); A. acinos (L.) Huth in Helios 11:132 (1893), nom. illeg.; S. hispidula (Boiss. & Reut.) Briq. in Engler &

Prantl, Nat. Pflanzenfam. 4,3a:303 (1897); M. arvensis (Lam.) Bub., Fl. Pyr. 1:411 (1897); S. villosa (Pers.) Dorfler, Herb. Norm. no. 3459 (1898); Calamintha thracica Vel., Sitz. Bohm. Ges. Wiss. 1899:7 (1899); Calamintha villosa (Pers.) Terracc. in Bull. Ort. Bot. Napoli 3:164 (1913); A. subcrispus Klokov, Fl. RSS Ucr. 9:662 (1960); A. eglandulosus Klokov, loc. cit. 661 (1960); A. arvensis (Lam.) Dandy ssp. villosus (Gaud.) Sojak in Cas. Nar. Muz. (Prague) 140(3-4):129 (1972); A. arvensis (Lam.) Dandy ssp. eglandulosus (Klokov) Tzvelev in Nov. Sist. Vyssh. Rast. 10:365 (1973); A. patulus Jord., in schaed.

Ic: Hegi, Ill. Fl. Mittel-Eur. 5(4):2296, f.3201a, b (1927), as Satureja acinos; Rech. f., Fl. Iranica 150: t.413 (1982).

Fl. 5-9. Limestone rocks, scrub, open pine woods, roadsides, sandy and gravelly banks, 300-2200 m.

Type: Described from Europe, on gravel, chalk, dry places (Hb.Linn. 744\14, microfiche!)

Gen. distrib.: Europe, except far north and south, N Turkey, Iran and neighbouring USSR.

Although this species is highly variable it does not appear to be divisible into meaningful infra-specific taxa.

3.11.S. 4. A. rotundifolius Pers., Syn. Pl. 2:131 (1806)

Syn: Acinos purpurascens Pers., Syn. Pl. 2:131 (1806); Thymus purpurascens (Pers.) Poir. in Lam., Encycl. Meth. 7:654 (1806); T. canus Steuen ex M. Bieb., Fl. Taur. Cauc. 2:60 (1808); T. graveolens M. Bieb., loc. cit. (1808); T. exiguus Sibth. & Sm., Fl. Graec. Prod. 1:421 (1809); A. graveolens (M. Bieb.) Link, Enum. Pl. Hort. Berol. Alt. 2:117 (1822); A. canus (Steuen) Reichenb., Fl. Germ. Exc. 1:327 (1830); Melissa graveolens (M. Bieb.) Benth., Lab. Gen. Sp. 390 (1834); M. purpurascens (Pers.) Benth., loc. cit. 391

(1834); M. rotundifolia (Pers.) Benth., loc. cit. (1834); A. erectus Friv. in Flora 18:333 (1835); Calamintha cana Auct. ex Heynh., Nom. 2:104 (1840-46); A. exiguus (Sibth. & Sm.) D. Don ex Steud., Nom. ed.2, 1:23 (1841); A. incanus Griseb., Spicil. Fl. Rum. Bithyn. 2:123 (1844); Calamintha graveolens (M. Bieb.) Benth. in DC., Prod. 12:231 (1848); Calamintha maritima Benth., loc. cit. (1848); Calamintha purpurascens (Pers.) Benth., loc. cit. (1848); Calamintha rotundifolia (Pers.) Benth., loc. cit. 232 (1848); M. maritima (Benth.) Nym., Syll. Fl. Eur. 101 (1855); A. transsilvanica Schur, Enum. Pl. Transs. 529 (1866); Calamintha exigua (Sibth. & Sm.) Nym., Consp. Fl. Eur. 589 (1881); Satureja graveolens (M. Bieb.) Caruel in Parl., Fl. Ital. 6:143 (1884); Clinopodium canum (Steuen) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Clinopodium graveolens (M. Bieb.) O. Kuntze, loc. cit. (1891); Clinopodium maritimum (Benth.) O. Kuntze, loc. cit. (1891); Clinopodium rotundifolium (Pers.) O. Kuntze, loc. cit. (1891); S. rotundifolia (Pers.) Briq., Lab. Alp. Mar. 453 (1895); S. maritima (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:303 (1897); S. exigua (Sibth. & Sm.) Holmboe, Veg. Cyprus 161 (1914); S. graveolens (M. Bieb.) Pau in Bol. Soc. Arag. 15:170 (1916); A. fominii Schost-Desiat. in Symp. Mem. Fomin. (Acad. Sc. Ukr.) 39 (1938); S. crassinervis Lindl. f., Arsbok Soc. Sci. Fenn. 20B, 7:6 (1942); A. infectus Klokov in Fl. RSS Ucr. 9:663 (1960); A. schizodontus Klokov, loc. cit. (1960).

Ic: Rech. f., Fl. Iranica 150: t.414 (1982), as A. graveolens.

Fl. 3-7. Igneous, limestone or serpentine rocky slopes, Quercus scrub, roadside, fallow and grain fields, 50-2500 m.

Type: Described from Spain, Richard.

Gen. distrib.: SE Europe, S Italy, S & C Spain, NW Africa, SW Asia.

This species is very variable in stature, leaf shape and size, calyx tube and teeth length, and indumentum. The only species it could be confused with is A. nanus, but as indicated in the table below it is quite easily distinguished on leaf, calyx and corolla characters. Dwarf montane and densely hairy littoral ecotypes have been described as distinct species. A. graveolens [illustrated as Thymus exiguus in Sibthorp & Smith (1826)] is one such montane form and A. incanus is a littoral ecotype.

3.11.6. 5. A. nanus P. H. Davis & A. Doroszenko, sp. nov.

Syn: Acinos graveolens (M.Bieb.) Link var. integrifolia Raulin, Desc. Phys. L'Ile Crete 828 (1858), nom. nud., non Satureja (sect. Acinos) exigua (Sibth. & Sm.) Holmboe var. integrifolia Holmboe, Veg. Cyprus 161 (1914).

Annual herb, stems 1-4(-6.5) cm, erect, simple or with few widely spreading branches, densely retrorse-puberulent. Leaves broadly ovate or orbicular, 2.0-4.5 x 1.8-4.3 mm, base broadly cuneate or truncate, apex obtuse, entire, with a prominent marginal vein and 3- 4 distinct lateral veins, pubescent on both sides. erticillasters 2-4, crowded, 2(-4)-flowered; pedicels 1.0-2.2 mm, corolla exceeding bracts. Calyx strongly gibbous at base, mouth narrow; tube 3.5-4.0 mm, densely puberulent and with more robust hairs on nerves; upper and lower lips 1.5-2.3 mm; upper teeth 0.8-1.2 mm; lower 1.5-2.3 mm. Corolla tube c. 4.3 mm; upper lip c. 0.6 mm; lower lip c. 1.5 mm. Fl. 3-5. Rocky calcareous slopes, 1150-1340 m.

Type: Crete, Sitia: In lapidosis montis Tavoutsi [Kavoutsi], 1220 m, v 1846, Heldreich (holo. E!).

Gen. distrib.: Crete, Is. Samos.

Specimens seen: Crete: Mt. Kavoutsi, 1340 m, iv 1846, Heldreich (E, K, MANCH); In montis Kavoutsi, Apr., Heldreich 1449 (K); No locality, ann. 1821, Sieber (K). Samos: In declivibus montis ad Vathy, 1 iv 1934, K. H. Rechinger 3532 (K); In lapidosis calc. prope Vathy, 31 iii 1934, K. H. Rechinger 3519 (K).

This new species might appear at first sight to be one of the dwarf forms of A. rotundifolius Pers., but there are distinct characters which clearly separate them. The table sets out the differences.

	A. nanus	A. rotundifolius
Stems	1-4(-6.5) cm	(3-)7-30 cm
Leaves	2-4.5 x 1.8-4.3 mm, entire, with a thick marginal vein.	5-18 x 3-14.5 mm, serrulate, sometimes scarcely so; marginal vein absent.
	Lateral veins not prominent.	Lateral veins prominent.
	Apex obtuse	Apex abruptly acuminate or acute.
Verticillasters	2(-4)-flowered.	3-12-flowered.
Calyx	Strongly gibbous.	Moderately gibbous.
Corolla	c. 6 mm.	8-12(-14) mm.

Dwarf forms of A. rotundifolius have previously been named A. graveolens (M. Bieb.) Link or as the synonymous Thymus exiguus Sibth. & Sm. Raulin (1858) first noted that our new taxon was distinct from typical A. graveolens; he gave no description of his "var. integrifolia", but cited the specimen (or specimens) "Fl. April-May, sub-alpine zone, 1400-1500 m, summit of Aphendi Kavoutsi. Heldreich." It is very likely, therefore, that Raulin based his variety on the same collection cited above as the holotype of A. nanus. The illustration of Thymus exiguus in Sibthorp & Smith's Flora Graeca 6:61, t. 575 (1826) is superficially very similar to "var. integrifolia Raulin" and this is probably why Halacsy (1902) and Rechinger (1943) placed "var. integrifolia Raulin" under Calamintha exigua (Sibth. & Sm.). Hayek.

Holmboe (1914) validly published Satureja exigua (Sibth. & Sm.) Holmboe var. integrifolia Holmboe from Cyprus, describing it as "Humilior, foliis integerimus", citing the illustration of Sibthorp in Flora Graeca t. 575, and specimens from the top of Chionistra and Trooditissa (Sintenis & Rigo 737 and Kotschy 762). We have seen these specimens and they have been correctly assigned by Holmboe to S. exigua (i.e. A. rotundifolius), and are therefore not equivalent to A. nanus or "var. integrifolia Raulin". Boissier in Flora Orientalis cited Kotschy 762 under C. graveolens (M. Bieb.) Benth. but there is no mention of a Heldreich specimen from Aphendi Kavoutsi.

The thick marginal vein of A. nanus is unusual in Acinos and is only shared with A. corsicus (Pers.) Getliffe. This appears to be a case of convergent evolution rather than an indication of close affinity.

A. nanus seems to be a local endemic restricted to Aphendi Kavoutsi and Samos, though it may have been overlooked on other Eastern Aegaean islands. The new species seems to belong to the montane element. There are few Aegaean islands with mountains over 1000 m (Crete, Aphendi Kavoutsi 1476 m, Karpathos 1215 m, Rhodos 1216 m, Samos 1433 m (near Vathy 1150 m), Ikaria 1037 m, Chios 1297 m) and all of these are in the eastern island arc, which may explain the known distribution of the novelty. There are a number of species more or less restricted to these islands and adjacent

Anatolia. Useful lists are given by Rechinger (1949).

3.119. 6. A. troodii (Post) Leblebici in Bitki 1:405 (1974).

Syn: Calamintha troodii Post in Mem. Herb. Boiss. 3(18):97 (1900); Satureja troodii (Post) Holmboe, Veg. Cyprus 161 (1914).

Ic: Holmboe, Veg. Cyprus 160 (1914), as S. troodi.

Fl. 7. Serpentine, igneous or limestone screes, 1520-2200 m.

Calyx tube 5.0-5.5 mm; bract width 3.0-5.0, broadly ovate [Cyprus]	ssp. troodii
Calyx tube 6.0-6.5 mm; bract width2.0-3.0 mm, narrowly elliptic [Turkey]	ssp. vardaranus

ssp. troodii

Type: [Cyprus:] habitat in monte troodi, fl. julio., Post 914 (G).

Gen. distrib.: Cyprus.

ssp. vardaranus Leblebici in Bitki 1:405 (1974).

Type:[Turkey C2 Mugla] Sandras Da. near Gokce ova, on serpentine, 1700 m, 23 vii 1947, Davis 13499 (holo. E!).

Gen. distrib.: SW Anatolia.

The few specimens available for study show that the two sub-species are clearly separable on calyx tube length and shape and width of bracts. Indumentum differences are a less certain guide: the calyx and stem of ssp. troodii are shortly velutinous and minutely glandular-papillose, while in ssp. vardaranus the calyx is minutely glandular-papillose or sparsely puberulent.

3.11.8. 7. A. corsicus (Pers.) G. Don in Sweet, Hort. Brit., ed.3, 768 (1839).

Syn: Thymus corsicus Pers., Syn. Pl. 2:131 (1806); Melissa microphylla Benth., Lab. Gen. Sp. 390 (1834); Calamintha corsica (Pers.) Benth. in DC., Prodr. 12:231 (1848); Satureja corsica (Pers.) Car. in Parl., Fl. Ital. 6(1):137 (1884); Micromeria corsica (Pers.) Levl., Dict. Invent. Fl. Fr. 22 (1916).

Ic: Coste, Fl. Fr. 3:95 (1906), as Calamintha corsica.

Fl. 8-9. Mountain rocks and screes.

Type: Described from Corsica. Richard (holo. P)

Gen. distrib.: Corsica.

A. corsicus is unusual in a number of respects. The low, woody habit, scarcely gibbous calyces, and entire leaves with a thick marginal vein make it quite unmistakable. It probably comes closest to A. troodii of Cyprus and SW Anatolia which has a similar habit and calyx shape but not the marginal leaf vein. Davis (1949) has suggested that these two species may have been derived from the polymorphic A. alpinus which is possible, since all the perennial species are woody at the base to some degree, and gibbosity of the calyx varies from very strongly gibbous in A. suaveolens, with the throat almost closed, to much more weakly gibbous in A. alpinus, with the throat wide open. A. nanus, endemic to E Crete and E Aegaean islands, appears to have developed a thick marginal vein similar to A. corsicus quite independently.

3.11.9. 8. A. simensis (Benth.) A. Doroszenko, comb. nov.

Syn: Calamintha simensis Benth. in DC., Prodr. 12:230 (1848); Calamintha cryptantha Vatke in Linnaea 37:328 (1872); Clinopodium simense (Benth.) O. Kuntze, Rev. Gen. Pl. 2:516 (1891); Clinopodium cryptanthum (Vatke) O. Kuntze, loc. cit. 515 (1891); ?Nepeta ehlersii Schweinf. ex Engler, Hochgebirgsfl. Trop. Afr. 368 (1892), nomen; Satureja simensis (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:303 (1897); Calamintha parvula S. Moore in Jour. Linn. Soc. Bot. 38:276 (1908); Calamintha cryptantha Vatke var. mildbraedii Perk. in Wiss. Ergebn. Deutsch. Zentr.-Afr. Exp. 1907-1908, 2:551 (1913).

Fl. All year. Grass and wasteland, margin of fens, Juniper, Olea, and Arundinaria forest, 1685-3975 m.

Type: [Ethiopia:] ad rupes regionis mediae montis Bachit, 21 v 1838, Schimper 999 (holo. K!).

Gen. distrib.: Ethiopia, Kenya, Sudan, Burundi, Uganda, Tanzania.

A. simensis is closely related to and has been much confused with A. pseudosimensis. It is most easily distinguished by its clearly petiolate leaves, smaller calyx tube, and the posterior stamens reduced to staminodes. In the Calaminthoid genera (Calamintha, Clinopodium, Cyclotrichium, and Acinos) only the Far Eastern Calamintha gracilis, C. ussuriensis, C. confinis, and C. micrantha have similarly reduced posterior stamens.

3.11.10. 9. A. pseudosimensis (Brenan) A. Doroszenko, comb. nov.

Syn: Satureja pseudosimensis Brenan in Mem. N.Y. Bot. Gard. 9:50 (1954).

Fl. All year. Grassland, igneous rocks, open woodland, damp and shady places, 1460-3350 m.

Type: Kenya: Kinangop, W Aberdares, growing in scrub, xii 1929, I.R. Dale 2157 (holo. K!).

Gen. distrib.: Cameroons, Fernando Poo, Tanzania, Ruanda-Urundi, Uganda, Kenya, Congo, NW Mozambique.

Similar to A. simensis but differing in its stems 15-60(-120) cm, leaves more broadly rounded or subcordate at base, petiole

0.5-1.5(-4.0) mm, longer calyx tube (3.6-4.8 mm) and upper calyx teeth (0.6-1.5 mm), longer upper corolla lip (1.5-3.2 mm), and posterior stamens fully fertile.

There is a strong facies similarity of this species to Calamintha uhligii, especially in habit and leaf shape. Yet A. pseudosimensis (and A. simensis) has a sigmoid, gibbous calyx with sessile pedicels typical of Acinos. Brenan (1954) believed that A. pseudosimensis hybridised with Satureja (Calamintha) uhligii. I have not seen any intermediates which might suggest hybridisation, but Brenan saw very many more specimens than I have. At the moment, the choice is between Acinos and Calamintha, with the evidence, in my opinion, weighted toward Acinos.

3.11.11. Nom. exclud.

A. herba-barona (Loisel.) G. Don ex Loud., Hort. Brit. 239 (1839) = Thymus herba-barona Loisel.

A. siso Siebold, Verh. Batav. Gen. 12:32 (1830) = ?Perilla arguta Siebold

3.11.12. Nom. dubia.

A. diffusus Boenningsh., Prod. Fl. Monast. 182 (1824).

A. grandiflorus G. Don ex Loud. Hort. Brit. 239 (1839).

3.12. Cyclotrichium (Boiss.) Manden. & Scheng., Not. Syst. (Leningrad) 15:336 (1953).

Syn: Calamintha Sect. Cyclotrichium Boiss., Fl. Or. 4:579 (1879); Satureja Sect. Cyclotrichium Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Perennial suffrutescent herbs. Leaves ovate to lanceolate, sometimes elliptic, entire or weakly crenulate, flat, veins usually prominent, camptodromous; palisade mesophyll dorsiventral or isolateral; shortly but distinctly petiolate. Inflorescence bracteate. Verticillasters dense, few- to many-flowered, distant. Bracteoles narrowly lanceolate or linear, up to as long as calyx tube. Calyx usually cylindrical-tubular, sometimes ampliate, straight or curved, 13-veined, throat usually glabrous, sometimes with a dense fringe of hairs, bilabiate, rarely almost regular, teeth all similar in shape or upper somewhat broader, upper half as long to almost as long as lower, lower teeth usually not ciliate. Corolla mauve, violet or pink, tube resupinate, annulate inside 1/2-2/3 way up tube, glabrous below the annulus, lips 1/4-1/2 as long as tube, upper (abaxial) lip as long as or slightly shorter than lower (adaxial) lip, upper lip emarginate or retuse, lower lip 3-lobed, lobes subequal. Stamens 4, all long exserted, of similar length or upper slightly shorter, usually inserted at same level, all fertile; thecae parallel. Style branches unequal, subulate. Nutlets oblong to ovoid, glabrous, apex rounded.

Type species: C. floridum (Boiss.) Manden. & Scheng. = C. origanifolium (Labill.) Manden. & Scheng.

An Irano-Turanian genus comprised of 8 species.

Cyclotrichium, as treated by Mandenova & Schengelia (1953), was related to Lophanthus Adans., a genus close to Nepeta. However, Lophanthus is distinguished by the deeply dentate to crenulate leaves, infundibuliform, 15-nerved calyx tube, exannulate corolla with unequal lobes of the lower (adaxial) lip, and thecae divergent. It seems unlikely, therefore, that Cyclotrichium can be closely related to Lophanthus.

In facies, leaf shape and structure (except C. niveum), verticillaster arrangement and calyx, Cyclotrichium is rather similar to Calamintha, the genus to which Boissier (1879) subordinated it. However, in corolla structure these genera are quite distinct.

3.12.1. 1. Plant densely white dendroid-haired tomentose 1. niveum

\+ Plant usually green; indumentum of simple hairs 2

2. Calyx tube glabrous or apparently so even under a lens 3

\+ Calyx tube distinctly hairy, sometimes minutely 4

3. Calyx teeth as long as or slightly shorter than calyx tube; calyx tube 3.0-3.5 mm; verticillasters with 3-9 flowers per floral leaf 2. haussknechtii

\+ Calyx teeth clearly shorter than calyx tube; calyx tube 5.0-6.0 mm; verticillasters of 1(-3) flowers per floral leaf 3. depauperatum

4. Calyx distinctly bilabiate, the upper triangular-acuminate teeth slightly divergent, half as long as lower teeth 4. origanifolium

\+ Calyx bilabiate but much less distinctly so, teeth porrect, generally narrowly triangular to lanceolate-subulate 5

5. Stems, especially upper part, and verticillasters also, very densely patent-pilose; leaves very broadly ovate to sub-orbicular 6

\+ Stems and verticillasters sparsely or not long-hairy; leaves ovate, mostly distinctly longer than broad 7

6. Calyx tube clearly ampliate, 3.0-3.5 mm; calyx teeth 1.0-1.5 mm; corolla 8.5-10.5 mm 5. straussii

\+ Calyx tube narrowly cylindrical, 4.7-7.5 mm; calyx teeth 2.0-4.5 mm; corolla 12.0-18.5 mm 7. longiflorum

7. Stems with long spreading hairs at least below or at nodes; lower calyx teeth 1.5-2.6 mm 6. leucotrichum

\+ Stems minutely glandular-pruinose, without long hairs; lower calyx teeth 3.0-3.4 mm 8. stamineum

3.12.2. 1. C. niveum (Boiss.) Manden. & Scheng., Not. Syst. (Leningrad) 15:337 (1953).

Syn: Calamintha nivea Boiss., Ann. Sci. Nat. ser. 4, 2:253 (1854); Clinopodium niveum (Boiss.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja nivea (Boiss.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Fl. 6-8. Rocky calcareous slopes, scree, 1400-1600 m.

Type: [Turkey B6 Malatya] in Cappadocia centrali inter Ketche-Mesara et Guruno (Gurun), Tchihatcheff (G?).

Gen. distrib.: E Turkey.

A very distinct species on account of its dense, white, dendroid indumentum. The isolateral leaf anatomy may also be unique in the genus.

3.12.3. 2. C. haussknechtii (Bunge) Manden. & Scheng., Not. Syst. (Leningrad) 15:337 (1953)!

Syn: Calamintha haussknechtii Bunge, Lab. Pers. 38 (1873); Clinopodium haussknechtii (Bunge) O. Kuntze, Rev. Gen. Pl. 2:515

(1891); Satureja haussknechtii (Bunge) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897).

Fl. 6-7. Dry ledges of limestone cliffs, rock fissures, 900-1130 m.

Type: [Iran] Teng, Tokab p. Behbehan, in fissur. rup., 3000 ped., 6 vi 1868, C. Haussknecht (K!).

Gen. distrib.: Iran.

3.12.4. 3. C. depauperatum (Bunge) Manden. & Scheng., Not. Syst. (Leningrad) 15:337 (1953)!

Syn: Calamintha depauperata Bunge, Lab. Pers. 38 (1873)! Clinopodium depauperatum (Bunge) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja depauperata (Bunge) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897)!

Fl. 8. Rocks, c. 900 m.

Type: [Iran] in rup. Bors vall. fl. Chyrsan, 3000 ped., viii 1868, C. Haussknecht (K!).

Gen. distrib.: Iran.

3.12.5. 4. C. origanifolium (Labill.) Manden. & Scheng., Not. Syst. (Leningrad) 15:337 (1953).

Syn: Clinopodium origanifolium Labill., Ic. Pl. Syr. Rar. 4:14 t.9 (1812); Melissa origanifolia (Labill.) Benth., Lab. Gen. Sp. 392 (1834); Micromeria origanifolia (Labill.) Benth. in DC., Prodr. 12:214 (1848); Calamintha glomerulosa Boiss. & Heldr. ex Benth. in DC., Prodr. 12:234 (1848); Calamintha origanifolia (Labill.) Boiss., Diagn. ser. 1(12):50 (1853); Calamintha florida Boiss., loc. cit. 51 (1853); Clinopodium floridum (Boiss.) O. Kuntze, Rev. Gen. Pl. 515 (1891); Satureja origanifolia (Labill.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); Satureja florida (Boiss.) Briq., loc. cit. (1897); Satureja labillardieri

Briq., Ann. Conserv. Bot. Geneve 2:187 (1898); Calamintha origanifolia (Labill.) Boiss. ssp. labillardieri (Briq.) Bornm., Beih. Bot. Centralbl. 31(2):248 (1914); Calamintha labillardieri (Briq.) Bornm., loc. cit. 249 (1914), nomen; Calamintha florida Boiss. var. villicaulis Bornm., Fedde Rep. 49:250 (1940); Cyclotrichium floridum (Boiss.) Manden. & Scheng., Not. Syst. (Leningrad) 15:336 (1953).

Fl. 7-9. Stony places, limestone scree, mountain slopes, 1200-4000 m.

Type: [Lebanon] in Libano, Labillardiere (holo. FI).

Gen. distrib.: S Turkey, Lebanon.

3.12.6. 5. C. straussii (Bornm.) Rech. f., Fl. Iranica 150:516 (1982).

Syn: Calamintha straussii Bornm., Beih. Bot. Centralbl. 22(2):119 (1907); Satureja straussii Bornm., loc. cit. (1907), nomen in herb.

Type: [Iran] Persia ditione oppidi, Nehawend m. m. Gerru, T. Strauss (K!).

Gen. distrib.: Iran.

Only known from the type.

3.12.7 6. C. leucotrichum (Stapf) Leblebici, Bitki 1:405 (1974).

Syn: Calamintha leucotrichum Stapf ex Rech. f., Oest. Bot. Zeitschr. 99:62 (1952).

Fl. 7. Cliffs and rock crevices, rocky slopes, 1000-1500 m.

Type: [Turkey C8 Mardin] Mardin, Rischemil (Rismil), 23 vii 1888, Sintenis 1352 (holo. WU, iso. E!, K!, LD, MANCH!).

Gen. distrib.: E Turkey, Iraq.

Very closely related to C. stamineum.

3.12.8. 7. C. longiflorum Leblebici, Bitki 1:406 (1974)!

Fl. 7. Calcareous mountain slopes, amongst rocks, rock crevices, 1200-1800 m.

Type: Iraq. Distr. Mosul (Kurdistan) ad confines Turciae prov. Hakari, in ditione pagi Sharanish, in montibus calc. a Zakho septentrionem versus Jabal Khantur, in saxosis, 1200 m, 4-9 vii 1957, K. H. Rechinger 10764 (holo. E!).

Gen. distrib.: Iraq.

Closely related to C. stamineum.

3.12.9. 8. C. stamineum (Boiss. & Hohen.) Manden. & Scheng., Not. Syst. (Leningrad) 15:337 (1953).

Syn: Micromeria staminea Boiss. & Hohen., Diagn., ser. 1(5):19 (1844); Calamintha staminea (Boiss. & Hohen.) Boiss. & Hohen., Diagn. 1(12):51 (1853); Clinopodium stamineum (Boiss. & Hohen.) O. Kuntze, Rev. Gen. Pl. 2:516 (1891); Satureja staminea (Boiss. & Hohen.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:299 (1897); Calamintha glabrescens Boiss. & Kotschy ex Rech. f., Oest. Bot. Zeitschr. 99:62 (1952); Cyclotrichium glabrescens (Boiss. & Kotschy ex Rech. f.) Leblebici, Bitki 1:406 (1974).

Fl. 6-8. Rock crevices, gravel terraces, rocky limestone slopes, 1200-1830 m.

Type: [N Iraq] in fissuris rupium montis Gara Kurdistaniae, Kotschy 311 (holo. G, iso. BM, K!).

Gen. distrib.: E Turkey, N Iraq.

3.13. Gardoquia Ruiz & Pav., Prod. 86, t. 17 (1794).

Syn: Rizoa Cav. in Anal. Cienc. Nat. 3:132 (1801); Satureja L. sect. Gardoquia (Ruiz & Pav.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897); Satureja L. sect. Calomelissa subsect. Coccineae Briq., loc. cit. 302 (1897), p.p.

Shrubs, prostrate to erect. Leaves ovate, lanceolate, elliptic, or obovate, rarely flabelliform or linear, clearly petiolate; flat, revolute at margins, or rarely conduplicate; entire, minutely toothed or crenulate, rarely serrate; lateral veins camptodromous, marginal veins absent; palisade mesophyll dorsiventral, rarely isolateral. Verticillasters usually single or few-flowered, sometimes many-flowered, approximate, rarely spike-like, flowers sessile to long pedunculate and pedicellate. Floral leaves shorter than flowers. Bracteoles linear to ovate, lanceolate or oblanceolate in shape, rarely absent. Calyx bilabiate, narrowly tubular, rarely ampliate, nearly always curved, rarely straight, 13-veined, throat glabrous or hairy; teeth straight, rarely upper curving upward, nearly always less than 1/2 tube length, usually not ciliate, upper teeth usually much shorter than lower. Corolla mostly red or red with yellow or orange-red, rarely purple, blue or white; tube very long narrowly tubular, not resupinate, not annulate inside, densely hairy on inside lower half, rarely glabrous; lips 1/20-1/3 x tube length; upper lip emarginate, longer than or +- equal to lower lip; lower lip 3-lobed, central lobe entire, very rarely bifid. Stamens 4, all fertile or rarely posterior pair reduced to staminodes, straight or convergent, all just exserted from tube, posterior stamens 1/2 to almost as long as anterior pair, inserted 1/2-3/4 way up tube; anthers divergent, sometimes parallel. Style branches mostly unequal, narrowly subulate or broad lanceolate, rarely one broadly lanceolate and the other narrowly subulate. Nutlets oblong or ovoid, glabrous or rarely minutely glandular or eglandular hairy.

Type species: G. multiflora Ruiz & Pavon.

35 species in N, C and S America.

In common with all the American genera recognised here, Gardoquia has been little used at generic level since De Candolle's Prodromus (Bentham, 1848) and even less so since Briquet's treatment in Naturlichen Pflanzenfamilien (1897). However, it is only the taxonomic rank, not the distinctness of Gardoquia as a group, which has been contended. Gardoquia was first published by Ruiz & Pavon in 1794 without descriptions but an illustration presented, clearly G. multiflora, validates the genus. The same authors jointly published six species shortly afterwards (Ruiz & Pavon, 1798). The next major work was by Kunth in Bonpland & Humboldt's Nova Genera et Species Plantarum vol. 2 (1817) where ten new species were published. By the time of De Candolle's Prodromus (1848) 25 species were known. Authors who recognised Gardoquia at generic level after 1848 include J. A. Schmidt in Martius' Flora Brasiliensis vol.8 (1858), Grisebach in Weddell's Chloris Andina vol. 2 (1860), Hemsley's Biologia Centrali Americana vol. 2 (1882), and Kuntze's Rev. Gen. Pl. (1891). After Briquet (1897), Gardoquia has nearly always been treated as a section of Satureja s.l. Epling, monographer of most American Labiatae, was most influential in maintaining Briquet's arrangement as far as Satureja s.l. was concerned. An exception is the recent Venezuelan Flora del Avila (Steyermark & Huber, 1978) which recognises Gardoquia as an independent genus.

The floral features particularly give Gardoquia a quite distinct and unmistakable facies. The calyx is narrowly parallel-sided, tubular, nearly always curved, the teeth short in comparison to the tube which rarely curve upward. Nearly all the species are adapted to pollination by birds and have distinctive, large, narrowly tubular, red or red with yellow corollas. The stamens are usually long and curved, and held under the upper corolla lip. Characteristically the stamen connective is very broad.

In leaf morphology the genus is extremely diverse, enabling one to distinguish nine sections using vegetative characters. There is a distinctive leaf shape, ptyxis, venation, and pubescence in each group. The sections are usually restricted in geographical distribution.

The infrageneric arrangement adopted here is very different from that of Epling & Jativa (1964, 1966) though rather closer to an earlier arrangement of Epling (1927). They divided Satureja sect. Gardoquia into 3 informal groups: Multiflorae, which included multiflora, elliptica, tomentosa, and rugosa (=pulchella), Ericoideae, which included the species with leaves generally less than 1 cm, and Ovalifoliae, with leaves generally over 1 cm long. These groups are very arbitrary and do not always bring closely related species together. Leaf size is extremely variable in the genus. However, I am certain that Epling & Jativa (1964) were quite aware of the limitations of their groups. Sometimes species placed next to each other in their work correspond with sections adopted in the present revision; for example, the species of my sections Plicatae and Sericifoliae. The sections described here are based primarily on leaf shape, teeth, revolution, venation, and pubescence. These characters are much more constant throughout the sections and of greater significance than size alone.

Briquet, because of over-emphasis of the length of the corolla, says that there is a transitional series from Gardoquia to Xenopoma. However, he was very unfortunate in his choice of examples to illustrate this transition. He says that Satureja breviflora (Benth.) Briq. and S. rugosa (Benth.) Briq., both placed in sect. Gardoquia, show an intermediate position. However, S. breviflora is probably a sterile sex form of Gardoquia incana, and having seen the type of Gardoquia rugosa this specimen also has small flowers due to sterility. Normally these species have very large corollas quite average in length for Gardoquia. Of the 35 species in Gardoquia and 20 species in Xenopoma, a couple of species do exhibit some intermediate features. One of these is the single species of Xenopoma sect. Sphenostachys which has the vegetative characteristics of Gardoquia but the floral features of Xenopoma. Gardoquia sect. Anomales is the other intermediate, but here the weight of similarity tends to Gardoquia even thought the corolla is white and the smallest in the genus. These two rather anomalous species were described after Briquet's death. The only other species Briquet treats as transitional is Satureja micromerioides (Hemsl.) Briq. Even though this species has a small corolla in comparison to other Gardoquias, it has a greater similarity to Gardoquia, as Hemsley (1882) recognised, than to Xenopoma. The calyx is long, narrowly tubular with narrowly triangular teeth, all + equal, which is not far removed from calices of some species of Gardoquia sect. Gardoquia. The corolla, though smaller than the average Gardoquia, has the arching, narrowly tubular appearance and large open throat typical of most Gardoquia species.

Gardoquia is more distantly related to the other American genera (of Satureja s.l.) than to Xenopoma, except for Obtegomeria which may be a specialised offshoot of Gardoquia. The similarity of Diodeilis coccinea (Nutt.) Rafin. to Gardoquia seems entirely due to similarities resulting from adaption to pollination by birds.

Nearly all Gardoquia species and D. coccinea have a large, narrowly tubular, red corolla typical of this mode of pollination. Alexander (1941) argued for the inclusion of D. coccinea in Gardoquia based on the similarity of the structure of the anthers, corolla, and structure and venation of the calyx. However, he does say that this species "is somewhat anomalous in the genus Gardoquia" on account of its unusual calyx. In fact the calyx of D. coccinea is quite different from that in Gardoquia. It is short, broad, straight tubular, the upper lip, with obsolescent teeth, curving upward until erect. The calyx of D. coccinea is, however, very similar indeed to D. dentata (Chapm.) A. Doroszenko and D. ashei (Weatherby) A. Doroszenko. In leaf structure and habit also D. coccinea plainly belongs to Diodeilis.

Some species of Gardoquia show a marked similarity to Poliomintha. If it were not for the sterility of the posterior stamens and the unusually thick, stellate pubescence of P. marifolia (Schauer) A. Gray one would have great difficulty in separating it from Gardoquia, especially from G. domingensis (Urb. & Ekman) A. Doroszenko of Sect. Pallidae. The calyx of G. maderensis is also very similar to Poliomintha. Epling & Stewart (1939) say of Poliomintha: "[a] genus too near Gardoquia not to be distinguished if that really becomes diandrous". G. jaliscana is a species which is consistently diandrous, but the unusually shaped calyx clearly associates it with G. macrostema, a species which has 4 fertile stamens. The relationship seems therefore to be very close.

3.13.1. 1. Leaves small, 1-5(-6) mm long, plicate, not revolute but halves of lamina somewhat recurved, ovate-lanceolate (e) sect. Plicatae

\+ Leaves usually much larger than 5 mm long flat or revolute, shape various 2

2\. Calyx teeth as long as or longer than tube 3

\+ Calyx teeth distinctly shorter than tube 4

3\. Leaves 30-54 x 11-19 mm, serrate; calyx throat glabrous; corolla white (c) sect. Anomales

\+ Leaves 4-20 x 5-7 mm entire or scarcely toothed; calyx throat with a dense ring of long, thin hairs; corolla purple (h) sect. Discolores

4\. Leaves with a complex reticulate pattern of minor veins between the main, usually very prominent, lateral veins; lower side of leaves densely white-short-tomentose, occasionally with longer hairs (b) sect. Tomentosae

\+ Leaves without or with few minor veins between the scarcely prominent or sometimes invisible main lateral veins; lower side of leaves glabrous, sparsely hairy or densely sericeous 5

5\. Leaves with distinctly revolute margins, narrowly elliptic to linear, rarely small ovate, densely sericeous or pubescent on lower side (d) sect. Sericifoliae

\+ Leaves flat or scarcely revolute just at margin, not narrowly elliptic, glabrous or sparsely hairy on lower side (rarely densely minute white-pubescent below) 6

6. Leaves broadly ovate to lanceolate, serrate to almost entire, lateral veins very narrow, + sunken on upper surface (a) sect. Gardoquia

\+ Leaves oblong-elliptic to broadly elliptic, or oblanceolate-spathulate, entire or scarcely toothed, lateral veins very narrow and faint or invisible on upper side 7

7. Upper calyx lip longer than lower lip 8

\+ Upper calyx lip as long as or shorter than lower lip 9

8. Leaves oblanceolate or very broadly elliptic, upper surface shiny; calyx hairy in throat (f) sect. Taxifoliae

\+ Leaves oblong-elliptic, upper surface pallid; calyx glabrous in throat (g) sect. Pallidae

9. Leaves oblanceolate to elliptic; calyx throat glabrous; upper and lower calyx teeth distinctly different in length; pedicels longer than peduncles (f) sect. Taxifoliae

\+ Leaves oblong-elliptic; calyx throat with a dense fringe of hairs; upper and lower teeth + equal; calyx peduncle 8-15 x pedicel length (i) sect. Micromerioides

313.2. (a) Sect. Gardoquia

Erect shrubs. Leaves broadly ovate to lanceolate, glabrous or sparsely hairy, 10-55 x 8-32 mm, flat, rounded to somewhat cuneate at base, long petiolate, margins serrate to almost entire, lateral veins very narrow, sunken above, scarcely or not prominent below. Calyx tube slightly ampliate, sometimes narrowly tubular, curved or straight; lower teeth 1/8-4/5 x tube length, upper teeth straight or somewhat curving upwards. (Chile, Peru, Mexico, Guatemala)

3.13.2.1. 1. Calyx throat without a ring of hairs 2

\+ Calyx throat with a sparse to dense ring of hairs 3

2. Calyx glabrous or minutely puberulent; lower calyx lip 1.8-2.5 mm 1. <u>multiflora</u>

\+ Calyx sparsely hirsute; lower calyx lip 3.0-4.0 mm 2. <u>elliptica</u>

3. Upper calyx teeth distinctly curved upward, tube clearly widening to mouth 4

\+ Upper calyx teeth straight, tube narrowly cylindrical or scarcely wider at mouth 5

4. Fertile stamens 4; corolla tube glabrous within; calyx 7-13 mm long 3. <u>macrostema</u>

\+ Fertile stamens 2; corolla tube densely retrorse-strigose within; calyx 4-5 mm 4. <u>jaliscana</u>

5. Lower calyx teeth apex broad, obtuse; (leaves small, 5-10 mm) [Peru] 5. <u>junctionis</u>

\+ Lower calyx teeth sharply acute [Mexico, Guatemala] 6

6. Leaves 5-10 mm long, serrulate, with sharply pointed teeth 6. <u>mexicana</u>

\+ Leaves 10-40 mm long, entire to sub-entire with small rounded teeth 7

7. Leaf, other than at margins, glabrous; lower calyx teeth 2.2-3.0 mm [Guatemala] 7. <u>seleriana</u>

\+ Leaf minutely hirtellous; lower calyx teeth 1.1-2.0 mm [Mexico] 8. <u>maderensis</u>

3.13.2.2. 1. G. multiflora Ruiz & Pav., Syst. Veg. 149 (1798).

Syn: Rizoa ovatifolia Cav. in Anal. Cienc. Nat. 3:133 (1801); Clinopodium multiflorum (Ruiz & Pav.) O. Kuntze, Rev. Gen. Pl. 3(2):259 (1898); Satureja multiflora (Ruiz & Pav.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897).

Ic: Paxt. Mag. 6:223 (1839); Bot. Mag. 66: t.3772 (1840).

Fl. 1-2, 12. Amongst shrubs, margin of forest, marshy places, 50-300 m.

Type: Chile: Concepcion, Pavon (iso. CONC, G, P).

Gen. distrib.: Central coastal Chile.

A very common species in low-lying parts of central Chile between 35° and 42° S (Marticorena & Quezada, 1977). This area has a mediterranean-like climate where G. gilliesii (sp. no. 28) is also endemic. There is an abrupt change in the flora at around 42° S related to the last glacial period. A further note is given under Xenopoma darwinii.

3.13.2.3. 2. G. elliptica Ruiz & Pav., Syst. Veg. 149 (1798).

Syn: Stachys speciosa Hook., Bot. Misc. 2:235 (1831)! Satureja elliptica (Ruiz & Pav.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897), non Briq., loc. cit. 299 (1897).

Fl. 1, 6. Rock ledges by rivers, 2750-3350 m.

Type: Peru: Cheuchin and Sayan, Dombey (holo. P).

Gen. distrib.: Peru.

Most closely related to G. multiflora and distinguished easily on pubescence and the form of the bracteoles.

3.13.2.4. 3. G. macrostema (Moc. & Sessé ex Benth.) A. Doroszenko, comb. nov.

Syn: Melissa macrostema Moc. & Sessé ex Benth., Lab. Gen. Sp. 395 (1834)! Calamintha macrostema (Moc. & Sessé ex Benth.) Benth. in

DC., Prodr. 12:234 (1848)! Clinopodium macrostemum (Moc. & Sessé ex Benth.) O. Kuntze, Rev. Gen. Pl. 515 (1891)! Satureja macrostema (Moc. & Sessé ex Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 1897)! Calamintha fuchsiifolia Gandoger in Bull. Soc. Bot. Fr. 65:65 (1918); Clinopodium laevigatum Standley in Contrib. U.S. Nat. Herb. 23:1273 (1925); Satureja laevigata (Standley) Standley in Field Mus. Publ. Bot. 11:173 (1936); Satureja macrostema (Moc. & Sessé ex Benth.) Briq. var. laevigata (Standley) McVaugh & Schmid in Brittonia 19:264 (1967).

Ic: McVaugh & Schmid in Brittonia 19:264, f.1 (1967).

Fl. All year. Dry wooded hills, steep banks, deep shade of Abies and oak wood, 1800-3500 m.

Syntypes: [Mexico] hort. Mexican., ann. 1830, Graham 110 (K!); [Mexico]: N[ueva] E[spana], ex herb. Sessé & Mocino (lecto. OXF, ex herb. Lambert).

The lectotype was designated by McVaugh & Schmid (1967).

Gen. distrib.: S Central Mexico. A map is presented by McVaugh & Schmid (1967).

G. macrostema has a number of unusual floral features. The straight, ampliate calyx with clearly upcurving upper lip is only shared with G. jaliscana, and the corolla inflating at the calyx mouth is unique in the genus. However, in overall facies the species clearly belongs to Gardoquia. Leaf shape, verticillaster arrangement, and overall appearance of the flowers are similar to G. multiflora and G. elliptica. There is, however, some similarity in the calyx to Diodeilis sect. Diodeilis, especially in the upcurving upper lip.

A specimen labelled Arsene 8593, Morelia, Michoacan, Mexico, is very unusual and may represent a new species. In calyx structure and dimensions it is very similar to G. macrostema. There are two immature corollas on the specimen and dissection of one of them showed that all four stamens would probably be fertile when mature. The very slender, recurved puberulent, sprawling stems are similar to G. jaliscana. The leaves are narrowly elliptic, 12-20 x 4-6 mm, entire and glabrous except for a few hairs along the margins.

3.13.2.5. 4. G. jaliscana (McVaugh & Schmid) A. Doroszenko, comb. nov.

Syn: Satureja jaliscana McVaugh & Schmid in Brittonia 19:266 (1967).

Ic: McVaugh & Schmid, loc. cit., f.2 (1967).

Fl. 4, 11. Humid deciduously forested ravines in narrow stream valleys, 1700-1900 m.

Type: Mexico: Jalisco: headwaters of Rio Mascota, 20-25 km SE of Talpa de Allende and 12-13 km S of the sawmill called El Rincon, in flower 3-4 iv 1965, McVaugh 23465 (holo. MICH).

Gen. distrib.: Mexico, Jalisco.

The posterior stamens are reduced to small staminodes. Briquet (1897) would probably have placed this species in the 2-staminate genus Hedeoma, since he argued that it was not possible to make clear diagnoses of the genera if one mixed tetrandrous and diandrous species in one genus. Even though it is very likely that Hedeoma and its related 2-staminate genera are the closest relatives of the American Satureja s.l., the strong similarity of G. jaliscana to G. macrostema, a species with completely fertile stamens, argues for its retention in Gardoquia. The illustrations in McVaugh & Schmid (1967) show this quite clearly.

The posterior stamens are always shorter than the anterior in Gardoquia (see table below; G. jaliscana excluded). Complete sterility of all the stamens has been noted throughout Satureja s.l. (see chapter 4 for complete details), but whenever there is only partial sterility it is the posterior pair which are sterile.

Length of the posterior stamens as a percentage of the anterior.

Percentage	Number of species
50 - 60	2
60 - 70	7
70 - 80	7
80 - 90	10
90 - 100	2

Mean percentage = 75%

3.13.2.6. 5. G. junctionis (Epling & Jativa) A. Doroszenko, comb. nov.

Syn: Satureja junctionis Epling & Jativa in Brittonia 16:400 (1964)!

Fl. 5. Margins of streams, 3100 m.

Type: Peru, La Libertad, Prov. Pataz, Tingo (La Sabana - Huayillas), 3100 m, 23 v 1961, Lopez & Sagastegui 3533 (holo. LA in UC!).

Other than in size the leaves are very similar to G. multiflora. The affinity of G. junctionis seems to be with G. multiflora/G. elliptica, but the low shrubby habit, and ampliate, curved calyx with obtuse teeth clearly distinguishes this species from the others in the section.

3.13.2.7 6. G. mexicana Benth., Pl. Hartw. 50 (1840).

Syn: G. helleri Peyr. in Linnaea 30:34 (1859); Satureja mexicana (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)! Calamintha oaxacana Fernald in Proc. Amer. Acad. Sc. 35:564 (1900); Clinopodium oaxacanum (Fernald) Standley, Contrib. U.S.

Nat. Herb. 23:1273 (1925); Satureja oaxacana (Fernald) Standley in Field Mus. Publ. Bot. 11:173 (1936).

Fl. 1, 7, 12. Steep rocky hillside, 1500-2745 m.

Type: Mexico: between Regla and the Barranco, ann. 1839, T. Hartweg 377 (holo. K!, iso. E!).

Gen. distrib.: Mexico.

The leaves are very variable in size in this species and larger ones are very similar to those of G. macrostema. The type specimen has much smaller, broadly ovate leaves but with the small, sharply pointed, outcurving teeth characteristic of the species.

3.13.2.8. 7. G. seleriana (Loesener) Doroszenko, comb. nov.

Syn: Satureja seleriana Loesener in Verh. Bot. Brandenb. 1909, 51:35 [213] (1910)! Satureja seleriana Loes. var. guatemalensis Loes., loc. cit. 36 [214] (1909); Satureja guatemalensis Standley ex Epling & Jativa in Brittonia 20:309 (1968).

Fl. 4, 9. 2600-3400 m.

Syntypes: Guatemala: dept. Chimaltenango, in cupresseto in Sierra Santa Elena apud Tecpam Guatemala, 3400 m, Seler 2352 (B?, lost?); dept. Quche apud Chiul, 2600 m, iv 1892, Heyde & Lux 3125 (K!).

Gen. distrib.: Guatemala.

In leaf shape this is most similar to G. macrostema, probably its nearest relative. The calyx widens gradually from the base which is unusual, most Gardoquia species having parallel-sided calices. The corolla tube is very narrow, most similar to G. multiflora and G. maderensis.

3.13.2.9. 8. G. maderensis (Henrickson) A. Doroszenko, comb. nov.

Syn: Satureja maderensis Henrickson in Brittonia 33:211 (1981).

Ic: Henrickson in Brittonia 33:212 (1981).

Ic: Henrickson in Brittonia 33:212 (1981).

Fl. 8-9. Steep calcareous slopes, frequently in shade, 2050-2600 m. Type: Mexico: Coahuila: c. 35 (air) km W of Cuatro Cienegas in Canon de la Hacienda in Sierra de la Madera along trail SE of road's end, near 27 03' N Lat., 102 24'W Long., 2200-2600 m, 5 viii 1973, J. Henrickson with T. Wendt 11888 (holo. LL, iso. ASU, MEX). Gen. distrib.: Mexico.

The very narrow, straight, parallel-sided calyx with short teeth is very similar to Poliomintha. Henrickson (1981) mentions that on one of the isotypes (at ASU) Irving, the monographer of Hedeoma (Irving, 1980) and Poliomintha (Irving, 1972), comments that "save for the four fertile stamens, this plant is remarkably like Hedeoma-Poliomintha". Judging from the excellent illustration in Henrickson (1981) I would have to agree.

Irving's comments imply that Hedeoma and Poliomintha are artificial and should be united together and with Gardoquia. The overall similarity of Gardoquia to Poliomintha is certainly close. However, Gardoquia and Hedeoma are quite different in calyx and corolla structure, as well as in habit and geographical distribution. My inclination would be to keep these genera apart, at least for the time being.

3.13.3 (b) Sect. Tomentosae A. Doroszenko, sect. nov.

Tall erect shrubs. Leaves broadly ovate, narrowly elliptic to obovate, lower surface densely white tomentose, the upper side much less densely adpressed hairy, or glabrous, 8-25 x 3-20 mm, with clearly revolute margins, crenulate or entire, lateral veins broad, prominent below, sunken above, with a complex reticulate pattern of minor veins between the laterals; petioles usually short but quite distinct. Calyx narrowly parallel-sided, curved tubular; lower teeth (1/4-)1/3-2/3 x tube length. (Ecuador, Peru, Colombia)

3.13.3.1. 1. Leaves 6.5-10.0 mm; calyx teeth parallel-sided in lower part, terminating in a broad obtuse apex 13. flabellifolia

\+ Leaves 10.0-35.0 mm; calyx teeth narrowly triangular, apex acute 2

2. Leaf apex sharply acute 9. acutifolia

\+ Leaf apex rounded to broadly obtuse 3

3. Lower calyx teeth 3.0-5.0 mm; leaves broadly to narrowly ovate 12. pulchella

\+ Lower calyx teeth 1.5-2.5 mm; leaves orbicular to broadly elliptic (rarely obovate) 4

4. Calyx tube 4.5-5.0 mm, glabrous in throat; lateral veins on lower side of leaf very narrow, hardly raised above leaf surface 10. tomentosa

\+ Calyx tube 5.6-6.5 mm, hairy in throat; lateral veins on lower side of leaf broad, prominently raised above lamina 11. cercocarpoides

3.13.3.2. 9. G. acutifolia Benth. in DC., Prodr. 12:236 (1848).

Syn: Satureja acutifolia (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)!

Fl. 1, 12. Cliffs and dry shrubland, c. 1700 m.

Type: Peru: Amazonas, Chachapoyas, ann. 1835, Mathews 1522 (holo. K!, iso. E!).

Mathews 1521 has very tightly revolute leaves, rather similar in aspect to some forms of G. sericea. Closer inspection shows that these are all very young leaves and that nearly all the older ones have fallen off. The few larger leaves remaining have the distinctive elliptic shape and unusual venation.

3.13.3.3. 10. G. tomentosa Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:314 (1817).

Syn: G. thymoides Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:314 (1817); G. elegans Kunth, loc. cit. (1817); G. grandiflora Kunth, loc. cit. 315 (1817); G. incana Willd. ex Benth. in Linnaea 11:331 (1837), nomen; G. quitensis Willd., loc. cit. 332 (1837), nomen; Satureja tomentosa (Kunth) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a: 300 (1897); Satureja thymoides (Kunth) Briq., loc. cit. (1897), non Brown ex Buch (1825), nomen, non Soland. ex Lowe (1831), nomen, non (De Not) Nyman (1854); Satureja elegans (Kunth) Briq., loc. cit. (1897); Satureja kunthii Briq., loc. cit. (1897), vars. crenata Briq., parvifolia Briq., subintegrifolia Briq. in Ann. Conserv. Jard. Bot. Geneve 2:189 (1898)!

Fl. 3, 6-8. Stony plains, sun-baked slopes, dry banks, 2440-3050 m.

Type: Ecuador: juxta Llactacunga, Hambato et Riobamba Nuevo, 2750 m, fl. Jun., Bonpland (holo. P!).

Gen. distrib.: Ecuador.

Rather variable in pubescence and corolla size (tube 12-27 mm, lips 3-5 mm) which accounts for the many synonyms.

3.13.3.4. 11. G. cercocarpoides (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja cercocarpoides Epl. in Fedde, Rep. Spec. Nov. Beiheft 85:153 (1936)! Satureja kunthii Briq. var. nervosa Briq. in Ann. Conserv. Jard. Bot. Geneve 2:189.

Fl. 2-5. Open grass and scrub, 2130-2750 m.

Type: Colombia: Taquina, ad Rio Hacha, 2750 m, ii 1844, I. Linden 1623 (holo. K!)

Gen. distrib.: Colombia.

Epling & Jativa (1964) have this species as a synonym of Satureja andrei Epl. However the latter taxon is entirely different and is synonymous with G. taxifolia. Examination of the types show that G. cercocarpoides has more broadly elliptic, adpressed or recurved densely tomentose leaves, (not glabrous or sparsely minutely hairy), more rounded at the apex, and the veins sunken above not raised as in S. andrei. The calyx is densely shortly recurved-pubescent with sharply pointed, lanceolate-subulate teeth, rather than the calyx sparsely minute-hairy, the teeth triangular not sharply subulate as in S. andrei.

3.13.3.5. 12. G. pulchella Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:315 (1817).

Syn: G. rugosa Benth., Lab. Gen. Sp. 399 (1834)! ?G. pilosa A. Gray in Proc. Am. Acad. Sci. 5:341 (1862); Satureja rugosa (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)! Satureja pulchella (Kunth) Briq., loc. cit. (1897)! Satureja panicera Epl. in Bull. Torrey Bot. Club 68:553 (1941)!

Fl. 3, 5-9, 11. Open shrubbery, 1270-3600 m.

Type: Peru: Contumasay, Bonpland 3717 (iso. P!)

Gen. distrib.: Peru.

Epling (1941), examining type material only, noted the close similarity of S. panicera Epl. to S. rugosa (Benth.) Briq. The main differences noted were in pubescence and corolla length. I have examined 9 specimens and the only noteworthy differences are in pubescence. The types of G. pulchella and S. panicera, and Sagastegui 2517 and 3885 have a very dense, white, extremely minute tomentose pubescence. The type of G. rugosa and Ferreyra 13299 have a much sparser, shortly villous pubescence. Even longer villous are the leaves of Ridoutt 476 & 845, and Hutchinson & Wright 5241. The type of G. pulchella and the Sagastegui specimens tend to have much narrower lanceolate and more shallowly crenate leaves than the rest, but the type of G. panicera has broadly ovate and deeply crenate leaves. The small corolla of the type of G. rugosa is due to sterility. All the other specimens have the typically large corollas of the genus.

3.13.3.6. 13. G. flabellifolia (Epl. & Jativa) A. Doroszenko, comb. nov.
Syn: Satureja flabellifolia Epl. & Jat. in Brittonia 16:399 (1964)!
Fl. 6. Montane shrubbery, 2100-2200 m.
Type: Peru: Dept. Piura, Prov. Huancabamba: Abra de Porculla, lado oriental, monte bajo, elemente dominante Barnadesia sp., 2100-2200 m, 28 vi 1959, Ferreyra 13740 (holo. LA in UC, iso. UC!).

This species, only known from the type, is most closely related to G. pulchella, but has much smaller more broadly ovate leaves, truncate at the base. The broadly lanceolate calyx teeth are very unusual; only G. junctionis has similar teeth.

3.13.4. (c) Sect. Anomales (Epl. & Jat.) A. Doroszenko, comb. nov.
Syn: Satureja L. sect. Anomales Epl. & Jat. in Brittonia 16:407 (1964).

Ascending shrubs. Leaves narrowly lanceolate to elliptic, flat, veins sunken above, prominent below, with numerous minor veins between the laterals, reticulate, petioles 3-6 mm. Calyx tube straight; lower teeth 1-1 1/4 x tube length. Monotypic. (Peru).

3.13.4.1. 14. G. sphenophylla (Epl.) A. Doroszenko, comb. nov.
Syn: Satureja sphenophylla Epl. in Fedde, Rep. Spec. Nov. Beiheft 85:152 (1936)!
Fl. 6. Margin of forest, 2700-3200 m.

Type: Peru: Junin, Carpapata road to Huacapistana, 2700-3200 m, 7 vi 1929, Killip & Smith 24443 (holo. US!, iso. LA in UC!).

Gen. distrib.: Peru.

Epling & Jativa (1964) noted that this distintive species has the habit of a Gardoquia but a corolla similar to Xenopoma. They described a new section for it, placed between Satureja sect. Gardoquia and sect. Xenopoma, noting also the multi-flowered cymes.

Although the small, white corolla is unusual for Gardoquia, there are similarities in calyx, leaf shape and leaf texture to sect. Tomentosae. However, a monotypic section for S. sphenophylla seems appropriate. The inflorescence is spike-like, and the narrowly triangular calyx teeth equal or shortly exceed the straight calyx tube. Such long teeth are only known in Sect. Discolores, and few species have a straight calyx tube (G. microphylla, G. seleriana, G. jaliscana, G. maderensis, G. macrostema, G. micromerioides).

Nearly all Gardoquias are adapted to bird pollination, but G. sphenophylla, G. weberbaueri (sect. Taxifoliae) and G. discolor (sect. Discolores) (the last two with small bluish-violet flowers) are probably adapted to insect pollination.

3.13.5. (d) Sect. Sericifoliae A. Doroszenko, sect. nov.

Procumbent or ascending shrublets. Leaves linear- or narrowly elliptic or very small ovate, shortly petiolate, entire or scarcely toothed, margins strongly revolute, densely white-sericeous or lanate below, sparsely sericeous or pilose, or minutely pubescent above; lateral veins very narrow, sunken above, prominent below, sometimes invisible, without minor veins between them. Calyx small, slightly ampliate or straight curved-tubular; teeth 1/4-2/5 x tube length. (Peru).

3.13.5.1. 1. Leaves ovate, 1-3(-4) mm long 20. revoluta

\+ Leaves linear, lanceolate to elliptic, (3-)4-20 mm long 2

2. Leaf veins on upper side deeply impressed, running ± parallel to centre vein; upper leaf surface with minute erect hairs only 19. impressa

\+ Leaf veins on upper surface not markedly sunken, running out towards margin; upper leaf surface with long, adpressed hairs 3

3. Leaves mostly 10-20 mm long; pubescent on all parts, hairs crisped-erect on stems 18. sericifolia

\+ Leaves mostly 3-10 mm long; adpressed-sericeous on all parts 4

4. Most leaves tightly revolute, very densely sericeous so that the underlying surface is invisible 15. sericea

\+ Most leaves lanceolate to elliptic, clearly revolute only at margins, sericeous but much less densely so, the hairs short 5

5. Leaves 3-6 mm long, ± lanceolate, punctate glands mostly obscured by hairs 16. argentea

\+ Leaves 6-10 mm long, elliptic, punctate glands few but plainly visible 17. clivorum

3.13.5.2. 15. G. sericea Presl ex Benth., Lab. Gen. Sp. 402 (1834).

Syn: Satureja sericea (Presl ex Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)!

Fl. 5-7, 12. Dry settled moraines, bushy thickets on mountain slopes, 2100-4580 m.

Type: Peru: Cordillera Scruvia, Haenke (holo. PR, iso. K!)

Gen. distrib.: Peru.

This species is closely related to and has been confused with G. argentea. A number of specimens identified as G. argentea are in fact this species [Woytkowski 18 (FM); Soukup 4138 (FM); Bonpland (FM ex P)]. G. sericea has much narrower leaves and much more revolute margins; the indumentum is long, fine, silvery and adpressed-pilose rather than very short, white (not shiny) recurved-puberulent.

3.13.5.3 16. G. argentea Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:313 (1817).

Syn: Satureja argentea (Kunth) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)!

Fl. 8. River cliff ledges, c. 2130 m.

Type: Peru: Micuipampa, around the base of Mt. Hualayoc, Bonpland (holo. B!).

Gen. distrib.: Peru.

3.13.5.4. 17. G. clivorum (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja clivorum Epl. in Brittonia 12:145 (1960)!

Fl. 5-6. Rocky hillsides, 2700- 3230 m.

Type: Peru: Dept. La Libertad, Prov. Otuzco, Shilte (Hda. Llaguen), 3150 m, 2 vi 1951, A. Lopez 1555 (holo. LA in UC!).

Gen. distrib.: Peru.

This is very close to G. argentea but may be distinguished by its larger leaves, and very much sparser pubescence. Only young leaves are densely hairy, but then these are most similar to G. sericea, with very fine shiny hairs. These hairs do not appear to be shed but the leaves enlarge so much that a sparse pubescence results. The brown punctate glands on the lower side of the leaves are also a distinctive feature of this species.

3.13.5.5. 18. G. sericifolia (Epl. & Jat.) A. Doroszenko, comb. nov.

Syn: Satureja sericifolia Epl. & Jat. in Brittonia 16:405 (1964).

Fl. 6-7. Moraines, sandy cliffs, steep dry slopes, 2300-4290 m.

Type: Peru: Dept. La Libertad, Prov. Bolivar, arriba de Longotea, 3200 m, 27 v 1960, Lopez & Sagastegui 3189 (LA in UC).

Gen. distrib.: Peru.

3.13.5.6. 19. G. impressa A. Doroszenko, sp. nov.

Shrub, stems slender, up to 60 cm tall, densely minute-patent-puberulent. Leaves elliptic to lanceolate, subsessile, 7.0-14.0 x 1.3-3.5 mm, base narrowly cuneate, apex acute, margins revolute, entire, veins narrow but strongly impressed on upper side, running parallel to margin, densely white minute-puberulent below, densely extremely minute-hairy above but shiny surface showing through. Verticillasters approximate on distal part of stems or on short lateral shoots, 1-8-flowered; peduncles 0.4-0.6 mm; pedicels 0.5-3.0 mm. Bracteoles filiform, 0.8-2.0 mm. Calyx narrowly parallel-sided, curved-tubular; tube 3.5-3.8 mm, densely white, minute, simple-hairy, throat glabrous; upper lip 1.6-2.0 mm; lower lip 1.3-1.7 mm; teeth narrowly triangular, upper 0.5-1.0 mm, lower 1.3-1.7 mm. Corolla dull yellow-scarlet, yellow toward base; tube 15-19 mm; lips 3.0-4.0 mm. Stamens 4, all fertile; anthers divergent. Style branches equal, both narrowly subulate.

Type: Ecuador: Cuenca, Quebrada de Chushkin, 2590 m, dry sandy cliffs among shrubs and Aloes, etc., also on steep dry sunny slopes amongst similar vegetation, 22 vi 1939, E.K. Balls 7079 (holo E!).

Only known from the type, G. impressa is related to G. sericifolia but clearly differs in the leaves, calyx and corolla.

G. sericifolia has consistently elliptic leaves, adpressed-pubescent on both sides, the lateral veins only a little sunken and running toward the margins. The calyx tube of G. impressa is much shorter, more hairy on the veins and the teeth are much narrower; also the corolla is much shorter.

The type specimen of G. impressa had been determined as Satureja [Gardoquia] taxifolia (Kunth) Briq. However the latter species is a much more robust plant with minutely toothed, (2.5-)4-9 mm broad leaves, not revolute at the margins and the veins slightly raised on the upper side. The leaves are often also shiny-glabrous above, giving G. taxifolia an entirely different aspect.

3.13.5.7. 20. G. revoluta Ruiz & Pav., Syst. Veg. 149 (1798).

Syn: Satureja revoluta (Ruiz & Pav.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897); S. insignis Mansfeld in Notizbl. Bot. Gart. Berlin 9:288 (1925).

Fl. 4, 8-10. Grassland, rock crevices, 2750-3800 m.

Type: Peru: pr. Huassahuasi, Panao et Huariaca, Dombey (holo. P).

Gen. distrib.: Peru.

The very small, broadly ovate leaves are very unusual and quite different from the rest of the section. Points of similarity, however, are the strongly revolute margins and dense tomentose pubescence on the lower side. The calyx, on the other hand, is very similar to G. sericea.

3.13.6. (e) Sect. Plicatae A. Doroszenko, sect. nov.

Erect or ascending shrubs. Leaves ovate-lanceolate, 1-6 x 1-4 mm, rounded or cordate at base, conduplicate, halves of lamina somewhat curved back, + prominently veined, entire or scarcely toothed, glabrous or with minute hairs on both sides. Calyx tube narrowly parallel-sided or slightly ampliate tubular; lower teeth 1/7-1/3 x tube length. (Peru, Ecuador, Colombia).

3.13.6.1. 1. Calyx glabrous outside; leaves very numerous, mostly 1-2 mm long 21. microphylla
\+ Calyx hairy outside; leaves few to many, mostly 2-6 mm long 2
2. Erect plants, 60-200 cm tall; leaves + glabrous, + entire; bracteoles absent; calyx throat with a dense fringe of hairs 22. striata
\+ Low, procumbent plants, 20-30 cm tall; leaves minutely hairy, minutely serrulate; bracteoles 1.6-1.8 mm; calyx throat glabrous 23. plicatula

3.13.6.2. 21. G. microphylla Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:311 (1817).

Syn: G. jamesonii Benth., Lab. Gen. Sp. 404 (1834)! Satureja ericoides Willd. ex Benth. in Linnaea 11:328 (1837), nomen; Satureja jamesonii (Benth.) Briq. in Engler & Prantl. Nat. Pflanzenfam. 4,3a:300 (1897)! Satureja microphylla (Kunth) Briq., loc. cit. (1897); Satureja connata Epl. in Ann. Missouri Bot. Gard. 14:70 (1927).

Fl. 7-9, 12. Mountain slopes, 2200-3500 m.

Type: Ecuador: crescit in Andibus Pastoensibus locis frigidus prope Rio Blanco, inter pagos Guachucal et Tulcan, 3200 m, fl. Dec., Bonpland 2186 (holo. P).

Gen. distrib.: SW Colombia, Ecuador.

This species is easily recognised by its very numerous, tiny leaves.

3.13.6.3. 22. G. striata Ruiz & Pav., Syst. Veg. 148 (1798).

Syn: Satureja striata (Ruiz & Pav.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897).

Fl. 2-8. Mountain slopes, 2700-3660 m.

Type: Peru, Pavon?

Gen. distrib.: Peru.

The species derives its name from the strongly developed leaf lateral veins which arch toward the leaf apex, and the strongly nerved, narrowly tubular calyx tube.

3.13.6.4. 23. G. plicatula (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja plicatula Epl. in Ann. Missouri Bot. Gard. 14:69 (1927)!

Type: Peru: Llata, pendant from river cliff ledges, 2130 m, 21 viii 1922, Macbride & Featherstone 2238 (holo. F, iso. K!).

Only known from the type.

3.13.7. (f) Sect. Taxifoliae A. Doroszenko, sect. nov.

Erect or ascending shrubs. Leaves flat, oblanceolate-spathulate to elliptic, sometimes broadly elliptic, subsessile, 3-25 x 1-14 mm, minutely toothed or entire, apex obtuse to rounded to acute, glabrous or with minute hairs on both sides, or glabrous above and minutely hairy below; lateral veins very narrow, hardly prominent or sometimes invisible. Calyx narrowly parallel-sided, sometimes slightly ampliate, curved tubular; lower teeth 1/9-4/5 x tube length. (Peru, Ecuador, Chile).

3.13.7.1. 1. Leaves oval-elliptic, obtuse at apex, for the most part over 10 mm long, the largest leaves 6-14 mm wide 2

+ Leaves oblanceolate and more or less rounded at apex, for the most part up to 10 mm long, 1-6 mm wide 3

2. Stem densely white-puberulent; leaves mostly narrowly elliptic; corolla red 24. taxifolia

+ Stem very sparsely minute-puberulent or glabrous; leaves mostly oval to broadly elliptic; corolla bluish-purple 25. weberbaueri

3. Stem densely shaggy-pubescent; leaves minutely serrulate, lateral veins very prominent; calyx tube 3.2-4.5 mm, upper calyx lobe about 1 1/2 x the lower lobe 26. cutervoensis

+ Stem minutely puberulent; leaves entire (rarely scarcely toothed), lateral veins invisible; calyx tube 4.5-6.5 mm, upper calyx lobe about the same length as lower lobe 4

4. Corolla tube 9-14 mm; leaves minutely puberulent (rarely with a few longer hairs); lower calyx teeth 3.0-5.5 mm; calyx throat glabrous 28. gilliesii

+ Corolla tube 14-22 mm; leaves essentially glabrous (rarely a few minute hairs); lower calyx teeth 1.3-1.7 mm; calyx throat with a fringe of hairs 27. obovata

3.13.72 24. G. taxifolia Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:312 (1817).

Syn: G. glabrata Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:313 (1817); Thymus taxifolius Willd. ex Benth. in Linnaea 11:342 (1837), nomen; Satureja taxifolia (Kunth) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897); Satureja glabrata (Kunth) Briq., loc. cit. (1897); Satureja andrei Epl. in Ann. Missouri Bot. Gard. 14:67 (1927)! Satureja lineata Epl. in Fedde, Rep. Sp. Nov. Beiheft 85:154 (1936).

Fl. 3-10. Dry rocky places, 1500-3000 m.

Type: Ecuador: Paramo de Saraguro pr. Ona, Bonpland 3310 (holo. B).

Gen. distrib.: Ecuador, Colombia, Peru.

S. andrei was associated with G. cercocarpoides by Epling & Jativa (1966) [see under that species (no. 11) for a further note], but is actually much closer to G. taxifolia. The label attached by Andre cites differences to distinguish the specimen from G. taxifolia and G. glabrata, thought to be the closest relatives, but these differences are trivial. Andre provisionally identified his specimen with G. obovata, but S. andrei may be distinguished from this species by its much larger, elliptic leaves, obtuse at the apex, and by its clearly visible, raised lateral veins.

3.13.73. 25. G. weberbaueri (Mansf.) A. Doroszenko, comb. nov.

Syn: Satureja weberbaueri Mansf. in Notizbl. Bot. Gart. Berlin 9:285 (1925); Satureja loeseneriana Mansf., loc. cit. 287 (1925); Satureja lopezii Epl. in Brittonia 12:145 (1960).

Fl. 5-9. Steep rocky slopes, 2600-3500 m.

Type: Peru: Santiago de Chuco, Hacienda Angasmarca, 3000-3100 m, Weberbauer 7016 (holo. B).

Gen. distrib.: Peru.

The species is closely related to G. taxifolia but differs in its almost glabrous stems, much broader leaves, and bluish-purple corollas. I have only seen one authenticated specimen of G. weberbaueri but additional differences seem to include a more erect, less woody and leafy habit, and up to 8 flowers in each bract rather than always 1-flowered. The unusually small, violet or purplish corolla possibly indicates a different mode of pollination for this species. Nearly all of the rest of Gardoquia have the typical floral features of bird pollination.

3.15.7.4. 26. G. cutervoensis A. Doroszenko, sp. nov.

Tall robust shrub, stems densely white shaggy-pubescent. Leaves obovate, rarely almost elliptic, 5.5-10 x 2.5-4.8 mm, base cuneate, apex obtuse to rounded, margins serrulate, both sides glabrous. Verticillasters approximating; flowers solitary in bract axils; peduncles absent; pedicels 0.5-0.7 mm. Bracteoles leaf-like, 3-7 mm long. Calyx narrowly parallel-sided curved-tubular; tube 3.2-4.5 mm, glabrous or sparsely hairy, throat densely hairy; upper lip 3.2-4.5 mm; lower lip 2.0-2.5 mm; teeth narrowly triangular, upper 2.2-2.7 mm, lower 2.0-2.5 mm. Corolla red; tube c. 16 mm; upper lip c. 5.0 mm; lower lip c. 5.5 mm. Style branches equal, one broad lanceolate, the other narrow subulate. Fl. 4-7. Stony slopes, 2320-2600 m.

Type: Peru: Dept. Cajamarca, Prov. Cutervo, Cutervo-Socota, en ladera escarpada de arbusto, 2320 m, 23 v 1965, Lopez & Sagastegui 5345 (holo. LA in UC!).

Specimens also seen: Peru: Dept. Cajamarca, Prov. Cutervo, cerros de Cutervo, monte bajo, 2500-2600 m, 31 vii 1946, R. Ferreyra 819 (LA in UC).

There is also a fragment of the new species collected by de

Jelski at Cutervo (LA in UC) in an envelope attached to an isotype sheet of Satureja guamaniensis Mansf.

This new species was confused by Epling & Jativa (1964) with G. obovata Ruiz & Pav. (Satureja guamaniensis Mansf.). They cited both the de Jelski and Ferreyra collections under this name, possibly because the de Jelski specimen is only a fragment contained in an envelope mounted on an isotype of S. guamaniensis, and Ferreyra 819 is a depauperate plant that has lost most of its lower leaves. However, comparison of the types of G. cutervoensis, S. guamaniensis and G. obovata clearly shows that there are two distinct species, G. cutervoensis and G. obovata, with S. guamaniensis synonymous with the latter. The novelty is readily distinguished by its shaggy haired stems, more broadly obovate, distally serrulate, distinctly veined, glabrous leaves, shorter calyx tube (3.2-4.5 mm, not 4.6-6.6 mm as in G. obovata), the upper calyx lip as long as the tube (not only 1/3 as long), and very much longer calyx teeth.

3.13.7.5. 27. G. obovata Ruiz & Pav., Syst. Veg. 150 (1798).

Syn: Satureja obovata (Ruiz & Pav.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)!, non Lag. (1816); Satureja guamaniensis Mansf. in Notizbl. Bot. Gart. Berlin 9:286 (1925)! Satureja ruizii Macbride in Field Mus. Publ. Bot. 13:761 (1960).

Fl. 5, 10. Grass steppe amongst evergreen shrubs, roadsides, 2950-3200 m.

Type: Peru: Pueblo Cheuchin, Dombey (holo. P!).

Gen. distrib.: Peru.

3.13.7.6. 28. G. gilliesii Grah. in Edinb. Phil. Jour. 1831:377 (1831).

Syn: G. chilensis Benth. in Hook. & Arn., Bot. Beechey's Voy. 58

(1841); Satureja gilliesii (Grah.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897), non (Benth.) Briq. (1897); Satureja chilensis Briq. in Ann. Conserv. Jard. Bot. Geneve 2:191 (1898).

Ic: Bot. Reg. 21: t.1812 (1835); Rafols in Thrower & Bradbury, Chile-California Mediterranean Scrub Atlas 140, fig. V-1k (1977).

Fl. All year. Coastal mountain slopes, 150-5000 m.

Type: Chile: A specimen cultivated in Edinburgh by Graham from nutlets sent by Gillies (holo. K!).

Gen. distrib.: Central Chile.

This is one of the most common and characteristic plants of the matorral in the mediterranean-like parts of central Chile. It is most similar to G. obovata, but easily distinguished by its proportionately narrower leaves, more attenuate at the base, and consistently minutely hairy, and by very much longer, narrowly triangular, sharply pointed calyx teeth.

3.13.8. (g) Sect. Pallidae A. Doroszenko, sect. nov.

Tall erect or ascending shrubs. Leaves oblong-elliptic to broadly ovate, 6-25 x 3-16 mm, flat or scarcely revolute at margin, entire or rarely minutely toothed or scarcely notched, apex obtuse to rounded or very abruptly and very shortly apiculate, glabrous or minutely hairy on both sides, more densely on lower side, lateral veins faint. Calyx very narrowly parallel-sided, rarely slightly ampliate, curved tubular; upper lobe longer than lower; lower teeth 1/7-2/5 x tube length. (Peru, Bolivia, Haiti).

The short pubescence and very numerous, tiny, punctate glands give the leaves a pallid appearance, hence the name of the section. The leaves are also flat and characteristically oval-shaped, sometimes broadly so.

3.13.8.1. 1. Lower side of leaf white-hoary, with very short dense hairs	33. incana
+ Lower side of leaf glabrous or apparently so	2
2. Leaves broadly ovate-orbicular, 10-20 x 6.3-16.6 mm; lower calyx teeth 2.4-2.7 mm	32. mathewsii
+ Leaves oval-elliptic, 6-13 x 3.3-6.6 mm; lower calyx teeth 0.8-1.8 mm	3
3. Lower calyx teeth 1.6-1.8 mm; bracteoles 1.8-2.3 mm	31. pallida
+ Lower calyx teeth 0.8-1.3 mm; bracteoles 0.5-1.8 mm	4
4. Stems with extremely minute adpressed hairs; leaves broadly oval, very densely glandular-punctate; calyx tube 5.5-6.7 mm [Haiti]	30. domingensis
+ Stems with minute patent hairs; leaves narrowly oval, sparsely minute-glandular-punctate; calyx tube 7.0-8.0 mm [Peru]	29. vargasii

3.13.8.2. 29. G. vargasii (Epl. & Math.) A. Doroszenko, comb. nov.

Syn: Satureja vargasii Epl. & Math. in Brittonia 8:304 (1957)!

Fl. 6. Dry stony places, 2600-3200 m.

Type: Peru: Cuzco, Paucartambo: Challabamba, 2600 m, 16-20 vi 1950, Vargas 9472 (holo. LA in UC!).

Gen. distrib.: Peru.

The closest relative is G. pallida (sp. no. 31). G. vargasii is distinguished by larger, narrowly elliptic, round-tipped leaves and very much shorter, deltoid, rather than narrowly triangular or lanceolate-subulate, calyx teeth.

3.13.8.3 30. G. domingensis (Urb. & Ekman) A. Doroszenko, comb. nov.

Syn: Satureja domingensis Urb. & Ekman in Arkiv Bot. 20A, 15:92 (1926)!

Fl. 1-2. Limestone ledges amongst pines, c. 1800 m.

Type: Haiti: Massif de la Selle, Marne de la Selle, c. 1800 m, 29 i 1925, E. L. Ekman 3137 (holo. S?, iso. K!).

Gen. distrib.: Haiti.

In leaf and calyx shape G. domingensis is clearly similar to G. vargasii and G. pallida, yet is very isolated in distribution from the rest of sect. Pallidae. Comparison with Mexican Gardoquia species does not reveal a closer relative.

3.13.8.4. 31. G. pallida (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja pallida Epl., Ann. Missouri Bot. Gard. 14:65 (1927)!

Type: Bolivia: Turedon, Bolivian plateau, Bang 1127 (holo. NY, iso. E!, K!).

Gen. distrib.: Bolivia.

This species, only known from the type collection, is most closely related to G. vargasii and G. mathewsii.

3.13.8.5. 32. G. mathewsii (Briq.) A. Doroszenko, comb. nov.

Syn: Satureja mathewsii Briq., Ann. Conserv. Jard. Bot. Geneve 2:189 (1898)!

Fl. 10. Rocky places, 1900-3350 m.

Type: Peru: Chachapoyas, Mathews (holo. G, iso. K!).

Gen. distrib.: Peru.

It is unusual to find yellow corollas in Gardoquia, but many other species have yellow blotches on a red background or are more orange in colour.

3.13.8.6. 33. G. incana Ruiz & Pav., Syst. Veg. 148 (1798).

Syn: Satureja incana (Ruiz & Pav.) Spreng., Syst. 2:719 (1825); G. breviflora Benth., Lab. Gen. Sp. 401 (1834); Thymus crenatus Willd. ex Benth. in Linnaea 11:342 (1837)! Satureja breviflora (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897); Satureja pavoniana Briq. in Ann Conserv. Jard. Bot. Geneve 2:189 (1898); Satureja mantaroensis Mansf. in Notizbl. Bot Gart. Berlin 9:287 (1925).

Fl. 2-4, 9, 12. Schistose stony soils, 1800-3600 m.

Type: Peru: Tarma, Dombey (holo. P).

Gen. distrib.: Peru.

The dense, greyish, minute indumentum easily distinguishes this species. It is more variable in leaf shape than the rest of the species in the section. Mansfeld (1925) described Satureja mantaroensis, a plant with small, narrowly elliptic leaves, and placed it near to G. incana and G. discolor. Gourley 134 closely matches this description but apart from the unusual leaf shape I can't find other differences to justify separation from G. incana. Woytkowski notes on his no. 34012 that this is a very common species in dept. Huanuco, Peru.

3.13.9. (h) Sect. Discolores (Epl. & Jat.) A. Doroszenko, comb. nov.

Syn: Satureja L. sect. Discolores Epl. & Jat. in Brittonia 16:406 (1964).

Ascending shrubs. Leaves elliptic, flat or a little revolute at margins, entire or scarcely toothed, apex obtuse or rounded, upper side sparsely or densely minute pubescent, the lower side dense, white tomentose, lateral veins very thin, hardly prominent below. Calyx slightly ampliate, curved tubular; lower teeth as long as tube. (Venezuela, Colombia). Monotypic.

3.13.9.1. 34. G. discolor Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:312 (1817).

Syn: Melissa marifolia Willd. ex Steud. in Nom. Bot. ed. 2, 2:122 (1841), nomen; G. foliolosa Benth. in DC., Prodr. 12:238 (1848)! Satureja discolor (Kunth) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897); Satureja foliolosa (Benth.) Briq., loc. cit. (1897)!

Ic: Steyermark & Huber, Flora del Avila 506, f.159 B. (1978).

Fl. 1-6, 12. Rocky slopes, 1675-3980 m.

Type: Venezuela: Silla de Caracas, Bonpland (holo. P).

Gen. distrib.: N Venezuela, N Colombia.

Leaf size in the species is very variable. The type of G. foliolosa has very numerous overlapping leaves only 4-5 mm long, whereas Linden 120 has leaves 10-20 mm long. At first sight these specimens appear to be of different species. Linden 120 has proportionately narrower elliptic leaves with a uniformly minute tomentose pubescence. Yet dissection of the flowers of these two specimens reveals practically identical calyx and corolla dimensions and structure. In indumentum G. discolor is rather similar to G. incana.

3.13.10. (i) Sect. Micromerioides A. Doroszenko, sect. nov.

Low ascending shrub. Leaves oblong-elliptic, glabrous, flat or slightly channelled, entire, apex acute, lateral veins invisible, densely punctate-glandular on both sides. Calyx slightly ampliate, straight tubular; teeth 1/2-2/3 x tube length. Monotypic. (Mexico)

3.13.10.1. 35. G. micromerioides Hemsl., Biol. Centr. Amer. 2:550 (1882).

Syn: Satureja micromerioides (Hemsl.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)! Hedeoma subequale Epl. in Bull.

Torrey Bot. Club 74:513 (1947).

Ic: Hemsley, Biol. Centr. Amer. 5: t.69A (1882).

Syntypes: Mexico: San Luis Potosi, 6000-8000 ft., ann. 1878, C. C. Perry & E. Palmer 244 (K!); San Luis Potosi, Schaffner 70 (E!, K!).

Gen. distrib.: Mexico (San Luis Potosi).

There would be little problem in arguing in favour of sectional rank for this species if one accepted it belonged to Gardoquia, but first appearances would make many doubt whether it belonged to Gardoquia at all. The low, slender habit and oblong-elliptic, channelled leaves, solitary flowers on long peduncles and relatively small corollas are the most remarkable features. This species is apparently the only Gardoquia to have isolateral leaf palisade parenchyma, also indicative of its isolation in the genus. Vegetative features aside, which in any case varies greatly in the genus, the floral structure is quite similar to the majority of Gardoquia. The calyx is narrowly tubular with narrowly triangular, equal teeth. The combination of such features is unique but the shape of the tube and teeth are not in themselves unusual. The corolla, though smaller than the average Gardoquia, is narrowly tubular at first, gradually widening to the throat, and similar to many other species.

3.13.11. Nom. exclud.

G. affinis Benth. in Linnaea 11:342 (1837).

This is cited in Index Kewensis, but no such name exists at the reference given.

G. betonicoides Lindl. in Bot. Reg. Misc. 24:86 (1838).

Apparently a synonym of Cedronella mexicana Benth. but I have not seen the type.

G. capitata Spreng. in Syst. Veg. ed. 16, 4(2):225 (1827).

Possibly an Agastache sp. or Cunila sp.

G. obovata Spreng. ex Benth. in DC., Prodr. 12:239 (1848).

This is the solanaceous species Brunfelsia ramosissima (Pohl) Benth.

G. origanoides Reichenb. ex Spreng. in Syst. Veg. ed.16, 4(2):225 (1827) = Lippia micromera Schau

G. racemosa Spreng. ex J. A. Schmidt in Mart., Fl. Bras. 8:170 (1858), nomen ex herb. Spreng. = Hedeoma multiflora Benth.

G. salviaefolia Colla, Herb. Pedem. 4:469 (1835).

Epling (1937) has this as a synonym of Lepechinia salviae (Lindl.) Epl.

G. spicata Spreng. in Syst. Veg. ed. 16, 4(2):225 (1827).

This is based on Rio Grande, Sello, which I have not seen. Sello's specimens were at B, and Sprengel's Labiatae are at Heidelberg.

3.14. Obtegomeria A. Doroszenko, gen. nov.

Syn: Satureja L. sect. Obtectae Epl. & Jat. in Brittonia 16:407 (1964).

Low shrub, stems many, erect. Leaves linear-oblong, replicate, sessile, entire; a single lateral vein per side parallel to mid-vein; palisade mesophyll dorsiventral. Verticillasters conferted. Flowers 1-2 in leaf axils, on short sessile pedicels. Floral leaves reaching to middle of calyx; bracteoles similar to leaves. Calyx curved, ampliate, 11-veined, densely hairy in throat; bilabiate, teeth straight, almost as long as tube, not ciliate, upper 1/3-1/2 x lower in length. Corolla bluish or pinkish, rarely white; tube short, straight, not resupinate, not annulate within, sparsely hairy on outside lower half; lips 1/2 to as long as tube; upper lip emarginate; lower lip 2 x upper, central lobe entire. Stamens 4, all fertile, posterior 2/5 x anterior in length, included or just exserted from tube; anthers widely divergent. Style branches unequal. Nutlets unknown. Monotypic.

3.14.1. O. caerulescens (Benth.) A. Doroszenko, comb. nov.

Syn: Hedeoma caerulescens Benth. in DC., Prodr. 12:245 (1848)! Calamintha caerulescens (Benth.) Wedd., Chloris Andina 2:149, t. 63 (1860)! Clinopodium caerulescens (Benth.) Kuntze, Rev. Gen. 2:515 (1891)! Satureja lindeniana Briq. in Ann. Conserv. Jard. Bot. Geneve 2:191 (1898); Satureja caerulescens (Benth.) Epl. in Fedde, Repert. Sp. Nov. Beih. 85:156 (1936)!

Fl. 2-3, 6. c. 3300 m.

Type: Colombia: Magdalena, Sierra de Santa Martha, vi 1844, Purdie (holo. K!, iso. E!).

Gen. distrib.: Colombia (Magdalena).

Obtegomeria consists of a single species which had hitherto been either placed in Hedeoma (Bentham, 1848) (though Bentham was doubtful about this and noted a similarity to Gardoquia), or within Satureja sect. Gardoquia (Epling, 1937), or as a distinct section of Satureja (sect. Obtectae) (Epling & Jativa, 1964). The concensus of opinion amongst these authors is, therefore, that the species falls within or near to Gardoquia. However, there are many differences in calyx, corolla and leaves which indicate a more isolated position for this species.

The curved, ampliate, 11-veined calyx tube, deltoid upper teeth, and narrowly triangular lower teeth as long as the calyx tube contrasts with Gardoquia which usually has a narrowly tubular 13-veined calyx, with teeth less than half the tube length. The aberrant G. discolor, which also has calyx teeth as long as the calyx tube, does not have the broadly ampliate calyx of Obtegomeria.

The bluish or purplish corolla with short straight tube and lips as long as the tube is quite unlike those of Gardoquia. Gardoquia typically has much larger, red or red with yellow corollas with narrower, curving tubes, and lips never longer than 1/3 of the tube in length.

Even with the extreme variability of the leaves in Gardoquia, the leaves are never linear-oblong and replicate as in Obtegomeria. These very numerous, small (4.0-6.0 x 0.8-1.0 mm) leaves give O. caerulescens a quite unmistakable facies.

3.15. Montereya A. Doroszenko, gen. nov.

Syn: Calamintha sect. Calomelissa (Benth.) Benth. in DC., Prodr. 12:229 (1848), p.p.; Satureja sect. Calomelissa subsect. Mimuloideae Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897); Satureja sect. Occidentalis Epl. & Jat. in Brittonia 18:244 (1966).

Tall, erect, perennial herbs. Leaves broadly ovate, flat, long petiolate; dentate or serrate; lateral veins camptodromous, narrow, not prominent, marginal veins absent. Verticillasters distant, many-flowered, very long pedunculate and pedicellate. Bracts shorter than or equalling flowers. Bracteoles similar to leaves in shape. Calyx large, straight, somewhat ampliate, 13-veined, sparsely hairy in throat; slightly bilabiate, teeth divergent, spinose, ciliate, c. 1/3 x tube length. Corolla large, red; tube broad, straight-flaring, not resupinate, nor annulate inside, hairy on inside lower half; lips large, 1/3-1/2 x tube length, upper emarginate, lower 3-lobed. Stamens 4, all fertile, inserted 1/3-1/2 way up tube, convergent, posterior 4/5 x anterior in length, all just exserted from tube; anthers divergent. Stylar branches equal, both narrowly subulate. Nutlets not seen. Monotypic.

3.15.1. M. mimuloides (Benth.) A. Doroszenko, comb. nov.

Syn: Calamintha mimuloides Benth., Pl. Hartweg. 331 (1849)! Clinopodium mimuloides (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Satureja mimuloides (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897)!

Fl. 6-7. Shaded and damp places, c. 1220 m.

Type: California: In shaded places near Carmel River, ann. 1848, Hartweg 1917 (122) (holo. K!)

Gen. distrib.: Coastal mountains between Monterey and San Gabriel, Central California.

Most recent Floras and revisions place this species under Satureja (Jepson, 1943; Abrams, 1951; Epling & Jativa, 1966) following the lead of Briquet (1897). However, the species was first described under Calamintha (Bentham, 1849) since the large, broadly tubular calyx tube with upcurving upper teeth and straight lower teeth are reminiscent of this genus. Oyster (1885) agreed with Bentham in the species' placement and Jepson (1925), in his earlier revision of the Californian flora, included the species under Clinopodium (closely related to Calamintha).

Briquet (1897) placed the species in the wholly American section Calomelissa, which in the present revision is synonymous with Diodeilis. Therefore, S. mimuloides (Benth.) Briq. was not related to the entirely Old World genera Satureja s.s. (sect. Sabbatia Briq.), Calamintha (sect. Calamintha Briq.) or Clinopodium (sect. Clinopodium Briq.).

In the American genera there is nothing quite like this Montereyan plant. The large orange-red corollas on long peduncles and pedicels, unusually large, broadly tubular calyx whose teeth are broadly triangular to lanceolate and ending in sharp setae, and the large, broadly ovate, dentate, long-petiolate leaves clearly separates it from both Calamintha and Diodeilis [sect. Calomelissa Benth.]. Epling & Jativa (1966) described a new section for it under Satureja s.l. and concluded that the resemblance to Calamintha was entirely superficial noting that both groups occupy similar "Mediterranean" habitats. I agree that the similarity to Calamintha is superficial, but believe that generic rather than sectional rank is justified for the Californian plant.

The coastal mountains between Monterey and just north of Los Angeles have a large number of endemics. The area immediately around Monterey has 13 endemic species (Raven & Axelrod, 1978) while Howitt & Howell (1973) report 20 species and 14 other subspecies and varieties endemic to Monterey County as a whole. The San Lucia Mountains just south of Monterey add another 6 endemic species, and the San Gabriel mountains north of Los Angeles have 30 endemic species (Raven & Axelrod, 1978). This whole region is an active centre of evolution but also a refuge for a large number of relict species. Its great diversity of habitat, climate, and soil types are some of the reasons for this. Of the 50 genera endemic to the Californian Floristic Province 34 are monotypic. Many of them have no close relatives, indicative of their relictual nature. Montereya is now added to this list.

3.16. Piloblephis Rafin., New Fl. N. Am. 3:52 (1836).

Syn: Satureja L. sect. Pycnothymus Benth., Lab. Gen. Sp. 354

(1834); Pycnothymus Small, Fl. S.E. U.S. 1042 (1903).

Low erect or ascending shrub. Leaves linear-lanceolate, tightly revolute, sessile, entire; veins camptodromous, scarcely visible, marginal veins absent; palisade mesophyll dorsiventral. Inflorescence condensed into a dense ovoid head, the calyces completely obscured by numerous bracts similar to leaves. Calyx tube straight, slightly ampliate, 15-veined, throat glabrous; teeth all similar, 1 1/2 x tube length. Corolla purple, small; tube straight, somewhat ampliate, not resupinate nor annulate inside, glabrous on inside lower half; lips c. 1/3 x tube length, upper entire, lower 3-lobed. Stamens 4, all fertile, inserted near top of tube, exserted beyond upper lip, posterior 2/3 x anterior in length; anthers parallel. Stylar branches unequal, both very short, broad lanceolate. Nutlets ovoid, glabrous. Monotypic.

3.16.1. P. rigida (Bartr. ex Benth.) Rafin., New Fl. N. Am. 3:52 (1836).

Syn: Satureja rigida Bartr. ex Benth., Lab. Gen. Sp. 354 (1834); Piloblephis ericoides Rafin., New Fl. N. Am. 3:53 (1836); Clinopodium rigidum (Bartr. ex Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Pycnothymus rigidus (Bartr. ex Benth.) Small, Fl. S. E. U. S. 1042 (1903).

Ic: Pellett, Amer. Honey Pl. 282 (1920); Long & Lakela, Flora of Tropical Florida 751 (1971); both as Satureja rigida.

Fl. All year. Dry pine barrens, sandy field, sand hills.

Type: In Florida orientali, W. Bartram (holo. BM).

Gen. distrib.: Florida, S. Georgia.

Piloblephis is very isolated from the rest of Satureja s.l. on account of the numerous linear-lanceolate, tightly revolute leaves, truncate at the base and obtuse at the apex, the inflorescence condensed into a dense ovoid head, the bracts completely obscuring the very small, 15-nerved, actinomorphic calyces with teeth longer than the tube, small corollas with stamens inserted near the top of the tube, all exserted beyond the upper corolla lip, with parallel anthers, and very short, broadly lanceolate stylar branches.

The species was first described by Bentham (1834) as a monotypic section of Satureja, but with a query as to its placement in that genus. The species was separated into its own genus, Piloblephis, shortly afterward by Rafinesque (1836). Ever since it has been separated into either its own section of Satureja (Bentham, 1848; A. Gray, 1886; Briquet, 1896; Epling & Jativa, 1966) or more rarely as a separate genus (Small, 1903).

Epling & Jativa (1966) mention that Piloblephis has a superficial resemblance to Satureja thymbra L. (Satureja L. sect. Tragoriganum Benth.). But even so, the structure of the inflorescence, calyx, and leaves are so different in these two species to make a close link quite impossible.

Florida was isolated from continental America by a strait of sea from at least the Oligocene to Pliocene when it was then reconnected. However, the sea level has fluctuated widely since then due to numerous glacial periods and shoreline features, dunes, and other marine deposits, are now present at various elevations. It is on such deposits that Piloblephis is principally found.

3.17. Hesperothymus (Benth.) A. Doroszenko, gen. nov.

Syn: Micromeria sect. Hesperothymus Benth., Lab. Gen. Sp. 371 (1834); Satureja sect. Hesperothymus (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897).

Prostrate sprawling or repent herbs. Leaves broadly ovate or orbicular, flat, long petiolate; serrate or crenate to crenulate;

lateral veins camptodromous, narrow, faint to almost invisible, marginal veins absent; palisade mesophyll dorsiventral. Flowers solitary in leaf axils on very long peduncles and pedicels. Bracts shorter than or exceeding flowers. Bracteoles linear or absent. Calyx straight or slightly curved tubular, 13-veined, glabrous or hairy in throat; bilabiate, teeth straight, ciliate or not, 1/3-1/2 x tube length, upper much shorter than lower. Corolla white or violet; tube short, straight, not resupinate nor annulate inside, glabrous or sparsely hairy on inside lower half; lips 1/4-3/5 x tube length; upper lip emarginate; lower lip longer than upper, central lobe entire or bifid. Stamens 4, all fertile, convergent, posterior 1/2-2/3 x anterior in length, inserted 2/3 way up tube, all just exserted from tube; anthers divergent. Style branches unequal, sometimes very much so, both narrowly subulate. Nutlets sub-orbicular, glabrous or minutely eglandular hairy.

Type species: H. brownei.

The two species included here were either placed under Micromeria (Bentham, 1834; Hooker, 1838; Grisebach, 1861; Oyster, 1885; A. Gray, 1886; Macoun, 1889; Small, 1903; Jepson, 1925; Moscoso, 1943) or under Satureja (Briquet, 1896; Epling, 1927; Jepson, 1943; Pittier, et al., 1947; Abrams, 1951; Leon & Alain, 1957; Hitchcock, et al., 1959; Epling & Jativa 1964, 1966; Adams, 1972; Shetler & Skog, 1978; Scoggan, 1979). It is clear from these cited references that the more recent opinion tends to place these species in Satureja following the lead of Briquet (1896). However, Briquet recognised the distinctness of S. brownei and S. douglasii, placing them in their own section Hesperothymus, and noted the 2-flowered verticillasters, with lengthy peduncles, campanulate calyx, equally or nearly equally 5-toothed, 13-nerved calyx tube, and small corollas not greatly exserted from the calyx.

In facies Hesperothymus is similar to Micromeria. However, the entirely New World Hesperothymus is distinguished from Micromeria, an Old World genus, by its always solitary, long pedicellate and pedunculate flowers, the calyx with broadly lanceolate-subulate or broadly lanceolate teeth, bracteoles absent or small and filiform, the leaves petiolate, broadly ovate or orbicular, crenate to crenulate.

The problem still remains, however, as to the rank of Hesperothymus, whether sectional or generic rank is preferable. Since all the American sections of Satureja s.l. in the treatments of Epling & Jativa (1964, 1966) (except the monotypic sections Sphenostachys, Discolores and Anomales) have been raised to generic rank in the present revision, for the sake of consistency I have done the same with Hesperothymus. Admittedly it is weakly defined at the generic level. However, there is no other American genus into which Hesperothymus could be placed with confidence. The closest American relative is probably Diodeilis, but the differences in calyx structure and verticillaster arrangement are too great for Hesperothymus to be placed at sectional rank within Diodeilis.

3.17.1. Slender repent herb; leaves sub-orbicular;
bracteoles absent; calyx throat hairy 1. brownei
More robust decumbent herb; leaves ovate;
bracteoles present; calyx throat glabrous 2. douglasii

3.17.2. 1. H. brownei (Sw.) A. Doroszenko, comb. nov.

Syn: Thymus brownei Sw., Prodr. Veg. Ind. Occ. 89 (1788); T. xalapensis Kunth, Nov. Gen. 2:316 (1818); Micromeria stolonifera Benth., Lab. Gen. Sp. 371 (1834)! M. brownei (Sw.) Benth., loc.

cit. 372 (1834); M. xalapensis (Kunth) Benth., loc. cit. (1834); Apozia chamaedryoides Willd. ex Benth. in Linnaea 11:328 (1837), nomen! T. gracilis Willd. ex Benth., loc. cit. 341 (1837), nomen; M. brownei (Sw.) Benth. var. pilosiuscula A. Gray, Syn. Fl. N. Am. 2(1):359 (1878); Clinopodium brownei (Sw.) O. Kuntze, Rev. Gen. Pl. 2:514 (1891); C. stoloniferum (Benth.) O. Kuntze, loc. cit. 516 (1891)! C. xalapense (Kunth) O. Kuntze, loc. cit. (1891); Satureja brownei (Sw.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897); S. stolonifera (Benth.) Briq., loc. cit. (1897)! S. xalapensis (Kunth) Briq., loc. cit. (1897); M. pilosiuscula (A. Gray) Small, Fl. S.E. U.S. 1042 (1903); Hedeoma gracillima Jones in Contr. West. Bot. 15:150 (1929); M. bahamensis Shinners in Sida 1(2):96 (1962); M. domingensis Shinners, loc. cit. (1962); Stachys uniflora, nomen in schaed. (LA in UC)!

Ic: Small, Man. S.E. Fl. 1168 (1933), as Micromeria pilosuiscula.

Fl. All year. Meadows, Quercus scrub, river banks, ditches, wet places, 230-2700 m.

Type: Jamaica, P. Browne 259 (holo. BM)

Gen. distrib.: SE USA, S California, Mexico, Guatemala, Caribbean Islands, Colombia, Venezuela, Ecuador, N Argentina, Paraguay.

This is a very widespread and variable species. Most of the synonyms are based on variants of pubescence and habit. A summary of the variation is given by Epling & Jativa (1966).

3.17.3 2. H. douglasii (Benth.) A. Doroszenko, comb. nov.

Syn: Thymus douglasii Benth. in Linnaea 6:80 (1831)! T. chamissonis Benth. in Linnaea 6:80 (1831)! Micromeria douglasii (Benth.) Benth., Lab. Gen. Sp. 372 (1834)! M. barbata Mey. in Fisch. & Mey., Ind. Sem. Hort. Petrop. 8:67 (1842), non Boiss. & Kotschy (1859); Clinopodium douglasii (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515

(1891)! M. chamissonis (Benth.) Greene, Man. Bot. San Franc. Bay 289 (1894)! Satureja douglasii (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)!

Ic: Armstrong, Field Book West. Wild Fl. 437 (1915); Jepson, Manual Fl. Pl. Calif. 875 (1925), both as Micromeria chamissonis; Rickett, Wild Fl. U.S. 4:563 (1970), as Satureja douglasii.

Fl. 5-8. Shady forests in damp situations, 100-250 m.

Type: Canada: Shady pine woods near Fort Vancouver, ann. 1826, Douglas (holo. K!)

Gen. distrib.: SW Canada, W USA.

3.18. Xenopoma Willd. in Ges. Naturf. Fr. Berl. Mag. 5:399 (1811).

Syn: Nostelis Rafin., Sylva Tellur. 76 (1838); Micromeria sect. Xenopoma (Willd.) Benth. in DC., Prodr. 12:222 (1848); Satureja L. sect. Xenopoma (Willd.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897).

Erect perennial herbs, sometimes shrubby. Leaves small, linear to orbicular, flat, sometimes revolute, entire or shallowly toothed, shortly petiolate; veins camptodromous, usually very narrow and faint, rarely more prominent, marginal veins absent; palisade mesophyll dorsiventral. Inflorescence lax or very dense, 1- to many-flowered, sessile or on long peduncles and/or pedicels. Bracts exceeding or shorter than flowers. Bracteoles linear or elliptic, smaller than or as long as pedicels and peduncles. Calyx straight, ampliate, tubular to urceolate, 13-veined, throat glabrous or hairy; actinomorphic or sub-bilabiate, teeth straight, nearly always not ciliate, 1/4-3/4 x tube length; upper teeth (1/2-)3/4 x to as long as lower teeth. Corolla white or shades of purple, rarely yellow; tube 1.3-8.0 mm, very rarely longer (to 18 mm), ampliate, not resupinate nor annulate inside, glabrous or sometimes hairy on inside lower half; lips (1/9–)1/5–1/3 x tube in length; upper lip mostly emarginate, sometimes retuse or entire; lower lip 3-lobed, central lobe entire or bifid. Stamens 4, all fertile, inserted near mouth of corolla, all included or just exserted from tube; anthers parallel or divergent. Style branches slightly unequal, rarely equal, both narrowly subulate, rarely one broader than the other. Nutlets oblong or ovoid, glabrous or strongly hairy.

Type species: X. obovatum [=viminea].

20 species in western N & S America, and the Caribbean.

Six sections are described here which very closely match the species-groups (section in the case of Sphenostachys) recognised by Epling & Jativa (1964, 1966a, 1966b) in Satureja, the generic name which has generally been applied here. (This is in complete contrast to Gardoquia where there is little agreement in subgeneric groups). It seemed sensible, therefore, to use Epling & Jativa's informal species-groups' names for the new sections described here. Only sect. Prostratae looks a bit eccentric since X. brevicalyx can be up to 1 m tall and X. vana up to 2 m tall. The sections of Xenopoma are just as distinct as those in Gardoquia, and to be consistent in treatment of the American genera, sections are preferable to species groups.

Although one can quite easily recognise a number of sections, it is difficult to find features that are constant throughout the genus; yet Xenopoma has a distinctive facies which makes it easily separable from the other genera of Satureja s.l. This, though, is what one might expect when one constructs groups based on overall similarity, where no single feature is deemed necessary when forming groups. Xenopoma is usually herbaceous, with small, shallowly toothed leaves, the calyx small, straight, ampliate, tubular to urceolate, actinomorphic, and the corollas white or purple, little exserted from the calyx.

In calyx structure some Xenopoma species (e.g. sects. Xenopoma and Sphenostachys) are similar to Micromeria. However, the majority of Xenopoma have more ampliate tubular calyces, tending to become urceolate (e.g. sect. Xenothymus). Xenopoma has a slender, herbaceous habit, with narrowly ovate elliptic or oblanceolate, nearly always toothed, flat or only slightly revolute leaves. Micromeria sect. Micromeria tends to be shrubby, with small ovate or elliptic, entire leaves often clearly revolute and with distinct marginal veins. Micromeria sect. Pseudomelissa is mostly herbaceous with broadly ovate or orbicular leaves. The other three sections of Micromeria that I recognise are specialised, local endemic groups of the Canaries, Madagascar, and E Turkey. Micromeria is an entirely Old World genus, concentrated around the Mediterranean, while Xenopoma is of western N and S America and the Caribbean Islands. Associations proposed between Xenopoma and Micromeria, such as suggested by Briquet for his Satureja sect. Piperella (Briquet, 1896) [now placed in Micromeria sect. Micromeria], are ill founded and ignore the marked differences between these two genera. The closest relative of Xenopoma is Gardoquia; the descriptions above of the calyx and corolla of Xenopoma are sufficient to distinguish them.

Babu (1969) proposed conserving the name Micromeria Benth. (1829) against Xenopoma Willd. (1811). This is only necessary if one wishes to unite the two genera. The present treatment, of course, does not. There is an omission in Babu's proposal. He says that no author could be traced who had taken up the name Xenopoma while in fact Grisebach (1874) has done so.

3.18.1. 1. Inflorescence a dense spike, not interrupted or only shortly so at base; verticillasters sessile, multi-flowered; calyx lips straight 2

\+ Inflorescence not spike-like, interrupted; verticillasters shortly pedunculate, multi-flowered or solitary; calyx teeth straight or not 3

2. Leaves broadly ovate, 13-34 mm, petioles 4-6 mm; veins on lower side of leaves prominent, white (f) sect. Sphenostachys

\+ Leaves linear or orbicular-ovate, 3-20 mm, petioles up to 1 mm; veins on lower side of leaf invisible or prominent but not white (c) sect. Spicatae

3. Leaf hairs robust, pustulate-dendritic or stellate (a) sect. Xenopoma

\+ Leaf hairs, if any, simple, fine 4

4. Leaves narrowly ovate or elliptic to linear-oblong, 3-7 x as long as broad, entire or minutely serrulate with sharply pointed teeth (d) sect. Xenothymus

\+ Leaves broadly ovate to orbicular, 1-2 x as long as broad, entire or crenulate to serrulate with rather rounded teeth 5

5. Calyx broadly tubular, infundibuliform, teeth broadly lanceolate; corolla 7-15 mm [California] (e) sect. Pauciflorae

\+ Calyx narrowly tubular or somewhat ampliate but not infundibuliform; teeth narrowly triangular to lanceolate; corolla 3.5-9.5 mm [S. America] (b) sect. Prostratae

3.18.2. (a) Sect. Xenopoma

Erect or ascending suffruticose herbs or shrubs. Leaves ovate, elliptic to oblanceolate, shortly petiolate or sessile, revolute at margin, entire, serrulate or crenate, all parts of leaf densely verrucose-dendritic or with robust dendritic or stellate hairs, veins sunken above, prominent below if not obscured by hairs, with numerous minor veins between the laterals. Calyx lower teeth 1/4-3/4 x tube length. Corolla white, rarely yellow; anthers parallel. (Caribbean Islands).

3.18.2.1. 1. Corolla c. 20 mm, yellow; leaves orbicular to broadly ovate, 5-10 mm ..... 3. bucheri

\+ Corolla 3-8 mm, white; leaves broadly or narrowly obovate, elliptic or lanceolate, or triangular-ovate, 2.5-20 mm 2

2. Flowers in multi-branched pedunculate cymules (6-17 flowers per cymule); leaves crenate ..... 5. schusteri

\+ Flowers mostly solitary (up to 4 per cyme); leaves entire or scarcely toothed 3

3. Leaves broadly triangular ovate, distinctly revolute ..... 4. alpestris

\+ Leaves oval to obovate, only slightly revolute 4

4. Leaves 5-20 mm long; upper calyx teeth distinctly shorter than lower ..... 1. viminea

\+ Leaves 2.5-5.0 mm long; all calyx teeth + the same length ..... 2. ekmaniana

3.18.2.2. 1. X. viminea (L.) A. Doroszenko, comb. nov.

Syn: Satureja viminea L., Syst. Veg. ed.10, 1096 (1759)! Xenopoma obovatum Willd. in Ges. Naturf. Fr. Berl. Mag. 5:399 (1811); Zygis aromatica Desv. in Ham., Prod. Pl. Ind. Occ. 46 (1825); Micromeria obovata (Willd.) Benth., Lab. Gen. Sp. 381 (1834); Nostelis viminea (L.) Rafin., Sylva Tellur. 76 (1838)! Nostelis arborea Rafin., loc. cit. (1838); Nostelis minor Rafin., loc. cit. (1838); Satureja sideritis Lunan ex Benth. in DC., Prodr. 12:212 (1848), nomen; Clinopodium vimineum (L.) O. Kuntze, Rev. Gen. Pl. 2:516 (1891)! Micromeria viminea (L.) Druce in Rep. Bot. Exch. Cl. Brit. Isles 3:421 (1914)!

Ic: Colla, Hort. Ripul. t.25 (1824), as X. obovatum.

Fl. 1-4, 7-11. Amongst pines, limestone or serpentine, 305-1530 m.

Type: Jamaica, P. Browne 258 (Hb. Linn. 723/12, microfiche!)

Gen. distrib.: Caribbean Islands.

The publication of Satureja viminea in Syst. Veg. ed.10 (May-June 1759) is no more than a short diagnosis without designation of a type specimen. Baum (1968) discusses the typification of a large number of species published in this work including S. viminea. He notes that Linnaeus published a short dissertation later in the same year entitled Plantarum Jamaicensium Pugillus (Nov. 1759) (there is a copy at E) which contains a full description and cites a type specimen. All the Browne specimens cited in this latter work were purchased by Linnaeus in 1758.

In most Floras of the W Indies this is called Satureja viminea.

3.18.2.3. 2. X. ekmaniana (Epl. & Alain) A. Doroszenko, comb. nov.

Syn: Satureja ekmaniana Epl. & Alain in Brittonia 20:156 (1968)!

Fl. 8. Mountain slopes, 1500-2350 m.

Type: Haiti: Massif de la Selle, Marigot, top of Morne Cabaio, 2350 m, 24 viii 1924, Ekman H1608 (holo. US!).

Gen. distrib.: Haiti.

This is most closely related to X. viminea and may be distinguished by its smaller, more broadly obovate to orbicular leaves, completely actinomorphic calyces more densely hairy in the throat, and smaller corolla. Epling & Alain (1968) say that the staminal filaments are subequal. Dissection of a flower of the holotype revealed posterior stamens c. 1.2 mm long and anterior stamens c. 2.0 mm long.

3.18.2.4. 3. X. bucheri (P. Wilson) A. Doroszenko, comb. nov.

Syn: Micromeria bucheri P. Wilson in Journ. N.Y. Bot. Gard. 23:93 (1922)! Satureja bucheri (P. Wilson) Urb. in Fedde, Repert. Sp. Nov. 20:349 (1924)! Satureja cubensis Urb., Symb. Antill. 9:249 (1924)! Satureja suborbicularis Alain in Contrib. Ocas. Mus. Hist. Nat. Col. "de la Salle", Habana 15:13 (1956).

Fl. 4-7. Stony places, 1800-1850 m.

Type: Cuba: Prov. Oriente: in Sierra Maestro ad latus septentr. Pico Turquino in saxis arduis, 1850 m, 24 vii 1922, Ekman 14586 (iso. LA in UC!).

Gen. distrib.: Cuba.

Epling & Jativa (1966) placed too much emphasis on the size and colour of the corolla and treated this species under Satureja L. sect. Gardoquia (Ruiz & Pav.) Briq. Apart from the corolla the similarity is clearly with X. viminea. The very unusual pubescence, shared by all of sect. Xenopoma, and the geographical distribution also strongly argue in favour of Xenopoma rather than Gardoquia.

3.18.2.5. 4. X. alpestris (Urb.) A. Doroszenko, comb. nov.

Syn: Micromeria alpestris Urb. in Fedde, Repert. Sp. Nov. 16:143 (1919); Satureja alpestris (Urb.) Epl. & Jat. in Brittonia 18:248 (1966).

Fl. 9. Amongst pines, 2270-2500 m.

Type: Santo Domingo: prope Constanza in Valle nuevo, 2270 m, Eggers 2223.

Gen. distrib.: Santo Domingo.

In leaf shape X. alpestris is quite different from the preceding 3 species which tend to have oblanceolate or elliptic leaves with rounded apices. However, in floral structure and indumentum it clearly belongs to sect. Xenopoma.

Jimenez in Arkiv Bot., Forli 42:87 (1966) also made the combination S. alpestris and he may have published this earlier than Epling & Jativa.

3.18.2.6. 5. X. schusteri (Urb.) A. Doroszenko comb. nov.

Syn: Hyptis schusteri Urb. in Fedde, Repert. Sp. Nov. 16:145 (1919); Satureja schusteri (Urb.) Epl. & Jat. in Brittonia 18:248 (1966).

Fl. 8-10. Amongst pines, 1500-2350 m.

Type: Haiti: Morne de la Selle ad Terlonge in fruticeto denso, 1600 m, fl. Aug., Buch 1356.

Gen. distrib.: Santo Domingo, Haiti.

This species is by far the tallest in Satureja s.l., growing to an incredible 500 cm. It was first described in Hyptis but the following table shows how it may be separated from that genus.

	Hyptis	X. schusteri
Flowers	In heads or in congested verticillasters	Multi-branched, long-pedunculate cymules
Calyx tube	Usually 10-veined	13-veined

Calyx throat	Naked or pilose-annulate about middle (sect. Apodotum)	Sparsely hairy at top
Calyx teeth	Subequal, rarely posterior larger	Anterior slightly longer
Nutlets	Rounded or truncate at apex	Apiculate at apex

3.18.3. (b) Sect. Prostratae A. Doroszenko, sect. nov.

Syn. Satureja L. sect. Xenopoma (Prostratae) Epling & Jativa in Brittonia 16:410 (1964).

Mostly prostrate or low shrubs but sometimes erect to 2 m tall. Leaves petiolate, sometimes + sessile, broadly ovate to orbicular, rounded to cuneate at the base, apex obtuse to rounded, entire, crenulate, or serrulate margins, minutely hairy to pubescent on both sides (rarely glabrous above), lateral veins not visible or very narrow and scarcely prominent, without veins between. Calyx tube actinomorphic or sub-bilabiate, teeth 1/4-1/2 x tube length. Corolla white or purple, anthers divergent, sometimes parallel. (Venezuela, Colombia, Ecuador, Peru, Argentina, Chile).

3.18.3.1. 1. Leaves (5.0-)8.0-15.0 mm; cymes 1-6 flowered ... 2

\+ Leaves 2.0-6.0(-8.0) mm; flowers always solitary in leaf axils ... 3

2. Prostrate herb, 8-20 cm tall; leaves with long hairs; lower calyx teeth 1.4-1.6 mm, narrowly triangular, ciliate; corolla 6-7 mm ... 8. grisea

\+ Erect shrub, 100-200 cm tall; leaves with minute hairs only; lower calyx teeth c. 0.9 mm, lanceolate-subulate, not ciliate; corolla 7-9.5 mm ... 11. vana

3. Erect shrubs, 50-100 cm; calyx teeth narrowly linear, filiform, the lower 1.2-1.3 mm 10. brevicalyx

\+ Prostrate herbs or shrubs, 10-30 cm tall; calyx teeth broadly triangular to lanceolate, the lower 0.6-1.1 mm 4

4. Stem densely recurved-hairy; calyx 4.0-5.0 mm (Patagonia) 9. darwinii

\+ Stem densely and very shortly patent-pubescent; calyx 2.0-3.5 mm (NW South America) 5

5. A delicate herb, thin-leaved; leaves mostly 4-8 mm, orbicular, hairs on upper side extremely minute, hardly visible (x 10 lens); calyx 2.0-2.6 mm 7. tenella

\+ A much-branched, + robust shrub, with leaves not especially thin; leaves 2-4 mm, ovate to orbicular, obviously hairy under a x10 lens; calyx 2.8-3.5 mm 6. nubigena

3.18.3.2. 6. X. nubigena (Kunth) A. Doroszenko, comb. nov.

Syn: Thymus nubigenus Kunth in Humboldt & Bonpland, Nov. Gen. Sp. Pl. 2:316 (1817); Micromeria nubigena (Kunth) Benth., Lab. Gen. Sp. 381 (1834); Apozia serpyllacea Willd. ex Benth. in Linnaea 11:328 (1837), ex nomen in schaed.! Thymus humifusus Willd. ex Benth. in Linnaea 11:342 (1837), nomen; Micromeria nubigena (Kunth) Benth. var. glabrescens Benth. in DC., Prodr. 12:222 (1848)! Clinopodium nubigenum (Kunth) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja nubigena (Kunth) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897).

Fl. 1, 3-8, 11. Dry open slopes, overhanging rocks, 1060-4580 m.

Type: Colombia: Purace volcano, Bonpland 2023 (B, P).

Gen. distrib.: Venezuela, Colombia, Ecuador, Peru.

A very common and widespread species.

3.18.3.3. 7. X. tenella (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja tenella Epl. in Fedde, Repert. Sp. Nov. Beih. 85:161 (1936)!

Fl. 9-11. Plains and rocky slopes, 2890-3600 m.

Type: Ecuador: Plains of Quito, Jameson 140 (holo. K!).

Gen. distrib.: Colombia, Ecuador.

3.18.3.4. 8. X. grisea (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja grisea Epl. in Brittonia 7:139 (1950)!

Fl. 4. Mountain slopes, 3400-3550 m.

Type: Colombia: El Valle: Cordillera Central, vert. occid.; Rio Bugalagrande, Barragan, Paramo de Bavaya, Corrales, 3550-3400 m, 11 iv 1946, J. Cuatracasas 20590 (LA in UC!).

Gen. distrib.: Colombia.

3.18.3.5. 9. X. darwinii (Benth.) A. Doroszenko, comb. nov.

Syn: Micromeria darwinii Benth. in DC., Prodr. 12:222 (1848)! Clinopodium darwinii (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Micromeria pusilla Phil. in An. Univ. Chile 90:556 (1895) [typ. err. pasilla]; Satureja darwinii (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)! Micromeria darwinii Benth. vars. typica Speg., imbricatifolia Speg., and pusilla (Phil.) Speg. in An. Soc. Ci. Arg. 1902:75 (1902); Satureja pusilla (Phil.) Macl. in Rept. Princeton Univ. Exp. Patagonia 8:698 (1905).

Ic: W. B. Scott, Rep. Princeton Univ. Exped. Patag. 1896-99, 8 II Bot. t.24 (1905).

Fl. 1-3, 11-12. Hot, dry, sunny rocks, steep granite schist ledges, eroded sandstone, 60-700 m.

Type: Argentina: Santa Cruz, iii 1834, C. Darwin (holo. K!).

Gen. distrib.: S Argentina, S Chile.

X. darwinii is a lowland plant which contrasts with most of the rest of the genus. A map presented by Epling & Jativa (1964) shows that the species is confined to Chile and Argentina south of 44 S but not on the western coastal mountains between 44 S and 47 S. This is interesting since it has been noticed that there is an abrupt change in the flora at about 42 S (Simpson, 1973). Virtually all of the land west of the Andes south of 44 S was covered in ice during the last glaciation. Judging by the distribution of Perezia (Compositae), Simpson (1973) suggested that there may have been glacial refugia east of the Andes south of 44 S. Markgraf (1980) also suggested that Tierra del Fuego, based upon a palynological study of the region, may have been a glacial refugium.

3.18.3.6. 10. X. brevicalyx (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja brevicalyx Epl. in Ann. Missouri Bot. Gard. 14:82 (1927).

Fl. 1, 3, 5, 7, 12. Open limestone hills, 3050-4270 m.

Type: Peru: Cuzco, iii 1925, Herrera 825 (holo. US).

Gen. distrib.: Peru.

Although differing in habit from the other species of the section there is a strong similarity to X. nubigena (sp. no. 6). The leaves are of similar size and shape but differ in pubescence. The calyx is more campanulate than X. nubigena, with a shorter tube and longer, much narrower teeth.

3.18.37. 11. X. vana (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja vana Epl. in Ann. Missouri Bot. Gard. 14:79 (1927)!

Fl. 1-3. Roadside, E facing mountain slopes, 3100-3350 m.

Type: Peru: Prov. Moquegua: Carumas, 3100 m, 21 ii - 6 iii 1925. Rainy green formation, A. Weberbauer 7259 (holo. F, iso. K!)

Gen. distrib.: Peru.

This very tall plant seems misplaced in a section named Prostratae. Epling & Jativa (1964) associated the species with sect. Pauciflorae, but I have reduced this section to include only two Californian plants. X. vana is rather similar in leaf shape, verticillaster arrangement and calyx to X. grisea (sp. no. 8). In pubescence it is similar to the preceding X. brevicalyx.

3.18.4. (c) Sect. Spicatae A. Doroszenko, sect. nov.

Syn: Satureja L. sect. Xenopoma (Spicatae) Epling & Jativa in Brittonia 16:411 (1964).

Tall erect herbs with woody bases. Leaves linear or broadly ovate-orbicular, entire or crenulate, revolute, minutely hairy above, long pubescent below, veins invisible in tightly revolute leaves, in less revolute leaves narrow, rather prominent below. Inflorescence a dense spike, interrupted at base only. Calyx teeth all very narrowly triangular, lower 1/2-3/4 x tube length, throat glabrous but a fringe of hairs situated half way up the teeth. Corolla white or purple. (Ecuador).

In leaf shape the two species are very different but are similar in verticillaster arrangement and calyx structure. The band of hairs half way up the calyx teeth is unusual, and is found in no other Xenopoma species.

3.18.4.1. Leaves linear-lanceolate, very tightly
revolute, 2-4 mm long 12. fasciculata

Leaves ovate-orbicular, revolute at the
margins, 3-20 mm long 13. mutabilis

3.18.4.2. **12. X. fasciculata (Benth.) A. Doroszenko, comb. nov.**

Syn: Gardoquia fasciculata Benth., Pl. Hartweg. 243 (1846)! Satureja fasciculata (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)!, non Rafin. (1814), non Tausch (1828); Satureja rigidula Epl. in Ann. Missouri Bot. Gard. 14:72 (1927), non Jard. & Fourv. (1866); Satureja stachyodes Epl. in Fedde, Rep. Sp. Nof. Beih. 85:156 (1936).

Fl. 4-8. Steep, dry, sunny slopes, 1700-3500 m.

Type: Ecuador: Pichincha: Rumibamba, and at the bridge of Guapulo, near Quito, Hartweg 1338 (holo. K!, iso. E!).

Gen. distrib.: Ecuador.

Jaramillo & Coello (1982) who studied the vegetation throughout Ecuador reported that this species is a typical component of the flora between 3000 m and 3500 m in Chimborazo province.

3.18.4.3. **13. X. mutabilis (Epl.) A. Doroszenko, comb. nov.**

Syn: Satureja mutabilis Epl. in Fedde, Rep. Sp. Nov. Beih. 85:157 (1936); Satureja breviflora sensu Epl. in Ann. Missouri Bot. Gard. 14:59 (1927), non Briq. (1897).

Fl. 4-9. Chaparral, river banks, 2300-3050 m.

Type: Ecuador: Pichincha: in andibus quitensis, Jameson (holo. S).

Gen. distrib.: Ecuador.

Epling (1940) mentions two leaf forms for this species: one with broadly ovate leaves, truncate at the base, the other with narrowly elliptic leaves. He says that otherwise they are very similar.

3.18.5. (d) Sect. Xenothymus Griseb. in Goett. Abh. 19:188 (1874).

Syn: Oreosphacus Phil. ex Leyb., Excurs. Pampas 45 (1873); Ceratominthe Briq. in Bull. Herb. Boiss. 4:875 (1896); Satureja L. sect. Xenopoma (Ceratominthe) Epl. & Jativa in Brittonia 16:413 (1964).

Tall erect suffruticose herbs with woody bases, or shrubby. Leaves narrowly ovate to linear-oblong, cuneate at base, entire or minutely serrulate, glabrous or minutely hairy above only, or hirsute on both sides, lateral veins not visible or very narrow and faint, without veins between. Calyx only slightly zygomorphic, lower teeth 2/5-2/3 x tube length. Corolla purple or white; anthers parallel or divergent. (Peru, Bolivia, Argentina).

Grisebach (1874) described sect. Xenothymus to include X. odorum, X. eugenioides (= X. gilliesii), and X. verticillatum. The latter species belongs to the independent genus Minthostachys which is distinguished by its inflorescence of sub-scorpioid verticillasters, in the leaf axils, terminating the stem in a spike-like inflorescence, and the calyx narrowly tubular with narrow, porrect teeth.

3.18.5.1. 1. Corolla tube 5.0-7.0 mm; calyx 2.2-3.5 mm, tube slightly ampliate, teeth + erect 14. bolivianum
\+ Corolla tube 1.3-2.0 mm; calyx 1.4-2.3 mm, tube broadly ampliate, teeth somewhat spreading 2
2. Flowers 4-21 per cyme; lateral veins narrow but plainly visible on larger leaves; leaves (8-)15-45 x 4-7 mm 15. odorum
\+ Flowers 1-3 per cyme; lateral veins invisible on all leaves; leaves 3-14 x 1.5-4 mm 3

3. Plant almost glabrous; leaf apex sharply acute 16. axillare

\+ Plant shortly hirsute; leaf apex +- obtuse 17. gilliesii

3.185.2. 14. X. bolivianum (Benth.) Griseb. in Goett. Abh. 25:272 (1879).

Syn: Micromeria boliviana Benth., Lab. Gen. Sp. 731 (1835); Gardoquia obovata Griseb. ex Wedd., Chlor. And. 2:150 (1860), nomen, et in schaed., Pl. Peruv. exsicc. Lechl., non Ruiz & Pav. (1798); M. boliviana Benth. var. angustifolia Wedd., loc. cit. (1860); X. bolivianum var. tarijense Wedd. in Griseb., loc. cit. (1879); Clinopodium bolivianum (Benth.) Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja kuntzeana Briq. in Bull. Herb. Boiss. 4:874 (1896); Satureja boliviana (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897); Clinopodium kuntzeanum (Briq.) Kuntze, Rev. Gen. Pl. 3(2):259 (1898); Satureja simulans Epl. in Ann. Missouri Bot. Gard. 14:81 (1927).

Fl. 1, 4-12. Rocky hillsides, moist roadside, 1000-4000 m.

Type: Bolivia: no data, Pentland (holo. G).

Gen. distrib.: Peru, Bolivia, Argentina.

X. boliviana differs from the three other species of the section in its longer more narrowly tubular calyx tube and relatively shorter, more erect teeth. But in leaf shape it is very like X. odora and X. axillare; it also has the tiny, sharply pointed, outcurving teeth characteristic of these two species. X. boliviana had been placed in species-group Pauciflorae by Epling & Jativa (1964). However, this group seems better delimited if it includes only two Californian endemics. Sect. Pauciflorae has an infundibuliform calyx with narrowly lanceolate, subulate teeth quite different from X. boliviana.

Very young leaves on short lateral shoots are oblanceolate-elliptic. Identification of specimens whose lower leaves have fallen off may be more difficult because of this. Buchtein 438 is one such and one's first impression is that there has been a misidentification.

3.1853. 15. X. odorum Griseb. in Goett. Abh. 236 (1874).

Syn: Micromeria odora (Griseb.) Hieronym. in Bot. Acad. Nac. Cordoba 4:413 (1881); Ceratominthe achalensis Briq. in Bull. Herb. Boiss. 4:877 (1896); Ceratominthe kuntzeana Briq., loc. cit. (1896); Ceratominthe odora (Griseb.) Hauman in Bull. Soc. Bot. Belg. 64:56 (1931); Satureja odora (Griseb.) Epl. in Fedde, Rep. Sp. Nov. Beih. 85:158 (1936).

Ic: Briquet, Bull. Herb. Boiss. 4:876 (1896), floral parts only, as Ceratominthe achalensis.

Fl. 1-4, 10-12. Roadside banks, fallow fields, 2250-3000 m.

Type: Argentina: Tafi, Jan. 1872, Lorentz 373 (holo. GOET).

Gen. distrib.: NW Argentina, Bolivia.

Briquet (1896) described a new genus to accomodate this species based entirely on floral features. If he had compared X. odora with X. axillare and X. gilliesii more closely he would have noticed a very close similarity in calyx and corolla. In leaf structure and nutlets it is also close to X. axillare and X. boliviana.

Ugent & Cardenas 4985 is a very small-leaved form. All the leaves are on short, slender, lateral shoots, and larger leaves may have been shed. As Epling & Jativa (1966 b) have suggested, it may be a xeric form.

3.1854. 16. X. axillare (Rusby) A. Doroszenko, comb. nov.

Syn: Bystropogon axillare Rusby in Mem. Torrey Bot. Club 6:108 (1896)! Bystropogon uniflorus Rusby ex Briq. in Bull. Herb. Boiss. 4:802 (1896); Satureja axillaris (Rusby) Epl. in Ann. Missouri Bot.

Gard. 14:82 (1927)!

Fl. 5. c. 1600 m.

Type: Bolivia: bolivian plateau, ann. 1891, Bang 1125 (iso. E!, FM!, K!, MANCH!, NY).

Gen. distrib.: Bolivia.

Only known from the type collection.

3.18.5.5. 17. X. gilliesii (Benth.) A. Doroszenko, comb. nov.

Syn: Micromeria gilliesii Benth., Lab. Gen. Sp. 381 (1834)! Oreosphacus parvifolia Phil. ex Leyb., Excurs. Pampas 45 (1873)! Xenopoma eugenioides Griseb. in Goett. Abh. 19:237 (1874); Micromeria eugenioides (Griseb.) Hieronym. in Bol. Acad. Nac. Cordoba 4:413 (1881); Clinopodium gilliesii (Benth.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891)! Bystropogon minutus Briq. in Bull. Herb. Boiss. 4:803 (1896); Satureja gilliesii (Benth.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:300 (1897)! S. oligantha Briq., loc. cit. 380 (1897); S. eugenioides (Griseb.) Loes. ex R. Fries in Nov. Acta Soc. Upsal. ser.4, 1:107 (1905); S. parvifolia (Phil. ex Leyb.) Epl. in Fedde, Rep. Sp. Nov. Beih. 85:159 (1936)!

Ic: Marticorena & Quezada in Bol. Soc. Biol. Concepcion 51:145 (1977), as Satureja parvifolia.

Fl. 1-5, 10-12. Grassy plains, 2000-4575 m.

Type: Argentina: Mendoza: Andes of Mendoza, Gillies (holo. K!, iso. E!).

Gen. distrib.: Argentina, Peru, Bolivia, N Chile (rare).

A very common plant of the eastern slopes of the NW Argentinian Andes.

3.18.6. (e) Sect. Pauciflorae A. Doroszenko, sect. nov.

Syn: Satureja L. sect. Xenopoma (Pauciflorae) Epl. & Jativa in

Brittonia 16:411 (1964).

Erect semi-shrubs. Leaves broadly ovate, flat, long-petiolate, crenulate, minutely or long densely hairy above and below, lateral veins very narrow, sometimes hardly visible. Calyx broadly tubular, infundibuliform, the teeth narrowly lanceolate, subulate, 1/3-2/5 x tube length. Corolla pink or white. (S California & Mexico).

Epling & Jativa (1966 a) thought that the two species included here "strongly resemble" X. vana and X. brevicalyx from Peru. Although there is some similarity in leaf shape to X. vana, there is a difference in calyx and corolla. Sect. Pauciflorae has distinctly infundibuliform calyces with lanceolate, subulate, outcurving teeth. The corollas are larger and more broadly tubular. In addition to these morphological differences there is a large disjunction in distribution.

3.18.6.1. Calyces naked in the throat; plant subglabrous;
calyx hirtellous 18. ganderi
Calyx with a ring of hairs in the throat; plant
clearly pubescent on all parts 19. chandleri

3.18.6.2. 18. X. ganderi (Epl.) A. Doroszenko, comb. nov.

Syn: Satureja ganderi Epl., in Amer. Midl. Nat. 24:748 (1940)!

Fl. 4-6. Chaparral, 150-425 m.

Type: Baja California: Pine Canon, 6 miles S of San Vicente, 25 iv 1940, C. Epling & H. Lewis (iso. LA in UC!).

Gen. distrib.: Mexico, Baja California.

3.18.6.3. 19. X. chandleri (Brandeg.) A. Doroszenko, comb. nov.

Syn: Calamintha chandleri Brandeg. in Zoe 5:195 (1905); Satureja chandleri (Brandeg.) Druce in Rep. Bot. Exch. Club Brit. Isles

1916:644 (1917).

Ic: Wiggins, Flora of Baja California 434, f.400 (1980), as Satureja chandleri.

Fl. 4.

Type: ?

Gen. distrib.: San Diego & Los Angeles Co., California & Mexico, Baja California.

3.18.7. (f) Sect. Sphenostachys (Epl. & Jat.) A. Doroszenko, comb. nov.

Syn: Satureja L. sect. Sphenostachys Epl. & Jativa in Brittonia 18:263 (1966).

Erect herbs. Leaves broadly ovate, flat, crenate, sparsely long hairy above, rather more densely long-hairy below. Inflorescence a terminal spike. Verticillasters dense, multi-flowered. Calyx tube slightly curved, lower teeth 2/5 x tube length. Corolla white; anthers divergent. Monotypic. (Peru).

There is a similarity in vegetative features to Gardoquia, especially G. multiflora of sect. Gardoquia. The inflorescence, however, is much more reminiscent of Xenopoma even though it has an unusual spike-like arrangement.

3.18.7.1. 20. X. cylindristachys (Epl. & Jat.) A. Doroszenko, comb. nov.

Syn: Satureja cylindristachys Epl. & Jat. in Brittonia 18:263 (1966)!

Fl. 1. Steep mountain slopes, c. 1700 m.

Type: Peru: Amazonas. Bongara. Pomacochas road, c. km 315 E of Olmos, between Pomacochas and Rio Utcubamba, 29 i 1964, Hutchison & Wright 3869 (holo. LA, iso. F, K!, M, MICH, MO, NY, P, US, USM).

Gen. distrib.: Peru.

3.18.8. Nom. exclud.

Xenopoma verticillatum Griseb. in Goet. Abh. 19:237 (1874) = Minthostachys verticillata (Griseb.) Epl.

3.19. Diodeilis Rafin., Fl. Tellur. 3:82 (1836).

Syn: Melissa sect. Calomelissa Benth., Lab. Gen. Sp. 388 (1834); Rafinesquia Rafin., Fl. Tellur. 3:83 (1837), non Rafin., Fl. Tellur. 2:96 (1837), non Rafin., Sylva Tellur. 79 (1838), non Nutt. in Trans. Am. Phil. Soc. 7:429 (1841); Calamintha sect. Calomelissa (Benth.) Benth. in DC., Prodr. 12:229 (1848), p.p.; Satureja sect. Calomelissa (Benth.) Briq. subsect. Coccineae Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897).

Annual or perennial herbs or low shrubs. Leaves orbicular to ovate, elliptic to linear, or obovate-spathulate, subsessile to long-petiolate; entire or serrulate-crenulate; veins camptodromous, invisible or scarcely visible, marginal veins absent; palisade mesophyll dorsiventral. Verticillasters distant or approximate, flowers solitary or few-flowered, on long, sessile or subsessile pedicels. Bracts usually shorter than flowers. Bracteoles like the leaves in shape or linear, shorter than pedicels. Calyx distinctly bilabiate; tube broad, straight, + parallel-sided, 13(-15)-veined, throat densely, rarely sparsely, hairy; upper lip curving upward, entire or with small teeth; lower lip straight, teeth 1/3 to as long as tube. Corolla shades of purple, sometimes red; tube straight, ampliate, not resupinate nor annulate inside, glabrous or hairy on inside lower half; lips 1/4 - 4/5 x tube length, upper emarginate, sometimes entire, lower lip 3-lobed, central lobe entire or bifid. Stamens 4, all fertile, inserted 1/2 - 3/4 way up tube, convergent or straight, posterior 1/2 - 3/4 x length of anterior, included or exserted from tube; anthers parallel to widely divergent. Style branches unequal, rarely equal, both narrowly subulate. Nutlets ovoid to suborbicular, glabrous, rarely minutely eglandular hairy.

Type species: D. coccinea.

Diodeilis is a North American genus which in the past has been dealt with as a synonym of Calamintha or else the species placed in Satureja s.l. (sect. Calomelissa). However, in calyx and leaf structure Diodeilis and Calamintha are definitely separable. The calyx of Diodeilis is remarkable for its sharply upcurving, ± erect upper lobe which either has short teeth or may be entire. The calyces are long-pedicellate but the peduncle is short or absent. This is in contrast to Calamintha which tends to have a less broadly tubular calyx tube, the upper lobe only a little curved upwards and always toothed, the calyx clearly pedunculate. Calamintha never has obovate leaves as occur in sect. Diodeilis, tending to be ovate-lanceolate with + definite teeth.

The distinctness of this North American group has, in fact, always been recognised. Both Bentham (1834, 1848) and Briquet (1897) described sections within Melissa, Calamintha or Satureja (see generic synonymy above) to accommodate them. Sectional rank within Satureja was also supported by Epling & Jativa (1966). However, generic rank seems justified, particularly because the unusual calyx features will not allow the group to be comfortably placed within any of the other American genera. An association with an Old World genus is also ruled out by the unusual floral features and by geographical distribution. The nearest relative to Diodeilis is probably Gardoquia, with the closest similarities in the woody sect. Diodeilis.

The name Diodeilis has never been used since its original publication. The name appears as an alternative for Rafinesquia Raf. in Fl. Tellur. (Rafinesque, 1836). There are no less than four genera named Rafinesquia, three of which Rafinesque modestly named after himself; all are now rejected, but the fourth, Rafinesquia Nutt., is conserved. Merrill (1949) maintains that all these Rafinesque alternative names are invalid. However, the Code of Botanical Nomenclature (1972), article 34, does not reject these names. Diodeilis is also accepted as validly published by Farr, Leussink, & Stafleu's Index Nominum Genericorum (Plantarum) (1979).

3.19.1. 1. Shrubs, with obovate-spathulate leaves, 4-15 x 1-5 mm, entire or tridentate, minutely hairy on upper side (Sect. Diodeilis) 2

\+ Herbs, sometimes rather woody at base, leaves not obovate-spathulate, 7-45 x 1-25 mm, entire or serrulate to crenulate, glabrous or long-haired on upper side (Sect. Herbaceae) 4

2. Corollas 35-60 mm, red 1. coccinea

\+ Corollas 10.5-18 mm, purple 3

3. Leaves narrowly oblanceolate, entire; upper calyx lip entire 2. ashei

\+ Leaves spathulate, apex tridentate; upper calyx lip with three teeth, 0.2-0.5 mm long 3. dentata

4. Calyx teeth all very narrowly triangular or deltoid, pungent 5

\+ Upper calyx teeth absent or very short, broadly triangular 7

5. Annual herb with orbicular-ovate leaves 8. amissa

\+ Perennial herbs with linear to elliptic leaves 6

6. Stoloniferous, the stolons leafy; nodes beardless or nearly so; primary leaves linear to linear-oblanceolate, the larger 10-25 x 1-5 mm — 4. arkansana

\+ Non-stoloniferous; nodes of stems bearded; primary leaves elliptic or oblong-lanceolate, the larger 25-50 x 5-17 mm — 5. glabella

7. Plant 30-50 cm tall; leaves oblanceolate-elliptic 9-45 x 5-25 mm; pedicels 1.5-4.5 mm; calyx tube 4.0-4.5 mm — 6. georgiana

\+ Plant 10-20 cm tall; leaves orbicular-ovate, 7-11 x 4-9 mm; pedicels 4.0-4.5 mm; calyx tube 3.5-4.0 mm — 7. procumbens

3.19.2. Sect. Diodeilis

Shrubs, with obovate-spathulate leaves, 4-15 x 1-5 mm, entire or tridentate, minutely hairy above, minutely hairy or glabrous below. (SE U.S.A.)

A close-knit section of three species centred on Florida and S Georgia. All are most often found on sandy soils, often amongst pines.

3.19.2.1. 1. D. coccinea (Nutt.) Rafin., Fl. Tellur. 3:83 (1837).

Syn: Cunila coccinea Nutt. ex Hooker, Exotic Flora 2: t.163 (1825)! Melissa coccinea (Nutt. ex Hooker) Spreng., Syst. 4(2):224 (1827)! Gardoquia hookeri Benth., Lab. Gen. Sp. 401 (1834)! Rafinesquia coccinea (Nutt. ex Hooker) Rafin., Fl. Tellur. 3:83 (1837)! R. angustifolia Rafin., New Fl. Am. 3:52 (1838); Calamintha coccinea (Nutt. ex Hooker) Benth. in DC., Prodr. 12:229 (1848)! Satureja coccinea (Nutt. ex Hooker) Bert., in Misc. Bot. 8:23 (1849)! Clinopodium coccineum (Nutt. ex Hooker) O. Kuntze, Rev. Gen. Pl.

2:515 (1891)! Clinopodium macrocalyx Small, Fl. S.E. U.S. 1043 (1903); Satureja macrocalyx (Small) Druce in Rep. Bot. Exch. Cl. Brit. Is. 4:644 (1917); Gardoquia coccinea (Nutt. ex Hooker) Alexander in Addisonia 21:45, t.695 (1941).

Ic: Bot. Reg. 21, t.1747 (1835), as Gardoquia hookeri.

Fl. 4-8. Sand ridges, open grassy pineland, c. 60 m.

Type: E Florida, Nuttall (holo. K!).

Gen. distrib.: SE U.S.A.

This species is remarkable for its large, narrowly tubular, crimson-red flowers which are very reminiscent of Gardoquia. However, in calyx structure it is very different. The broad, straight tube and sharply upcurving and very small-toothed upper lip clearly distinguishes D. coccinea from Gardoquia. In habit and leaves there is a very close similarity to D. ashei and D. dentata.

3.19.2.2. 2. D. ashei (Weatherby) A. Doroszenko, comb. nov.

Syn: Satureja ashei Weatherby in Rhodora 26:80 (1924); Clinopodium ashei (Weatherby) Small in Bull. Torr. Bot. Club 51:385 (1924); Calamintha ashei (Weatherby) Shinners in Sida 1(2):73 (1962).

Fl. 4-6. Fixed sand dunes.

Type: Florida: sandy pine woods near Ocala, Marion Co., iv 1923, W.W. Ashe (holo. GH).

Gen. distrib.: Florida, Georgia.

3.19.2.3. 3. D. dentata (Chapm.) A. Doroszenko, comb. nov.

Syn: Calamintha dentata Chapm., Fl. Southern U. S. ed.1, 318 (1860); Clinopodium dentatum (Chapm.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja dentata (Chapm.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897).

Fl. 5-8. Sand ridges in pine plantations and scrub.

Type: ?

Gen. distrib.: Florida.

Easily identified by its 3-dentate, sometimes 5-dentate, leaf apices.

3.19.3. Sect. Herbaceae (Benth.) A. Doroszenko, comb. et stat. nov.

Syn: Calamintha sect. Calomelissa subsect. Herbaceae Benth. in DC., Prodr. 12:230 (1848); Satureja sect. Calomelissa subsect. Glabellae Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897).

Herbs, sometimes rather woody at base, with orbicular or elliptic to linear leaves, 7-45 x 1-25 mm, entire or serrulate to crenulate, glabrous on both sides, or long hairy above only or on both sides. [NW Mexico, South & East U.S.A., Canada (Ontario)].

3.19.3.1. 4. D. arkansana (Nutt.) A. Doroszenko, comb. nov.

Syn: Hedeoma arkansana Nutt. in Trans. Amer. Phil. Soc. 5:186 (18..); Hedeoma glabra Nutt., Gen. Am. 1:16 (1818), non Pers. (1807); Cunila glabella sensu Torr., Fl. N. U.S. 23 (1823); Micromeria arkansana (Nutt.) Benth., Lab. Gen. Sp. 730 (1835); Micromeria glabella (Michx.) Benth. var. angustifolia Torrey, Fl. N.Y. 2:67 (1843); Calamintha nuttallii Benth. in DC., Prodr. 12:230 (1848); Micromeria nuttallii Torr. & A. Gray ex Benth. in DC., Prodr. 12:230 (1848), nomen; Calamintha glabella (Michx.) Benth. var. nuttallii (Benth.) A. Gray, Man. ed.2, 307 (1857); Cunila glabra (Nutt.) A. Gray, Syn. Fl. N. Am. 2:360 (1878); Calamintha glabra (Nutt.) Trelease ex Branner & Coville in Ann. Rep. Geol. Surv. Arkans. 1888(1):211 (1891); Clinopodium glabrum (Nutt.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja arkansana (Nutt.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4,3a:302 (1897);

Satureja glabra (Nutt.) Fern. in Rhodora 10:85 (1908); Clinopodium arkansanum (Nutt.) House in Am. Midl. Nat. 7:130 (1921); Satureja glabella (Michx.) Briq. var. angustifolia (Torr.) Svenson in Rhodora 42:7 (1940); Calamintha glabella (Michx.) Benth. var. angustifolia (Torr.) DeWolf in Baileya 2:150 (1954); Calamintha arkansana (Nutt.) Shinners in Sida 1(2):72 (1962).

Ic: Stevens, Ill. Fl. Pl. Mid. Atl. N. Engl. St. t.132 (1930), as Clinopodium glabrum; Gleason, New Britton & Brown, Ill. Fl. N.E. U.S. & Canada 3:175 (1952), as Satureja glabella var. angustifolia.

Fl. 5-9. Moist swamp clearings, damp places, 100-600 m.

Type: ?

Gen. distrib.: E U.S.A. & SE Canada.

3.19.3.2 5. D. glabella (Michx.) A. Doroszenko, comb. nov.

Syn: Cunila glabella Michx., Fl. Bor.-Am. 1:13 (1803); Hedeoma glabrum Pers., Syn. Pl. 2:131 (1807); Ziziphora glabella (Michx.) Roem. & Schult., Syst. Veg. 1:209 (1817); Micromeria glabella (Michx.) Benth., Lab. Gen. Sp. 371 (1834); Calamintha glabella (Michx.) Benth. in DC., Prodr. 12:230 (1848); Clinopodium glabellum (Michx.) O. Kuntze, Rev. Gen. Pl. 2:515 (1891); Satureja glabella (Michx.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897).

Ic: Britton & Brown, Ill. Fl. N. States & Canada 3:110 (1898), as Clinopodium glabellum.

Fl. 6. Cedar barrens, river banks, 300-400 m.

Type: [U.S.A.] in ripariis fluvii Tennassee, juxta Nashville, Micheaux (holo. P?).

Similar to D. arkansana but non-stoloniferous, with nodes of stems bearded, leaves broadly elliptic or oblong-lanceolate, 25-50 x 5-17 mm, apex obtuse to rounded, margins shallowly toothed to entire, upper side sparsely hairy, petiole 2-5 mm; bracteoles 5-7 mm; calyx tube 3.0-3.5 mm, upper and lower lips 2.0-2.5 mm, upper teeth 1.0-1.5 mm, lower teeth 2.0-2.5 mm.

3.19.3.3. 6. D. georgiana (Harper) A. Doroszenko, comb. nov.

Syn: Clinopodium georgianum Harper in Bull. Torr. Bot. Club 33:243 (1906); Thymus carolinianus (non "Walter") Michx., Fl. Bor.-Am. 2:9 (1803); T. grandiflorus sensu Sims. in Bot. Mag. 25: t. 997 (1807), non (L.) Scopoli (1772); Calamintha grandiflora (Sims.) Pursch, Fl. Am. Sept. 2:414 (1813), non (L.) Moench (1794); Calamintha caroliniana (Michx.) Nutt., Gen. N. Am. Pl. 2:39 (1818); Melissa caroliniana (Michx.) Benth., Lab. Gen. Sp. 388 (1834); Satureja caroliniana (Michx.) Briq. in Engler & Prantl, Nat. Pflanzenfam. 4, 3a:302 (1897); Clinopodium carolinianum (Michx.) A.A. Heller, Cat. N. Am. Pl. 7 (1898), non Miller (1768); Calamintha georgiana (Harper) Shinners in Sida 1(2):74 (1962); S. georgiana (Harper) Ahles in Journ. E. Mitchell Sci. Soc. 80:173 (1964).

Fl. 8-11. Deciduous woodland in sandy soil, dry pine woods, 60-140 m.

Type: [U.S.A.] Carolina, Micheaux (holo. P?, iso. G-DC, microfiche!).

Gen. distrib.: SE U.S.A.

Some comment is required on the correct citation of this species. Micheaux (1803) has Thymbra caroliniana Walter in synonymy but this is quite different and is synonymous with a Macbridea species. It is clear that Micheaux (1803) intended to make a new combination but his description of Thymus carolinianus is definitely not of Macbridea but what I am here renaming Diodeilis georgiana. Therefore caroliniana cannot be used as the specific epithet here. Shinners (1962) discusses the nomenclature of this species more fully and includes a more detailed "sensu" synonymy.

In sect. Herbaceae D. georgiana is the most similar in calyx structure to sect. Diodeilis. Leaf size is very variable. The isotype at G-DC is a small-leaved, rather poorly preserved specimen.

3.19.3.4. 7. D. procumbens (Greenm.) A. Doroszenko, comb. nov.

Syn: Satureja procumbens Greenm. in Proc. Amer. Acad. Sci. 41:245 (1906)!

Fl. 5. Shady banks, c. 1680 m.

Type: Mexico: Hidalgo, below Trinidad Iron Works, 1680 m, 5 v 1904, Pringle (holo. K!, iso. E!).

Gen. distrib.: Hidalgo, Mexico.

This low, creeping plant has a calyx very similar to D. georgiana.

3.19.3.5. 8. D. amissa (Epl. & Jat.) A. Doroszenko, comb. nov.

Syn: Satureja amissa Epl. & Jat. in Brittonia 20:310 (1968).

Type: Mexico: Sinaloa: Varomena and vicinity, volcanic foothills, cut-over short-tree forest, 300-450 m, Gentry 7146 (holo. UC!).

This species is the only annual in Satureja s.l. in the Americas. In leaf shape and habit D. amissa is most like D. procumbens, but in calyx very like D. arkansana.

Appendix

The characters used in the data tables.

What follows here is a detailed description of the characters used in the codified data tables.

Habit and Stem Characters.

Character 1. Longevity. 1. Annual/ 2. Perennial.

1. Annual - a plant that completes its whole life cycle within one year, from seed germination to seed production, followed by death. Generally there is no difficulty in determining whether a plant is annual or not, but the following circumstances may cause problems: (a) in adverse conditions, plants normally perennial may only survive one year (e.g. desert plants); (b) rare perennials may only be known from one or a few collections of juvenile plants; and (c) poor collecting of specimens (e.g. if only the top of a plant is collected) may not make it obvious if a plant is annual or perennial). None of these difficulties have caused a problem in Satureja s.l.

2. Perennial - a plant which continues growth from year to year. See notes under 1. Annual above.

Character 2. Habit. 1. Herbaceous/ 2. Herb, but base rather woody/ 3. Semi-shrubby/ 4. Shrubby.

1. Herbaceous - a plant without persistent stems above ground, including plants with soft stems only, which have not become obviously lignified. All the annuals of Satureja s.l. are herbaceous. The perennials encompass all four of the above character states. In the case of herbaceous perennials, the

perennating buds are on rhizomes below or at ground level, falling into the categories of either cryptophytes or hemicryptophytes in the classification of life forms of Raunkiaer (1934).

2. Herb, but base rather woody - the stems in the unfavourable season dying back to almost ground level, with the perennating buds on these remnant shoots. This character state is only found in perennials. These are chamaephytes in Raunkiaer's classification of life forms.

3. Semi-shrubby - falling half way between the last category and the next; the perennating buds are rather higher above the ground and the new shoots are not woody. During the unfavourable season these shoots die back to near to where they arose. Most of this category are chamaephytes.

4. Shrubby - the perennating buds are well above ground and the new shoots tend to become woody by the end of the year. These new shoots tend not to die in the unfavourable season, with the perennating buds somewhere along the length of these shoots. In many species the length of these new shoots surviving to the next year is not very great, so that a compact, bushy habit is attained. Most Satureja s.l. species here are chamaephytes, but many are also nanophanerophytes (Raunkiaer, 1934).

Note that a species may have a range of shrubbiness or herbaceousness, and may not fall into only one habit category.

Character 3. Stem height (cm).

The height in cm is taken from the point where the stem joins the rootstock to the apex of the inflorescence.

Character 4. Stolonifery. 1. Stoloniferous/ 2. Not stoloniferous.

Stolons are horizontally growing stems which root at their nodes. Rather few species in Satureja s.l. are stoloniferous.

Character 5. Stem hairs. 1. ± Patent/ 2. Recurved or adpressed/ 3. Absent or very minute/ 4. Crisped or of no preferred direction.

1. ± Patent - hairs ± perpendicular to the stem surface. The only difficulty which could arise is when the patent hairs are very long, and become flattened during picking and mounting, if one is examining a herbarium specimen. See fig. App. 1a.

2. Recurved or adpressed - There is a difference between recurved and adpressed, but they are brought together here for simplicity and because intermediate forms sometimes exist. Recurved hairs always arch away from the stem before curving backward toward the stem. Adpressed hairs bend abruptly near their base and are pressed against the stem, without much gap between hair and stem. See fig. App. 1b.

3. Absent or very minute - Sometimes the hairs are so minute that the direction of curvature, if any, is not apparent; this category covers them. It was thought best to included these minute hairs with "hairs absent" since, with a hand lens only, the minute hairs may be missed. See fig. App. 1c.

4. Crisped or no preferred direction - the hairs are bent but

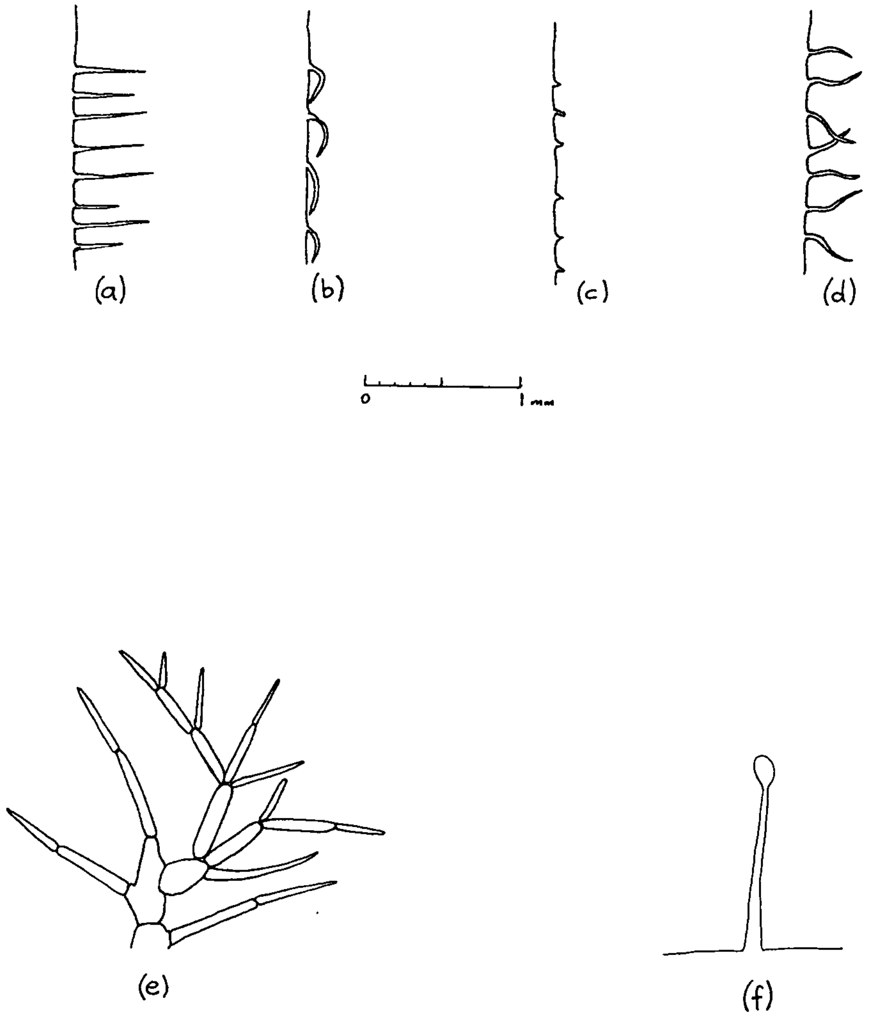


Figure App. 1. Hairs [scale bar = 1 mm for (a) - (d)]. (a) long, patent; (b) recurved; (c) microhairs; (d) crisped with no preferred direction; (e) dendroid hair of Cyclotrichium niveum, x30; (f) simple glandular hair.

not in any particular direction, giving a rather shaggy appearance. This condition is less common in Satureja s.l. than one might expect. See fig. App. 1d.

Leaf Characters.

Hickey (1979) has devised a detailed scheme for the unambiguous classification of leaf architecture. It was unfortunate, however, that I only saw this work long after I chose the characters to describe the leaves of Satureja s.l. Nevertheless, the descriptive terms used by me do not contradict Hickey.

Character 6. Leaf shape. 1. Orbicular/ 2. Ovate/ 3. Obovate/ 4. Spathulate/ 5. Linear/ 6. Oblong/ 7. Lanceolate/ 8. Oblanceolate/ 9. Elliptic.

The shapes understood by these terms are shown diagrammatically in fig. App. 2a-2i. The following notes should be read along with these figures.

1. Orbicular - the length of the leaf similar to its breadth, the apex ± rounded.

2. Ovate - the leaf longer than broad, with the broadest part below the middle of the leaf, i.e. measured from the junction of the lamina and petiole to the leaf apex along the midrib. The apex is usually obtuse. Length:width ratio < 2:1.

3. Obovate - similar to ovate but the broadest part above the middle of the leaf.

4. Spathulate - similar to obovate but below the broadest part abruptly narrowed, then gradually attenuate to the base and

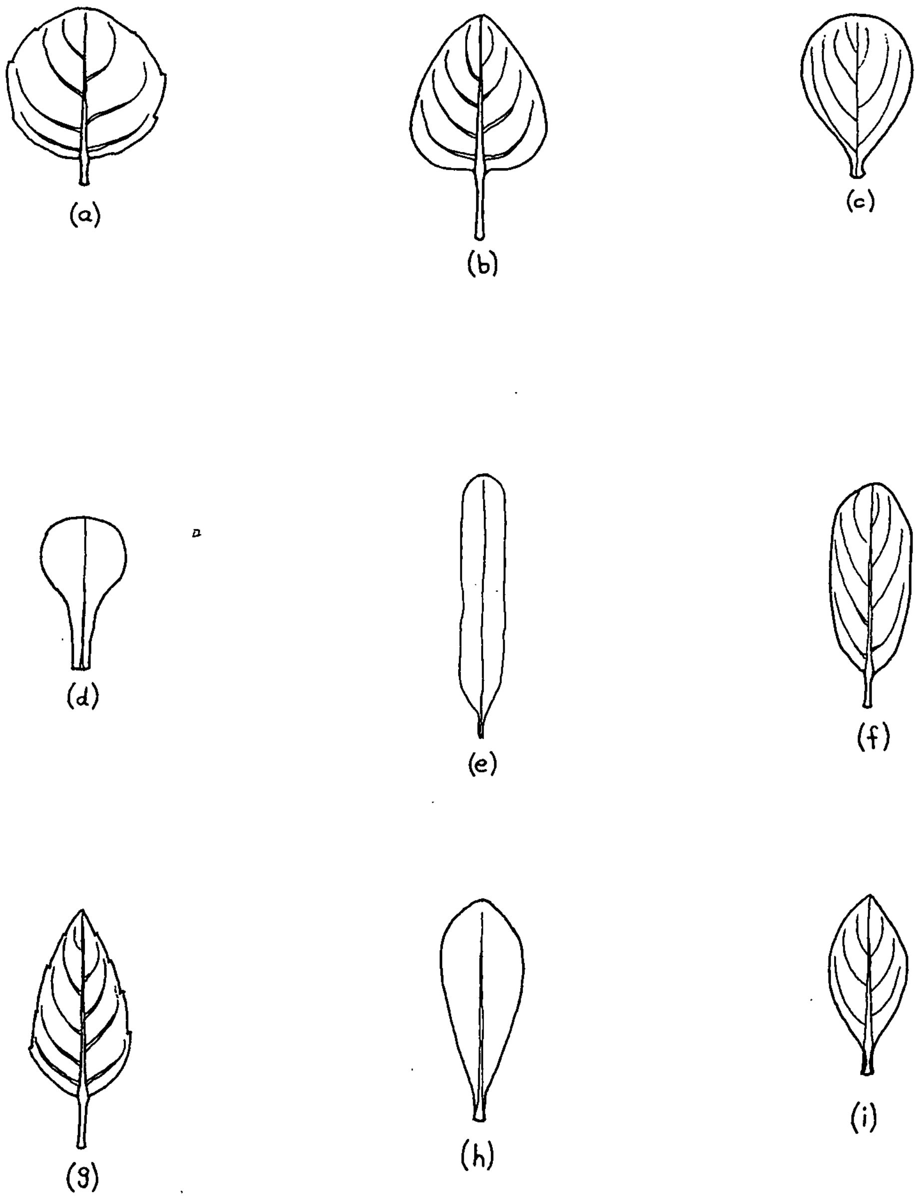


Figure App. 2. Leaf shape. (a) Orbicular; (b) Ovate; (c) Obovate; (d) Spathulate; (e) Linear; (f) Oblong; (g) Lanceolate; (h) Oblanceolate; (i) Elliptic.

merging with the petiole.

5. Linear - the leaf much longer than broad with ± parallel sides. Linear includes the term "lorate" of Hickey (1979). Length:width ratio > 6:1.

6. Oblong - similar to linear but broader. Length:width ratio < 3:1.

7. Lanceolate - rather similar to ovate but narrower, shaped like the head of a spear, the apex usually acute. Length:width ratio > 2:1.

8. Oblanceolate - similar to obovate, but much narrower, the lamina, below its broadest part, gradually attenuate to the base. Length:width ratio > 2:1

9. Elliptic - leaf longer than broad, the broadest part half way between the apex and junction of lamina and petiole.

Character 7. Leaf margin. 1. Entire/ 2. Serrulate/ 3. Serrate/ 4. Dentate/ 5. Crenate/ 6. Crenulate.

See figures App. 3a-3f.

1. Entire - margin without noticeable projections or indentations.

2. Serrulate/ 3. Serrate - projections from leaf margin with pointed apices, with their axes inclined toward the apex. No precise definition of the difference between serrulate and serrate has been attempted in this work. Serrulate is used when

very small teeth are present, and serrate with large teeth. Such lack of precision is of little taxonomic significance in Satureja s.l. The two terms have been adopted since some indication of teeth size does help on occasion with identification. Precise definition of the two terms would be rather artificial in any case.

4. Dentate - this term has been used in a way slightly different from Hickey (1979). It has been used to describe very large teeth which slightly point toward the leaf apex, rather than the teeth perpendicular to the trend of the margin. An example of the usage of the term adopted here is found in some leaf forms of Calamintha ussuriensis Regel & Maack.

5. Crenate/ 6. Crenulate - similar to serrate/serrulate but the apices of the teeth rounded. Similar comments as to relative sizes apply to crenate/crenulate as to serrate/serrulate.

Character 8. Leaf ptyxis. 1. Flat/ 2. Conduplicate/ 3. Slightly revolute/ 4. Revolute to tightly revolute.

The folding of the leaf lamina here refers to leaves that have opened, rather than still in bud. See figures App. 4a-4d.

1. Flat - the margins of the lamina and mid-vein are all in the same plane, without folding or rolling of the lamina.

2. Conduplicate - the lamina folded upward along the mid-rib, the halves flat, without any rolling. Conduplicate leaves are frequently easier to see in small leaves rather than in fully opened leaves, especially if the mature leaves are large. However, there is little likelihood of confusing conduplicate

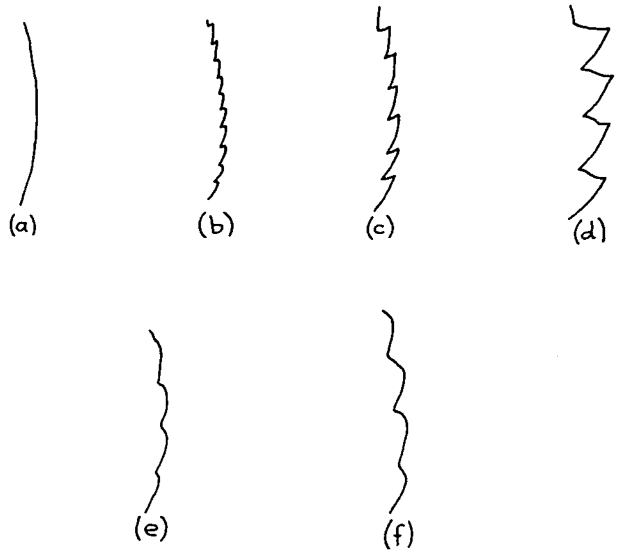


Figure App. 3. Leaf margin. (a) Entire; (b) Serrulate; (c) Serrate; (d) Dentate; (e) Crenulate; (f) Crenate.

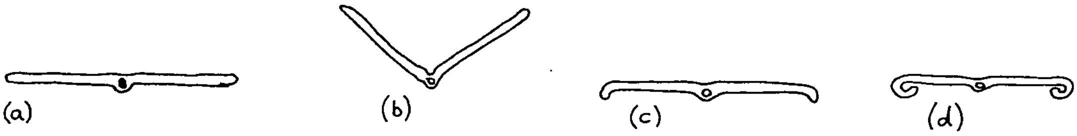


Figure App. 4. Leaf ptyxis. (a) Flat; (b) Conduplicate; (c) Slightly revolute; (d) Clearly revolute.

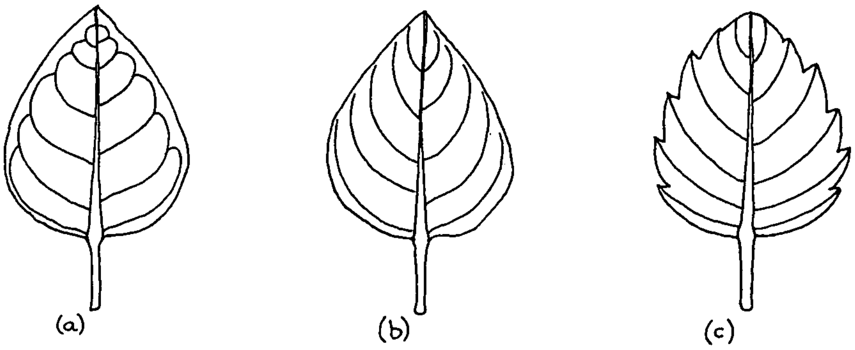


Figure App. 5. Venation. (a) Brochidodromous; (b) Eucamptodromous; (c) Craspedromous.

with flat leaves in Satureja s.s. and Gardoquia, the two genera to which conduplicate leaves are confined.

3. Slightly revolute - refers to leaves where the leaf margin only is slightly or clearly rolled under. In some cases the leaves of dried herbarium specimens have slightly inrolled margins, but this is due to uneven drying of the leaf; these have been excluded from this category.

4. Revolute to tightly revolute - leaves quite clearly rolled under at the margins, and in some cases replicate, i.e. the under-surface of the leaf is completely obscured.

Character 9. Leaf apex. 1. Acute/ 2. Obtuse/ 3. Rounded.

1. Acute - the apex forming an angle < 90°.

2. Obtuse - the apex forming an angle > 90°.

3. Rounded - the apex a continuous arc.

Character 10. Marginal vein. 1. Present/ 2. Absent.

1. Marginal vein present - the margins of the lamina with a distinct thickening, sometimes of a lighter colour than the lamina. This vein begins at the base of the leaf and continues all the way round to the apex. The thickening is not the distal part of a lateral vein. Leaves with marginal veins are always entire, whereas leaves which have thickened distal parts of lateral veins which are united to appear like a marginal vein are slightly or clearly lobed.

Character 11. Venation. 1. Brochidodromous/ 2. Eucamptodromous/ 3. Craspedromous.

Hickey (1979) gives a very detailed account of leaf venation. Leaf venation can be very complex. In Satureja s.l. there are basically only two arrangements of leaf veins, Camptodromous and Craspedromous. The three above-mentioned categories are of the pinnate type, i.e. the mid-vein is the primary vein from which the secondary and higher order veins originate. Note that in some species the secondary veins are invisible. In these cases clearing of the leaf is necessary to determine the type of venation.

A. Craspedromous type - the secondary veins not terminating at the margin.

1. Brochidodromous/ 2. Eucamptodromous - The brochidodromous condition, where the secondaries are joined together to form a series of arches (see fig. App. 5a), though expected at the beginning of the study, has, in fact, never been found in Satureja s.l. By far the greatest number of species are eucamptodromous, where the secondaries are upturned and gradually diminishing toward the margin, but are not joined together into loops (see fig. App. 5b).

B. Craspedromous - 3. Simple craspedromous - secondary veins terminating at the margin (see fig. App. 5c). This condition is confined to the Calaminthoid genera.

Character 12. Vein visibility. 1. Primary vein visible, secondaries invisible/ 2. Primary and secondary veins all ± visible.

1. Mid-vein only visible - There is usually no difficulty in observing the mid-vein except in the few cases where the leaf

is densely hairy. Invisible secondary veins are characteristic of certain genera and sections of Satureja s.l. and is not simply due to observation of under-developed leaves. Occasionaly a few leaves will have very faint secondary veins in species where they are normally invisible.

2. Primary and all secondary veins visible - There should be no difficulty again in seeing secondary veins. In some species, in Acinos for example, the proximal part of the secondary vein is much less prominent than the distal part. These species are included here.

Character 13. Petiole length (mm).

Measurement of the length of the petiole may not always be accurate in the case where the leaf base is decurrent and merges with the petiole. However, such inaccuracy is usually of little significance taxonomically. Measurement is made from the base of the lamina to the point where the petiole attaches to the stem.

Characters 14 and 15. Hairs of upper and lower side of leaf respectively. 1. Absent/ 2. Simple micro-hairs/ 3. Long simple/ 4. Long dendroid/ 5. Stellate/ 6. Pustulate dendritic.

All hairs have been observed at x20 magnification. Drawings are given in figures App. 1a-1e.

2. Simple micro-hairs - Micro-hairs are taken to be, rather arbitrarily, less than 0.1 mm in length. These are not papillae, which have not been observed on the leaf surface of any Satureja s.l. species.

3. Long simple - unbranched hairs longer than 0.1 mm.

4. Long dendroid - This type of hair is very rare in *Satureja* s.l., but is distinguished by its many fine branches. See fig. App. 1e.

5. Stellate - The fine hairs branch from the base. This condition is very rare in *Satureja* s.l.

6. Pustulate dendritic - This type of hair is distinguished from long dendroid hairs by its very robust central column with short, thick branches. This type is only found in species of *Xenopoma* sect. *Xenopoma*.

Character 16. Leaf margin ciliation. 1. Not ciliate/ 2. Ciliate.

2. Ciliate - Cilia are long (>0.1 mm) hairs, distinct from the laminar hairs, if any, and confined to the edge of the margins.

Character 17. Type of hairs. 1. All ± glandular/ 2. Some eglandular, some glandular/ 3. All eglandular.

Although there are very shortly stalked glands, these appear similar to punctate glands and are not likely to be confused with glandular hairs which are always clearly stalked. All glandular hairs are simple. Glandular leaf hairs are rather uncommon. The gland is always apical and usually quite small. See figure App. 1f.

1. All hairs ± glandular - nearly all the hairs glandular with possibly very few hairs apparently non-glandular.

2. Mixture of glandular and non-glandular hairs - If any glandular hairs at all are observed in an overwhelmingly eglandular hairy leaf, then these would fall into this category. At the other extreme, if more than approximately 1-2% are eglandular and of slightly different morphology, then these are also covered by this category.

3. All hairs eglandular - the hairs without glands at the apex, tapering gradually to the tip. By far the greatest number of species fall into this category.

Character 18. Punctate glands. 1. Absent/ 2. Very shortly stalked/ 3. Sessile/ 4. Sunken.

See figures 2.58 and 2.59 in Chapter 2 (Leaf Anatomy).

2. Very shortly stalked - This state could be ascertained definitely only by making leaf sections since the gland head is so much larger than the stalk. The stalk is at least one cell in height above the level of the epidermis. Very few species have this type of gland.

3. Sessile - glands without a stalk, attached to an enlarged epidermal cell, the epidermis not or a little sunken so that the gland does not rest in a little hollow or pit.

4. Sunken - glands without a stalk and sunken into a pit lower than the general level of the epidermis.

Character 19. Palisade mesophyll. 1. Isolateral/ 2. Dorsiventral.

Palisade cells are often dorsiventrally elongated in section and are mostly without airspaces between neighbouring cells. Spongy mesophyll cells are often of apparently random shape in section with large airspaces between adjacent cells.

1. Palisade mesophyll isolateral - palisade parenchyma adjacent to both upper and lower epidermal layers. Spongy mesophyll is confined to between the two layers of palisade mesophyll, or is absent. The palisade mesophyll may be one or more cells thick.

2. Palisade mesophyll dorsiventral - palisade parenchyma adjacent to only the upper epidermal cells, with spongy mesophyll below the palisade.

Character 20. Leaf length (mm).

The length is taken from the junction of the lamina and petiole to the apex of the lamina along the leaf axis. (See also the comments for Character 13, Petiole length). Mid stem leaves were measured in 10-20 plants, or as many as possible if fewer specimens were available.

Character 21. Maximum leaf width (mm).

The width was measured perpendicular to the axis at the widest point of the leaf lamina. The same leaves measured for length were measured for width.

Inflorescence Characters.

Character 22. Number of flowers per floral leaf.

The only problem that may arise here is that often in a multi-flowered verticillaster not all of the calyces will mature enough to flower before the season ends. When examining a herbarium specimen one cannot tell if a flower bud would have opened or not. In the multi-flowered verticillasters, however, the inaccuracy introduced by this is of little consequence. When the flowers in a verticillaster are few, the number are more or less constant within a species, e.g. most <u>Gardoquia</u> species have 1-3 flowers per floral leaf.

<u>Character 23. Verticillaster density. 1. Very dense/ 2. Rather crowded/ 3. Lax.</u>

<u>1. Very dense</u> - verticillasters globose to hemispherical, the pedicels and peduncles very short, usually not visible from above, the calyces tightly pressed against one another.

<u>2. Rather crowded</u> - less compact than above, with distinct spaces between the calyces, pedicels and peduncles longer.

<u>3. Lax</u> - pedicels and peduncles long, with clear spaces between the flowers. In the case of solitary flowers these are always counted as lax unless the verticillasters themselves are aggregated and thus are very crowded or dense.

<u>Character 24. Distance separating verticillasters.</u>

The distance between verticillasters is taken as multiples of the length of the immediate subtending floral leaf lamina. This provides for a better comparison between different species, and compensates for differences in floral leaf size due to reasons other than genetic ones (e.g. the effects of shading). The distances are arbitrarily categorised as follows.

1. > 2 floral leaf lengths apart.

2. 1-2 floral leaf lengths apart.

3. c.1 floral leaf length apart.

4. < 1 floral leaf length apart.

The measurements were made in the lowermost part of the inflorescence, i.e. that part which had fully expanded.

Character 25. Length of the peduncle (mm).

The cymes of the verticillasters in *Satureja* s.l. are often compound. Therefore, the peduncle length was taken to be the lowermost stalk supporting the flowers, i.e. from the point at which the inflorescence is attached to the leaf axil to the lowermost bracteole. See figure App. 6 d.

Character 26. Length of the pedicel (mm).

The pedicel is the ultimate stalk supporting the calyx. Measurement was made from the junction with the calyx down to the first bracteole.

Bracteole Characters.

Character 27. Bracteole shape. 1. Absent/ 2. Narrow linear, filiform/ 3. Narrowly elliptic, lanceolate or oblanceolate/ 4. Similar to the leaves.

Since the cymes are often compound there may be more than one pair of bracteoles per cyme. One could distinguish these as the primary, secondary, tertiary, etc. bracteoles; however, one gains little by so differentiating them. The bracteole shape varies little between each order. Rather than differentiating a large number of bracteole shapes, as for leaf shapes, it is more useful to distinguish just four categories.

<u>1. Absent</u> - this is a very rare condition. One should check, when the bracteoles appear to be absent, if the pedicel has a scar on either side, which would indicate that the bracteoles have merely fallen off.

<u>4. Leaf-like</u> - here the bracteoles are almost indistinguishable from the true leaves. This situation is found in a few species, widely scattered and unrelated to one another.

Character 28. Bracteole length (mm).

The length is taken of all bracteoles which are on peduncles supporting fully opened flowers.

Calyx Characters.

Character 29. Calyx tube ampliation. 1. Parallel sided cylindrical/ 2. Slightly ampliate/ 3. Ampliate/ 4. Broadly ampliate/ 5. Obconical.

These are better described by illustrations. See figures App. 7a-7e. Use these figures to judge which comes closest to the specimen at hand.

Character 30. Tube curvature. 1. Straight/ 2. Curved/ 3. Sigmoid.

All observations of curvature should be made looking from the side of the calyx, i.e. when the three teeth of the upper lobe are uppermost.

<u>1. Straight</u> - no appreciable curvature of the tube. See figure App. 6f.

2. Curved - the curvature is in one continuous arc from the base of the calyx to the teeth. The curve does not change direction. The only difficultly which may arise is when a broadly ampliate calyx tube is curved as in *Euhesperida thymbrifolia*. See figure App. 6c.

3. Sigmoid - the tube is curved into an S-shape. The basal part of the tube curves downward first of all, then curves back upward, curving back downward when near the teeth. The teeth themselves may curve back up again. See figures App. 6a-6b.

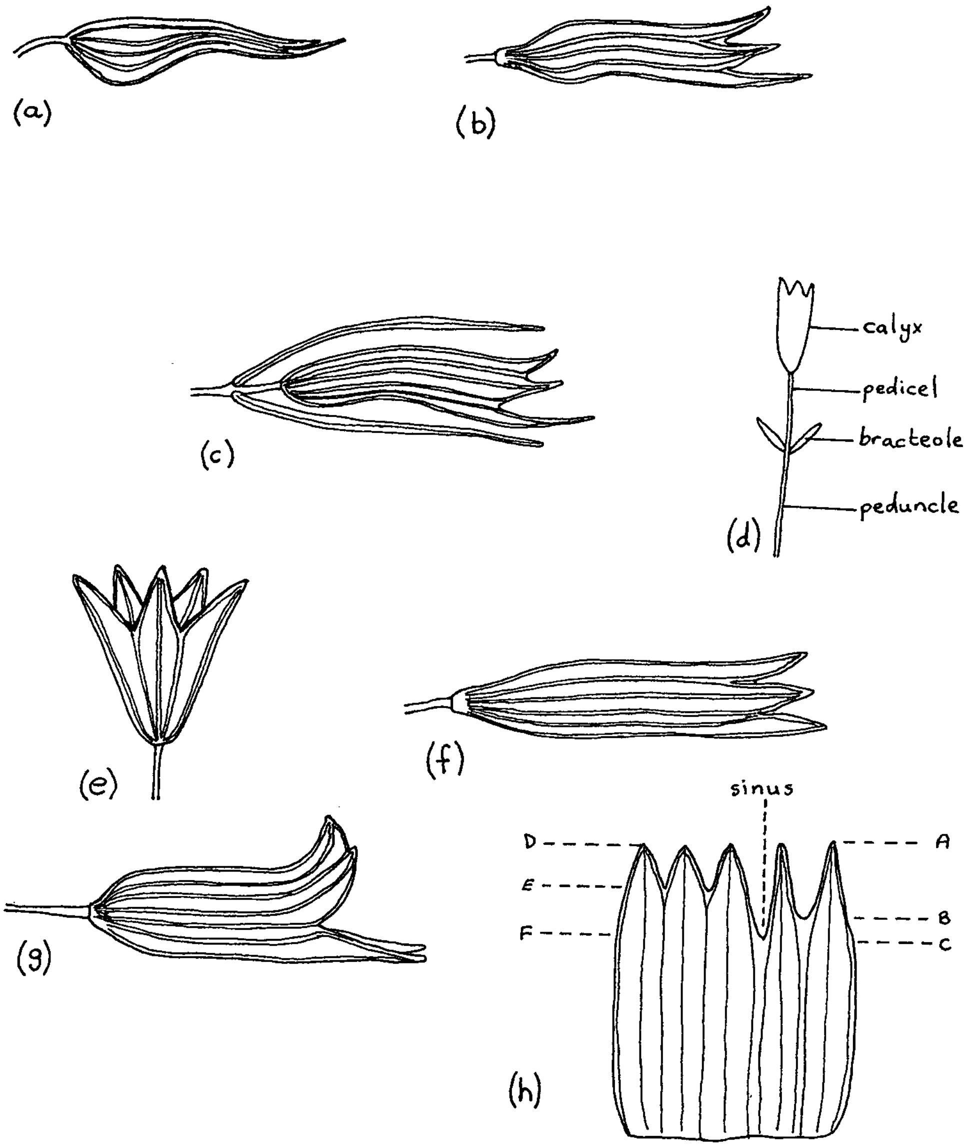
Character 31. Calyx tube length (mm).

The tube is measured from the junction between the calyx and pedicel to the sinus between the upper and lower lips. When the calyx is curved a slight compensation should be made when measuring across the arc. The curvature in *Satureja* s.l. is slight enough to make this a permissable estimate of tube length. In sigmoid calyces the measurement is taken as if it were a straight calyx. This is acceptable if one always uses this method. Non-comparability between, say, a straight calyx and a sigmoid one, as far as length is concerned, is of little taxonomic consequence since the organisation of the calyx is so different. See figure App. 6h.

Character 32. Calyx gibbosity. 1. Gibbous/ 2. Not gibbous.

1. Gibbous - the calyx base is swollen and saccate, bulging downward (in *Satureja* s.l.). The character state was only ascertained in flowering calyces and not in older fruiting calyces, which may bulge out due to the growth of ripening nutlets. See figure App. 6a.

Figure App. 6. Calyx Characters.



(a) *Acinos suaveolens*, sigmoid, strongly gibbous at base; (b) *A. troodii*, sigmoid, hardly gibbous at base; (c) *Clinopodium vulgare*, curved, not gibbous; (d) Calyx and supporting structures; (e) *Killickia reptans*, obconical, actinomorphic; (f) *Micromeria elliptica*, straight, tubular; (g) *Diodeilis dentata*, broadly straight tubular, upper lip erect; (h) Calyx tube opened out: left of sinus = upper lip; right of sinus = lower lip; AC = lower lip length; AB = lower teeth length; DF = upper lip length; DE = upper teeth length; the calyx throat is below FC.

Characters 33 and 34. 33. Length of upper calyx lip (mm).

34. Length of lower calyx lip (mm).

Characters 35 and 36. 35. Length of upper calyx lip teeth (mm).

36. Length of lower calyx lip teeth (mm).

The terms "lip", "lobe" and "teeth" have been used rather imprecisely in the past, leading to the misapplication of the terms "actinomorphic" and "zygomorphic". The lip refers to that portion of the calyx distal to the tube, often divided into an upper and lower, as is always the case in Satureja s.l., separated by a distinct sinus (see figure App. 6h). The use of the term "lobe" is incorrect when applied to the whole lip. "Lobe" may be used when it refers to a rounded sub-division of the lip, in distinction to pointed subdivisions when the term "teeth" are preferable. The teeth of the upper and lower lips are ± of the same length in all species of Satureja s.l. If the upper and lower lips and teeth are all of the same length, then the calyces are said to be actinomorphic. In such calyces there are 5 planes of symmetry. If the upper and lower lips and/or teeth are of different lengths then the calyx is said to be zygomorphic. A zygomorphic calyx has only one plane of symmetry. Using such a precise definition of actinomorphy, very few species of Satureja s.l. have truly actinomorphic calyces.

Characters 37 and 38. 37. Upper calyx teeth shape.

38. Lower calyx teeth shape.

1. Narrowly triangular to setaceous/ 2. Lanceolate-subulate/ 3. Deltoid or broadly triangular/ 4. Lanceolate, but not subulate.

1. Narrowly triangular to setaceous - teeth much longer than broad, the sides straight or concave, or the teeth rigid filiform, the very base broad but quickly narrowed. See figure

App. 8a.

2. Lanceolate-subulate - the tooth base lanceolate, ending in a long, sharp point. See figure App. 8b.

3. Deltoid or broadly triangular - teeth about as long as broad, the sides concave or straight, without a sharp pointed apex. See figure App. 8c.

4. Lanceolate, not subulate - teeth lanceolate but the apex obtuse or sub-obtuse, without a sharp seta at the apex. See figure App. 8d.

Character 39. Hairs on outside of calyx tube. 1. Absent/ 2. Only simple micro-hairs/ 3. At least some hairs long, simple/ 4. Long dendritic/ 5. Stellate.

See the descriptions of the hair types for characters 14 and 15.

Character 40. Calyx throat hairs. 1. Absent/ 2. With a dense fringe of hairs/ 3. With a sparse fringe of hairs.

These hairs are situated on the inside of the calyx tube but confined to just below the mouth of the tube.

2. With a dense fringe of hairs - with at least two rows of hairs which are tightly packed together giving the impression of a continuous band at the calyx throat.

3. With a sparse fringe of hairs - the hairs few or with distinct spaces between the hairs, not giving the impression of a tight continuous band at the calyx tube mouth.

Fig. App. 7. Calyx tube ampliation. (a) Parallel-sided cylindrical; (b) Slightly ampliate; (c) Ampliate; (d) Broadly ampliate; (e) Obconical.

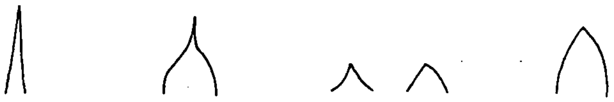


Figure App. 8. Calyx teeth shape. (a) Narrowly triangular to setaceous; (b) Lanceolate-subulate; (c) Deltoid and broadly triangular; (d) Lanceolate, but not subulate.

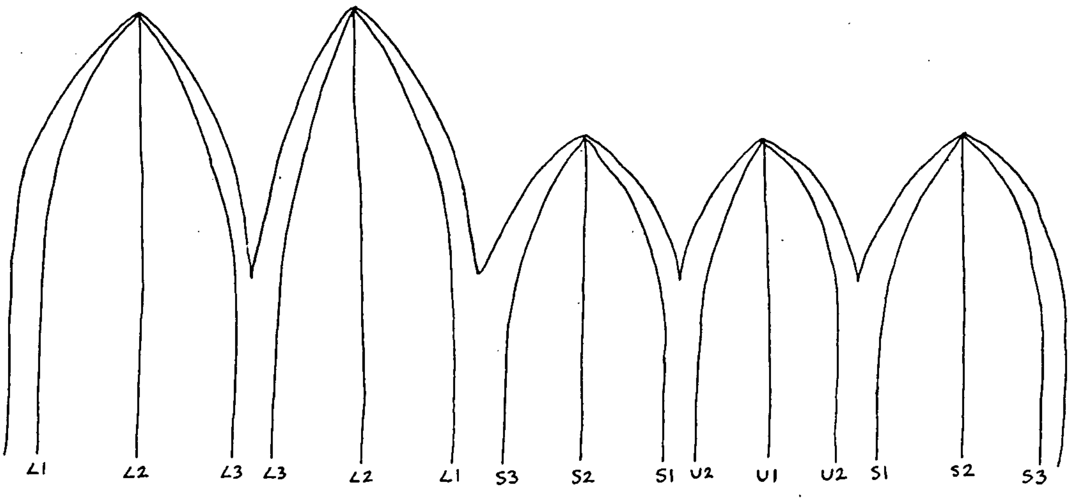


Figure App. 9. Calyx tube veins.

Character 41. Lower teeth ciliation. 1. Teeth ciliate/ 2. Teeth not ciliate.

1. Teeth ciliate - the cilia are usually long hairs quite distinct from the other hairs of the calyx, on the margins of the lower teeth, ± equally spaced out in a single row.

2. Teeth not ciliate - hairs on the teeth, if any, not different from the other calyx hairs.

Character 42. Glands on calyx. 1. Absent/ 2. Sunken/ 3. Sessile or sub-sessile.

These glands are similar in structure to the punctate leaf glands.

2. Sunken - see under Character 18 - 4. Sunken.

3. Sessile or sub-sessile - see under Character 18 - Very shortly stalked - and 3. Sessile, which are here taken together under one category.

Characters 43 and 44.

For each of the five calyx teeth the basic number of veins is three so that the calyx may be up to 15-veined in Satureja s.l. However, in the great majority of species there are fewer than 15 veins on the tube due to veins uniting at different heights up the tube.

Since the veins are always symmetrical about the plane through the centre of the uppermost tooth and the sinus between the two lowermost teeth, there are only eight distinct veins. The veins of the upper lip's central tooth are designated U1 and U2, the three veins of the two side teeth of the upper lip, S1, S2 and S3, and the veins of the lower lip teeth L1, L2 and L3 (see figure App. 9).

Character 43. Veins U2 and S1.

Character 44. Veins S3 and L1.

1. United to the very top/ 2. United to near the top or middle/ 3. United near the bottom or just at the top or not at all.

1. United to the very top - diverging only at the sinus between the teeth.

2. United to near the top or middle - diverging somewhere between half way up the tube and below the sinus of the two teeth.

3. United near the bottom or just at the top or not at all - the veins diverging below the middle of the tube, or not united at all. Rarely the veins are ununited for the whole length of the tube but bridge across at the sinus to meet but then diverge into their appropriate teeth.

Character 45. Hairs inside the tube. 1. Absent/ 2. Present.

This character refers to hairs, if any, that are on the inside of the calyx tube below the throat, i.e. excluding any hairs of the annulus.

2. Hairs present - the hairs are very small and high magnification (> x20) is necessary to see them.

Corolla Characters.

The states of all the following corolla characters should be determined from fully fertile, fully opened flowers.

Character 46. Length of the corolla tube (mm).

The length should be measured from the base of the tube to the sinus between the upper and lower lips taking account of any corolla curvature. Particular attention should be paid to the flower's fertility since infertile flowers are generally much smaller than fertile flowers.

Character 47. Length of upper corolla lip (mm).

The length is measured perpendicularly from a line drawn across the sinuses to the apex of one of the lobes if divided, or to the apex of the lip if entire. See also the note for Character 46.

Character 48. Length of lower corolla lip (mm).

The length is measured perpendicularly from a line across the sinuses to the apex of the central lobe or to the apex of one of the lobules of the central lobe if bifid. See also the note for Character 46.

Character 49. Upper lip lobes. 1. Emarginate/ 2. Retuse/ 3. Entire.

1. Emarginate - lip with a distinct notch in the middle. See figure App. 10a.

2. Retuse - lip with a shallow depression in the middle. See figure App. 10b.

3. Entire - lip apex a complete rounded arc. See figure App. 10c.

Character 50. Lower central lobe. 1. Entire/ 2. ± Bifid with two lobules.

1. Entire - the lower central lobe not itself lobed.

2. ± Bifid with two lobules - the middle lobe clearly emarginate (rare) or retuse (frequent).

Character 51. Corolla annulus. 1. Present/ 2. Absent.

1. Present - the annulus is a distinct ring of hairs on the inside of the corolla tube approximately half way between the base and the throat.

2. Absent - the hairs not in a distinct ring, though the inside of the corolla tube may be densely hairy.

Character 52. Corolla resupination. 1. Resupinate/ 2. Not resupinate.

1. Resupinate - the corolla tube is twisted about 180° so that the real upper lip appears to be the lower lip. This is most readily determined by removing the corolla from the calyx, soaking in water, attaching it to a slide and holding it up to the light. The nine main veins of the tube will be seen to cross over one another in a spiral fashion (see figure b, Mandenova & Schengelia, 1953).

2. Not resupinate - the corolla tube not twisted.

Character 53. Hairs on inside lower half of corolla tube. 1. Glabrous/ 2. Sparsely hairy/ 3. Hairy/ 4. Densely hairy.

2. Sparsely hairy - a few hairs only present.

3. Hairy - many hairs present with clear spaces between the hairs.

4. Densely hairy - hairs very dense, entirely hiding the inside lower half of the corolla tube surface.

Observations of these hairs should be made in corolla dissections that are as dry as possible. When there are only a few hairs, they stick to the side of the corolla if wet rendering them very difficult to see.

Character 54. Corolla colour. 1. Red, or red with yellow, or various shades of red/ 2. Various shades of purple or blue/ 3. White, or mainly white/ 4. Yellow.

Ideally the corolla colour should be determined from living specimens. The colours tend to change on drying. The red coloured flowers tend to become much darker in colour. Those corollas with yellow mixed with red lose the yellow colour entirely. Purple flowers often fade so that a very light purple may appear white in dried corollas. For this reason, although white flowers do not lose their colour, one cannot be certain if an apparently white flower was white or light purple. In poorly dried specimens, white flowers may become brown.

Stamen Characters.

All stamen characters have been determined for fully fertile stamens only.

Character 55. Stamen insertion. 1. Posterior inserted below anterior stamens/ 2. Anterior inserted below posterior stamens/ 3. All stamens inserted at the same level.

The point of insertion of the stamen is the point that the base of the filament joins with the corolla tube. In a few cases the lower part of the filament is adnate with the corolla tube for a short distance. The point of insertion is still taken to be the very base of the filament, and not the point where the filament separates from the corolla.

Characters 56 and 57. 56. Posterior stamen filament length (mm).
57. Anterior stamen filament length (mm).

The measurement is made from the point of insertion to the base of the anther connective.

Characters 58 and 59. Stamen exsertion.

The exsertion of the stamens is measured relative to the corolla tube and apex of the upper lip.

Character 58. Posterior stamens.

Character 59. Anterior stamens.

1. Included in the tube - the anthers of both stamens not projecting beyond the level of the sinus between the upper and lower corolla lips.

2. Exserted, but not beyond upper lip - the anthers of both stamens projecting out of the tube beyond the level of the

sinus between upper and lower lips, but not beyond the apex of the upper corolla lip.

3. Exserted beyond the upper lip - the anthers of both stamens projecting beyond the apex of the upper corolla lip.

Character 60. Anther divergence. 1. ± Parallel/ 2. Divergent/ 3. Widely divergent.

The angle between the inner margins of each anther lobe was measured only in anthers which were shedding pollen.

1. Parallel - the angle between the anthers < 15° (i.e. one third of a 45° angle).

2. Divergent - the angle between the anthers > 15° but < 90°.

3. Widely divergent - the angle between the anthers > 90°.

Character 61. Anther fertility. 1. All fertile/ 2. Posterior sterile, anterior fertile/ 3. Anterior sterile, posterior fertile/ 4. All sterile.

Anther fertility is not so easy to determine as one might at first think. Even if an anther is shedding pollen, one still does not know if the pollen is fertile. However, although this may be so, "anthers fertile" here means any anther which is shedding pollen and "anthers sterile" means anthers not shedding, and will never shed, pollen. Sterile anthers are usually much reduced in size and supported on much reduced filaments, making them easy to spot. In the case where on one stamen one anther is fertile and the other sterile, the stamen is counted as fertile.

Character 62. Stamen curvature. 1. Convergent/ 2. Straight or parallel/ 3. Divergent.

1. Convergent - either the upper or lower stamen pair filaments curving toward one another.

2. Straight or parallel - the filaments of either the upper or lower stamens straight, not curving away or toward one another. The stamens may point toward or away from each other but the filaments are straight.

3. Divergent - the filaments of either the upper or lower stamens curving away from one another.

Style Characters.

Character 63. Style length (mm).

The length is measured from the point at which it is connected to the ovary to the tips of the stigma lobes, if equal, or to the longer lobe if unequal.

Character 64. Stigma lobes relative length. 1. ± Equal/ 2. Unequal/ 3. Very unequal.

Only the styles of fully fertile flowers should be observed since male sterile flowers in gynodioecious species may differ in the stigma relative lengths.

1. ± Equal - the stigma lobes equal or very slightly unequal.

2. Unequal - one stigma (always the lower) up to two times the

length of the other.

3. Very unequal - lower stigma lobe at least twice as long as the upper.

Character 65. Stigma lobe shape. 1. Very narrow subulate/ 2. One very broad lanceolate, the other narrow subulate/ 3. Both broad lanceolate/ 4. Both very short and stubby.

See figures App. 11a-11d.

Nutlet Characters.

Character 66. Nutlet shape in outline. 1. Oblong/ 2. Ovate or obovate/ 3. Sub-orbicular to orbicular.

1. Oblong - sides of the nutlets parallel, and the length longer than the width (see Pl. 12.10).

2. Ovate or obovate - the nutlet broader at the base than toward the apex, or vice versa, and longer than broad (see Pl. 17.3).

3. Sub-orbicular to orbicular - the nutlets a sphere or a slightly flattened sphere (see Pl. 16.1).

Character 67. Nutlet hairs and glands. 1. Non-glandular hairy/ 2. Glabrous/ 3. Glandular hairy/ 4. With sessile glands.

Even with a good binocular microscope (x20) the nutlet hairs are difficult to see. A light source should be placed at such an angle so that light is reflected from the surface on which the nutlets are placed. In this way a back lighting effect is produced. This technique makes the hairs more easy to see. The hairs may be confined to the apex or cover the entire surface except the hilum.

Character 68. Nutlet surface. 1. Reticulate/ 2. Tuberculate/ 3. Smooth.

1. Reticulate - surface with a netted appearance at x20 magnification. The majority of the species which appear to have a smooth surface do, in fact, when studied with the SEM, have a reticulate surface. In rare cases this reticulation may be visible at low magnification.

2. Tuberculate - the surface entirely covered with small, rounded protuberances. This is a rare condition in *Satureja* s.l.

3. Smooth - without any apparent sculpturing at x20 magnification, though, as can be plainly seen from the SEM photographs, most species have, in fact, a reticulate sculpturing of the surface.

Character 69. Nutlet apex. 1. Blunt or obtuse/ 2. Rounded/ 3. Apiculate to sub-apiculate.

1. Blunt or obtuse - see Plate 17.3.

2. Rounded - see Plate 18.14.

3. Apiculate to sub-apiculate - see Plates 7.8 and 12.10.

Chromosomes

Character 70. Chromosome number (2n).

All the chromosome numbers have been extracted from the literature. The counts taken from pollen have been doubled.

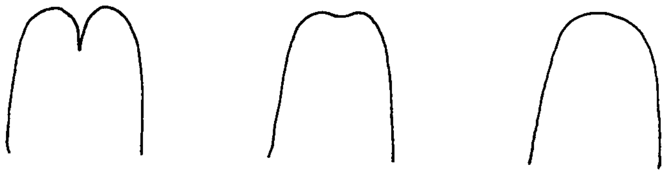


Figure App. 10. Upper corolla lip. (a) Emarginate; (b) Retuse; (c) Entire.

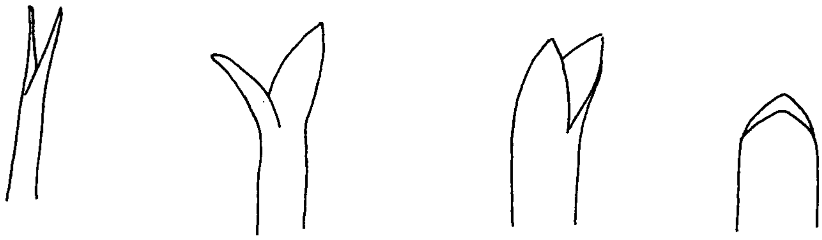


Figure App. 11. Stigma lobe shape. (a) Very narrow subulate; (b) One very broad lanceolate, the other narrow subulate; (c) Both broad lanceolate; (d) Both very short and stubby.

		montana	cuneifolia	obovata	cilicica	wiedemanniana	parnassica	athoa	pilosa	icarica	amani
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	3	3	3	3	4	4	4	4	4
Stems	3.	7-40(-70)	10-50	15-45	15-30	6-15	4-11(-15)		7-23	5-10	8-15
	4.	2	2	2	2	2	2		2	2	2
	5.	2	2-4		2	1	1-4		2	2	2-4
Leaves	6.	8(-3)	8	3-4	6-8	3-8	3-4		3-8	8	8
	7.	1	1	1	1	1	1	1	1	1	1
	8.	2	2	2	2	2	2	2	2	2	2
	9.	1-2	1(-2)	2-3	2(-1)	1-2	2-3		1-2	1	1
	10.	2	2	2	2	2	2		2	2	2
	11.	2	2	2	2	2	2		2	2	
	12.	1(-2)	1	1	1	2-1	1		1-2	1	1
	13.	0-0.5	0	0	0	0	0		0-1.5	0	0
	14.	1(-2)	3	3	3	3	3		3	3	3
	15.	1(-2)	3	3	3	3	3		3	3	3
	16.	2	2-1	1	1	1	1		1	1	1
	17.	3	3	3	3	3	3		3	3	3
	18.	4	4	4	4	4	4		4	4	4
	19.	1	1			1	1				
	20.	8.0-41.0	5.0-19.0	2.0-10.0	10.0-23.0	6.0-14.0	2.5-7.5		8.0-21.0	6.0-18.0	10.0-15.0
	21.	1.0-9.7	1.2-4.5	0.7-4.0	2.0-6.0	2.0-5.0	1.0-3.2		2.3-8.0	2.0-4.0	2.0-3.5
Inflorescence	22.	1-7	1-3	1-4	1-3	1-3	1		1-3	1	1
	23.	1-3	2	2	3	2	2		2	1-2	2
	24.	4	2-4	1-2	2-4	4	4		4	4	4
	25.	0.5-9.0	0.4-0.8	0.2-1.5	0.5-4.0	0-0.2	0-0.6		0.2-1.5	0-0.1	1.0-1.1
	26.	0.5-1.5	0.2-0.5	0.6-1.5	0.5-2.0	0-0.2	0.2-0.6		0.2-1.7	0-0.1	0.5-0.9
	27.	3	3	4	3	3	4		2	3	4
	28.	2.6-4.5	0.8-2.5	0.7-1.7	0.5-2.5	2.5-4.5	2.0-2.7		1.5-3.0	2.3-3.4	1.6-3.4
Calyx	29.	3-4	3		3	2-3	3-4		3		3
	30.	1	1	1	1	1	1		1	1	1
	31.	1.0-5.0	0.8-3.0	1.5-2.4	1.4-1.8	1.4-2.0	1.7-2.0		2.5-2.8	1.5-2.4	1.8-2.0
	32.	2	2	2	2	2	2		2	2	2
	33.	1.0-4.0	0.8-3.0	0.7-1.7	1.0-1.5	1.5-2.0	1.7-2.0		1.8-2.0	1.3-1.4	1.8-2.0
	34.	1.0-4.5	0.8-3.0	0.7-1.7	1.0-1.5	1.5-2.0	1.7-2.0		1.8-2.3	1.3-1.4	1.8-2.0
	35.	0.9-3.8	0.6-2.5	0.3-1.3	0.7-1.2	1.0-1.8	1.2-1.5		1.3-1.5	0.9-1.0	1.3-1.5
	36.	1.0-4.5	0.8-3.0	0.7-1.7	1.0-1.5	1.5-2.0	1.5-1.8		1.7-2.1	1.3-1.4	1.8-2.0
	37.	1	1	3	3	1	1		1	2	1
	38.	1	1	1	1	1	1		2	2	1
	39.	3	3	3	3	3	3		3	3	3
	40.	3	3	3	3	3	3		3	3	3
	41.	1	1	+1	+1	1	1		1	2	2
	42.	3	3	2-3	3	2	3		2-3	2	2
	43.	1	1	1	1	1	1		1	1	1
	44.	2	2-3	2	3	1	1		2	1	2
	45.	1	1	1	1	1	1		1	1	1
Corolla	46.	2.0-11.0	3.0-7.5	3.5-4.5	4.6-6.0	4.0-7.0	4.0-4.8		5.0-6.8	3.6-5.0	4.9-5.1
	47.	2.0-3.0	2.0-2.6	1.5-2.2	1.5-2.8	2.0-2.5	1.3-1.5		2.4-2.6	1.6-2.2	2.5-2.8
	48.	2.5-4.0	2.3-2.6	1.5-2.0	1.5-2.5	2.0-2.2	1.8-2.0		2.5-3.0	1.6-2.2	2.5-2.8
	49.	2-3	1	2	1	1	1		1	1	1
	50.	1	1	1	1	1	1		1	1	1
	51.	2	2	2	2	2	2		2	2	2
	52.	2	2	2	2	2	2		2	2	2
	53.	1(-2)	1	1	1	1	1		1	1	1
	54.	3	3	(2-)3	3	3	3		3	3	3
Stamens	55.	2	2	2	2	2	2		2	2	2
	56.	1.5-3.4	2.4-2.5	c.1.9	c.3.0	c.2.3	c.2.2		c.2.7	c.3.0	c.2.4
	57.	2.6-5.4	3.5-4.0	c.3.0	c.4.0	c.4.0	c.2.7		c.5.0	c.4.3	c.3.8
	58.	2	2	2	2	2	2		2	2	2
	59.	3	3	2	3	2	3		3	3	3
	60.	2	2	2	2	2	2		2	2	2
	61.	1	1	1	1	1	1		1	1	1
	62.				1	1			1		
Style	63.	4.0-14.0	5.5-10.0	5.0-6.0	6.0-7.5	6.5-9.5	8.0-9.4		7.5-9.0	5.1-6.5	5.5-6.0
	64.	1	1	1	1	1	1		1(-2)	1	1
	65.	1	1	1	1	1	1		1	1	1
Nutlets	66.	1-2	2	1-2	2	2-1	1			1	
	67.	3+4	3	3	3	3	3			3	
	68.	3	3	3	3	3	3			3	
	69.	2	2	2	2	1	2			2	
2n	70.	30, 12		30							

		spinosa	mutica	boissieri	bachtiarica	sahendica	metastasiantha	edmondii	isophylla	rumelica	intermedia
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	4	2	2	3	3	3	3	4	4	3
Stems	3.	3-12	30-50	40-60	12-90	25-50	20-70	15-40	5.0-10.0	10-20	10-25
	4.	2	2	2	2	2	2	2	2	2	2
	5.	2-4	2-4	2			1(-2)	3(-1)	1		1
Leaves	6.	8-3	3-8	5-8	8	8	9-8	9-6	3-8	4	4
	7.	1	1	1	1	1	1	1	1	1	2
	8.	2	2	2	2	2	2	2	2	2	2
	9.	1-2	2	1(-2)	1(-2)	1	1	1-2	1-2	2	2
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2		2		2	2	2	2		
	12.	2	1	1	1	1	1	1	2		1
	13.	0	0-0.5	0-1.0	0-0.3	0-0.3	0.2-1.0	0.2-0.4	0		0-1.0
	14.	3	1(-3)	3	3	3	1-3	3	2		3
	15.	3	1(-3)	3	3	3	3	3	2		3
	16.	2	+1	1	1	1	1	1	1		1
	17.	3	3	3	3	3	3	3	3		3
	18.	4	4	4	4	4	4	3	4	4	4
	19.	1	1								
	20.	1.0-10.0	14.0-18.0	11.0-24.0	4,0-9.0	8.0-15.0	8.0-18.0	6.0-16.0	6.0-10.0	c.15.0	8.0-15.0
	21.	0.7-3.0	2.5-6.5	2.5-7.5	1.2-2.2	2.0-3.3	2.0-5.0	1.7-6.3	1.6-4.0	c.5.0	2.5-5.0
Inflorescence	22.	1	1-4	1-8	1-3	1-4	1-7	1-3	1-3	3-5	1
	23.	3	3	3	1	1	3	3	3	2	2
	24.	1-2	1-2	1	1-3	1-2	1-2	1-3	4		4
	25.	0.4-1.0	2.3-6.7	4.0-9.0	0-1.2	0-0.1	1.0-6.7	0.5-2.5	0.2-1.5		0.5-1.5
	26.	0.4-1.0	0.4-0.8	1.0-2.3	0.2-0.8	0-0.3	0.4-2.4	0.5-1.2	0.2-0.6		0.2-0.8
	27.	4	4	4	4	3	2	3	3		4
	28.	2.0-3.0	0.5-1.5	1.5-3.0	1.5-3.5	1.0-1.5	1.0-1.5	1.0-2.2	1.0-4.2		3.8-5.5
Calyx	29.	3	3	3-4		2-3	3	3	2-3		2-3
	30.	1	1	1	1	1	1	1	1		1
	31.	1.7-2.0	1.9-2.2	2.0-2.4	1.3-2.0	2.6-3.0	1.0-2.0	2.2-3.2	2.3-2.5		3.0-3.8
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.0-1.2	1.3-1.9	1.7-2.0	1.0-1.3	1.4-1.6	0.7-1.5	1.7-2.2	0.8-1.2		2.5-3.2
	34.	1.0-1.2	1.9-2.7	2.5-2.8	1.2-1.7	2.0-2.6	0.9-1.7	1.7-2.2	1.0-1.2		2.8-3.5
	35.	0.8-0.9	0.8-1.6	1.2-1.3	0.6-0.8	1.0-1.2	0.4-1.1	0.7-1.5	0.6-0.8		2.0-2.8
	36.	1.0-1.2	1.9-2.9	2.5-2.8	1.2-1.7	2.0-2.6	0.9-1.7	1.7-2.2	1.0-1.2		2.8-3.5
	37.	1	2	1	3	3	1	1-3	1		1
	38.	2	1	1	1	1	1	1-2	1	1	1
	39.	3	3	3	3	3	3	2	2		3
	40.	3	3	3	3	3	+1	1	3	3	3
	41.	2	1	1	2	2	2	2	2		1
	42.	2-3	3	3	3	3	3	3	3		3
	43.	1	1	1	1	1	1	1	1	1	1
	44.	2	3	2	3		2	2-3	3	2	2
	45.	1	1	1	1	1	1	1	1		1
Corolla	46.	3.0-5.0	4.0-4.5	5.0-6.0	3.5-4.0		3.0-5.6	7.0-10.0	4.5-5.0		5.2-6.3
	47.	1.5-1.7	1.5-1.7	2.0-2.2	1.2-1.3	c.12.0	1.3-1.6	1.0-2.5	1.6-2.2		1.5-2.2
	48.	1.7-2.0	2.2-2.6	2.5-3.0	1.2-1.3		1.3-2.2	1.0-2.5	2.0-3.5		2.3-2.8
	49.	1-2	1	1	2		1		2		1
	50.	1	1	1	1		2		1		1
	51.	2	2	2	2	2	2	2	2		2
	52.	2	2	2	2	2	2	2	2		2
	53.	1	1	1	1		1		1		1
	54.	3	3	3	3	2-3	3	2	3		2
Stamens	55.	2	2	2	2		2		3		2
	56.	c.2.6	c.1.5	c.2.0	c.1.3		c.2.0		c.2.0		c.1.8
	57.	c.4.0	c.2.6	c.3.0	c.2.5		c.2.4		c.3.5		c.3.0
	58.	2	2	2	2	2	2		2		2
	59.	3	3	3	3	3	2-3	2	3		3
	60.	2	2	2	2	2	2	2	2		2
	61.	1	+2	1	1		1	1	1		1+3
	62.			1			1		1		1
Style	63.	3.5-5.5	4.0-4.5	8.5-10.0	5.0-6.0		4.5-8.0	c.11.0	5.5-6.5		8.0-10.5
	64.	1	2	1	1	1	2		1		1
	65.	1	1	1	1	1	1	1	1		1
Nutlets	66.	2	2		1	1	1	1	1		
	67.	3	3	3	3	1-3	3	3	4		3
	68.	3	3		3	3	3	3	3		
	69.	2	2		1	1	2	1	1		
2n	70.										

		macrantha	bzybica	aintabensis	azerbaijanica	spicigera	coerulea	thymbra	salzmannii	hortensis	Gontscharovia
Habit	1.	2	2	2	2	2	2	2	2	1	2
	2.	3	3	3	3	3	3	4	4	2	4
Stems	3.	15-40	15-25	10-15	20-35	10-45	10-20	20-100	5-30	5-35	20-30
	4.	2	2	2	2	2	2	2	2	2	2
	5.	1-2	+2	1	3	2-4	2	2-4	2-4		1
Leaves	6.	9-5	(7-)9	5	5-8	5-8	5-7	3	5-4	5-8	9
	7.	1	2	1	1	1	1	1	1	1	1
	8.	2	2	2	2	2	2	2	2	2	1
	9.	1	1	2	1	1	1-2	1	3	1	1
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2			2	2	2	2		2
	12.	1	2	1	1	1	2	1	1	1	2
	13.	0(-1.0)	0	0(-0.5)	0	0-0.5	0	0-1.0	0	0-1.0	c.0.5
	14.	3	1	3	1	+1	1	3	1	3	2
	15.	3	1	3	1	+1	1	3	1	3	1
	16.	1	1	1	1	1	2	1	2	1	1
	17.	3	NA	3	NA	3	3	3	3	3	3
	18.	4	4	4	4	4	4	4	4	4	4
	19.	1	1	1		1	1	1	1	1	1
	20.	8.0-30.0	15.0-25.0	8.0-11.0	15.0-20.0	6-25(-37)	7.0-21.5	5.0-20.0	5.0-8.5	8.0-30.0	8.0-12.0
	21.	1.0-7.5	4.6-9.5	0.8-1.8	2.0-3.0	1.0-2.5	0.7-2.0	1.0-9.0	0.7-1.3	1.0-4.5	2.0-4.0
Inflor-escence	22.	1-3	3-6	1	3-4	1-3	1-2	3-17	1	1-10	1-6
	23.	3	3	3	2	3	2	1	2	2	2
	24.	1-2	4	1-2	2-4	2-4	4	1-2	4	1-4	
	25.	0.1-8.5	1.0-5.0	1.7-3.2	1.5-7.0	0.4-2.5	0.2-0.7	0.8-1.0(-3	0-0.2	0.5-5.0	0.5-2.0
	26.	0.8-3.0	0.7-1.5	0.5-0.7	0.3-0.7	0.5-1.5	0.2-0.4	0.3-0.6	0-0.2	0.5-1.0	0.5-1.0
	27.	3	2	3	3	3	4	4	4	3	2
	28.	1.0-2.0	3.5-8.5	1.5-2.0	1.3-2.7	0.4-1.6	2.5-5.0	5.0-9.0	3.5-6.0	1.0-2.5	2.0-4.0
Calyx	29.				3-4	3-4		3-4	3		3
	30.	1	1	1	1	1	1	1	1	1	1
	31.	1.7-3.5	3.4-4.0	1.5-1.7	1.8-2.6	1.5-1.8	2.0-3.3	2.0-3.5	3.0-3.3	1.0-1.6	2.5-3.0
	32.	2	2	2	2	2	2	2	2	2	2
	33.	0.7-2.4	4.5-5.0	c.1.4	1.0-1.4	1.3-1.5	1.1-2.2	2.0-3.8	1.6-1.8	1.8-2.9	c.1.0
	34.	1.0-2.7	5.0-5.5	c.1.5	1.0-1.4	1.3-1.7	1.3-2.3	2.0-3.8	1.6-1.8	1.8-2.9	c.1.0
	35.	0.5-1.6	4.0-4.2	c.1.0	0.8-1.2	0.6-1.0	1.1-2.2	2.0-3.8	1.3-1.5	1.4-2.5	c.1.0
	36.	1.0-2.7	5.0-5.5	c.1.5	1.0-1.4	1.3-1.7	1.3-2.3	2.0-3.8	1.6-1.8	1.8-2.9	c.1.0
	37.	1	1	1	1	3	1	2	4	1	1
	38.	1	1	1	1	1	1	2	4	1	1
	39.	3	1(-3)	3	2(-1)	3	3	3	1	3	3
	40.	3	3	3	3	3	3	1	3	1	1-3
	41.	2	2	2	2	1	2	1	1	1	2
	42.	2	2	2	3	2-3	3	2-3	2-3	2-3	3
	43.	1	1	1	1	1	2	1	1	1	3
	44.	2	3	2	2	3	3	3	1	3	2-3
	45.	1	1	1	1	1	1	1	1	1	
Corolla	46.	8.5-13.5	c.10.0	3.2-3.4	3.6-4.8	5.0-7.0	4.0-7.0	6.0-8.5	3.5-5.5	3.0-7.0	c.4.0
	47.	1.3-1.7	3.0-3.5	c.1.0	1.6-2.1	2.0-2.6	1.5-2.6	2.0-4.0	2.0-2.5	0.8-1.3	c.1.0
	48.	1.5-3.0	4.0-5.0	c.1.6	c.2.8	2.5-4.0	1.5-2.6	4.0-6.5	2.0-2.5	1.5-2.5	c.2.0
	49.	1	1	1	2	2-3	2-1	1	1	2-3	1
	50.	1	1	1	1	1	1	1	1	1	+1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1	1	1	1	1	1	1	1	1	
	54.	2	2	2		3	2	2	3	2	2
Stamens	55.	1	2	2	2	2	2	2	1	2	
	56.	c.1.3	c.3.5	0.5-0.6	c.2.0	c.4.0	c.3.0	c.2.4	1.2-1.3	c.0.6	c.1.0
	57.	c.2.0	c.6.0	c.1.0	c.3.0	c.5.5	c.4.5	c.4.2	1.5-1.6	c.1.4	c.1.5
	58.	1	2	1	2	3	2	2	2	1	1
	59.	2	2-3	2	2	3	3	2	2	2	2
	60.	2	2	2	2	2	2	2	2	2	2
	61.	1+4	1		1	1	1	1	1	1	1
	62.	1			1				1		
Style	63.	10.5-15.0			6.0-8.5	8.0-10.0	6.0-9.0		4.5-5.0	4.5-8.5	5.0-6.0
	64.	1			2	1	1	1	1	1	1
	65.	1			1	1	1	1	1	1	1
Nutlets	66.	1	2		1	2	1	2		1	1
	67.	3	4+3		3	3+4	3	3		3	
	68.	3			3	3	3				
	69.	2	1		2	2	2	1		2	3
2n	70.							30		45,46,48	

		filiformis	microphylla	acropolitana	hispida	marginata	croatica	nervosa	macrosiphon	fontanesii	weilleri
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	4	4	3	4	4	4	3-4	4	3	2-3
Stems	3.	5-25	10-30	10-30	10-30	8-20	7-20	5-50	15-100	18-45	20-40
	4.	2	2	2	2	2	2	2	2	2	2
	5.	(2)	2	2	1	1	1	2	2	1	1
Leaves	6.	2	2	6-7	2-7	2	2	2	3-5	2-7	2
	7.	1	1	1	1	1	1	1	1	1	1
	8.	1	1	1	1	1	1	3	3-4	1-3	3-4
	9.	2-3	2	2	2	2-3	1-3	1-2	1	1	2
	10.	1	1	1	1	1	1	1	1	1	1
	11.	2	2		2	2	2	2		2	2
	12.	2	2		2	2	2	2	1	2	2
	13.	0.3-1.0	0.3-0.5		0.5-1.0	0.4-1.3	0.4-1.0	0.5-1.2	0.5-1.0	0.5-1.7	0.5-1.0
	14.	1	3	3	3	1-2	3	3	3	(1-)3	3
	15.	1(-3)	3	3	3	1-3	3	3	3	3	3
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	3	3	3	3	3	3	3	3
	18.	3			3	4	3	4	3	4	4
	19.					2		2	2	2	
	20.	2.0-4.5	3.0-6.0	c.5.0	2.5-4.0	3.0-12.0	5.0-10.0	6.0-10.0	4.0-8.0	5.5-10.0	5.5-15.5
	21.	1.5-4.0	2.0-4.0	1.0-2.0	1.5-2.8	3.0-6.0	2.5-8.0	3.0-5.0	0.6-2.4	2.3-7.0	1.0-6.2
Inflorescence	22.	1-2	1-6	2-5	1-3	1-6	1-9	2-10	1	2-5	4-18
	23.	3	2	3	2	3	2	1-2	3	2-3	1
	24.	1	1		2-4	2	2-4	2-4	3-4	1-3	1
	25.	0	1.8-2.2		1.0-3.0	0.8-4.0	0.5-6.0	1.0-3.0	0.1-1.0	1.5-3.0	2.0-6.5
	26.	2.0-3.0	0.8-1.4	2.0-5.0	0.8-1.0	0.5-1.5	1.5-3.0	0.5-1.0	0.5-1.0	0.6-1.4	0.2-0.5
	27.	2	2		3	3	3	2	3	2	3
	28.	0.7-1.0	1.0-1.5		1.0-1.4	0.7-2.5	1.6-3.0	0.5-1.0	1.2-2.8	0.8-2.5	1.0-2.5
Calyx	29.	1	1		1	1	1	2	1	1	
	30.	1	1	1	1	1	1	1	1	1	1
	31.	2.0-2.4	2.0-2.4	1.8-2.0	2.0-2.4	3.5-4.5	2.5-3.0	1.5-2.3	4.0-5.2	1.8-2.2	1.5-1.7
	32.	+2	+2		2	2	2	2	2	1	2
	33.	1.1-1.3	0.9-1.3		1.0-1.5	1.7-2.0	1.8-2.2	1.3-1.5	1.4-1.8	0.7-1.0	0.6-1.0
	34.	1.5-2.0	1.0-1.5	0.9-1.0	1.0-1.5	2.0-2.5	2.4-2.7	1.3-1.8	1.4-1.8	0.7-1.0	0.6-1.0
	35.	0.7-0.9	0.6-1.0		0.6-1.0	1.2-1.7	1.8-2.2	1.0-1.3	0.7-1.0	0.5-0.7	0.5-0.7
	36.	1.5-2.0	1.0-1.5	0.9-1.0	1.0-1.5	1.9-2.5	2.4-2.7	1/3-1.8	1.4-1.8	0.7-1.0	0.6-1.0
	37.	1	1	1	1	1	1	1	3-1	3	1
	38.	1	1	1	1	1	1	1	1	1	1
	39.	2	3	3	3	3	3	3	3	3	3
	40.	2	3	3	3	+2	2	3	3	3	3
	41.	1	1	1	1	2	1	1	2	+2	1
	42.	3	3		3	3	3	3	3	3	3
	43.	2	2		1	2	2	1	1	1	1
	44.	3	3		3	3	3	3	3	3	3
	45.	1	1		1	1	1	1	1	1	1
Corolla	46.	3.0-3.5	4.8-5.0	4.8-5.0	4.0-5.0	10.0-14.0	6.5-10.0	3.6-5.0	9.5-11.0	2.5-3.2	c.2.5
	47.	0.9-1.1	c.1.5	c.1.5	c.1.5	1.5-4.0	1.5-2.0	0.7-1.0	1.5-2.5	0.6-0.8	c.0.5
	48.	1.4-1.6	c.3.0	c.3.0	c.2.0	2.0-5.0	2.0-4.0	1.0-2.0	2.0-3.8	1.2-1.3	c.1.3
	49.	1	1		1	1	1	1	1	1	1
	50.	1	2		1	2	2	1	1	1	2
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1	1		1	1	1	1	1	1	1
	54.	3	2	2	2	2	2	2	2	2	
Stamens	55.	1	1		1	1	1	1	1	1	1
	56.	0.1-0.2	c.1.0		c.0.2	c.0.6	c.0.7	0.3-0.4	c.2.5	c.0.2	
	57.	0.3-0.4	c.1.8		0.5-0.6	c.0.8	c.1.5	c.1.2	c.3.2	c.0.5	
	58.	1	1		1	1	1	1	2	1	
	59.	1	2		2	2	2	2	2	1	
	60.	2	2		2	2	3	2	2	2	
	61.		1		1	1+4	1	1	1	1	1+4
	62.	1				1	1	1		1	
Style	63.				c.3.0	10.0-14.0			10.5-12.0	c.1.3	c.2.3
	64.	2	2	1	1	1	1	1	1	1	1
	65.	1		3	3	3	3	1	+3	+3	1
Nutlets	66.	1	1	2		1	1	2	1	1	1
	67.	1?	1	1		2	2	2	2	2	2
	68.	3					3	3	3	3	3
	69.	1	3	2		3	1	1	1(-3)	1(-3)	3
2n	70.		30,60					30			

		debilis	hochreutineri	brivesii	conferta	myrtifolia	juliana	cristata	kerneri	cremnophila	parviflora
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	3	3	4	3	4	3	3-4	3	3
Stems	3.	15-30	8-45	7-20	15-25	10-45	7-43	3-20	20-30	5-27	5-25
	4.	2	2	2	2	2	2	2	2	2	2
	5.	2(-1)	2		+2	2	1-2	1	1	1-2	2
Leaves	6.	2-7	2-5-7	7-2	(2-)7	2-5	5-7	2-7	5-7-2	9-6-2	6-5+1-2
	7.	1	1	1	1	1	1	1	1	1	1
	8.	3	3	4	4	3	4	4	4	4-3	4
	9.	1	1	2	+1	1	1-2	1	1	1-2	2-3
	10.	1	1	1	1	1	1	1	1	1	1
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	1	1	2	2	1	2	2	2
	13.	0.1-2.0	0.5-1.5	0.2-0.5	0.1-0.3	0.5-1.5	0.3-1.0	0.2-0.5	0.1-0.6	0.2-1.5	0.5-1.2
	14.	2-3	2(-3)	3	3	3	3	2+3	3	1-3	1
	15.	3	2(-3)	3	3	3	3	3	3	3	3
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	3	3	3	3	2	3	3	3
	18.	4	4	3	3	3	3	3	3	4	4
	19.					2	2	2			
	20.	2.7-9.0	3.0-10.0	4.5-7.0	3.5-7.0	5.0-11.0	3.0-8.0	5.0-12.0	3.0-9.0	4.0-12.0	2.5-10.0
	21.	1.0-5.3	1.0-3.4	1.3-1.5	1.2-2.5	1.5-5.5	0.7-3.3	0.5-3.0	1.5-5.0	0.5-3.0	1.0-5.0
Inflorescence	22.	1-5	1-5	1-2	2-3	1-15	2-10	1-5	2-6	1-5	1-4
	23.	2	1-2	3	1	1-2	1	2	2	2-3	3
	24.	1-2	1-2	3-4	4	1-3	2-4	3-4	2-3	2	4
	25.	0.6-2.7	0.4-2.7	0-0.3	0.2-0.4	0.5-2.6	1.0-3.0	0.5-1.7	1.2-2.2	0.5-2.7	1.0-5.0
	26.	0.3-0.7	0.3-0.6	1.0-1.7	0.1-0.4	0-1.5	0-0.5	0.1-1.7	1.5-3.0	0.7-1.4	1.7-3.5
	27.	2	2	4	2-3	2	2	3	3	2	3
	28.	0.6-1.7	0.6-1.6	1.0-1.2	1.5-2.0	1.5-3.7	2.3-3.5	2.0-3.0	2.0-2.5	1.0-1.4	0.7-2.3
Calyx	29.	1	1		1	1	1	1	1	1	1
	30.	1	1	1	1	1	1	1	2	1(-2)	1
	31.	1.6-1.9	1.4-1.9	c.3.4	1.7-1.9	1.8-2.5	1.7-2.0	1.6-3.5	2.0-2.5	1.6-2.0	1.8-2.2
	32.	2	2	2	2	2	2	2	2	2	2
	33.	0.5-0.6	0.5-0.7	c.1.4	0.7-0.8	1.0-1.3	0.8-0.9	0.6-1.8	1.0-1.4	0.6-0.8	0.8-1.2
	34.	0.5-0.7	0.5-0.7	c.1.4	0.7-0.8	1.0-1.3	0.9-1.0	0.6-0.8	1.2-1.6	0.6-0.8	1.3-1.8
	35.	0.3-0.4	0.4-0.6	c.0.9	0.5-0.6	0.5-1.1	0.8-0.9	0.6-1.8	0.6-1.2	0.4-0.6	0.4-1.0
	36.	0.5-0.7	0.5-0.7	c.1.4	0.7-0.8	1.0-1.3	0.9-1.0	1.0-1.8	1.2-1.6	0.6-0.8	1.3-1.8
	37.	3	3	3	1	1	1	1	1	1	1
	38.	3	1	2	1	1	1	1	1	1	1
	39.	3	3	3	3	3	3	3	3	3	3
	40.	2	2	3	3	3	1	2	3	3	3
	41.	2	+2	2	2	1	1	2	1	2	1
	42.	3	3	3	3	3	3	3	3	3	3
	43.	1	1	1	1	1	1	3-2	1	2	1
	44.	3	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	2.3-2.4	2.4-3.2	c.8.0	3.0-4.3	3.0-3.7	3.0-3.5	2.5-7.5	2.5-4.0	2.0-3.4	3.0-3.5
	47.	c.0.6	c.0.6	c.2.5	1.0-1.3	0.9-1.0	0.7-1.2	1.0-1.3	c.1.0	0.7-0.9	0.8-1.7
	48.	1.0-1.2	c.1.5	c.2.7	1.5-2.0	1.1-1.3	0.7-1.5	1.5-2.0	c.1.5	1.0-1.3	2.5-3.0
	49.	1	1	1	1	1	1-2	1	1	1	1
	50.	1	1	1	1	1	1	+1	+1	1	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1	1	1	1	1	1	2	1	1	1
	54.	2	2	3?	2	2	2	2	2	2	2
Stamens	55.	1	1	2	1	1	1	1	1	1	1
	56.	0.1-0.2	0.1-0.2	c.2.2	c.0.2	c.0.6	c.0.3	c.0.5	c.0.3	c.0.2	c.0.2
	57.	0.3-0.4	0.3-0.4	c.2.7	c.0.7	c.1.2	c.1.1	c.1.6	c.1.0	0.4-0.5	c.0.3
	58.	1	1	2	1	1	1	1	1	1	1
	59.	1	1	2	2	2	2	2	2	1	1
	60.	2	2	2	2	2	3	2	2	2	1
	61.	1+4	1	1	1	1	1	1	1	1	1
	62.	1	1	1	1		1				
Style	63.	1.4-1.6	1.6-1.8	c.10.5	c.2.7	2.5-4.3	3.0-5.0	7.0-7.5	2.5-4.0	1.3-1.5	1.3-1.5
	64.	1	1	1	1	1	1	1	1	1	1
	65.	3	3	1	1	1	1	3	1	3	4
Nutlets	66.		1		2	1	1	1	2-1	1	1
	67.	2	2		2	2	2	2	2	2	2
	68.	3			3	3	3	3	3		
	69.		1-2		1	1	1	3	1	3	1
2n	70.					30	30	30		30	

		elliptica	persica	cypria	sinaica	hedgei	graeca	fruticulosa	inodora	cinerea	longiflora
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	3	3	3	3	3	4	4	3	4
Stems	3.	8-20	10-30	10-40	10-30	40-55	8-50	10-35	10-50	5-25	30-40
	4.	2	2	2	2	2	2	2	2	2	2
	5.	2	2	1	2	2	2(-1)	1	1	1	
Leaves	6.	9(-2-7)	9-7	2	2	2-9	2-5-7	2-5	5-7	2	2
	7.	1	1	1	1	1	1	1	1	1	1
	8.	3	3	1	3-4	1	3-4	4	4	3-4	3
	9.	1	1	1	2	1	1	+1	1	2	1
	10.	1	1	1	1	1	1	1	1	1	1
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	2	2	2	2	2	1	2	2
	13.	0.3-0.6	0-0.4	0.5-1.5	0.4-1.0		0.5-1.0	0.2-0.8	0-0.2	0.3-0.8	1.0-2.0
	14.	3	3	2-3	2-3	1	3	3	2-3	3	3
	15.	3	3	2-3	3	1	3	2-3	2	3	3
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	2	3	NA	3	3	3	3	3
	18.	4	3	3	3		4	4	3	3	4?
	19.						2				2
	20.	5.0-10.0	2.5-7.7	4.5-6.5	2.0-7.0	6.0-11.0	6.0-14.0	2.6-8.3	1.5-3.5	3.0-6.5	10.0-16.0
	21.	1.0-3.5	0.8-2.5	1.9-4.4	0.5-5.0	2.0-6.0	2.0-7.0	0.7-3.0	0.3-1.2	1.2-3.3	2.0-3.6
Inflorescence	22.	1-3	1-3	1-6	1-8	c.6	1-9	1-2	1	1-6	1-4
	23.	3	2-3	2-3	2		2-3	2-3	2	2	2
	24.	2	1-3	2-4	1-2		2-4	4	4	2-3	4
	25.	2.0-3.6	1.0-2.3	0.7-2.0	1.0-1.6		1.0-5.0	0.5-2.0	0	0.5-0.7	0.5-1.2
	26.	1.4-2.0	0.7-2.9	0.5-1.7	0.4-1.0	0.5-1.0	0.5-1.5	0.5-2.0	2.0-3.3	0.5-1.0	1.0-1.6
	27.	2	2	2	2	2	2	2	3	2	2
	28.	1.2-1.6	0.7-2.4	0.6-1.5	0.8-1.5	0.5-1.0	1.5-2.5	1.0-5.0	1.8-2.7	0.5-1.0	0.6-2.3
Calyx	29.	1	1	1	1	2			1	1	
	30.	1	1(-2)	1-2	1	1	1-2	+1	2	1	1
	31.	2.8-3.0	1.6-2.2	2.5-3.2	1.7-2.2	1.6-2.0	2.5-3.5	2.7-3.2	3.0-3.5	1.6-2.0	3.8-4.2
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.0-1.3	0.6-0.9	1.3-1.7	0.6-1.2	0.4-0.5	1.5-2.0	1.0-2.2	1.3-1.9	0.8-1.0	1.7-2.0
	34.	1.2-1.5	0.7-1.1	1.5-1.7	0.8-1.2	0.4-0.5	1.8-2.3	1.3-2.5	1.3-1.9	0.9-1.4	1.8-2.1
	35.	0.6-1.0	0.5-0.6	0.7-1.2	0.6-1.0	0.4-0.5	1.5-2.0	0.7-1.7	0.9-1.1	0.7-0.8	1.3-1.5
	36.	1.2-1.5	0.7-1.1	1.5-1.7	0.8-1.2	0.4-0.5	1.8-2.3	1.3-2.5	1.3-1.9	0.9-1.4	1.8-2.1
	37.	1	1	1-2	1	3	1	1	1-2	1	2
	38.	1	1	2	1	3	1	1	1	1	2
	39.	2-3	3	3	3	3	3	3	3	3	3
	40.	2	3	2-3	3		+2	+2	2	3	+2
	41.	+2	2	1	1		1	1	1	1	2
	42.	3	3	3	3		3	3	3	3	3
	43.	1	1	2	1	2	1	1	1	2	1
	44.	3	3	3	2-3	3	3	3	3	3	3
	45.	1	1	1	1		1	1	1	1	1
Corolla	46.	6.0-7.0	3.3-4.0	4.8-5.7	3.8-4.3		5.5-8.5	6.0-8.0	6.3-7.2	3.0-4.5	9.0-10.0
	47.	c.1.5	1.2-1.3	1.0-1.5	0.5-0.9		1.0-1.5	1.7-2.0	2.5-3.0	1.0-1.5	1.6-2.0
	48.	2.0-2.5	1.3-1.5	2.0-3.4	1.5-2.0		1.5-3.5	2.5-3.4	2.8-4.0	1.5-2.5	3.0-3.5
	49.	1	1	1	1		1	1	2	1	1
	50.	1	1	1	1-2		1	1	1	1	1
	51.	2	2	2	2		2	2	2	2	2
	52.	2	2	2	2		2	2	2	2	2
	53.	1	1	1	1		1	1	1	1	1
	54.	2	2	2	2		2	2	2	2	
Stamens	55.	1	1	1	1		1	1	1	1	1
	56.	c.1.2	c.1.0	c.1.6	c.0.4		c.0.5	c.0.8	c.2.5	c.0.4	c.0.6
	57.	c.1.7	c.1.1	c.2.5	c.1.2		c.1.5	c.2.5	c.3.0	c.1.5	c.2.4
	58.	1	1	2	1		1	1	2	1	1
	59.	2	2	2	2		2-3	2	2	2	2
	60.	2	2	2	2		2-3	2-3	2-3	2	2
	61.	1	1	1	1		1	1	1	1	1
	62.			1	1					1	
Style	63.	7.0-9.0	4.5-5.3	7.0-8.0	4.0-5.0		6.5-9.5	7.5-9.0	8.3-10.0	c.4.5	11.0-12.0
	64.	1	1	1	1		1	1	1	1	
	65.	1	1	1	1		1	1	1	1	
Nutlets	66.	1	2	2	1		2	2	2	1	
	67.	2	2	2	2		2	2	2	2	
	68.	3					3		3	3	
	69.	3	3	1-2	1		1(+3?)	1	2	3	
2n	70.						20,60		26,48		

		serbaliana	imbricata	contardoi	pineolens	leucantha	cymuligera	madagascarensis	flagellaris	sphaerophylla
Habit	1.	2	2	2	2	2	1	2	2	2
	2.	3	3-4	4	4	4	1	1	1	1
Stems	3.	5-20	5-25	2-5	50-100	15-50	4-25	15-50	40-70	25-70
	4.	2	2	2	2	2	2	2	2	2
	5.	1(-2)	2	2	1		2	2-3	1-4	1-4
Leaves	6.	2	7-2	2	7	6-7	2	5-6	2	1-2
	7.	1	1	1	1	1	1	1	1+2	1
	8.	3	1	1	4	4	1+3	1(-3)	3-4	1-3
	9.	2-3	1	2	1	1	1	2-3	(1-)2	+3
	10.	1	1	1	1	1	2	2	2	2
	11.	2	2	2?	2	2	2	2	2	2
	12.	1	2	1	2	2	2	1	1(-2)	2
	13.	0.1-0.6	0.4-0.6	0.4-0.7	1.5-2.0		1.0-3.5	0.2-0.6	0.2(-0.5)	0.3-0.6
	14.	2-3	+1	2	3	3	2	1	2(-3)	3
	15.	3	3	2	3		1	1	2(-3)	3
	16.	1	1	1	1	1	1	1	1	1
	17.	3	3	3	3	3	3	NA	3	3
	18.		3	4	3	2	3	4	3	3
	19.				2	2	2			
	20.	3.0-4.0	3.0-6.5	1.0-2.3	14.0-30.0	25.0-30.0	7.0-11.0	4.0-11.5	1.5-5.3	3.0-6.8
	21.	1.7-2.7	1.5-4.0	0.8-2.2	3.3-13.0	4.0-5.0	2.0-6.0	0.7-3.2	1.0-4.8	3.0-7.2
Inflorescence	22.	1-10	1-3	1	3-10	1-3	4-10	1	1	1
	23.	2	3	3	1	2	2	3	3	3
	24.	1-2	4	1-2	4	4	3-4	2-4	1-2	2-3
	25.	1.0-1.6	0-0.2	0.4-0.9	c.0.5		1.8-2.5	1.0-2.0	1.2-3.5	0.9-2.0
	26.	0.4-1.4	1.0-1.6	0.7-1.2	c.0.5	c.0.5	0.3-0.6	8.0-10.0	1.0-5.5	1.5-2.4
	27.	2	2	2	3	2	4	4	4	4
	28.	0.8-1.4	0.5-1.0	0.4-1.0	3.5-7.0	7.0-8.0	3.0-4.0	2.5-3.5	1.0-3.8	1.6-3.0
Calyx	29.		1-2		1			3	2-3	3
	30.	1	1-2	1	1	1	1	1	1(-2)	1
	31.	1.8-2.0	2.0-2.7	1.7-2.2	4.0-5.0	c.7.5	1.7-1.9	2.7-3.0	2.2-2.8	3.0-3.6
	32.	2	2	2	2	2	2	2	2	2
	33.	0.6-0.7	1.0-1.4	0.7-1.0	1.2-1.4	c.4.0	1.4-1.5	c.0.8	1.0-1.5	1.8-2.0
	34.	0.7-0.8	1.4-1.6	0.8-1.2	0.8-1.0	c.4.0	1.5-1.6	c.0.8	1.0-1.6	1.8-2.3
	35.	0.5-0.6	0.8-1.0	0.5-0.6	0.5-0.6	c.2.5	1.2-1.3	0.4-0.5	1.0-1.3	1.8-2.0
	36.	0.7-0.8	1.4-1.6	0.8-1.2	0.8-1.0	c.4.0	1.5-1.6	c.0.8	1.0-1.6	1.8-2.3
	37.	1	1	3	3	1	1	3	1	1
	38.	1	2-1	1	2	1	1	3	1	1
	39.	3	3	+2	3	3	3	3	2(-3)	3
	40.	2-3	2	3	3	1	3	1	1	1
	41.	1	1	1	2	2	1	2	2	2
	42.	3	3	3	3		3	3	3	3
	43.	2	2	1	2	2	1	1	1	3
	44.	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1
Corolla	46.	3.0-4.0	3.5-6.5		10.0-1.2.0	c.15.0	2.0-2.5	3.5-4.2	5.0-7.0	5.8-7.0
	47.	0.9-1.0	1.5-1.7		2.5-3.0	c.3.5	c.0.5	c.1.4	1.7-2.2	c.2.0
	48.	1.5-1.6	2.0-4.0		3.2-4.0	c.5.0	c.0.4	c.4.0	4.0-5.0	c.4.0
	49.	1	1		1	1	1	1	1	1
	50.	2	2		1	1	1	1	1	2
	51.	2	2		2	2	2	2	2	2
	52.	2	2		2	2	1	2	2	2
	53.	1	1		1		1	1	1	1
	54.	2	2		2	3	2		2	2
Stamens	55.	1	1		2		2	3	1	1
	56.	c.0.7	c.1.0		c.1.3		c.0.4	c.1.0	c.2.7	c.1.6
	57.	c.1.3	c.2.0		c.4.0		c.0.7	c.2.3	c.3.6	c.3.0
	58.	1	1		1	1	2	1	1	1
	59.	2	2		2	2	2	2	2	+2
	60.	2	2		2	2	2	1	2	2
	61.	1	1		1		1+2	1	1	1
	62.		1		1	1		1		1
Style	63.	4.5-5.5	3.5-6.0		10.0-11.0		c.1.7	c.4.0	5.0-7.5	6.0-7.5
	64.	1	1		1	1	1	3	3	3
	65.	1	1		3		1	2	2	2
Nutlets	66.	2		2	2	2	3			
	67.	2		2	2		2			
	68.	3		3			3			
	69.	1		1	2	1	2			
2n	70.									

		teneriffae	forbesii	helianthemifolia	rivas-martinezii	glomerata	lanata	benthamii	tenuis	lepida	varia
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	4	4	4	4	4	4	4	4	4	4
Stems	3.	10-35	10-20	10-35	20-30(-50)	10-40	7-30	20-40	15-60	10-30	10-60
	4.	2	2	2	2	2	2	2	2	2	2
	5.	1	1	3+1		1	4	4	2-4	1-4	1(-2-4)
Leaves	6.	2-7	2-7	2-7	6-7	9-6	5	5-7	5	5-7	5-7-9
	7.	1	1	1	1	1	1	1	1	1	1
	8.	1	1-3	(1-)3-4	1	1-3	4	4	4	4	4(-1)
	9.	1(-2)		1	1(-2)	2	1	1	1	1	1(-2)
	10.	1	1	1	1	1	1	1	1	1	1
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	2	2	2	1	2	2	2	1
	13.	0.3-0.9		0.5-0.8		0.7-1.8	0.1-0.6	0.3-0.6	0.4-0.6	0.3-0.7	0-0.2
	14.	1	3	2+3	1(-3)	1	3	3	3	2-3	3
	15.	1	3	2+3	1(-2)	2	3	3	3	2-3	3
	16.	1	1	1	1	1	1	1	1	1	1
	17.	NA		2	(3)	3	3	3	3	2	3
	18.	4	3	3	4	3	3	3		3	3
	19.	2		2	2	2	2	2	2		2
	20.	4.5-8.0	6.0-12.0	10.0-15.0	3.0-15.0	8.0-14.0	4.5-9.0	6.0-9.0	6.5-14.0	3.0-14.0	2.0-12.0
	21.	1.5-5.5	4.0-8.0	1.5-5.0	1.0-8.0	4.5-6.0	1.0-1.5	0.9-1.5	0.8-2.5	1.0-4.0	0.5-4.0
Inflorescence	22.	2-8	3-6	2-8	1-8	3-10	4-9	1-3	3-11	3-15	2-13
	23.	2-3		3	3	2	1	2	3	2-3	2
	24.	2-4		4	4	4	2-3	3-4	2-4	4	1-4
	25.	1.5-3.6		2.0-13.5	3.0-5.0	2.0-5.5	0.5-4.5	c.0.4	2.8-6.0	1.5-10.0	0.5-5.0
	26.	0.5-0.9		1.5-3.0		1.0-1.5	0.2-0.3	0.5-1.2	1.0-2.8	0-1.8	0-0.5
	27.	2	2	2	3	2	2	2	2	2	2
	28.	0.7-1.8	0.5-2.0	2.0-3.8	1.0-5.0	2.0-6.0	0.9-1.4	2.0-3.0	0.5-2.5	1.0-4.5	1.0-2.0
Calyx	29.	2	1	1	1	1-2	1-2	1	1	1	1-2
	30.	1	1	1	1	1	1	1	1	1	1
	31.	1.7-2.0	1.3-2.0	5.3-6.6	c.4.4	4.3-5.5	1.6-1.8	2.7-2.9	2.5-3.7	2.9-3.6	1.5-2.6
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.0-1.2	0.7-0.9	2.8-3.4	c.2.4	1.8-2.3	c.0.7	1.9-2.0	1.3-2.5	0.9-1.2	0.7-1.4
	34.	1.0-1.2	0.7-0.9	3.0-3.7	c.2.4	2.0-2.6	c.0.7	1.9-2.0	1.3-2.5	0.9-1.2	0.7-1.5
	35.	0.6-0.7	0.5-0.7	1.0-1.2	c.1.7	1.7-2.0	0.4-0.5	1.5-1.6	0.6-1.1	0.6-0.8	0.5-1.0
	36.	1.0-1.2	0.7-0.9	3.0-3.7	c.2.4	2.0-2.6	c.0.7	1.9-2.0	1.4-2.8	0.9-1.2	0.7-1.5
	37.	1	1	1	1	1	3	1	1	1	1
	38.	1	1	1	1	1	3	1	1	1	1
	39.	3	3	2-3	3	2	3	3	3	3	3
	40.	3		(3)	1	1	1	(3)	1	+1	1
	41.	2	2	2	2	2	2	2	2	2	2
	42.	(3)		3		3	3		3	3	3
	43.	2	2	2	2	2	1	2	1	2	2
	44.	3	3	3	3	3	3	3	3	3	3
	45.	1		1	1	1	1	1	1	1	1
Corolla	46.	2.8-3.7		9.0-12.0	c.10.0	8.5-9.5	1.7-1.8	5.0-6.0	4.1-7.2	3.5-5.0	2.2-4.2
	47.	c.0.7		1.0-1.5	c.2.5	c.3.0	c.0.6	1.0-1.1	1.5-1.8	0.9-1.3	0.7-0.9
	48.	c.1.5		3.0-4.4	c.3.0	c.5.5	c.1.0	1.3-1.5	1.5-2.7	1.0-2.3	1.0-1.8
	49.	1	1	1	1	1	1	3	1	1	1
	50.	1	+2	1	2	2	1	1	1	2	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1		1		1	1	1	1	1	1
	54.	2	3	2(-3)	2	2	2-3	2	3(-2)	2	2-3
Stamens	55.	1		1	1	1	1	2	1	1	1
	56.	c.0.6		c.0.5	c.0.6	1.3-1.7	c.0.5	c.0.5	0.6-1.0	0.5-0.6	c.0.3
	57.	c.0.7		c.1.6	c.2.0	2.3-4.1	0.8-0.9	c.2.0	1.6-2.0	1.0-1.3	c.0.7
	58.	1		1	1	1	1	1	1(-2)	1	1
	59.	2		2	1	2	2	2	2	2	2
	60.	2		2	1	2	2	2	2	2	2
	61.	1		1	1	1	1	1	1	1	1+4
	62.	1		1		1		1	1	1	1
Style	63.	3.3-4.2		9.0-12.0		10.0-11.0	1.7-1.8	4.5-5.5	4.8-8.5	3.5-4.5	3.0-5.0
	64.	1		1	1	1	1	1	1	1	1
	65.	3		1		3	3	3	3	3	1
Nutlets	66.	2	2		2(-1)	1	2	1	1	1	2
	67.	2					2		2	2	2
	68.	3					3		3	3	3
	69.	3	3		1	1	2	1	1	3-2	1
2n	70.	30		30				30			

		hyssopifolia	herpyllomorpha	lachnophylla	lasiophylla	densiflora	pineolens	leucantha
Habit	1.	2	2	2	2	2	2	2
	2.	4-3	4	4	4	4	4	4
Stems	3.	10-40(-80)	15-70	15-40	10-25	20-40	50-100	15-50
	4.	2	2	2	2	2	2	2
	5.	1-4	1-2	2	1	+1	1	
Leaves	6.	5-7	5-2	5-7		5-7	7	6-7
	7.	1	1	1	1	1	1	1
	8.	4	4	4	4	4	4	4
	9.	1-2	1	2		1	1	1
	10.	1	1	1	1	1	1	1
	11.	2	2			2	2	2
	12.	2	2	1		1	2	2
	13.	0.4-0.6	0.4-2.0	0-0.4		0.1-0.3	1.5-2.0	
	14.	2-3	2	2-3	3	2-3	3	3
	15.	3	3	2-3	3	3	3	
	16.	1	1	1	1	1	1	1
	17.	3	3	3		3	3	3
	18.	3	4	3	2	3	3	2
	19.			2	2	2	2	2
	20.	3.0-10.0	5.5-12.0	3.0-7.0	6.0-12.0	3.0-6.0	14.0-30.0	25.0-30.0
	21.	1.0-2.8	0.5-1.5	0.5-1.3	1.5-3.0	0.6-1.3	3.3-13.0	4.0-5.0
Inflorescence	22.	3-20	4-23	2-12	2-12	1-4	3-10	1-3
	23.	2	1	1	1	1	1	2
	24.	2-3	1-4	1-2	4	4	4	4
	25.	0.5-4.0	1.0-6.5	0.6-6.0	0-0.5	0	c.0.5	
	26.	0.2-0.8	0.1-0.5	0-0.4		0.1-0.5	c.0.5	c.0.5
	27.	2	2	2	2	2	3	2
	28.	0.5-2.3	0.8-2.0	1.0-2.7	1.0-2.0	0.8-1.5	3.5-7.0	7.0-8.0
Calyx	29.	2	1-2	1	1-2	1-2	1	
	30.	1	1	1	1	1	1	1
	31.	1.8-2.3	1.5-1.7	1.4-2.6		2.0-2.3	4.0-5.0	c.7.5
	32.	2	2	2	2	2	2	2
	33.	0.8-1.4	1.0-1.3	0.6-1.3		0.8-1.2	1.2-1.4	c.4.0
	34.	0.9-1.4	1.0-1.3	0.6-1.3		0.8-1.2	0.8-1.0	c.4.0
	35.	0.4-0.8	0.8-1.1	0.4-0.9		0.5-0.8	0.5-0.6	c.2.5
	36.	0.9-1.4	1.0-1.3	0.6-1.3		0.8-1.2	0.8-1.0	c.4.0
	37.	1	1	1	1	3-1	3	1
	38.	1	1	1	1	2-1	2	1
	39.	3	3	2-3	3	3	3	3
	40.	1	1	1	3	3	3	1
	41.	2	2	2	2	2	2	2
	42.	3	3	3		3	3	
	43.	2	2-3	3	3	2	2	2
	44.	3	3	3	3	3	3	3
	45.	1	1	1		1	1	1
Corolla	46.	3.0-4.2	4.0-5.0	2.7-4.0	c.3.5	3.0-4.2	10.0-12.0	c.15.0
	47.	0.6-0.8	1.0-1.5	0.8-1.0	c.1.2	0.8-1.0	2.5-3.0	c.3.5
	48.	1.0-1.7	1.5-2.0	1.3-1.7	c.1.5	1.5-1.6	3.2-4.0	c.5.0
	49.	1	1	1	1	1	1	1
	50.	2	2	+1	+2	1	1	1
	51.	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2
	53.	1	1	1		1	1	
	54.	3-2	2	3	3-2	2	2	3
Stamens	55.	1	1	1		1	2	
	56.	c.0.2	c.0.5	c.0.4		c.0.2	c.1.3	
	57.	c.0.5	c.0.9	c.1.0		c.0.5	c.4.0	
	58.	1	1	1	1	1	1	1
	59.	2	2	2	2	2	2	2
	60.	2	2	+2	1	1-2	2	2
	61.	1+4	1	1	1	1	1	
	62.	1		1		1	1	1
Style	63.	3.5-4.7	4.5-6.0	3.0-4.3		3.0-3.5	10.0-11.0	
	64.	1	1	1	1	1	1	1
	65.	3	1	3		3	3	
Nutlets	66.	1	1	2			2	2
	67.	2	2	2			2	
	68.	1	3	3				
	69.	2(-1)	1	1	1		2	1
2n	70.							

		fruticosa	congesta	cilicica	thymifolia	libanotica	nummularifolia	taygetea	carica	mollis	dalmatica
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	2	1	3	3	3	3	3	3	3
Stems	3.	30-60	20-35	15-30	20-50	3-20	5-15	4-18	15-30	5-30	20-50
	4.	2	2	2	2	2	2	2	2	2	2
	5.	2	4(-1)	2	2	+1	1	2	1	1-2	2
Leaves	6.	2-7	1-2	2	2	2-1	1-2	2	2	2-1	2
	7.	1-2	1-2	1-2	1-2	1-2	1	1-2	+1	1-3	2-4
	8.	1	1	1+4	1	1	1	1	1	1	1
	9.	2	2-3	2	2	2-3	2	2-3	1-2	2	2-3
	10.	2	2	2	2	2	2	2	2	2	2
	11.	3	2	2	2	2	2	2	2	2	2
	12.	2	2	2	2	2	2	2	2	2	2
	13.	1.0-5.0	1.5-3.0	1.0-4.0	1.0-3.0	1.0-2.0	0.2-0.4	1.5-3.0	0.5-2.0	2.0-7.0	1.0-5.5
	14.	2	3	3	1	3	3	3	3	3	3
	15.	2	3	3	1	3	3	3	3	3	3
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	3	NA	3	3	3	3	3	3
	18.	4	3	3	4		4	4	4	4	4
	19.	2			2	2		2	2	2	2
	20.	5-35	7.0-17.0	10.0-20.0	5.0-20.0	4.0-15.0	4.5-9.0	7.5-10.0	5.0-10.0	5.0-15.0	10.0-20.0
	21.	2-17	6.0-12.0	5.0-10.0	3.0-12.0	2.8-11.0	3.2-6.8	2.5-6.0	2.5-6.5	5.0-15.0	3.0-15.0
Inflorescence	22.	5-25(-40)	3-30	3-20	1-15(-20)	1-8	1(-2)	1-5	3-5	1-3	5-30
	23.	3	1	2	2	2	3	2	3	3	2
	24.	1	1	2	2	1-3	2-4	1-4	1	1-2	1-2
	25.	2.0-6.0	0.1-0.3	1.2-3.6	1.0-3.5	1.7-4.7	0.2-0.4	1.0-2.5	3.0-5.0	4.0-13.0	2.0-4.0
	26.	0.3-1.0	0.2-0.5	0.3-0.6	0.2-1.0	0.5-1.5	0.2-0.4	0.4-0.8	1.5-3.6	2.5-3.5	0.5-1.2
	27.	3	2	2	4	2	3	3	3	2	3
	28.	0.7-1.3	1.0-1.5	0.7-1.6	0.5-1.0	1.0-1.5	c.0.4	1.0-1.5	0.8-1.0	1.0-1.5	1.0-2.0
Calyx	29.	3-2	2-3	2	2-3	1-2		2-3	3	2-3	
	30.	1	1	1	1	1	1	1	1	1	1
	31.	1.5-3.0	1.7-2.0	1.5-1.6	2.0-2.2	2.4-3.0	2.0-2.3	1.5-2.2	1.5-1.8	2.0-2.6	1.5-1.7
	32.	2	2	2	2	2	2	2	2	2	2
	33.	c.0.7	0.5-0.6	0.5-0.7	0.4-0.5	0.9-1.1	3.0-3.7	0.5-0.7	0.5-0.8	0.7-1.2	1.0-1.3
	34.	c.0.7	0.6-0.7	0.5-0.7	0.4-0.5	0.9-1.1	3.0-3.7	0.5-0.7	0.5-0.8	0.7-1.4	1.2-1.3
	35.	c.0.5	0.4-0.5	0.4-0.6	0.3-0.4	0.6-0.9	3.0-3.7	0.4-0.6	0.4-0.7	0.4-1.2	0.8-1.1
	36.	c.0.7	0.6-0.7	0.5-0.7	0.4-0.5	0.9-1.1	3.0-3.7	0.5-0.7	0.5-0.8	0.7-1.4	1.2-1.3
	37.	3	3	1	3	2	1	3	3	2	1
	38.	3	3	1	3	2	1	2	3	2	1
	39.	2	3	3	2	3	3	3	2-3	2-3	3
	40.	2	3	1	1	3	3	3	1	3	3(-1)
	41.	2	2	2	2	2	2	2	2	2	2
	42.	2-1	3	3	3	3	3	3	3	3	3
	43.	1	1	1	1	1	2	1	1	1	2
	44.	3	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1	
Corolla	46.	3.0-6.0	2.5-4.5	3.0-4.0	4.0-5.0	5.5-7.5	6.0-6.7	2.8-4.0	c.4.4	3.0-6.6	2.0-4.0
	47.	2.5-3.0	0.8-1.2	0.9-1.2	1.7-2.3	0.8-1.4	c.1.0	1.0-1.6	c.1.0	1.0-1.2	2.0-2.2
	48.	2.5-3.0	1.2-1.4	1.0-1.3	2.0-2.5	1.5-2.5	c.1.2	0.9-1.1	c.2.0	1.7-2.8	1.5-2.0
	49.	1	1	1	1	1	1	1	1	1	1
	50.	1	1	1	+2	1	1	1	1	1	1
	51.	2	2	2	2	2	2		2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1	1	1	1	1	1		1	1	1
	54.	3	3	3	2+3	2	2	2	2	2	2+3
Stamens	55.	2	2	1	2	1	1	1	1	2	2
	56.	c.3.0	1.0-1.5	c.1.0	c.3.5	c.2.3	c.0.5	1.3-1.5	c.1.4	1.6-2.0	c.2.0
	57.	c.4.5	2.0-2.5	c.2.2	c.5.0	c.2.8	c.1.2	c.2.0	c.2.4	2.6-3.0	3.0-3.3
	58.	2	(1-)2	2	3	2	1	2	+2	(1-)2	2
	59.	3	(2-)3	3	3	+3	2	2-3	+3	(2-)3	3
	60.	3	2	2	3	2	2	2	2-3	2	2
	61.	1	1+4	1	1	1	1	1+4	1	1	
	62.									1	
Style	63.	c.8.0	3.6-4.8	c.4.0	6.0-9.0	7.5-8.0	c.5.0	4.0-4.5	c.5.0	5.5-6.5	4.0-5.5
	64.	2	2	2	2	2		2	2	1	2
	65.	1	1	3	1	1	1	1	3	1	1
Nutlets	66.	1	1	1-2	1	2		2	1-2	1	1
	67.	1	3	1	1	1		1	1	3	1
	68.	1				2					
	69.	1-3	3	1	3	1		1	3	3	3
2n	70.				20						20

		dolichodonta	pulegium	frivaldskyana	abyssinica	hydaspidis	euosma	barosma	wardii	nepalensis	capitellata
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	3	2	2	1	2	2	1	1	1
Stems	3.	30-50	20-90	10-30	30-60	20-45	18-40	15-35	20-70	20-45	28-50
	4.	2	2	2	2	2	2	2	1	1	2
	5.	4	2	2	2-4	2	+2	2	2	2	+2-4
Leaves	6.	1-2	2	2	2-7	2	2	2-8	2	2	2
	7.	1-2	3-5	3-5	3	2	6	1(-2)	(1-)2	1-2	2
	8.	1	1	1	1	1	3	3	1-3(-4)	3	1
	9.	2-3	2-3	2	2-3	2	2	2	2-3	(2-)3	2
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	2	2	2	2	1	2	2	2
	13.	0.5-2.0	2.0-4.5	1.0-2.7	1.0-9.0	3.0-11.0	1.5-5.0	0.5-1.0	0.5-4.5	0.2-2.0	2.0-5.0
	14.	3	3	1-3	1-2	2(-3)	2	1(-2)	1(-2)	1(-2)	3
	15.	3	3	1(-3)	2	2(-3)	2	1(-2)	1	1	3
	16.	1	1	1	2	1	1	1	1	1	1
	17.	3	3	3	3	3	3	(3)	3	3	3
	18.	3	4	4	4	4	4	4	4	4	4
	19.	2	2	2		2					
	20.	13-24	10.0-30.0	7.0-12.0	9.0-27.0	14.0-32.0	8.0-17.5	2.0-6.0	8.3-30.0	10.0-21.0	8.0-24.0
	21.	8.0-17.0	5.0-20.0	9.0-22.0	5.0-19.0	6.0-17.0	5.0-12.5	0.7-2.8	2.5-20.5	2.5-8.4	5.0-16.0
Inflorescence	22.	5-15	5-35	3-7	1-7	3-8	1-5	1-3	2-9	1-4	2-20
	23.	3	2	3	3	3	3	2	2	3	1
	24.	1	3-4	3-4	1-2	3-4	1-2	2-4	1-2	2-4	1-2
	25.	2.5-4.0	1.0-1.8	2.0-3.0	2.5-6.5	0.3-1.7	4.0-9.0	0-0.7	0-0.4	0-0.3	1.0-13.0
	26.	0.5-1.5	0.5-0.8	0.7-1.0	0.1-0.5	1.5-7.5	2.0-3.5	0.6-2.0	1.0-3.5	1.0-3.3	0-1.4
	27.	3	3	2	3	2-3	2-3	2(-4)	2	2-3	2
	28.	1.0-1.7	1.5-3.0	1.2-2.0	1.2-1.5	0.7-5.5	1.0-2.5	1.5-3.5	0.5-2.2	0.6-1.5	0.6-1.5
Calyx	29.	2			1	1	1	1	1	2	1
	30.	1	1	1	1	1	1	2	2	2	1
	31.	1.4-1.6	1.5-2.0	3.4-3.6	4.8-5.7	4.0-5.2	3.7-4.4	4.5-6.8	4.4-5.2	2.7-3.1	1.5-1.7
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.0-1.4	1.3-1.8	1.0-1.1	1.4-1.6	1.7-2.7	1.0-1.5	1.9-2.7	0.7-0.9	1.2-1.7	c.0.8
	34.	1.4-1.8	1.3-1.8	1.6-1.7	1.4-1.6	1.7-3.0	1.4-2.0	1.9-3.0	0.7-0.9	1.2-1.7	c.0.9
	35.	0.7-1.0	1.0-1.3	0.7-1.0	1.4-1.6	1.5-2.2	0.6-1.4	1.7-2.5	0.4-0.6	1.2-1.7	0.6-0.7
	36.	1.4-1.8	1.3-1.8	1.6-1.7	1.4-1.6	1.7-3.0	1.4-2.0	1.9-3.0	0.7-0.9	1.2-1.7	c.0.9
	37.	1	1	2	2	1	1	1	3	1	1
	38.	1	1	2	2	1	1	1	3	1	1
	39.	3	3	(1-)2	2-3	2	3	1-2	2	1-2	+3
	40.	3	1	3(-1)	3	1	3	3	3	2	2
	41.	2	2	2	+1	2	1	2	2	2	1
	42.	3	3	3	3	3	3	3	3	3	3
	43.	1	1	2	1	2	1	1	1	2	2
	44.	3	3	3	3	3	3	3	3	3	2
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	3.5-4.0	3.0-5.7	3.6-4.6	6.2-7.5	10.0-11.5	6.4-7.0	11.5-17.0	9.0-12.0	7.2-8.8	c.2.5
	47.	1.0-1.2	1.0-2.8	c.1.4	2.0-2.7	1.7-2.0	1.5-2.0	2.8-3.2	1.5-2.0	2.5-4.6	c.0.6
	48.	1.7-2.0	1.0-2.5	c.1.4	2.8-3.5	1.7-2.0	4.0-4.5	3.0-4.0	2.0-2.5	1.8-2.5	c.1.3
	49.	1-2	1	1	3	1	1	1	1	1	1
	50.	1	1	1	1	1	2	1	1	2	2
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1	1	1-2	1	1	1	3	3	1	1
	54.	3	2+3	2+3	2	3	1	1	2	4	2
Stamens	55.	2	2	3	1	3	1	1	3	2	1
	56.	1.7-2.2	2.5-3.0	c.0.7	c.0.2	c.3.5	c.0.4	c.4.0	c.2.2	c.4.0	c.0.2
	57.	3.0-3.1	4.0-4.5	c.1.4	c.0.7	c.4.5	0.8-1.0	c.4.8	c.3.2	c.5.6	c.0.5
	58.	2	2-3		1	2	1	2	1	2	1
	59.	3	3		1	2	1	2	2	2(-3)	1
	60.	2	2	2	1	2	2	1	2	2	1
	61.	1	1	1	1	1	1	1	1	1	1
	62.	1	1	1	1	+2	1	1	1	2	1
Style	63.	6.5-7.5	c.7.0		c.4.0	12.0-15.0	4.2-4.5	13.5-22.0	12.0-15.0	10.5-14.0	c.1.2
	64.	2	2	2	1	1	1	2	2	2	1
	65.	1	1	1	1	1	4	1	1	1	4
Nutlets	66.	1	2	1	2	1	2	1	1	1	2
	67.	1	1	1	2	2	4	2	4	4	2
	68.			3	3	+3	3	3	3	3	3
	69.	3	1	1	2	2	1	1	1	1	2
2n	70.										50

		robusta	masukuensis	myriantha	verneyana	cacondensis	wellmanni	rungwensis	grandiflora	pilosa	compacta
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	1-3	3	1	1	3	3	1	1	1
Stems	3.	90-300	60-120	90-180	40-105	35-120	50-100	100-150	15-34	20-75	15-35
	4.	2	2	2	1	2	2	2	2	1	
	5.	4	4	4	2-4	4	4	3	1	1	1
Leaves	6.	2	2	2	9-3	2-7	2-7	7	1-2	(1-)2	1-2
	7.	3-2	2	2	1-2	2-3	2	2	3-2	2	2
	8.	1	1	1	1	1	1	1	1	1	1
	9.	2	1	1	3	1	1	1	2-3	2-3	2-3
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	2	+2	2	2	2	2	2	2
	13.	1.5-2.5	0.5-2.0	1.0-6.0	0.7-2.3	1.0-4.0	2.0-4.0	2.0-4.5	1.0-3.0	1.5-5.0	1.5-7.0
	14.	3	3	3	1	1	1(-3)	2	3	3	3
	15.	3	3	3	1	1	1(-3)	2	3	2+3	3
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	3	(3)	(3)	3	3	2	2	3
	18.	3-4	4	4	4	4	4	4	4	4	4
	19.	2		2						2	
	20.	9.0-43.0	7.0-23.0	16-40(-65)	7.0-18.0	12-45	12-47	14.0-23.0	12.0-25.0	6.0-23.5	7.0-17.0
	21.	8.0-31.0	5.0-17.0	9-30(-41)	3.0-11.5	7.5-20.0	6.0-19.5	6.0-11.0	10.0-22.0	5.5-21.5	6.0-17.0
Inflorescence	22.	4-15	4-10	5-15	1-10	3-12	3-9	2-6	1	1-5	1(-6)
	23.	1	1	1	1	1	1	2	3	3	3
	24.	3-4	2	2	1-2	2	2-4	2-3	2-4	1-2	2
	25.	0-0.2	0	0-0.7	0	0.3-1.0	0.5-1.7	0.3-0.5	7.0-11.0	1.5-22.0	4.0-20.0
	26.	0.2-0.6	0-0.6	0.2-1.0	0-0.4	1.8-3.0	0-0.7	0.9-1.5	5.0-7.0	1.5-5.0	1.5-5.0
	27.	3	3	3	3	3	3	3	4	3	3
	28.	3.5-5.0	3.0-5.5	1.5-7.0	1.0-7.5	2.0-5.0	3.0-8.0	1.5-4.0	7.0-11.0	1.0-1.8	1.0-2.0
Calyx	29.	2	2	2	2	2	2	2	5	5	5
	30.	1	1	1	1	1	1	1	1	1	1
	31.	2.4-3.2	2.5-3.5	3.2-4.0	3.0-3.8	3.0-3.5	2.5-3.5	3.6-4.0	3.5-5.0	2.0-3.5	1.3-2.0
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.0-2.0	1.7-2.7	2.0-2.5	2.0-2.7	1.8-2.2	1.7-3.5	1.5-1.7	4.0-5.0	0.9-1.7	1.4-2.0
	34.	1.3-1.8	1.7-2.7	2.0-2.5	2.1-2.8	1.8-2.2	1.7-3.5	1.5-1.7	4.0-4.5	0.9-1.7	1.4-2.0
	35.	0.4-0.8	1.3-2.5	1.4-2.0	1.5-2.0	1.2-1.5	1.3-3.0	1.0-1.5	3.6-4.2	0.9-1.7	1.4-2.0
	36.	1.3-1.7	1.7-2.6	1.8-2.3	2.1-2.8	1.7-2.2	1.7-3.5	1.5-1.7	4.0-4.5	0.9-1.7	1.4-2.0
	37.	2	1	1	2	1	1	2	1	3	2
	38.	2	1	1	2	1	1	2	1	3	2
	39.	3	3	3	3	2	3	2	3	3	3
	40.	1	1	1	1	1	1	1	1	1	1
	41.	1	1	1	1	1	1	+1	2	2	2
	42.	3	3	3	3	3	3	1	3	3	3
	43.	1	1	1	1	1	1	1	3	2	2-3
	44.	3	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	4.5-5.5	5.7-8.0	5.5-7.5	4.5-7.3	4.0-6.5	4.5-8.0	5.0-6.0	11.0-15.0	5.0-12.0	3.0-5.0
	47.	1.4-3.2	2.8-4.5	2.5-4.0	3.5-5.0	2.5-4.5	3.0-4.5	2.7-3.8	2.0-4.0	1.0-3.0	1.5-2.0
	48.	1.0-2.4	2.1-3.0	2.0-3.0	2.5-3.0	1.7-2.5	2.0-2.8	2.8-4.0	5.0-6.0	3.0-7.0	1.5-2.2
	49.	1	3-2	1-2	1	1	1	3-2	1	1-2	1
	50.	1	1	1	+2	1	1	1	2	2	2
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1	1	1	1	1	1	1	2	1	1
	54.	3	3	3	3	3	3	3	2	2-3	2
Stamens	55.	2	2	2	2	2	2	2	1	1	1
	56.	c.2.5	c.3.7	c.3.5	c.3.0	2.7-3.0	c.5.5	c.3.0	c.4.0	0.9-1.5	1.4-2.0
	57.	c.3.5	c.5.5	c.5.5	c.4.0	3.5-5.0	c.7.0	c.3.7	c.5.0	c.3.0	2.0-3.0
	58.	2	2	2	2	2	2	2	1	1	1
	59.	2	2	3	2	2	+3	2	1	2	2
	60.	1	1	1	2	+1	+1	1	1	1	1
	61.	1+4	1	1	1+4	1	1	1	1	1+2	1
	62.	2	1	2	1		1	2	1	1	1
Style	63.	5.5-8.0	8.5-12.5	8.0-13.5	7.0-10.0	5.5-10.0	6.0-10.0	7.0-8.5	10.0-15.0	6.0-13.0	3.0-5.0
	64.	+1	2	2	+2	2	2	1	2	3	2
	65.	1	2	1	1	1	1	1	1	2	1
Nutlets	66.	1	1	1	1	1	2		1	1-2	1-2
	67.	2	4	2	2	1+4	4		1	1	1
	68.	3	3	3	3	3	3			1	1
	69.	3	3	3	3	3	2			2	2
2n	70.	42									

		linearifolia	thymbrifolia	vulgare	atlanticum	chinense	umbrosum	macranthum
Habit	1.	2	2	2	2	2	2	2
	2.	4	4	1	3	1	1	1
Stems	3.	11-25	10-40	20-80	8-20	25-70	15-60	50-60
	4.	2	2	2	2	2	2	
	5.	1	4	1-2	1	2	2-1	2
Leaves	6.	5-6	5-6	7-2	2	7	2-7	2-7
	7.	1	1	2-6	2-6	3	6-2(-3)	3-4
	8.	1	1	1	1	1	1	1
	9.	2	2	1-2	2	2(-1)	2-1	1(-2)
	10.	2	2	2	2	2	2	2
	11.	NA	NA	2	2	2	2	2
	12.	1	1	2	2	2	2	2
	13.	0	0	1.5-14.0	1.3-4.0	6.0-21.0	1.5-9.0	4.0-9.0
	14.	3	3	3	3	3	3	3
	15.	3	3	3	3	3	3	3
	16.	1	1	1	1	1	1	1
	17.	3	3	3	3	3	3	3
	18.	3	3	4	3	3	4	4
	19.	1	1	2			2	
	20.	5.0-8.0	7.5-13.0	10-65(-80)	4.5-16.0	(25-)30-67	10.0-45.0	36-58
	21.	1.5-2.3	1.6-2.4	3.5-30(-40	4.0-11.5	(12-)16-31	6.0-31.0	20-38
Inflorescence	22.	1-3	3-5	3-20	2-7	4-15	3-20	6-10
	23.	2	1	1	2	1-2	1-2	3
	24.	4	4	1-2	1-2	1-3	1-4	3-4
	25.	0-0.3	0	0.5-0.8	0.3-0.8	0-0.5(-2.0	0.2-1.0	1.5-2.0
	26.	0	0	0.8-1.5	1.0-2.8	0.8-2.0(-4	1.0-2.9	2.5-6.0
	27.	4	3	2	2	2	2	2
	28.	2.0-2.5	2.0-3.0	5.5-12.0	2.0-4.6	(2.0-)3.0-	(1.0-)3.0-	4.0-6.5
Calyx	29.	2	2		2	2		2
	30.	+2	+2	2	2	2	2	2
	31.	1.6-1.9	c.1.8	4.5-6.5	2.5-3.4	3.5-6.3	2.8-7.5	5.3-5.6
	32.	2	2	2	2	2	2	2
	33.	1.1-1.3	c.1.0	2.0-5.7	2.5-3.0	1.4-3.2	1.3-3.7	3.0-4.2
	34.	1.1-1.3	c.1.0	2.0-6.0	2.6-3.5	1.5-3.6	1.8-3.6	3.5-4.0
	35.	1.1-1.3	c.1.0	1.5-4.0	1.5-2.0	1.0-1.7	0.7-2.2	2.5-3.0
	36.	1.1-1.3	c.1.0	2.0-6.0	2.6-3.5	1.5-3.6	1.8-3.6	3.5-4.0
	37.	1	1	2	1	2	2	1-2
	38.	1	1	1	1	1	1	1
	39.	3	3	3	3	3	3	3
	40.	2	1	3	3	3	3	3
	41.	2	2	1	1	1	1	1
	42.	3	3	3	3	1	3	1
	43.	3	3	1	1	1	1	1
	44.	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1
Corolla	46.	c.6.4	c.6.0	9.0-15.5	c.5.5	6.5-16.3	5.5-15.5	12.5-16.5
	47.	c.2.4	c.3.4	2.0-2.7	c.1.5	1.0-4.0	1.3-3.0	2.0-2.7
	48.	c.2.8	c.3.4	2.0-4.5	c.2.0	1.0-4.0	1.5-3.5	4.0-4.5
	49.	1	1	1	1	1	1	1
	50.	1	1	1	2	2	2	2
	51.	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2
	53.	1	1	1	1	1	1	1
	54.	3-2	3	2	3	2	2-1	
Stamens	55.	3	3	3	1	3	1	3
	56.	c.2.0	c.4.0	0.7-2.7	c.1.0	c.1.6	0.6-2.0	c.1.6
	57.	c.3.2	c.4.5	1.5-4.5	1.7-2.0	c.2.5	1.6-4.4	c.4.5
	58.	2	2	1-2	1	+1	1	1
	59.	2-3	+2	2	2	2	2	2
	60.	2	+2	2	2	2	2	2
	61.	1	1+4	1	1+2	1+4	1+2	1
	62.	2	2		1	1	1	1
Style	63.	c.7.0	c.9.5	10.0-20.0	c.6.0	8.5-21.5	5.5-18.0	16.0-17.5
	64.	2	2	2	2	2	2	2
	65.	1	1	2	2	2	2	2
Nutlets	66.		2	3	3	2	3	3
	67.		2	2	2	2	2	2
	68.		3	3	3	3	3	3
	69.		2	2	2	2	2	2
2n	70.			20			20,36,38	

		grandiflora	betulifolia	tauricola	pamphylica	piperelloides	sylvatica	nepeta	rouyana	candidissima	cretica
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	1-2	2	2	2	3	1	1	3	2	2
Stems	3.	15-60	15-40	10-40	10-25	5.0-12.0	15-80	20-80	2-10	25-60	10-40
	4.	2	2	2	2	2	1	2	2	2	2
	5.	1	1	1	1		1-4	1-2	4	NA	1
Leaves	6.	2	2	2	2	2	2	2	2	2	2-1
	7.	3-4	3-4	2-3	2	2	2-3-6	2-3-6	2	6-5	2
	8.	1	1	1	1	1(-3)	1	1	1	1	1
	9.	2	2	1-2	2	2	2	2	2	3	2
	10.	2	2	2	2	2	2	2	2	2	2
	11.	3	3	3	3	3	2	2	2	2	2
	12.	2	2	2	2	2	2	2	2	2	+2
	13.	6.0-17.0	5.0-20.0	1.0-5.0	2.5-11.0	1.0-3.0	4.0-16.0	1.5-9.0	1.0-2.6	1.0-6.0	1.0-4.5
	14.	3	2-3	2(-3)	3	2	3	3	3	4	3
	15.	(1-)3	2-3	2(-3)	3	2	3	3	3	4	3
	16.	+1	+1	1	1	1	+1	1	1	1	1
	17.	3	2	2	3	3	3	3	3	3	3
	18.	4	4	1	3	4	3	3	4	3	3
	19.	2					2		2		
	20.	25-85	17-37	9.0-29.0	8.0-24.0	4.5-9.3	12-70	8.5-45.0	2.7-8.0	6.0-16.0	6.0-15.0
	21.	16-49	10-28	5.0-22.0	8.5-21.0	4.0-8.0	9-45	6.0-30.0	1.5-6.5	6.0-16.0	5.5-14.5
Inflor-	22.	1-6	1-5	1-4	1-6	1	3-9(-15)	2-20	1	1-8	1-7
escence	23.	3	3	3	3	3	3	2-3	3	3	3
	24.	2-4	2-3	2-4	2-4	4	1-2	1-2	2	1	1-4
	25.	0.5-9.5	1.7-10.0	1.0-1.5	1.6-2.7	1.7-2.0	0-15.0	0-18.0	0.7-1.2	1.0-13.0	0-4.0(-7.0)
	26.	1.2-7.0	1.0-3.6	0.4-0.5	3.5-4.5	1.0-1.8	0-5.0	0-10.0	0.7-1.6	1.0-6.7	1.0-4.5
	27.	3	3	3	3	3	3	3	2	3-4	2
	28.	3.0-6.5	2.4-10.0	0.6-6.0	2.3-4.3	1.7-2.3	1.5-2.7	0.8-3.0	0.6-0.7	1.5-3.0	1.0-2.3
Calyx	29.	1-2	1(-2)	2	1				2		2
	30.	1	1	1	1	1	1	1	1	1	1
	31.	5.0-10.0	7.5-11.0	4.5-7.7	6.0-8.0	6.5-8.0	4.0-6.2	2.5-3.8	2.0-2.5	3.0-4.2	2.9-3.5
	32.	2	2	2	2	2	2	2	2	2	2
	33.	2.0-4.0	2.0-2.8	1.3-2.0	1.7-2.0	2.8-3.2	1.5-2.6	0.7-2.0	0.7-0.8	1.3-1.5	1.0-1.5
	34.	2.5-5.0	2.0-2.8	1.3-2.0	1.7-2.0	3.0-3.5	2.0-4.0	1.0-2.6	1.0-1.3	1.8-2.5	1.5-2.1
	35.	0.8-2.5	1.0-1.5	0.7-1.7	0.8-1.5	2.0-2.2	0.9-1.9	0.5-1.0	0.4-0.6	0.6-0.7	0.5-0.9
	36.	2.5-4.5	2.0-2.6	1.3-2.0	1.7-2.0	3.0-3.5	2.0-4.0	1.0-2.6	1.0-1.3	1.8-2.5	1.5-2.1
	37.	2	2	2	2	2	3	2-3	2	3	2-3
	38.	1	2	2	2	2	1	1-2	2	2	3
	39.	2-3	2-3	2-3	3	2	3	3	3	2	3
	40.	3	1	1	1	1	3	2-3	3	2	3
	41.	1	1	1	+1	1	1	1	+1	+2	1
	42.	1	3	1	3	1	3	3	3	3	3
	43.	1	2	2	2	2	2	2	1	1	2
	44.	2	2	2	2(-3)	2	3	3	3	2-3	3
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	12.5-33.5	13.0-22.5	12.0-16.0	11.0-20.5	16.5-17.0	9.0-17.0	6.0-10.5	3.0-4.6	6.0-14.2	5.0-7.0
	47.	3.0-6.0	1.5-2.0	2.0-2.5	2.0-3.0	c.3.2	2.0-5.5	2.0-2.5	1.0-1.3	1.5-3.0	1.0-1.5
	48.	4.0-11.0	2.0-4.5	3.5-4.0	3.5-6.0	c.6.7	2.0-2.5	3.0-3.5	1.4-1.5	1.5-3.0	1.5-3.0
	49.	1	1	1	1	1	1	1	1	1	1
	50.	1	2	2	+1	2	+2	2	2	1	1(-2)
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	2	2	1	2	1	2	2	1	3	1
	54.	1-2	2	2	2		2	2		2	3
Stamens	55.	1	1	1	1	1	1	1	1	1	1
	56.	1.5-2.5	c.1.0	c.0.6	c.2.3	c.1.3	1.6-2.5	1.4-1.9	c.0.5	c.2.1	c.1.2
	57.	7.0-12.0	c.3.5	c.2.0	c.3.8	c.3.0	5.5-6.0	3.3-4.3	c.1.3	5.3-6.5	c.2.0
	58.	1	1	1	1	1	1	1	1	1	+1
	59.	2	2	2	2	2	2	2	2	2-3	2
	60.	2	2	2	2	2	2	2	2	2	2
	61.	1	1	1-2	1	1	1-4	1	1	1	1
	62.	1	1	1	1	1	1	1		1	1
Style	63.	20.0-36.0	15.0-22.0	13.5-17.5	12.0-20.5	20.5-21.0	11.0-20.0	9.0-15.0	3.5-5.0	8.0-20.0	5.0-9.0
	64.	2	2	2	2	2	2	2-3	2	2	3
	65.	2	2	2	2	2	2	2	2		2
Nutlets	66.	2-3	3	3	3		3	2	2	2	3
	67.	2	2	2	2		2	2	2	2	2
	68.	3	3	3				3	3	3	3
	69.	1-2	2	2	2		2	2	2	2	2
2n	70.	22					24,48	24,42,48,72			

		incana	kilimandschari	uhligii	paradoxa	gracilis	micrantha	confinis	ussuriensis	debilis	piperita
Habit	1.	2	2	2	2	2	2	2	2	1	2
	2.	2	1-2	2	1	1	1	1	1	1	1
Stems	3.	10-32	8-27	15-150	12-50	10-40	30-40	8-30	10-65	7-20	40-100
	4.	2	1	2	2	2	2	2	1	2	2
	5.	4	1	1	4	2	2	2	2	+1	2-1
Leaves	6.	2-1	+1	2	2	2	2	2	2-7	9	7-9
	7.	1-6	2-6	6-2(-5)	2-6	2	2-3	2-6	3-4	2	2-6
	8.	1	3	1	1	1	1	1	1	1	1
	9.	2	2-3	2-3	3-2	2(-1)	1	2(-1)	1(-2)	2	2-1
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	3	2	2	2	2	2	3	2
	12.	2	2	2	2	2	2	2	2	2	2
	13.	0.5-2.5	0.5-3.5	0.5-2.0	1.0-5.5	2.5-8.0	4.0-12.0	3.0-9.0	5.0-25.0	5.0-15.0	4.0-11.0
	14.	3	3	+1-3	1	1(-3)	1(-3)	1(-3)	1-3	1(-3)	(1-)3
	15.	3	3	+1-3	1(-3)	1(-3)	1(-3)	1(-3)	1-3	1(-3)	(1-)3
	16.	1	1	1	1	1	1	1	1	1	+2
	17.	3	3	1-3	3	3	3	3	3	3	3
	18.	3	3	3	3	1(-4)	4	1(-4)	4	4	4
	19.			2							
	20.	3.0-14.0	4.0-8.0	8.5-21.0	14.0-32.0	8.0-30.0	17.0-30.0	10.0-33.0	12-57	10.0-20.0	9.0-38.0
	21.	3.0-14.0	3.3-7.5	6.3-19.0	11.0-27.0	5.5-18.5	9.0-19.0	7.5-19.0	7.0-29.0	4.0-10.0	3.5-19.5
Inflorescence	22.	1-4	1	1-7	2-7	3-10	3-12	2-9	1-9	1-3(-5)	1-4
	23.	3	3	3	1	1-2	2	1-2	2	3	3
	24.	1-2	3-4	3-4	4	1-4	1-3	2-4	3-4	3-4	4
	25.	0-2.5	0.4-1.0	0.7-1.0	0	0-0.3	0-0.5	0-0.5	0-0.3	0-0.5	0-2.0
	26.	1.5-6.5	0.8-1.8	1.5-3.5	1.7-2.4	0.5-5.0	1.3-3.0	1.0-4.0	0.8-5.0	1.0-3.5	1.3-2.1
	27.	3	2	2	2	2	3	2	2	3	2
	28.	1.0-1.5	0.5-0.6	1.5-3.8	1.0-2.5	1.0-5.0	1.0-2.8	0.3-0.7	1.0-2.3	0.5-1.0	0.8-2.0
Calyx	29.	2	1	1	1	1	1	1	1-2	1	2
	30.	1	1	1	1	1	1	1	1	1	+2
	31.	2.2-3.2	2.4-2.9	4.5-6.0	3.3-4.5	1.7-2.7	2.5-3.0	2.7-3.2	2.5-3.7	2.7-3.6	5.3-7.6
	32.	2	2	2	2	2	2	2	2	+2	2
	33.	0.8-1.6	1.1-1.5	1.7-2.7	2.0-2.5	1.2-1.7	1.3-1.6	1.0-1.3	1.3-2.2	1.8-2.3	2.2-3.0
	34.	1.3-2.6	1.5-1.9	1.7-2.7	2.0-2.5	1.4-1.8	1.5-1.7	1.1-1.5	1.5-2.2	1.8-3.0	2.2-3.0
	35.	0.4-0.6	0.5-0.7	0.5-1.2	0.8-1.0	0.3-0.6	0.3-0.5	0.3-0.5	0.3-0.7	1.0-1.5	1.3-2.6
	36.	1.3-2.6	1.5-1.9	1.7-2.7	2.0-2.5	1.4-1.8	1.5-1.7	1.1-1.5	1.5-2.2	1.8-3.0	2.2-3.0
	37.	3	1	3	3	3	3	3	3	2	2
	38.	1	2	2	1	1	1	1	1	1	1
	39.	3	3	3	3	3	3	1	3	3	3
	40.	2	3	3	1	3	3	3	3	3	3
	41.	1	1	1	1	1	1	1	1	1	1
	42.	3	3	3	3	1	3	1	3	3	1-3
	43.	2(-3)	1	1	1	1	1	1	1	1	1
	44.	3	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	5.0-8.3	4.7-5.3	8.0-12.0	5.5-7.6	2.8-4.0	c.1.7	3.5-3.8	4.0-5.4		9.0-16.0
	47.	1.5-3.5	1.0-1.3	2.5-4.5	2.0-2.6	0.4-0.7	c.1.0	0.8-1.0	1.0-1.5		2.5-2.7
	48.	2.0-3.5	1.5-2.5	3.0-6.5	1.6-2.4	0.7-1.5	c.0.8	1.0-1.4	2.0-2.3		3.5-4.5
	49.	1	1	1	1	1	1	1	1	1	1
	50.	+1	2	2	1	1	2	1	2	2	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	1	1	1	1	1	1	1	1		1
	54.	2	2	2-4	2	2-3	3-2	2	3-2	3	2
Stamens	55.	1		3	2	3		3	1		3
	56.	1.7-3.4	c.0.5	3.0-3.5	c.2.3	c.0.4		c.0.5	c.1.0		c.2.7
	57.	2.6-5.6	c.1.7	5.8-6.0	c.3.2	c.1.6		c.1.4	c.2.0		c.4.5
	58.	2	1	1	2	1	1	1	1		1(-2)
	59.	3	+2	2	2	2	1	2	+2		2-3
	60.	2	2	2	1	2	1+2	2	2	2	1+2
	61.	1	2	1	1	2	2	1	1	1+2	1
	62.	1	1	1		1		1	1	1	1
Style	63.	7.0-11.0	5.0-5.5	10.0-16.0	7.5-13.0	2.8-4.0		4.0-4.3	5.0-6.5		11.5-21.5
	64.	2	3	2	1	2	3	2	2		1
	65.	2	2	1	1	2	2	2	2		1
Nutlets	66.	3	2	2		2-3	3	3	3	2	2
	67.	2	2	2		2	2	2	2	2	2
	68.	3	3	3		3	3	3	3	3	2
	69.	2	2	1		1	2	2	2	2	2
2n	70.										

		alpinus	suaveolens	arvensis	rotundifolius	nanus	troodii	corsicus	simensis	pseudosimensis
Habit	1.	2	2	1-2	1	1	2	2	2	2
	2.	2	2	1	1	1	3	4	1	1-2
Stems	3.	5-45	10-45	10-40	3-30	1-4(-6.5)	3-10	2-10	12-30	15-60(-120)
	4.	2	2	2	2	2	2	2	2	2
	5.	2-4	2-4	+4	2-4	2	3	1	1	1
Leaves	6.	2-9(-1)	2	2	1-2	2-1	1-2(-7)	1-2	2	2
	7.	2	2	2	2	1	1(-6)	1	2-3	2-6
	8.	1	1	1	1	1	1	1	1	1
	9.	1-2	1	1	1	2	1-2	2	2	2
	10.	2	2	2	2	1	2	1	2	2
	11.	3	3	3	3	3	3	3	3	3
	12.	2	2	2	2	2	2	1	2	2
	13.	1.5-5.0	1.0-5.0	1.0-3.5	1.5-9.0	0.7-2.5	1.0-3.0	1.5-3.3	2.0-5.0	0.5-1.5
	14.	(1-2-)3	3(-1)	(2-)3	3	3	2	3	3	3
	15.	(1-2-)3	3(-1)	(2-)3	3	3	2	3	3	3
	16.	1	1	1	1	1	1	1	1	1
	17.	3	3	2-3	2	3	2	3	3	3(-2)
	18.	4	4	4	3	1	1	1	4	3
	19.	2			2	2		2		2
	20.	3.5-20.0	9.0-19.0	8.0-15.0	5.0-18.0	2.0-4.5	2.3-7.0	3.0-10.0	6.0-25.0	5.0-25.0
	21.	2.5-16.0	2.0-8.0	3.2-7.5	3.0-14.5	1.8-4.3	1.5-5.5	2.6-5.0	4.0-20.0	3.0-22.0
Inflorescence	22.	1-4	1-4	1-5	1-6	1-2	1-2	1-2	1-11	2-8
	23.	3	2	2	2	2	3	3	3	3
	24.	2-4	2-4	2-4	2-4	4	4	4	1-4	2-4
	25.	0	0	0-0.3	0	0	0-0.8	0	0	0-0.3
	26.	1.6-3.0	2.0-3.0	1.0-2.7	1.3-4.0	1.0-2.2	0.5-3.0	1.0-1.6	1.4-5.0	1.7-5.5
	27.	2	3	2	2	2	2-3	2	2	2
	28.	0.7-1.2	0.5-2.0	0.5-1.0	0.6-1.5	0.7-1.5	0.5-3.6	0.7-1.0	1.0-2.2	1.0-4.0
Calyx	29.									
	30.	3	3	3	3	3	3	3	3	3
	31.	3.5-4.5	4.3-5.5	3.0-4.3	3.5-6.0	3.5-4.0	5.5-7.0	4.3-4.6	2.0-4.2	3.6-4.8
	32.	1	1	1	1	1	+2	+2	1	1
	33.	1.5-2.6	2.3-3.2	1.0-2.5	3.0-4.0	1.5-2.3	1.8-2.7	2.0-2.3	1.5-2.3	1.7-2.3
	34.	1.5-3.3	2.3-3.5	1.0-2.5	2.5-3.5	1.5-2.3	2.0-3.2	2.3-2.5	1.6-2.6	1.5-2.3
	35.	0.5-2.0	1.3-1.8	0.5-1.5	1.3-2.5	0.8-1.2	1.1-2.0	0.9-1.3	0.3-0.7	0.6-1.5
	36.	1.5-3.3	2.3-3.5	1.0-2.5	2.5-3.5	1.5-2.3	2.0-3.2	2.3-2.5	1.6-2.6	1.3-2.1
	37.	2	2	2	2-1	2	1	2	1	+2
	38.	1	1	1	1	1	1	1	1	1
	39.	3	3	3(-2)	3	3	3	3	3	3
	40.	2	2	2	2	2	2	2	3	+2
	41.	1	1	1	1	1	1	1	1	1
	42.	1(-3)	3	1	1	1	1	1	3-1	3
	43.	1	1	1	1	1	2	1	1	1
	44.	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1
Corolla	46.	7.0-13.5	8.0-13.0	6.5-10.5	5.5-11.0	c.4.3	9.0-14.0	9.5-11.0	3.5-8.0	5.0-8.0
	47.	1.4-3.3	2.0-2.8	0.7-2.5	1.2-1.7	c.0.6	1.6-2.0	2.5-3.2	0.6-1.7	1.5-3.2
	48.	3.2-6.0	2.0-3.5	1.5-3.0	1.5-3.0	c.1.5	2.4-4.0	3.2-3.5	0.6-3.5	1.8-3.5
	49.	1	1	1	1	1	1	1	1	1
	50.	+2	2	1(-2)	+2	+1	1	1	1	1
	51.	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2
	53.	2	1	2		1	1	3	1	1
	54.	2	2	2	2		2	2	2	2
Stamens	55.	1	1	1	1	1	1	1	2	2
	56.	c.1.8	c.2.4	1.2-1.4	c.1.4	c.0.4	c.2.0	c.2.0	0.4-0.8	1.5-4.0
	57.	c.3.3	c.4.0	2.5-2.8	c.2.5	c.0.6	c.4.2	c.4.3	c.3.0	3.5-5.0
	58.	1	2	1	1	1	1	1	1	2
	59.	2	2	2	2	+2	2	2	2	2
	60.	2	3	3	3	2	2	2	2	2
	61.	1	1	1	1	1	1	1	2	1
	62.	1		1		1		1	1	1
Style	63.	7.0-13.5	10.0-16.0	7.5-13.0	7.0-12.0	c.6.0	9.0-14.0	12.0-14.0	3.3-7.5	6.0-11.0
	64.	2	2	2	2	2	2	2	3	3
	65.	2	2	2	2	2	1	2	2	2
Nutlets	66.	2	2	2	2	2	2		2	2
	67.	2	2	2	2	2	2		2	2
	68.	3	1	3	1	1	3		3	3
	69.	1	1	+2	1	1	2		2	2
2n	70.	18	18	18	36					22

		niveum	origani-folium	leuco-trichum	stamineum	longi-florum	hauss-knechtii	depauperatum	straussii
Habit	1.	2	2	2	2	2	2	2	2
	2.	2	2	2	2	2	3	2	2
Stems	3.	20-50	7-40	15-34	14-55	13-35	20-30	20-30	25-30
	4.	2	2	2	2	2	2	2	2
	5.	4	1(-3)	1	3	1	1	4	1
Leaves	6.	9(-2)	2	2-7	2(-7)	2	7	2	2
	7.	1(-2)	1(-6)	1(-2)	1(-6)	1(-6)	2	2	1(-6)
	8.	1	1	1	1	1	1	1	1
	9.	2-1	2	1	1-2	2	1	2	2
	10.	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2
	12.	+2	2	2	2	2	2	2	2
	13.	1.0-2.0	0.5-2.5	0.6-3.5	1.5-5.0	0.7-5.5	1.0-3.0	1.5-3.0	1.5-3.0
	14.	4	2-3	2+3	2	3	2-3	3	2+3
	15.	4	2-3	2+3	2	3	2-3	3	2+3
	16.	1	1	1	1	1	1	1	1
	17.	3	2	2	3	3	2	3	2
	18.	3	3	3	3	+4	3		3
	19.	1		2	2		2		
	20.	6.0-16.0	6.0-18.0	14.0-25.0	14.0-30.0	9.0-22.0	8.0-17.5	8.0-12.0	10.0-15.0
	21.	5.0-10.5	4.0-13.0	7.5-15.5	8.0-19.0	5.0-20.0	4.0-9.0	7.5-10.0	8.0-14.0
Inflor-escence	22.	3-8	1-14	1-9	1-7	3-12	3-9	1(-3)	4-10
	23.	2	1	1	1	1	1	3	1
	24.	1	1	1-2	1-2	1-2	2	1	1
	25.	0.7-2.0	0.8-2.0	0.4-0.6	0.2-0.8	0-0.5	0-0.5	0.5-1.7	0-3.0
	26.	0.5-1.2	0.2-1.7	0.5(-1.5)	0.2-1.0	0-0.5	0-0.3	0.3-0.6	0-0.8
	27.	2	3	3	3	3	3	3	3
	28.	1.6-3.0	2.5-7.0	2.5-5.0	3.0-5.5	3.0-7.5	3.0-4.5	2.0-3.5	2.5-3.0
Calyx	29.	1	1	1	1	1	2	1	3-2
	30.	2	2	1	2	1	1	1	1
	31.	4.0-6.0	3.3-5.0	4.3-4.6	4.4-5.8	4.7-7.5	3.0-3.5	5.0-6.0	3.0-3.5
	32.	2	2	2	2	2	2	2	2
	33.	0.9-1.3	1.0-2.1	1.5-2.6	3.0-3.4	2.5-4.0	2.9-3.2	1.5-3.0	c.1.5
	34.	1.0-1.5	1.0-2.1	1.5-2.6	3.0-3.4	3.0-4.5	2.9-3.2	1.5-3.0	c.1.5
	35.	0.4-0.9	0.5-1.0	1.3-2.0	2.0-2.5	2.0-3.5	1.9-2.4	1.5-2.8	c.1.0
	36.	1.0-1.5	1.0-2.1	1.5-2.6	3.0-3.4	3.0-4.5	2.9-3.2	1.5-3.0	c.1.5
	37.	3-2	2	1-2	1-2	2	1	1	+1
	38.	2	1	1	1-2	1	1	1	1
	39.	4	3	3	3	3	2	1	2
	40.	2	+2	1	1	1	1	1	1
	41.	+1	1	2	+1	1	1	1	1
	42.	3	3	1(-3)	3	3	1?	3	1?
	43.	2	1	1	1	1	1	1	1
	44.	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1
Corolla	46.	5.0-6.5	5.0-8.0	7.0-9.0	7.5-8.8	9.0-15.0	7.0-8.0		6.5-7.5
	47.	2.0-2.5	2.5-3.5	2.0-2.5	2.0-3.5	3.0-3.5	2.0-2.6		2.0-2.5
	48.	2.0-2.8	3.0-4.0	2.0-2.5	2.5-4.0	3.0-3.5	2.5-3.7		2.0-3.0
	49.	2	1	2	2	1	1		1
	50.	1	1	1	1	1	1		1
	51.	1	1	1	1	1	1	1	1
	52.	1	1	1	1	1	1	1	1
	53.	1	1	1	1	1	1		1
	54.	2	2	2	2	2	2		
Stamens	55.	1	2-3	3	3	3	1		
	56.	3.5-5.0	5.0-7.5	5.0-6.0	6.0-8.0	5.0-9.0	c.8.5		c.5.0
	57.	4.0-5.5	5.0-8.0	5.0-6.0	6.0-8.0	6.0-10.0	c.9.0		c.5.0
	58.	3	3	3	3	3	3	3	3
	59.	3	3	3	3	3	3	3	3
	60.	1	1	1	1	1	1		1
	61.	1	1	1	1	1	1		1
	62.	2	2	2	2	2	2		2
Style	63.	8.5-10.0	10.0-15.0	10.0-15.0	12.0-18.0	16.0-20.0	10.0-11.5		c.13.0
	64.	2	2	2	2	2	2		2
	65.	1	1	1	1	1	1		1
Nutlets	66.		1		1	2	2	1	
	67.		2		2	2	2	2	
	68.		3		3	3	3	3	
	69.		2		2	2	2	2	
2n	70.								

		multiflora	elliptica	macrostema	jaliscana	junctionis	mexicana	seleriana	maderensis	acutifolia	tomentosa
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	4	4	4	4	4	4	3	1(-2?)	4	4
Stems	3.	100-150	100-150	60-180	200-300			100-200	10-30	50-150	50-150
	4.	2	2	2	2	2	2	2	2	2	2
	5.	1	3	+1		2	3	2	2	2	2
Leaves	6.	2-7	2-7	2-7	9	2	2	2-7	2	9	1-9
	7.	3-2	3-2	2	2	2	2	2	1(-6)	1	2
	8.	1(-3)	1(-3)	1-3	3	1	1-3	3	1	4	3-4
	9.	2	2	1	1	2	2	2	2-3	1	2
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2		2	2	2	2	2	2
	12.	2	2	2	2	2	2	2	2	2	2
	13.	2.0-8.0	1.0-6.0	2.5-7.0	1.0-2.0	1.0-2.0	1.0-5.0	2.5-4.5	3.0-9.0	1.0-4.0	1.0-2.0
	14.	+1	3	1-3	3	2	1	1	(2-)3	3	2+3
	15.	1	1	1-3	3	2	1	1	(2-)3	3	3+2
	16.	1	1	1	1	1	1	+2	1	1	1
	17.	3	3	3	3	3	NA	(3)	3	3	3
	18.	3	3	3		4	3	4	+4	1	3
	19.	2					2	2		2	2
	20.	20-50	15-50	10-55	12-26	5.0-10.0	3.0-19.0	15-25	12-20(-39)	10-25	10.0-15.0
	21.	9-20	8-20	3-30		3.0-6.0	2.5-12.0	6.3-12.0	6-14(-30)	3.0-8.0	7.0-11.0
Inflor-escence	22.	3-15	3-15	3-8	1	1-3	1	1	1	1-3	3-6
	23.	3	2	2	3	3	3	3	3	2	2
	24.	2	2	2-4		2-4	4	3-4	3	4	4
	25.	5.0-10.0	3.0-10.0	2.0-4.0	c.0.3	0.4-0.6	0.2-1.0	1.0-3.0	0-2.0	0-0.5	0-1.5
	26.	2.0-4.0	2.0-4.0	4.0-8.0	5.0-10.0	1.0-2.5	1.0-4.0	3.0-7.0	3.0-6.5	1.0-2.0	1.0-4.0
	27.	3	4	3	3	3	3	2	2	3	2
	28.	c. 1.0	5.0-11.0	1.0-2.5	c.0.3	1.5-5.0	c.2.0	0.5-0.9	1.0-1.5	2.0-5.0	1.0-2.0
Calyx	29.	2	(1-)2	3(-4)	3	3	2	3	1	1	1
	30.	2	2	1	1	2	2	1		2	2
	31.	5.0-7.0	5.0-8.0	4.0-4.5	2.5-3.5	4.0-4.7	4.0-6.0	3.8-5.0	5.9-8.0	5.0-6.0	4.5-5.0
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.8-2.5	3.0-4.6	3.0-5.0		1.4-1.6	0.5-2.5	1.8-2.3		2.0-4.0	c.2.0
	34.	1.8-2.5	3.0-4.0	3.0-5.5	c.0.5	1.2-1.6	0.5-3.0	2.2-3.0	1.1-2.0	2.0-4.0	c.2.0
	35.	1.0-1.2	1.0-2.5	1.0-1.3		0.4-0.6	0.3-1.2	1.3-2.1		1.0-2.0	0.7-0.8
	36.	c. 2.0	2.0-2.5	2.0-4.0	c.1.5	1.2-1.6	0.5-2.0	2.2-3.0	1.1-2.0	2.5-4.0	1.5-1.8
	37.	3	3	2	3	4	2	1	3	1	3
	38.	2	3	1	2	4	2	1	2	1	3
	39.	2	3	2+3	2	2	2	2	3	3	2(+3)
	40.	1	1	3	2	2	2	3	3	1	1
	41.	2	1	2		2	2	+1	2	2	2
	42.	3	3	3		3	3	2	3	3	3
	43.	2	2	2		1	2	1	1	2	2
	44.	3	3	3		3	3	3	3	3	3
	45.	1	1	1		1	1	1	1	1	1
Corolla	46.	17-22	25-34	18-21	19-24	13.5-19.5	17-25	28-33.5		22-25	12-27
	47.	4.0-5.0	5.0-8.5	5.0-6.0	8.0-9.0	1.5-7.0	3.0-4.0	c.2.0		c.5.0	3.0-5.0
	48.	4.0-5.0	3.0-4.5	4.0-6.0		3.0-7.5	5.0-6.0	c.2.0		c.5.0	3.0-5.0
	49.	1	1	1	1	1	1	1	1	1	1
	50.	1	1	1	1	1	1	1	1	1	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	4	3	1				4	4	4	4
	54.	1	1	1	1	1	1	1	1	1	1
Stamens	55.	1	1	2	1	2	1		2	2	1
	56.	c.10.0	8.0-18.5	c.16.0	2.0-3.0	c.12.0	4.0-4.5	c.14.0	4.0-4.5	c.5.5	c.6.0
	57.	c.11.0	11.0-20.0	c.21.0	17-20	c.15.0	5.0-5.5	c.17.0	6.5-8.0	c.9.5	c.10.0
	58.	3	2-3	3	1	(2-)3	2	3	2	2	2
	59.	3	3	3	3	3	2	3	2	3	3
	60.	3	2	1	1	2	2	1	1-2	2	2
	61.	1	1	1	2	1	1	1	1	1	1
	62.	2	2		1	2		2	1		1
Style	63.	20-25	c.40	25-40	c.40	20-26	20-28	28-40	33-40	25-30	30-40
	64.	2	2	2		2	2	2		2	2
	65.	3	1	1		1	1			3	1
Nutlets	66.	1	1	2				2		1	1
	67.	2	2	2				2		2	2
	68.	2	3	3				3		3	1
	69.	1	2	2				2		2	2
2n	70.										48

		cercocarpoides	pulchella	flabellifolia	sphenophylla	sericea	argentea	clivorum	sericifolia	impressa	revoluta
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	4	4	4	4	4	4	4	4	4	3
Stems	3.	30-100	60-150		90-120	60-150	20-30	25-30	50-100	30-60	20-50
	4.	2	2		2	2	2	2	2	2	2
	5.	2	2	2	2	2	2	2	4	1	4
Leaves	6.	9(-3)	(1-)2	2	9(-2)	5-7	7	9	9	9-7	2
	7.	1(-2)	3-5	5	3	1	1	1	1	1(-2)	1
	8.	3-4	1-3	3	1	4	3-4	4	4	4	4
	9.	2	2	2	2-1	2	1	2	1	1	3
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2	2	
	12.	2	2	2	2	2	2	2	2	2	1
	13.	1.0-3.0	2.0-10.0	2.0-4.5	3.0-6.0	0-0.5	0-0.3	0.6-1.4	2.0-5.0	0.4-1.0	0.2-0.8
	14.	2-3	2-3	3	3	3	3	3	3	2	1-3
	15.	3	3	3	3	3	3	3	3	2	3
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	3	3	3	3	3	3	3	3
	18.	4	3		4	1	3	4	3	3	1
	19.	2	2			2		2	2		2
	20.	8.0-22.0	11-35	6.5-10.0	30-54	4.0-12.0	3.0-6.0	5.0-10.0	7.0-20.0	7.0-14.0	1.2-4.0
	21.	4.5-12.0	8.5-32.5	6.0-11.0	11.5-19.0	1-2(-3.2)	1.3-2.0	1.0-4.2	1.5-4.0	1.3-3.5	1.0-2.0
Inflorescence	22.	1-5	3-6	1	5-16	1-3	1	1	1-3	1-4	1
	23.	3	3-2	3	2	3	3	3	2	3	3
	24.	4	2-4	4	4	4	3-4	4	2	3-4	2
	25.	0.5-3.5	0.5-5.0	0-0.2	2.0-4.5	0		0.7-0.8	0-1.0	0.4-0.6	NA
	26.	1.0-5.0	0.5-7.0	1.6-2.3	0.5-1.2	1.0-2.0		0.7-1.2	1.0-5.0	0.5-3.0	2.5-4.0
	27.	2	3-2	2	3	4		3	3-4	2	1
	28.	0.5-1.5	1.5-5(-9)	1.0-1.5	1.3-4.0	3.0-4.0		1.2-3.5	2.0-7.0	0.8-2.0	NA
Calyx	29.	1	1	1	1	2	1	1	2	1	2
	30.	+2	2	2	+1	2	2	2	2	2	2
	31.	5.6-6.5	5.0-7.5	c.3.5	2.4-4.2	4.0-4.5	c.3.8	4.5-5.0	4.0-6.0	3.5-3.8	3.0-4.0
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.2-2.0	3.2-6.0	2.5-3.0	3.1-4.2	1.0-2.0	c.1.8	1.4-1.8	1.8-2.0	1.6-2.0	c.1.2
	34.	1.6-2.5	3.0-5.0	2.3-2.6	3.1-4.2	1.0-2.0	c.1.5	1.4-1.8	1.8-2.0	1.3-1.7	c.1.2
	35.	0.7-1.0	1.6-4.0	1.5-2.0	2.0-2.7	0.5-1.0	c.1.0	0.5-1.0	0.7-2.0	0.5-1.0	c.0.7
	36.	1.6-2.5	3.0-5.0	2.3-2.5	2.8-3.8	1.0-1.5	c.1.5	1.4-1.8	1.0-2.0	1.3-1.7	c.1.0
	37.	1	1	4	1	3	1	1	3	1	3
	38.	2	1	4	1	3	1	1	3	1	3
	39.	3	+2-3	3	3	3	3	3	3	2	3
	40.	2	1	1	1	3	1	1	1	1	3
	41.	2	2	2	1	2	2	2	2	2	2
	42.	3	3-2	1	3	3		2	3	3	3
	43.	1	1	2	1-2	1	1	1	1	1	2
	44.	3	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1		1	1	1	1
Corolla	46.	16-24	13-24	c.16.5	8.0-10.5	13-18	c.13.0	9.0-14.0	20-27	15-19	20-25
	47.	3.0-6.5	3.5-5.7	2.8-3.0	3.0-3.5	1.5-2.0	c.3.0	2.2-4.5	3.0-5.0	3.0-4.0	2.5-3.0
	48.	2.5-5.0	4.7-7.2	4.0-4.5	4.0-4.5	1.0-1.8	c.3.0	2.2-5.5	1.0-4.0	3.0-4.0	2.0-3.0
	49.	1	1	1	1	1	1	1	1	1	1
	50.	1	1	1	1	1	1	1	1	1	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	4	4-3	3	1	3		4	4	3	3
	54.		1	1	3	1	1	2	1	1	1
Stamens	55.	3	1	1	3	1		1	1	3	1
	56.	c.10.0	8.0-11.0	c.5.0	c.4.0	c.5.0		c.5.5	c.11.0	c.5.5	4.0-10.0
	57.	c.11.7	9.5-13.5	c.8.0	c.5.5	c.8.0		c.6.8	c.15.0	c.8.0	6.0-10.0
	58.	2	2	2	2	2		2	2	2	2
	59.	3	3	3	2	3		3	3	2	3
	60.	2	2	2	2	2		2	2	2	2
	61.	1	1	1	1	1	1	1	1	1	1
	62.		1-2	+1	1					2	
Style	63.	27-35	20-34	22-24	11.5-14.0	18-24	19-22	15-20	29-37	22-25	30-32
	64.	2	2	2	2	2	2	2	2	1	2
	65.	1	1	1	2	1	1	1	3	1	1
Nutlets	66.	1	1		1	2				1	1
	67.	2	2		2	2			2	2	2
	68.	3	3		3	3				3	3
	69.	3	1		3	1			1	1	2
2n	70.										

		jamesonii	striata	plicatula	taxifolia	weberbaueri	cutervoensis	obovata	gilliesii	vargasii	domingensis
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	4	4	3	4	4	4	3	4	4
Stems	3.	30-75	60-200	20-30	50-200	50-100		30-50	60-120	80-120	c.100
	4.	2	2	2	2	2	2	2	2	2	2
	5.	4	2	2	1	3	4	3	2	1	3
Leaves	6.	2	2	2-1	9-8	9(-2)	3(-9)	4-8	3-4	9	9-2
	7.	1	1	1-2	1-2	(1-)2	2	1(-2)	1	1	1(-2)
	8.	2+3	2+3	2	3-4	3	3	1	3	1	3
	9.	2	2(-1)	1	2	2	2-3	2-3	3	3	2-3
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	2	2	2	2	1	1	+2	2
	13.	0-0.3	0-0.3	0.2-0.5	1.0-2.0	0.2-1.0	0.2-0.5	0-0.6	0-0.5	1.5-3.0	1.0-2.5
	14.	+1	1(-2)	2	1-2	1-2	1	1(-2)	2(-3)	2	2
	15.	1	1(-2)	2	2-3	1-2	1	1(-2)	2(-3)	2	2
	16.	2	1	1	1	1	1	1	1	1	1
	17.	3	(3)	3	3	(3)	NA	(3)	3	3	3
	18.	1	4	4	3	4	4	4	3	4	4
	19.	2	2	2	2	2			2		2
	20.	1.0-3.0	3.5-6.0	1.7-5.0	9-18	6.0-25.0	5.5-10.0	4.0-10.0	5.0-17.0	10.0-13.0	6.0-10.0
	21.	1.0-1.5	2.2-3.8	1.5-4.0	2.5-9.0	2.5-14.0	2.5-4.8	1.3-4.7	1.0-5.0	4.0-6.6	3.5-6.5
Inflorescence	22.	1	1	1-2	1	1-8	1	1	1-3	1-3	1
	23.	3	3	3	3	2	3	3	1	3	3
	24.	3	4	1-2	4	3-4	4	2-4	4	4	3-4
	25.	0	NA	0.2-0.5	0.5-1.0	0.5-1.0	0	0.0.5	0.2-0.8	0.6-1.0	0.5-1.2
	26.	1.0-2.0	1.0-2.0	1.5-3.0	1.0-2.0	1.0-3.0	0.5-0.7	1.0-3.0	0.5-1.3	1.3-2.0	1.3-3.2
	27.	3	1	3	2	2	4	4	3-4	3	2
	28.	1.0-1.2	NA	1.6-1.8	1.0-2.5	0.5-2.0	3.0-7.0	3.0-6.5	3.0-6.0	0.5-1.8	0.5-1.2
Calyx	29.	2	1	2	1	1	1	1-2	2	1	2
	30.	1	2	2	2	2	2	2	2	2	2
	31.	3.5-5.0	3.0-7.0	4.0-4.4	4.0-6.0	4.5-6.0	3.2-4.5	4.6-6.6	4.5-6.5	7.0-8.0	5.5-6.7
	32.	2	2	2	2	2	2	2	2	2	2
	33.	c.1.5	1.3-1.4	1.2-1.5	1.5-4.0	1.0-2.4	3.2-4.5	1.7-2.0	3.0-5.5	1.7-1.8	1.5-2.0
	34.	c.1.5	1.0-1.2	0.9-1.6	1.5-4.0	1.0-2.4	2.0-2.5	1.3-1.7	3.0-5.5	1.0-1.3	0.8-1.2
	35.	c.0.5	0.3-0.8	0.6-0.7	1.0-2.5	0.5-1.0	2.2-2.7	1.0-1.4	2.0-4.0	0.5-0.6	0.6-1.0
	36.	c.1.2	1.0-1.2	0.9-1.6	0.7-2.0	1.0-2.4	2.0-2.5	1.3-1.7	3.0-5.5	1.0-1.3	0.8-1.2
	37.	3	3	3	1	1	1	1	1	3	3-1
	38.	3	3	2	1	1	1	1	1	2	2-3
	39.	1	2-3	3	(2-)3	2	1(-2)	2	2	2	2
	40.	1	2	2	1	1	2	2	1	1	1
	41.	1	2	2	2	2	2	2	2	2	2
	42.	1	2	3	3	2	2	2	3	3	2
	43.	2	1	1	2	2	1	1	2	2	1
	44.	3	3	3	3	3	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	12-15	13-20	20-22	15-18	12-20	c.16	14-22	9.0-14.0	19-23	20-21
	47.	1.5-2.5	3.3-6.0	4.0-4.5	3.0-6.0	2.7-3.8	c.5.0	4.0-6.5	2.0-4.0	2.0-4.5	c.4.5
	48.	1.5-2.5	4.0-4.5		3.0-5.0	2.5-4.7	c.5.5	3.0-6.0	3.0-5.0	2.0-3.0	c.4.5
	49.	1	1	1	1	1	1	1	1	1	1
	50.	1	1	2	1	1	1	1	1	1	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	3	4		3	3	4	3	1	4	4
	54.	1	1	1	1	2	1	1	2	1	1
Stamens	55.	1	2		3	3	1	1	1	2	2
	56.	c.5.0	c.8.5		c.5.5	c.5.3	c.6.5	10.5-11.0	c.3.0	c.7.0	7.0-7.5
	57.	c.6.0	c.12.5		c.8.5	c.7.5	c.8.0	c.14.0	4.0-5.0	c.10.0	9.0-11.0
	58.	2	2		2	2	2	2	2	2	2
	59.	2	3		3	2	2	3	3	2	2
	60.	2	2	2	3	2	3	3	2	1	2
	61.	1	1		1	1	1	1	1	1	1
	62.		1		2		1			2	1
Style	63.	22-23	23-25	25-27	20-25	14-23	c.20.0	20-35	15-17	24-26	
	64.	2	2		1	2	1	2	2	2	2
	65.		1		1	1	2	1	1	1	1
Nutlets	66.			1	1	1			2	1	
	67.			2	2	2			3	2	
	68.			3	3	3				1	
	69.			1	1	3			1	1	
2n	70.										

		pallida	mathewsii	incana	discolor	micromerioides	Obtegomeria	Montereya	Piloblephis	Hesperothymus	
										brownei	douglasii
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	3	4	3	4	4	1	4	1	1
Stems	3.	30-100	50-100	60-300	30-150	18-36	10-40	50-150	20-70	10-50	15-50
	4.	2	2	2	2	2	2	2	2	2	1
	5.	3	1	2	2	2	2	1	+1	3-4	2-4
Leaves	6.	9	2-1	9	9-2	6-9	5-6	2	5-7	1-2	2-1
	7.	1	1	1-2	1-2	1	1	3-4	1	1-2-6	3-2
	8.	3	3	1-3	3	+1	4	1	4	1	1
	9.	2	2	2	2-3	1-2	3	2	2	2-3	3
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	2	2	1	1	2	1	2	2
	13.	1.0-3.5	2.5-6.0	1.0-4.0	1.0-2.0	0-0.2	0.1-0.2	3.0-15.0	0-0.2	3.0-10.0	3.0-6.0
	14.	1(-2)	2	2	2	1(-2)	1-2	3	2+3	1(-3)	3
	15.	1(-2)	2	2	3	1(-2)	3	3	2	1(-3)	1
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	3	3	3	3	2	3	3	3
	18.	4	4	3	3	4	1	3	3	3	3
	19.	2	2	2	2		2		2	2	2
	20.	6.0-10.5	10-20	8.0-25.0	4.0-20.0	6.5-16.0	4.0-6.0	30-70	5.0-9.0	6.0-22.0	10.0-30.0
	21.	3.3-6.4	6.3-16.6	5.0-14.0	2.5-7.0	1.3-4.5	0.8-1.0	13-40	0.7-1.8	2.5-17.0	7.0-24.0
Inflorescence	22.	1-3	1-3	1-3	1	1	1-2	3-9	1-2	1	1
	23.	3	3	3	3	3	2	3	1	3	3
	24.	2-4	4	4	4	3-4	4	1-2	4	1-2	2
	25.	1.0-1.7	0.3-1.0	0.2-0.5	0.2-0.3	4.0-7.0	0-0.2	5.0-21.0	0	NA	3.0-5.0
	26.	1.0-1.7	1.6-2.3	2.0-3.0	1.5-2.0	0-0.5	2.0-3.0	15.0-30.0	0.3-0.5	3.0-12.0	5.0-10.0
	27.	2-3	2-3	3-4	4	3	4	4	4	1	2
	28.	1.8-2.3	2.0-4.0	2.5-7.0	2.0-3.0	2.0-2.8	3.0-3.5	9.0-16.0	5.0-7.0	NA	1.5-2.0
Calyx	29.	1	1	1	2	2	3-4	2	3	1-2	1
	30.	+2	2	2	2	1	2	1	2	1	2
	31.	7.0-7.8	6.5-7.0	4.5-6.0	2.0-2.5	4.0-4.4	3.0-4.0	12.0-13.5	0.7-1.0	2.5-3.5	3.0-4.0
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.7-2.0	3.0-3.3	1.5-3.0	2.0-2.5	2.0-2.5	2.5-3.0	3.8-4.2	c.1.2	1.3-1.5	1.3-1.5
	34.	1.6-1.8	2.4-2.7	1.0-2.5	2.0-2.5	2.0-3.0	3.0-3.5	3.6-4.0	c.1.5	1.3-1.5	1.3-1.5
	35.	0.9-1.4	1.6-1.8	0.8-1.5	0.8-1.2	2.0-2.5	1.0-1.5	3.5-4.0	c.1.2	0.6-0.9	0.8-1.0
	36.	1.6-1.8	2.4-2.7	1.0-2.5	2.0-2.5	2.0-3.0	2.8-3.3	3.8-4.2	c.1.5	1.3-1.5	1.3-1.5
	37.	1	1	3	1	1	3	2	2	2	1
	38.	2	2	2	1	1	1	2	2	3	1
	39.	2	2	3	3	1	3	3	3	1	3
	40.	1	1	1	2	2	2	3	1	2	1
	41.	2	2	2	2	2	2	1	2	1	2
	42.	2	2	3	1	3	3	3	3	1(-3)	1
	43.	1	2	2	1	2	1	1	3	2	2
	44.	3	3	3	3	3	2	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1	2
Corolla	46.	20-22	18-22.5	17-30	10.0-20.0	9.5-12.5	6.0-7.0	26-31	7.0-8.0	4.5-5.0	6.0-8.0
	47.	c.4.0	3.0-5.0	2.5-6.0	1.5-3.0	3.0-4.5	c.3.0	8.0-14.0	c.2.0	1.0-1.5	c.2.0
	48.	c.4.0	1.5-2.5	2.5-6.0	1.2-2.7	3.0-4.5	c.6.0	8.0-15.0	c.3.0	2.0-3.0	c.2.5
	49.	1	1	1	1	1	1	1	+3	1	1
	50.	1	1	1	1	1	2	1	1	2	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.		3	4	3	3	1	3	1	1	1
	54.	1	4	1	2-3		2(-3)	1	2	2	3
Stamens	55.		2	1	2	2	1	2	2	1	1
	56.		c.5.0	c.7.5	c.1.4	c.2.3	c.0.8	c.14.0	c.2.0	1.0-2.0	c.2.0
	57.		c.7.0	c.8.0	c.3.0	c.4.0	c.2.0	c.18.0	c.3.0	2.0-3.0	c.3.0
	58.		2	2	3	2	1	2	3	2	2
	59.	3	3	2	3	2	2	2	3	2	2
	60.	2	2	2	2	2	3	2	1	2	2
	61.	1	1	1	1+4	1	1	1	1	1	1
	62.		1			1		1		1	
Style	63.	28-31	24-33	25-35	12-22	12.5-17.0	c.9.0	42-45	8.0-9.0	6.0-7.0	c.9.0
	64.	1	1	2	2	2	2	1	2	3	2
	65.	1	1	3	2	1		1	4	1	1
Nutlets	66.	2							2	3	3
	67.	2							2	2	2
	68.	3							1	2	1
	69.	2							2	2	2
2n	70.			46							20

		viminea	ekmaniana	bucheri	alpestris	schusteri	nubigena	tenella	grisea	darwinii	brevicalyx
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	4	4	3	3	2	1	1	3	3
Stems	3.	30-100				300-500	10-30	15-30	8-18	3-15	50-100
	4.	2			2	2	2	2	2	2	2
	5.	1	1	1	1	4	1	1	1	2	+2
Leaves	6.	2-3	3-1	1-2-9	7-2	2	2-1	1	2	2-1	9
	7.	1(-2)	1	1(-2)	1	5	1-6	2-6	6	1-6	1(-2)
	8.	3	3	3	4	4	3	1	1	1	3
	9.	2-3	2	3	2	2	2-3	3	2	2-3	2
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2		2
	12.	2	2	2	2	2	1	2	2	1	+2
	13.	0.3-1.5	0.6-1.2	1.0-2.5	0.5-1.0	0.5-2.0	0.5-1.0	1.0-3.5	2.0-6.0	2.0-2.5	0.6-1.0
	14.	(3+)6	(1-)6	6	6	3	2-3	1-2	3	3	2
	15.	(3+)6	6(+3)	6	6	3(+5)	3	2	3	3	2
	16.	1	1	1	1	1	1	1	1	1	1
	17.	3	3	3	3	3	3	3	3	3	3
	18.	3	3	3	3	3	3	4	4	3	4
	19.	2			2	2	2	2		2	2
	20.	5.0-20.0	2.5-5.0	5.0-10.5	3.0-4.2	5.0-11.0	2.0-4.0	2.0-8.0	7.5-15.0	3.0-6.0	2.5-5.7
	21.	2.5-9.0	1.7-4.0	3.0-9.0	2.0-3.6	3.7-8.5	1.7-3.4	2.5-8.0	5.0-11.0	1.8-3.3	2.5-4.2
Inflor-escence	22.	1-4	1-3	1	1	6-17	1	1	2-4	1	1
	23.	2	3	3	2	3	2	3	3	2	3
	24.	4	4	4	4	2-4	2-4	1-2	2-3	2-4	4
	25.	0-1.0	c.0.5	0.3-0.5	0-0.4	4.0-8.0	0	0.2-0.3	0.2-0.5	0.5-3.0	0-0.2
	26.	0.3-0.5	0.5-0.7	1.8-2.5	0	0.2-1.2	0.8-1.0	0.4-1.5	1.0-2.0	0.4-0.5	0.6-1.5
	27.	3	2	2	2	3	2	2	2	3	2
	28.	0.5-2.0	0.4-1.0	0.9-1.1	0.5-0.7	0.9-1.3	0.3-0.4	0.4-0.6	1.0-2.2	1.0-1.5	1.2-1.6
Calyx	29.	2	2	3	2	3	3	1	2	2-3	4
	30.	1	1	1	1	1	1	1	1	1	1
	31.	1.5-2.0	1.5-2.5	3.0-4.7	2.3-2.4	c.1.6	2.0-2.5	1.3-1.8	2.2-2.3	3.0-4.0	1.8-2.0
	32.	2	2	2	2	2	2	2	2	2	2
	33.	1.0-1.3	0.6-1.3	1.3-1.8	c.0.6	c.0.4	0.8-1.3	0.5-0.7	1.5-1.6	c.1.0	1.0-1.2
	34.	1.0-1.5	0.6-1.3	1.3-1.8	c.0.6	c.0.5	0.8-1.3	0.6-0.8	1.4-1.6	c.1.0	1.2-1.3
	35.	0.5-1.0	0.6-1.3	0.3-0.5	0.4-0.5	c.0.4	0.5-0.8	0.4-0.5	c.1.2	c.1.0	0.8-1.0
	36.	1.0-1.5	0.6-1.3	1.3-1.8	c.0.6	c.0.5	0.8-1.1	0.6-0.8	1.4-1.6	c.1.0	1.2-1.3
	37.	1	1	2	3	3	3	3	1	3	1
	38.	1	1	2	3	3	3	1	1	3	1
	39.	5	5	+5	4	3	3	3	3	3	2
	40.	3	2	3	1	3	2	3	2	2	1
	41.	2	2	2	2	2	2	2	1	2	2
	42.	3	3	3	3	3	3	3	3	3	2-3
	43.	1	1	1	1	1	2	3	1	2	1
	44.	2	3	3	3	2	3	3	3	3	3
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	5.0-6.0	4.5-5.2	c.18.0	4.0-5.0	2.3-2.5	3.0-5.0	2.8-3.5	4.3-4.7	4.0-5.0	4.5-4.7
	47.	1.0-2.0	1.2-1.5	c.2.0	0.7-0.8	c.0.6	c.1.0	0.5-0.7	c.1.3	0.8-1.0	0.8-1.3
	48.	1.0-1.5	1.0-1.2	c.2.0	1.2-1.4	0.8-1.0	c.1.2	0.6-0.8	1.5-2.3	0.8-1.0	0.8-1.5
	49.	1	1	1	1	1	1	1	1	1	3
	50.	1	1	2	1	1	2	1	1	1	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	3	1		1	1	1	1	1	1	1
	54.	3	3	4	3	3	2	3	3	2	3
Stamens	55.	2	1		2	2	2	1	3	1	2
	56.	c.1.5	c.1.2		c.1.1	0.3-0.4	c.0.4	c.0.4	c.1.2	0.8-1.0	c.0.6
	57.	c.2.0	c.2.0	c.9.0	c.1.4	0.5-0.6	c.0.8	c.0.5	c.2.0	1.0-1.5	c.1.2
	58.	2	1		2	1	1	1	1	1	1
	59.	2	2	2	2	2	2	1	+2	2	2
	60.	1	1	1	1	1	2	2	2	2	1
	61.	1	1		1	1	1	1+4	1		1
	62.	2	1			1	1		3		
Style	63.	6.5-8.5	5.0-6.0	c.20.0	5.2-6.4	c.1.7	c.3.0	3.0-3.2	c.4.5	c.4.5	c.5.0
	64.	2	2	2	2	2	2	2	2	2	2
	65.	1	1	2	1	1	1	2	2	1	1
Nutlets	66.	1	1		2	1	2				2-3
	67.	1	1	1	1	2	2				1
	68.	3	3		3	3					
	69.	3	3		3	3	2				1-2
2n	70.										

		vana	fasciculata	mutabilis	bolivianum	odorum	axillare	gilliesii	ganderi	chandleri	cylindristachys
Habit	1.	2	2	2	2	2	2	2	2	2	2
	2.	3	3	3	3	4	3	3	3	3	1
Stems	3.	100-200	100-130	50-100	50-100	100-200	50-100	25-200	30-100	50-100	30-50
	4.	2	2	2	2	2	2	2		2	2
	5.	+1	4	4	3	3	3	2	2	1	1
Leaves	6.	2	7-5	1-2	9(-2)	9-7	5-7	6-7	2	1-2	2
	7.	2-6	1	5	2	2	1-2	1	2	5	6-2
	8.	3	4	4	3	1-3	3	3	1	1-3	3
	9.	2-3	3	2	2(-3)	1	1	2	2-3	3	2
	10.	2	2	2	2	2	2	2	2	2	2
	11.	2	2	2	2	2	2	2	2	2	2
	12.	2	2	2	2	2	1	1	+2	2	2
	13.	0.6-1.5	0-1.0	0.5-1.0	1.0-2.0	0.5-7.0	1.0-1.5	1.0-2.0	3.0-10.0	2.0-3.0	4.0-6.0
	14.	2	2	2	2	2	1	3	2(-1)	3	3
	15.	2	3	3	1	1	1	3	2(-1)	3	3(+5)
	16.	1	1	1	1	1	2	1	1	1	1
	17.	3	3	3	3	3	3	3	3	3	3
	18.	4	1	1	3	4	3	3	4	3	3
	19.	2	2	2	2	2	2	2		2	2
	20.	8.0-12.0	2.0-4.0	3.0-20.0	5.0-28.0	15.0-45.0	10.0-14.0	3.0-13.0	6.0-12.0	5.0-8.0	13.0-34.0
	21.	3.5-9.0	0.5-1.0	3.0-18.0	2.5-9.0	4.0-7.0	1.5-2.0	1.5-4.0	4.0-8.5	5.0-10.0	8.7-27.0
Inflor-escence	22.	3-6	6-15	6-21	1-3	4-21	1	1-3	1-3	1-3	4-9
	23.	2	1	1	2	3	3	3	3	2	1
	24.	2-4	2-4	1-4	4	2-4	3-4	4	1-2	3-4	(2-3-)4
	25.	0.2-0.4	0	0-0.1	0-0.5	0.2-0.5	0.2-0.5	0.5-1.0	0.9-3.0	c.0.5	0-0.2
	26.	0.2-0.4	0.5-1.0	0-0.1	0-0.5	0.8-1.5	0.6-1.0	0.8-1.0	1.5-2.3	c.2.0	0-0.2
	27.	2	4	2	3	3	2	2	2	2	3
	28.	0.6-1.2	2.0-3.0	0.5-2.2	1.0-2.0	0.3-0.5	0.2-0.3	0.8-1.0	1.5-3.7	1.0-2.0	1.3-1.7
Calyx	29.	3	1	2	3	4	4	4	2	4	+1
	30.	1	1	1	1	1	1	1	1	1	2
	31.	2.3-2.6	3.0-4.0	2.0-2.2	1.5-2.5	0.8-1.6	1.0-1.3	1.0-1.2	5.0-6.0	2.5-3.5	3.0-3.2
	32.	2	2	2	2	2	2	2	2	2	2
	33.	c.0.9	c.2.0	c.1.4	0.5-0.7	0.5-0.6	c.0.3	0.5-0.7	1.6-2.3	1.0-1.3	c.1.5
	34.	c.0.9	c.2.0	c.1.3	0.7-1.0	0.6-0.7	c.0.5	0.7-0.8	1.8-2.5	1.0-1.3	c.1.2
	35.	c.0.7	c.1.5	1.2-1.3	0.5-0.7	0.5-0.6	c.0.2	0.5-0.6	0.7-1.0	c.0.6	0.5-0.7
	36.	c.0.9	c.2.0	c.1.5	0.7-1.0	0.6-0.7	c.0.5	0.7-0.8	1.6-2.3	c.0.7	c.1.2
	37.	2	1	1	3	1-2(-3)	3	1	2	3	2
	38.	2	1	1	3	1-2	3	1	2	3	2
	39.	3	3	3	3	+1	1	3	2	3	3
	40.	3	1	1	1	1	1	3	1	3	1
	41.	2	2	2	2	2	2	2	2	2	2
	42.	2	1	1	3	2-3	3	3	3	3	3
	43.	1	1	1	1	1	1	1	2	2	1
	44.	3	3	3	3	3	3	1	3	3	3
	45.	1	1	1	1	1	1	1	1	1	1
Corolla	46.	5.0-7.0	7.0-8.0	3.5-4.5	5.0-7.0	1.3-1.4	1.5-2.0	1.3-1.8	9.0-11.6	6.0-9.0	4.0-4.2
	47.	0.9-1.0	1.5-3.0	1.0-1.5	c.1.0	0.5-0.6	0.5-0.7	0.7-0.8	2.0-3.0	1.5-2.5	c.1.3
	48.	2.0-2.5	1.5-2.2	1.5-2.3	1.5-2.0	0.8-0.9	0.5-0.7	0.7-0.8	2.0-3.5	1.5-3.0	c.1.4
	49.	1	1	1	1	3	1	1	1-2	1	1
	50.	1	1	1	1	1	1	1	1	1	1
	51.	2	2	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2	2	2
	53.	3	1	1	1	3	1	1	1	1	1
	54.	3(-2)	2	3	2	3		3	2-3	3	3
Stamens	55.	1	1	2	2	2	2	2	3	2	+1
	56.	c.1.6	1.5-1.8	c.0.6	c.1.5	0.1-0.2	c.0.3	c.0.1	c.2.8	c.2.5	c.0.8
	57.	c.2.3	c.2.5	c.1.0	c.3.0	0.2-0.3	c.0.4	c.0.1	c.4.2	c.3.5	c.1.4
	58.	(1-)2	1	1	2	1	1	1	2	2	2
	59.	3	2	2	3	1	2	1	2	2	2
	60.	2	2	1	2	1	1	1	1	2	2
	61.			1	1	1	1		1+4	1	1
	62.		1		1	1			+1		
Style	63.	6.5-11.0	c.10.0	c.3.8	c.9.0	1.4-1.5	1.5-2.0		11.0-14.0	c.10.0	5.5-6.2
	64.	2	1	2	2	2	2	2	2	2	2
	65.	1	1	1	1	1	1		1	1	1
Nutlets	66.	1		1	2	1	1	1	2	1	2
	67.	2		2	1	2	2	2	2	2	2
	68.	3		3	3	3	1		1	1	1
	69.	3		1	3	1-3	3	1	2	2	3
2n	70.		46								

		coccinea	ashei	dentata	arkansana	glabella	georgiana	procumbens	amissa
Habit	1.	2	2	2	2	2	2	2	1
	2.	4	4	2	1	1	1-2	1	1
Stems	3.	30-100	15-25	20-30	7-40	25-40	30-50	10-20	12-20
	4.	2	2	2	1	2	2	2	2
	5.	1	1	1	3	3	2	1	1
Leaves	6.	3	9	4	5(-9)	9	7-9	1-2	1-2
	7.	1	1	2	1(-2)	1-2	1-2	6	6-2(-4)
	8.	1-3	4	1-3	3	1	1-3	1	1
	9.	2-3	2	2	3	2-3	2-3	3	2
	10.	2	2	2	2	2	2	2	2
	11.	2			2	2	2	2	2
	12.	1	1	1	1	1	2	2	2
	13.	0-1.0	0-0.3	0.1-0.2	0-1.0	2.0-5.0	1.0-8.0	2.5-5.0	2.0-10.0
	14.	2	2	2	1	3	1(-3)	1-(3)	2(+3)
	15.	1	2	2	1	1	1	1(-3)	2(+3)
	16.	1	1	1	1	1	1	1	1
	17.	3	1	1	NA	3	3	3	3
	18.	3	3	3	3	3	3	3	3
	19.	2	2	2	2	2	2	2	
	20.	8.0-15.0	4.0-7.0	6.0-14.0	10.0-25.0	25-50	9.0-45.0	7.0-11.0	5.0-12.2
	21.	2.5-5.0	1.0-3.5	1.5-6.0	1.0-6.0	5.0-17.0	5.0-25.0	4.0-9.0	4.8-10.5
Inflor-escence	22.	1	1	1	1-3	1-3	1-4	1	2-6
	23.	3	3	3	3	3	2	2	3
	24.	2-4	3	2	3	3	2-3	1	1
	25.	0.5-1.0	0.2-0.3	0-0.2	0.4-0.5	0-0.2	0-0.3	0	0-0.2
	26.	2.5-4.5	2.0-3.0	4.0-6.0	3.0-8.0	5.0-10.0	1.5-4.5	4.0-4.5	3.0-9.5
	27.	4	4	4	4	3	3-4	2	2
	28.	2.0-2.5	2.0-3.0	1.8-2.5	2.0-3.0	5.0-7.0	2.0-5.0	0.8-1.2	0.4-1.0
Calyx	29.	2	1-2	1-3	1	1	1-2	2	2
	30.	1	1	1	1	1	1	1	1
	31.	7.0-8.0	3.0-3.5	4.0-5.6	2.0-2.5	3.0-3.5	4.0-4.5	3.5-4.0	1.8-2.3
	32.	2	2	2	2	2	2	2	2
	33.	1.0-1.5	1.5-2.5	1.0-2.0	1.7-2.0	2.0-2.5	1.0-2.5	1.2-2.1	1.2-1.4
	34.	2.5-3.0	2.5-3.5	2.0-3.0	1.7-2.0	2.0-2.5	1.0-3.0	2.5-3.0	1.5-1.6
	35.	0.2-0.5	0	0.2-0.5	0.4-1.2	1.0-1.5	0-0.4	0.4-0.5	0.6-0.9
	36.	2.0-3.0	2.5-3.5	2.0-3.0	1.6-1.9	2.0-2.5	0.8-2.5	2.4-2.8	1.5-1.6
	37.	3	NA	3	1	1	3	3	2
	38.	1	1	1	1	1	1	1	2
	39.	2	2	2	1	1	1	2+3	3
	40.	2	2	2	2	2	2	2	3
	41.	2	1	1	2	2	2	1	1
	42.	3	3	3	3	3	3	3	3
	43.	2	3	1	1	1	1	2	1
	44.	3	3	3	3	3	3	3	2
	45.	1	1	1	1	1	1	1	1
Corolla	46.	28-50	6.0-7.0	7.0-10.0	5.0-9.0	c.9.0	8.0-14.0	7.5-8.5	5.5-6.5
	47.	7.0-10.0	4.5-5.0	4.0-4.5	0.5-4.5	c.4.0	2.0-4.0	2.0-2.5	1.5-2.0
	48.	7.0-10.0	4.5-6.5	6.5-8.0	1.6-5.0	c.4.0	2.0-3.5	3.5-4.5	3.0-3.6
	49.	1	1	1	1	1	3	1	1
	50.	2	2	2	1	1	1	2	1
	51.	2	2	2	2	2	2	2	2
	52.	2	2	2	2	2	2	2	2
	53.	4	3	2	2		4	1	1
	54.	1	2	2	2	2	2	2	2
Stamens	55.	2	2	2	1		2	1	3
	56.	c.13.0	c.2.0	c.4.2	c.2.0		4.0-5.0	c.2.0	1.0-1.5
	57.	c.17.0	c.3.5	c.6.5	3.0-4.0		5.0-6.0	c.5.0	c.2.5
	58.	2	2	2	1		2	1	1
	59.	3	2	+3	2		2	2	2
	60.	1-2	1	1	2	2	3	2	1
	61.	1	1	1	1+4		1	1	1
	62.	1-2	2	2	1	1		1	1
Style	63.	40-46	9.0-11.0	11.0-13.0			11.0-15.0	10.0-11.0	5.5-7.0
	64.	1	2	2	2		2		2
	65.	1	1	1	1		1	1	1
Nutlets	66.	3	2	2	2		3(-1)	3	2
	67.	1	2	2	2		2	2	2
	68.		3						1
	69.	2	2	2	2		2	2	2
2n	70.				20				

Numerical Analysis

Intuitive methods of taxonomy, in which visual assessment of characters and experience in the group of concern combine to produce a practical and biologically plausible heirarchy, fail in two major respects: repeatability and objectivity. No two taxonomists will assess the characters in exactly the same way. Also, whether deliberate or not, some characters will be given more weight than others; even if a phenetic approach is intended this will occur. Such bias can be largely eliminated by numerical methods, and provided that observations are repeatable within an acceptable error and the taxonomic procedures are clearly defined different scientists should reach the same result. Various numerical methods are available, but I shall not discuss their relative merits here since this is dealt with at length by many text books on the subject, notably Sneath & Sokal, Numerical Taxonomy (1973).

Since much data had been gathered on a large number of characters for nearly all species of Satureja s.l. a numerical analysis seemed worthwhile. The results are presented as dendograms which represent graphically the similarity between taxa. These dendograms are compared with the taxonomic arrangement presented in Chapter 3. As an additional exercise I wrote all of the computer programs used for data input and processing. These programs are briefly described and fully documented listings provided.

Computer Programs

The programs were written in Digital Research ST BASIC on an Atari 520 ST with 512 K bytes of memory and one 500 K byte disk drive. The programs are as follows:

CHARDATA.BAS - accepts data typed in at the keyboard and produces sequential disk files for each species;

CONCAT.BAS - concatenates files with a specified file type name into one larger sequential file;

SIMILAR.BAS - calculates similarity values for all pairs of species using the general coefficient of similarity described by Gower in *Biometrics* 27:857-74 (1971);

PAIRSORT.BAS - performs group pairs sorting on the similarity values calculated by SIMILAR.BAS.

Since the programs are extensively commented, no further explanation will be given here on their operation.

Results and Discussion

Satureioid genera

The analysis (see Graph 1) suggests that *Euhesperida* is clearly distinct from *Satureja* s.s. while *Gontscharovia* and *Satureja* s.s. are more closely related. *G. popovii* is associated with species which are themselves distinct within *Satureja* s.s. (*S. thymbra*, *S. salzmannii*, *S. bzybica*, *S. coerulea* and *S. isophylla*). It could be argued, therefore, that *G. popovii* is just another of these distinct species. However, *Gontscharovia* has a combination of both floral and vegetative characters (see p. 211) which favour generic rank for this taxon.

Boissiers (1879) division of Satureja s.s. into 5 sections (see p. 177 for details) is not supported by the numerical analysis. For example, the species comprising Sect. Subbilabiatae Boiss., S. boissieri, S. subdentata [=S. intermedia], S. mutica, S. spicigera, S. macrantha, S. longiflora [=S. edmondii] and S. atropatana (of unknown affinity), are widely separated on the dendogram. My own informal division of the genus into 3 groups (see p. 178) is in somewhat closer agreement with the analysis. However, at best, groups comprising only 2 to 6 species are suggested by the dendogram. The species of these small groups are, in the main, placed near each other in the taxonomic account in Chapter 3.

Micromerioid genera

The species of the Micromerioid genera were too numerous to be dealt with by the computer programs as one block. Nevertheless, by dividing the species into more managable groups, the relationships between and within the 3 Micromerioid genera are still clearly shown in Graphs 2, 3 and 4.

Graph 4 shows that Brenaniella and Killickia are clearly separable from Micromeria sect. Pseudomelissa, the section most similar in facies to these genera (Brenan, 1954). Within Micromeria, sections Madagascarenses and Cymularia seem distinct from sect. Micromeria (Graph 3), whereas sect. Pineolentia, endemic to Gran Canaria, cannot be distinguished from the Canary Isles species of sect. Micromeria (Graph 3).

The similarity values between Micromeria sections Cymularia and Madagascarenses to sect. Micromeria (c. 70% on Graph 3) are of the same order as the distance between sect. Pseudomelissa to

Brenaniella and *Killickia* (Graph 4). Therefore, it could be argued that sections *Cymularia* and *Madagascarenses* are worthy of generic rank. Both sections are morphologically very distinct in *Micromeria* so generic rank could be sustained.

Numerous small species groups in *Micromeria* are suggested by the numerical analysis, and mostly these correspond with similarities between species noted in Chapter 3.

Calaminthoid genera

Analysis of the entire Calaminthoid group (see Graph 5) suggests that *Cyclotrichium* is the most distinct genus, and while *Calamintha*, *Clinopodium* and *Acinos* nearly separate into distinct groups intermediates occur.

A. simensis and *A. pseudosimensis* are related by the analysis to *C. uhligii*, *C. kilimandschari* and *C. debilis*. On p. 359 it is argued that the sigmoid, gibbous calyx and sessile pedicels of *A. simensis* and *A. pseudosimensis* suggest these taxa are better placed in *Acinos* than in *Calamintha*. Brenan (1954), however, noted their similarity to *C. uhligii* and believed that *A. pseudosimensis* hybridized with it. Therefore, my decision to place *A. simensis* and *A. pseudosimensis* into *Acinos* may be an error. Graph 7 shows, however, than in an analysis which excludes *Calamintha* these two species associate with *Acinos*.

Clinopodium is much more closely related to *Calamintha* than is *Acinos* (Graph 7), with the distinct *Cl. atlanticum* being associated with *C. rouyana* and *C. cretica*. There has been much discussion on the relationships between these two genera and much juggling of species between them (see pp. 324-327 for a detailed discussion). The analysis suggests that the relationship is indeed close, and it could be argued that *Clinopodium* is not sufficiently distinct to warrant generic rank. However, *Clinopodium* possesses a unique combination of floral characters. Sectional rank may, therefore, be more appropriate for *Clinopodium*, though traditionally vegetative characters are more usual in distinguishing sections.

Within *Calamintha*, *C. grandiflora*, *C. betulifolia*, *C. tauricola*, *C. pamphylica* and *C. piperelloides*, are closely related (see p. 303) and all share an 11-nerved calyx, large corollas and craspedromous leaf venation. These species are also identified as a distinct group by the numerical analysis (see Graph 6) and may merit sectional rank. The much confused species *C. confinis*, *C. gracilis*, *C. ussuriensis* and *C. micrantha* from the Far East, which are unusual in having the posterior stamens reduced to staminodes, also form a distinct group in the analysis (Graph 6).

American genera

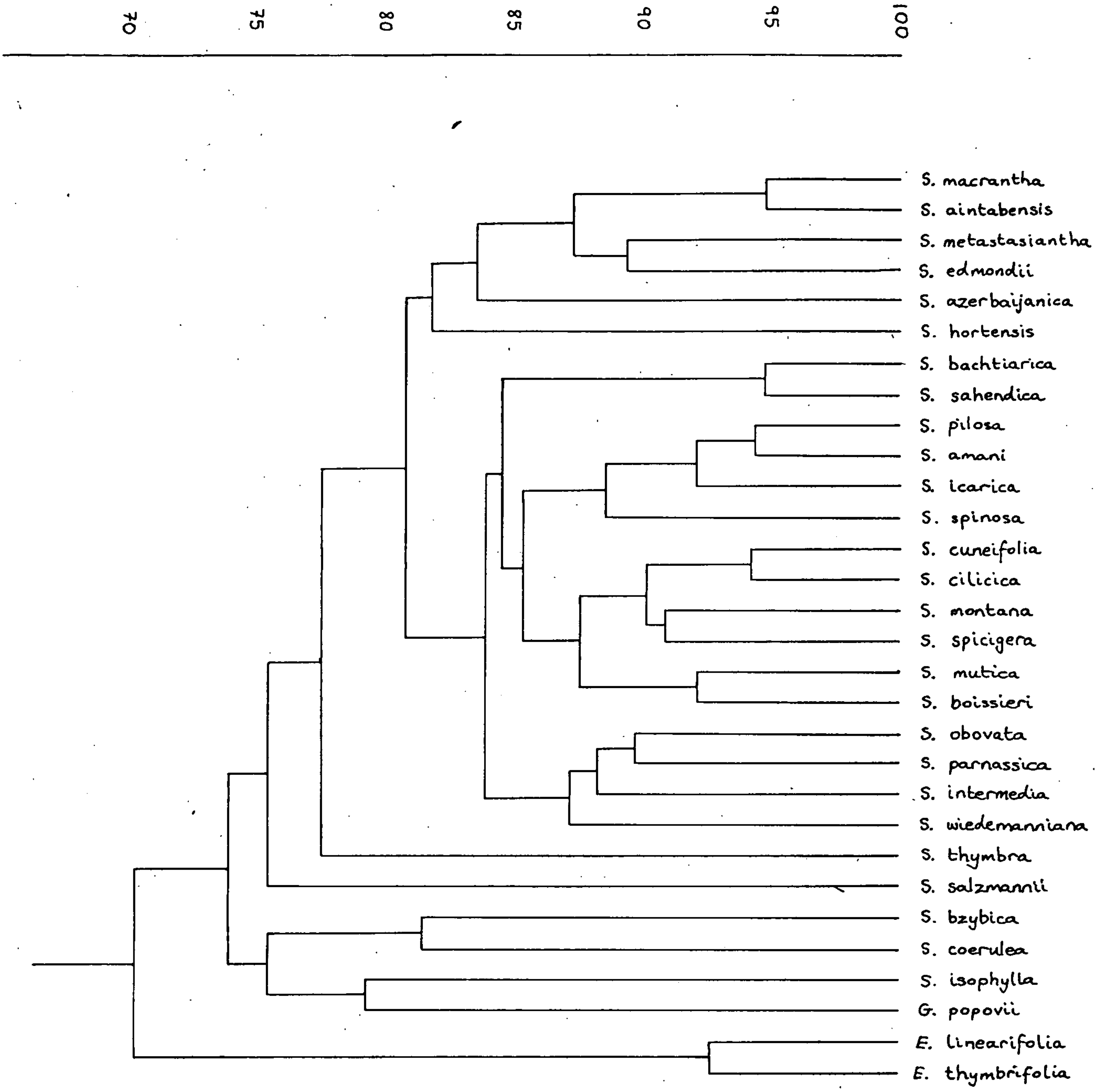
The monotypic genera *Montereya*, *Piloblephis* and *Obtegomeria* are clearly distinct from *Gardoquia* (Graph 8) and *Xenopoma* (Graph 9). However, the separation of the other American genera is not so clear cut. Graph 9 shows that *Xenopoma*, *Hesperothymus* and *Diodeilis* do not appear as fully separated groups.

It was stated earlier (p. 409) that *Hesperothymus* was a weakly defined genus which probably came closest to *Diodeilis*. This conclusion is supported by the numerical analysis (Graph 9), with *H. brownei* placed next to *D. procumbens* (sect. *Herbaceae*) and *H. douglasii* next to three more members of sect. *Herbaceae*. Graph 10 shows that *Diodeilis*, when analysed in isolation, is divisible into distinct groups which correspond with its two sections, *Diodeilis* (*D. ashei*, *D. dentata* and *D. coccinea*) and *Herbaceae*. Sect. *Diodeilis* also appears as a distinct group on Graph 9.

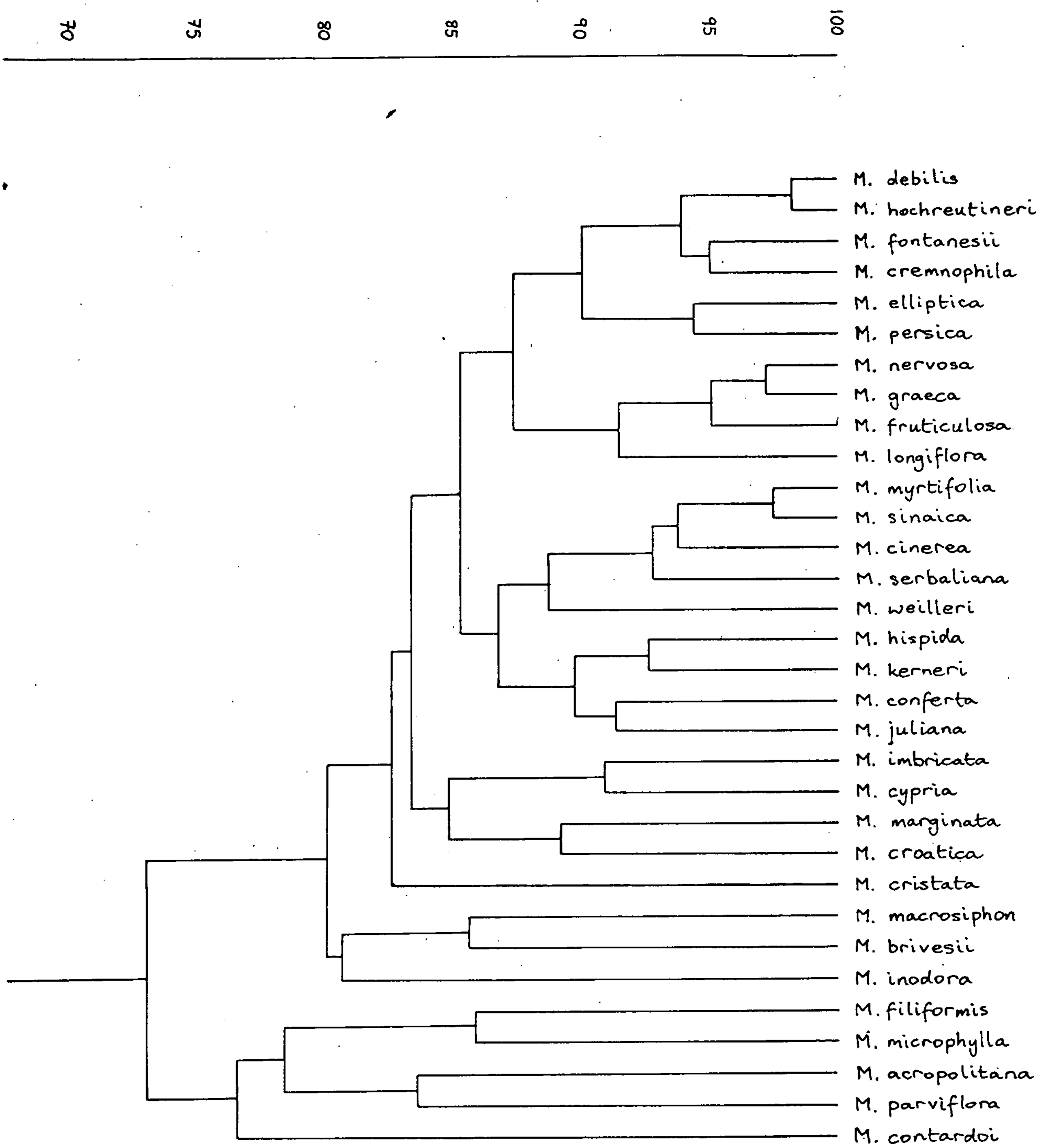
The sectional division of *Gardoquia* and *Xenopoma* adopted in this revision is not fully supported by the numerical analysis

(Graphs 8, 9 and 10). Nevertheless, the tendency is for the species of these sections to be placed near each other on the graphs. I suggest that part of the reason for this discrepancy is due to the characters chosen for the numerical analysis. The sections in Chapter 3 were mainly based on vegetative characters, while only 21 of the 69 characters chosen for the numerical analysis were vegetative; 47 were floral or inflorescence characters. The general similarity in floral characteristics may have obscured the differences in vegetative structure. An analysis of Gardoquia using vegetative characters only (graph not presented) suggested 3 major groups equivalent to the following: 1) sect. Gardoquia; 2) sections Tomentosae, Anomales and Sericifoliae united; and 3) sections Plicatae, Taxifoliae, Pallidae, Discolores and Micromerioides united. However, numerous anomalies occur, with species being placed together which one would not consider likely when based on the overall characteristics of the plants. The great variability in vegetative characters could be the reason for this.

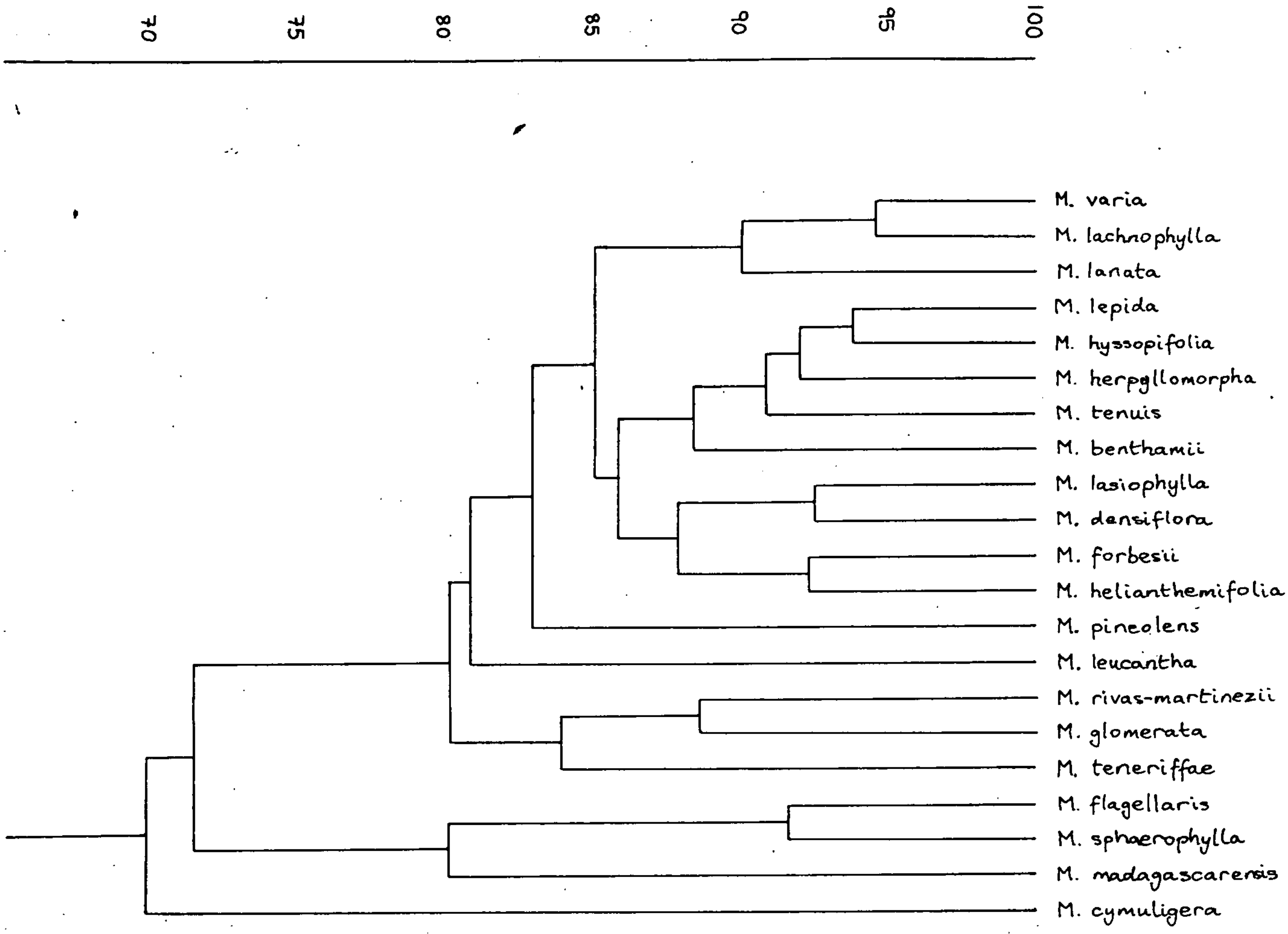
In the formation of my own sections of Gardoquia and Xenopoma I have judged that certain characters are worthy of more weight than others, particularly when they appear in combination with characters which are unlikely to be evolved independently in other parts of the genus. This would seem to fly in the face of the phenetic principle of equal weighting of characters. However, I feel this approach is defensible since one first of all forms the groups based on overall similarity, i.e. there is no a priori weighting of any particular character, and only then do certain characters lend themselves to describing these groups. To take a couple of examples, the distinctive indumentum and leaf venation of Gardoquia sect. Tomentosae and the unusual verrucose-dendritic indumentum of Xenopoma sect. Xenopoma are just some of the characters which support the recognition of these sections.



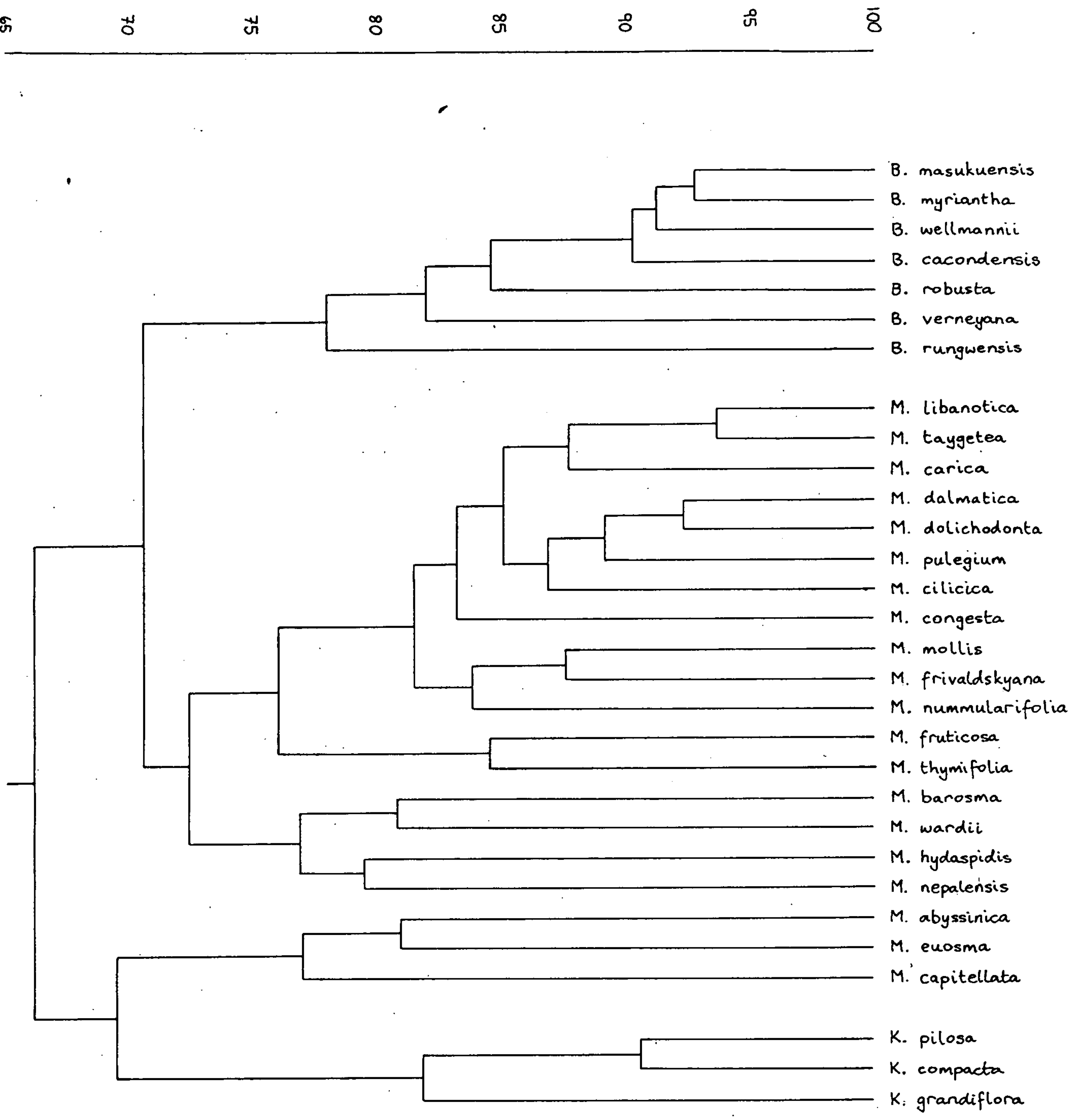
Graph 1. Satureioid genera: Satureja, Gontscharovia, Euhesperida.



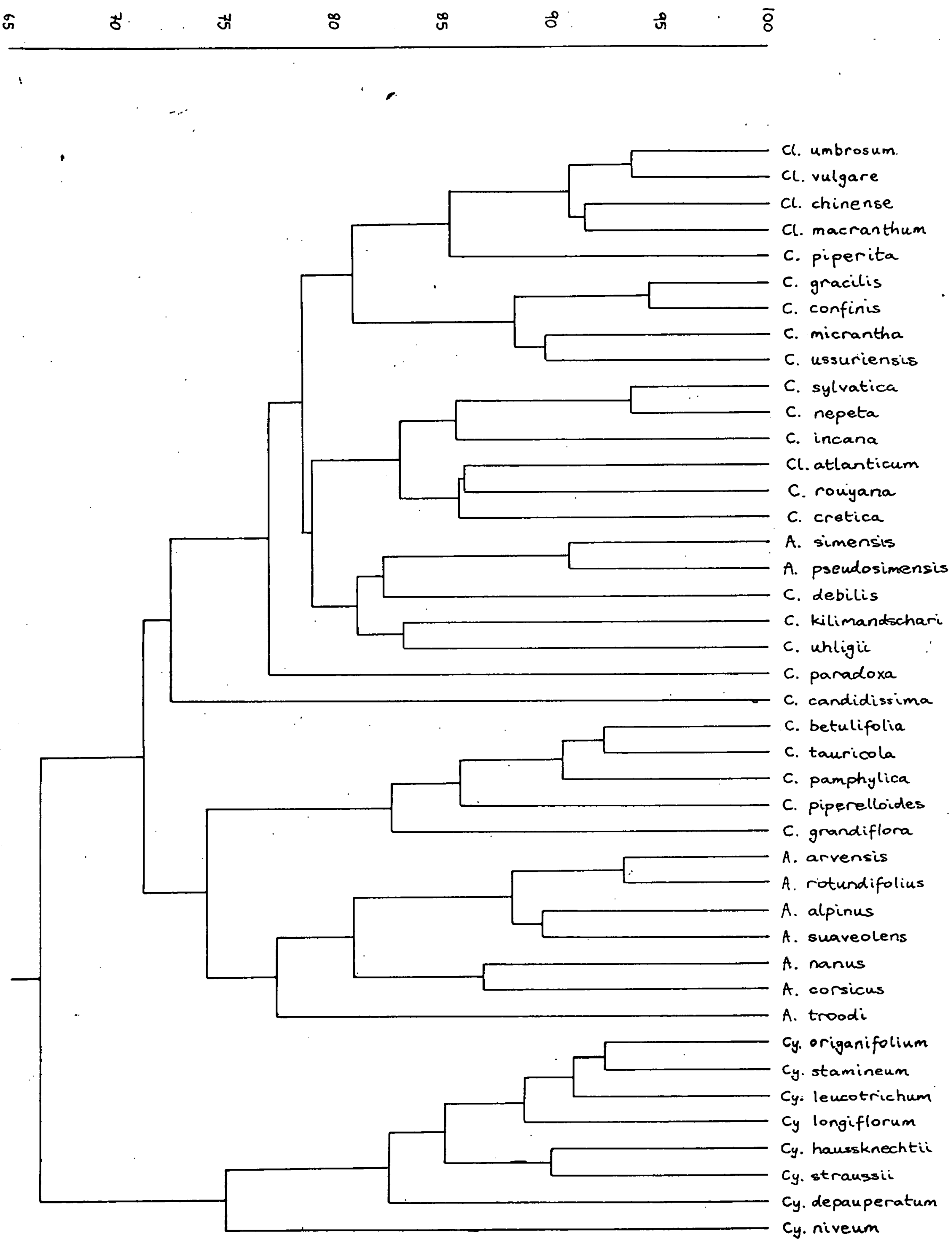
Graph 2. Micromerioid genera. Micromeria sect. Micromeria excluding Canary Isles species.



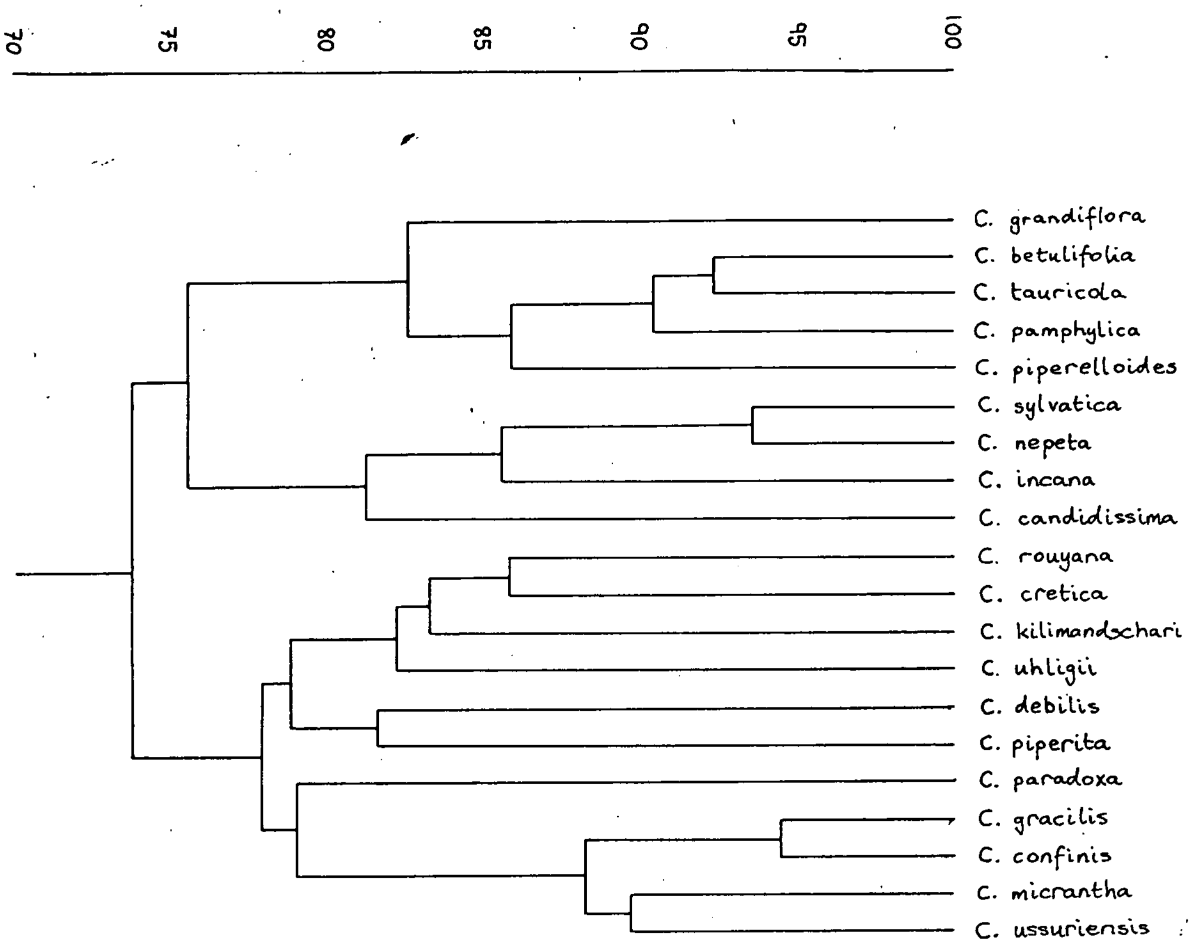
Graph 3. Micromerioid genera. Micromeria sect. Micromeria from the Canary Isles, Micromeria sect. Pineolentia, Micromeria sect. Madagascarenses, Micromeria sect. Cymuligera.



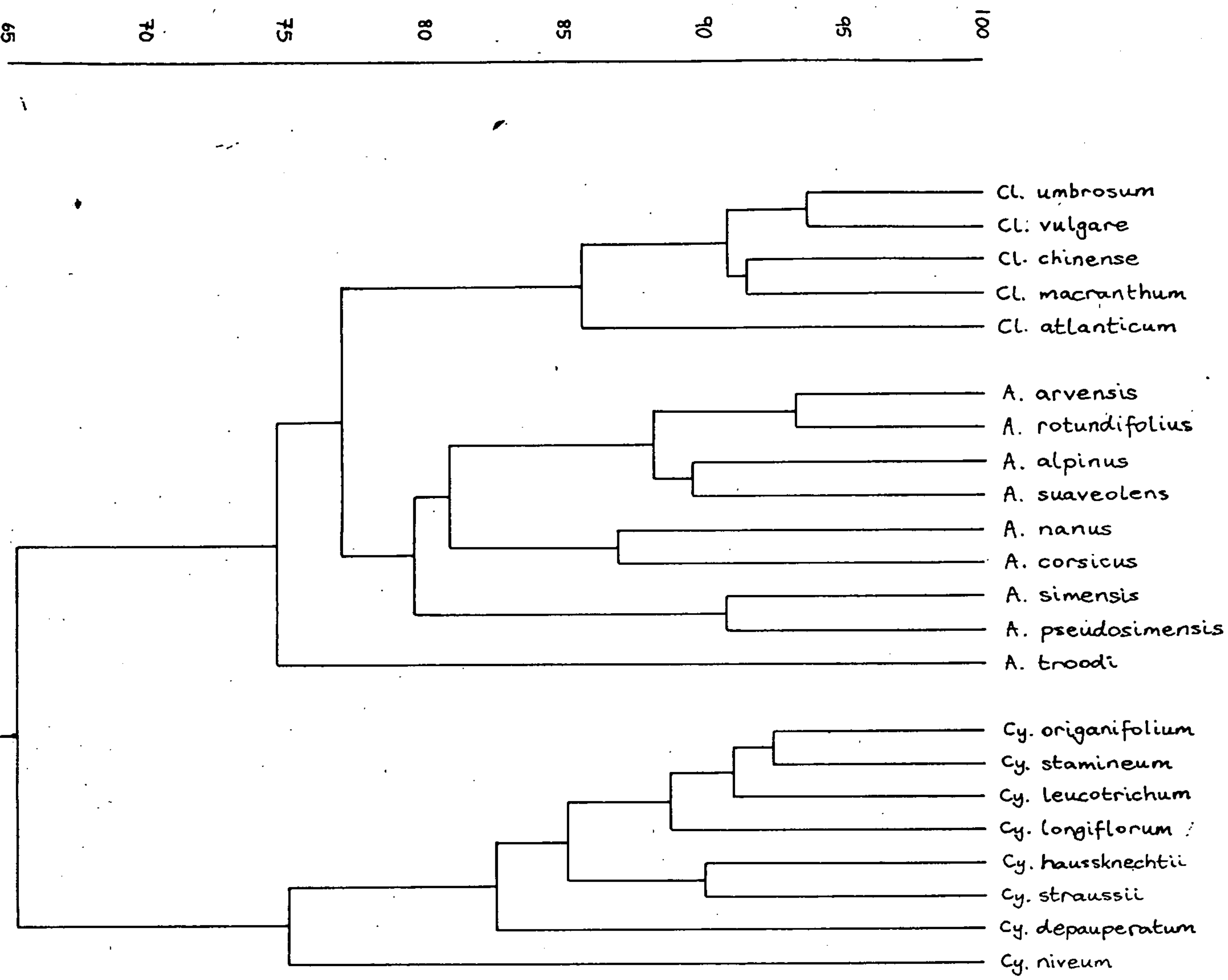
Graph 4. Micromerioid genera. *Brenaniella*, *Killickia*, *Micromeria* sect. *Pseudomelissa*.



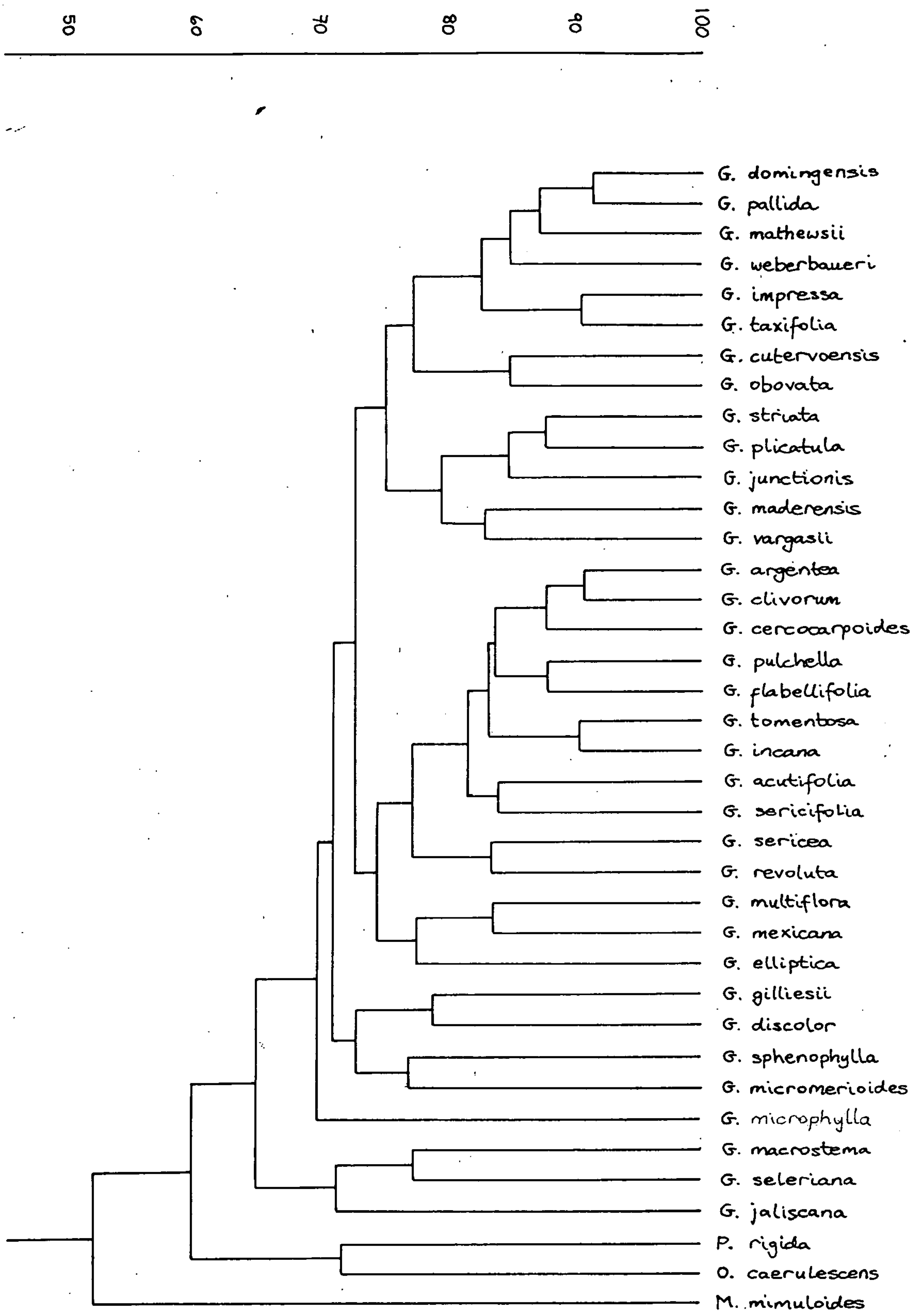
Graph 5. Calaminthoid genera. <u>Calamintha</u>, <u>Clinopodium</u>, <u>Acinos</u>, <u>Cyclotrichium</u>.



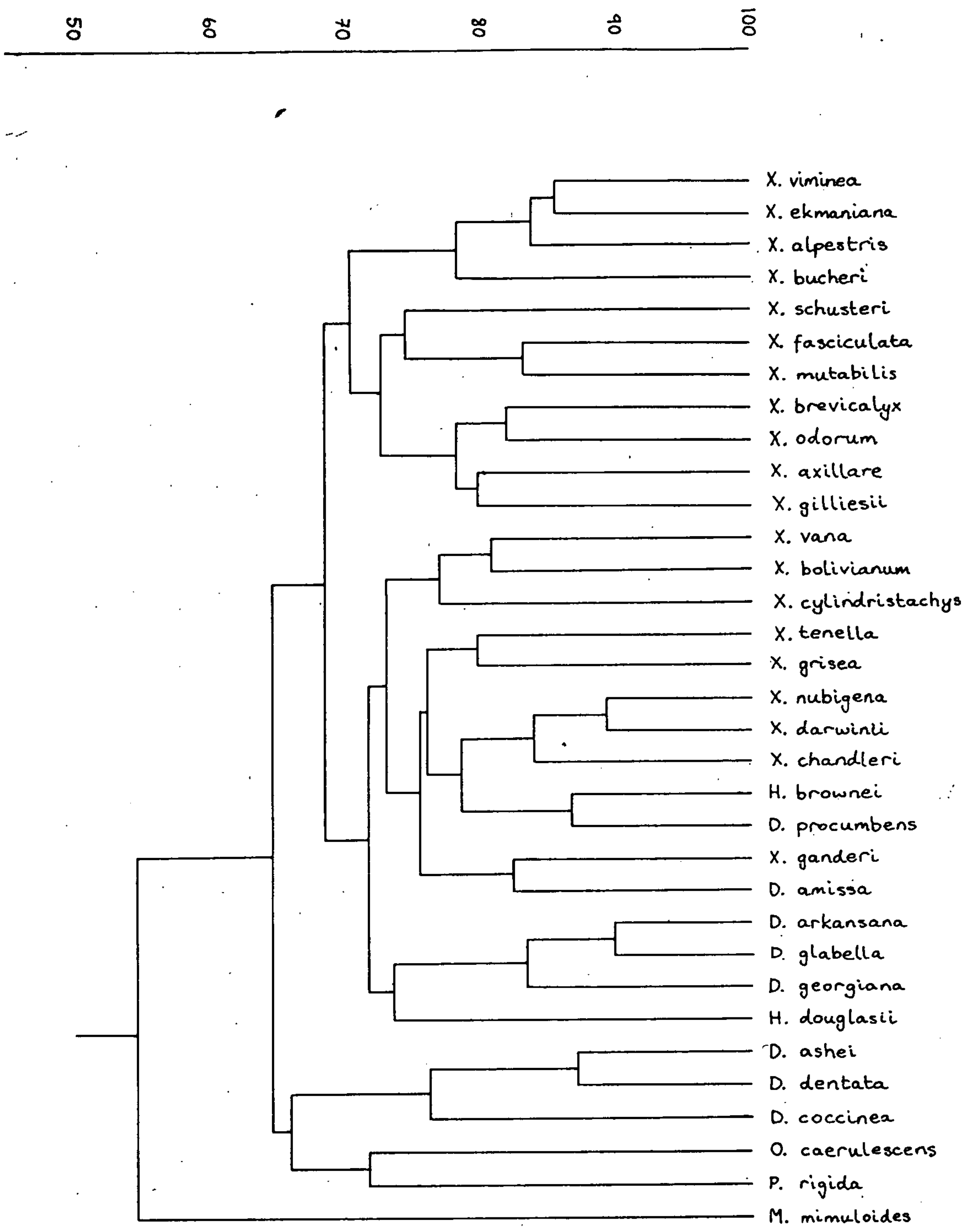
Graph 6. Calaminthoid genera. <u>Calamintha</u>.



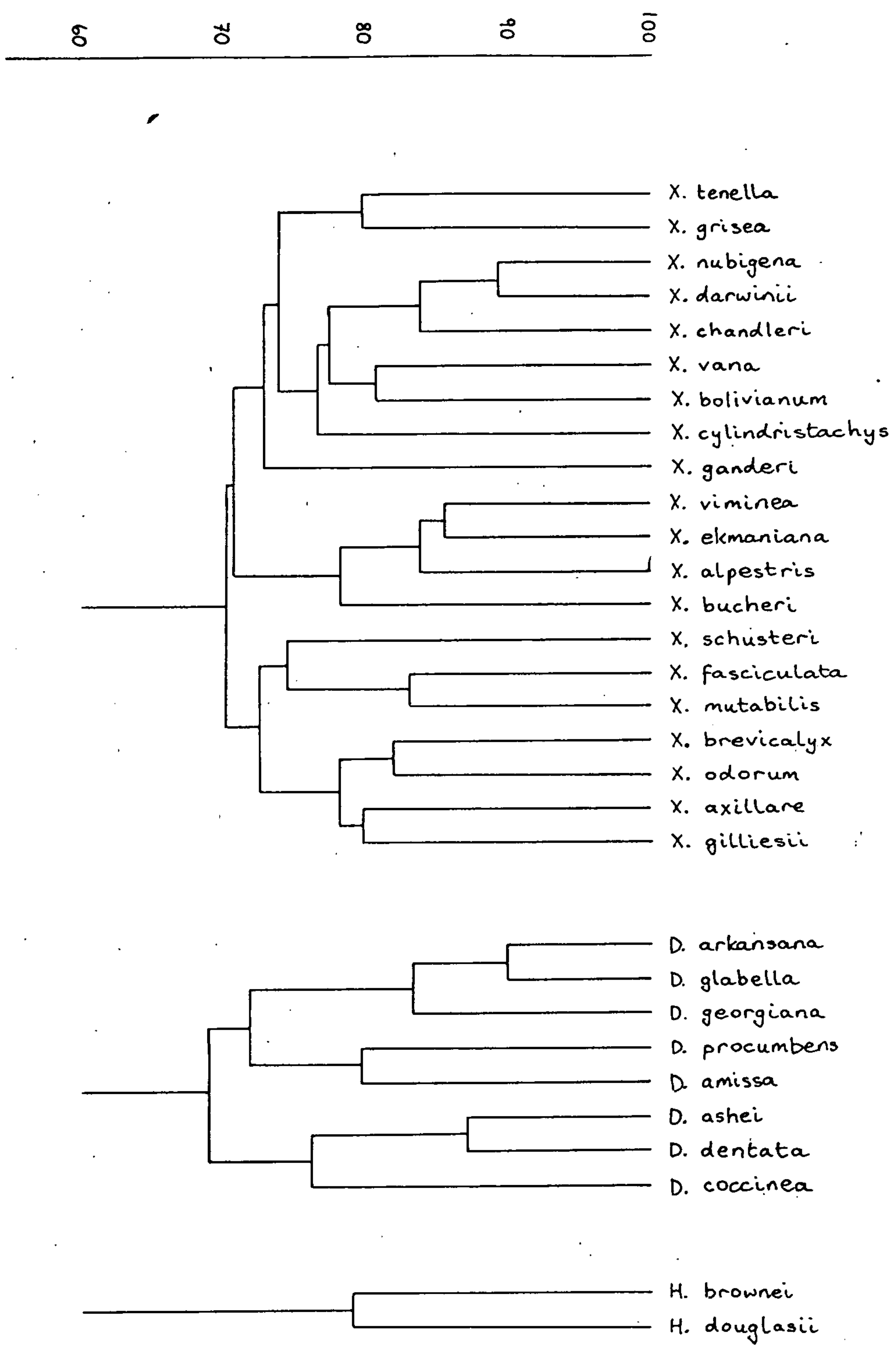
Graph 7. Calaminthoid genera. Clinopodium, Acinos, Cyclotrichium.



Graph 8. American genera. Gardoquia, Piloblephis, Obtegomeria, Montereya.



Graph 9. American genera. <u>Xenopoma</u>, <u>Diodeilis</u>, <u>Hesperothymus</u>, <u>Obtegomeria</u>, <u>Piloblephis</u>, <u>Montereya</u>.



Graph 10. American genera. *Xenopoma*, *Diodeilis*, *Hesperothymus*.

List of CHARDATA.BAS

```
10     REM -------------------------------------------------------------
20     REM *********************  DISK FILE DIRECTORY  ******************
30     REM -------------------------------------------------------------
40     REM CHARTYPE.DAT   = £1 = CHARACTER TYPES
50     REM [SPECIES NAME] = £2 = DATA FOR EACH SPECIES
60     REM SPECNAME.DAT   = £3 = NAMES OF SPECIES
70     REM MINMAX.DAT     = £4 = MINIMUM AND MAXIMUM VALUES
80     REM                       OF QUANTITATIVE CHARACTERS
90     REM TEMP.DAT       = £5 = TEMPORARY FILE OF SPECIES NAMES
100    REM -------------------------------------------------------------
110    NO.OF.CHAR% = 69                 : REM    NUMBER OF CHARACTERS
120    OPTION BASE 1                    : REM    ARRAY BASE VALUE
130    DIM MINMAX!(NO.OF.CHAR%,2)       : REM    MINIMUM/MAXIMUM VALUE ARRAY
140    DIM SPECDATA!(NO.OF.CHAR%)       : REM    SPECIES DATA
150    DIM TYPE$(NO.OF.CHAR%)           : REM    TABLE OF CHARACTER TYPES
160    REM -------------------------------------------------------------
170    REM *********  CHECK WHETHER FILE OF CHARACTER TYPES EXISTS  *****
180    REM -------------------------------------------------------------
190    ON ERROR GOTO 290                : REM    TRAP NON-EXISTENT FILE ERROR
200    OPEN "I", £1, "CHARTYPE.DAT"
210    CLOSE £1
220    GOTO ENTRY
230    REM -------------------------------------------------------------
240    REM *********************  READ IN DATA TYPES  ******************
250    REM                         Q = QUANTITATIVE
260    REM                         R = RANGE
270    REM                         B = BINARY
280    REM -------------------------------------------------------------
```

List of CHARDATA.BAS

```
290   CHARTYPE: OPEN "O", £1, "CHARTYPE.DAT"

300   FOR CHARACTER% = 1 TO NO.OF.CHAR%

310   PRINT "CHARACTER NO. "; CHARACTER%; " ";

320   INPUT "CHARACTER TYPE"; CHAR.TYPE$

330   WRITE £1, CHAR.TYPE$

340   NEXT CHARACTER%

350   CLOSE £1

360   REM -----------------------------------------------------------------

370   REM **************  CREATE INITIAL MINIMUM/MAXIMUM FILE  ***************

380   REM -----------------------------------------------------------------

390   OPEN "O", £4, "MINMAX.DAT"

400   MINMAX! = 99

410   FOR X = 1 TO 2

420   FOR CHARACTER% = 1 TO NO.OF.CHAR%

430   WRITE £4, MINMAX!

440   NEXT CHARACTER%

450   MINMAX! = 0

460   NEXT X

470   CLOSE £4

480   REM -----------------------------------------------------------------

490   REM *****************  CREATE EMPTY SPECIES NAME FILE ******************

500   REM -----------------------------------------------------------------

510   OPEN "O", £3, "SPECNAME.DAT"

520   CLOSE £3

530   REM -----------------------------------------------------------------

540   REM **********  GET CURRENT MINIMUM/MAXIMUM VALUES INTO ARRAY **********

550   REM -----------------------------------------------------------------

560   ENTRY: OPEN "I", £4, "MINMAX.DAT"
```

List of CHARDATA.BAS

```
570   FOR X = 1 TO 2
580   OPEN "I", £1, "CHARTYPE.DAT"
590   FOR CHARACTER% = 1 TO NO.OF.CHAR%
600   INPUT £4, MINMAX!(CHARACTER%,X)
610   INPUT £1, TYPE$(CHARACTER%)
620   NEXT CHARACTER%
630   CLOSE £1
640   NEXT X
650   CLOSE £4
660   REM ---------------------------------------------------------------------
670   REM *********************  GET DATA INTO FILE  *************************
680   REM ---------------------------------------------------------------------
690   FOR CHARACTER% = 1 TO NO.OF.CHAR%
700   CHAR.TYPE$ = TYPE$(CHARACTER%)
710   IF CHAR.TYPE$ = "Q" THEN GOSUB QUANTITATIVE
720   IF CHAR.TYPE$ = "R" THEN GOSUB RANGE
730   IF CHAR.TYPE$ = "B" THEN GOSUB BINARY
740   NEXT CHARACTER%
750   CLOSE £1
760   REM ---------------------------------------------------------------------
770   REM ******************  SAVE SPECIES DATA TO DISK  *********************
780   REM ---------------------------------------------------------------------
785   ON ERROR GOTO 790             : REM    TRAP INVALID FILE NAMES
790   INPUT "ENTER NAME OF DATA FILE"; SPECDATA$
800   OPEN "O", £2, SPECDATA$
810   FOR CHARACTER% = 1 TO NO.OF.CHAR%
820   WRITE £2, SPECDATA!(CHARACTER%)
830   NEXT CHARACTER%
840   CLOSE £2
```

List of CHARDATA.BAS

```
850   REM -------------------------------------------------------------------
860   REM ********************  SAVE NAME OF SPECIES  *********************
870   REM -------------------------------------------------------------------
880   REM *****************  LIST OF FILE TYPE ENDINGS  *******************
890   REM -------------------------------------------------------------------
900   REM       .SAT = SATUREJA
910   REM       .GON = GONTSCHAROVIA
920   REM       .EUH = EUHESPERIDA
930   REM       .MMO = MICROMERIA SECT. MICROMERIA (OLD WORLD)
940   REM       .MMC = MICROMERIA SECT. MICROMERIA (CANARIES)
950   REM       .MPS = MICROMERIA SECT. PSEUDOMELISSA
960   REM       .MPI = MICROMERIA SECT. PINEOLENTIA
970   REM       .MCY = MICROMERIA SECT. CYMULARIA
980   REM       .MMA = MICROMERIA SECT. MADAGASCARENSES
990   REM       .BRE = BRENANIELLA
1000  REM       .KIL = KILLICKIA
1010  REM       .CAL = CALAMINTHA
1020  REM       .CLI = CLINOPODIUM
1030  REM       .ACI = ACINOS
1040  REM       .CYC = CYCLOTRICHIUM
1050  REM       .GAR = GARDOQUIA
1060  REM       .OBT = OBTEGOMERIA
1070  REM       .XEN = XENOPOMA
1080  REM       .DIO = DIODEILIS
1090  REM       .MON = MONTEREYA
1100  REM       .HES = HESPEROTHYMUS
1110  REM       .PIL = PILOBLEPHIS
1120  REM --------------------------------------------------------------------
```

List of CHARDATA.BAS

```
1130  OPEN "I", £3, "SPECNAME.DAT"
1140  OPEN "O", £5, "TEMP.DAT"
1150  WHILE NOT EOF(3)
1160  INPUT £3, SPECIE$
1170  WRITE £5, SPECIE$
1180  WEND
1190  CLOSE £3
1200  WRITE £5, SPECDATA$
1210  CLOSE £5
1220  OPEN "O", £3, "SPECNAME.DAT"
1230  OPEN "I", £5, "TEMP.DAT"
1240  WHILE NOT EOF(5)
1250  INPUT £5, SPECIE$
1260  WRITE £3, SPECIE$
1270  WEND
1280  CLOSE £3, £5
1290  REM -------------------------------------------------------------------
1300  REM *************  SAVE MINIMUM/MAXIMUM VALUES TO DISK  ***************
1310  REM -------------------------------------------------------------------
1320  OPEN "O", £4, "MINMAX.DAT"
1330  FOR X = 1 TO 2
1340  FOR CHARACTER% = 1 TO NO.OF.CHAR%
1350  WRITE £4, MINMAX!(CHARACTER%,X)
1360  NEXT CHARACTER%
1370  NEXT X
1380  CLOSE £4
1390  INPUT "MORE DATA (Y/N)"; ANSWER$
1400  IF ANSWER$ = "Y" THEN GOTO ENTRY
1410  END
```

List of CHARDATA.BAS

```
1420  REM ------------------------------------------------------------
1430  REM *************  DATA INPUT --- QUANTITATIVE CHARACTER  *************
1440  REM ------------------------------------------------------------
1450  QUANTITATIVE: PRINT "QUANTITATIVE", CHARACTER%
1460  INPUT "LOWER LIMIT";LOWER!
1470  INPUT "UPPER LIMIT";UPPER!
1480  INPUT "NUMBERS CORRECT (Y/N)";ANSWER$
1490  IF NOT ANSWER$ = "Y" THEN GOTO QUANTITATIVE
1500  SPECDATA!(CHARACTER%) = (UPPER! + LOWER!)/2
1505  IF LOWER! < 0 THEN RETURN  : REM NEGATIVE NUMBER INDICATES MISSING DATA
1510  IF LOWER! < MINMAX!(CHARACTER%,1) THEN MINMAX!(CHARACTER%,1) = LOWER!
1520  IF UPPER! > MINMAX!(CHARACTER%,2) THEN MINMAX!(CHARACTER%,2) = UPPER!
1530  RETURN
1540  REM ------------------------------------------------------------
1550  REM ****************  DATA INPUT --- RANGE CHARACTER  ****************
1560  REM ------------------------------------------------------------
1562  REM     DATA OF UP TO 8 CHARACTER STATES COMBINED INTO ONE DATA BYTE
1564  REM   FOR EXAMPLE : 00010010 (binary) = 12 (hexadecimal) = 18 (decimal)
1566  REM  MEANS CHARACTER STATES 5 (BIT 5 SET) AND 2 (BIT 2 SET) ARE PRESENT
1568  REM ------------------------------------------------------------
1570  RANGE: PRINT "RANGE",CHARACTER%
1580  VALUE! = 0
1590  INPUT "FIRST VALUE";VALUE.1!
1600  INPUT "SECOND VALUE";VALUE.2!
1610  INPUT "THIRD VALUE";VALUE.3!
1620  INPUT "NUMBERS CORRECT (Y/N)";ANSWER$
1630  IF NOT ANSWER$ = "Y" THEN GOTO RANGE
1640  IF CHARACTER% = 6 THEN GOSUB LEAF.SHAPE
```

List of CHARDATA.BAS

```
1650  VALUE! = VALUE! OR 2^(VALUE.1! - 1)

1660  VALUE! = VALUE! OR 2^(VALUE.2! - 1)

1670  VALUE! = VALUE! OR 2^(VALUE.3! - 1)

1680  SPECDATA!(CHARACTER%) = VALUE!

1690  RETURN

1695  REM TOO MANY LEAF SHAPES -- COMBINE CHARACTER STATES 3 & 4

1700  LEAF.SHAPE: IF VALUE.1! > 3 THEN VALUE.1! = VALUE.1! - 1

1710  IF VALUE.2! > 3 THEN VALUE.2! = VALUE.2! - 1

1720  IF VALUE.3! > 3 THEN VALUE.3! = VALUE.3! - 1

1730  RETURN

1740  REM -------------------------------------------------------------------

1750  REM ****************  DATA INPUT --- BINARY CHARACTER  ****************

1760  REM -------------------------------------------------------------------

1770  BINARY: PRINT "BINARY",CHARACTER%

1780  INPUT "CHARACTER STATE";VALUE!

1790  INPUT "NUMBER CORRECT (Y/N)"; ANSWER$

1800  IF NOT ANSWER$ = "Y" THEN GOTO BINARY

1810  SPECDATA!(CHARACTER%) = VALUE!

1820  RETURN
```

List of CONCAT.BAS

```
10    REM ------------------------------------------------------------------
20    REM ***********************  CONCATENATE FILE  ************************
30    REM ------------------------------------------------------------------
40    ON ERROR GOTO 50             : REM     TRAP INVALID FILE NAMES
50    INPUT "NAME OF CONCATENATED FILE"; CONCAT.FILE.NAME$
60    INPUT "NUMBER OF FILES TO CONCATENATE"; NO.OF.FILES%
70    INPUT "ENTER GENUS NAME";GENUS$
80    INPUT "ENTER FILE TYPE ENDING (SEE TABLE IN CHARDATA.BAS)";FILE.TYPE$
90    OPEN "O", £1, CONCAT.FILE.NAME$
100   WRITE £1, NO.OF.FILES%
110   OPEN "I", £2, "SPECNAME.DAT"
120   WHILE NOT EOF(2)
130   INPUT £2, NAME$
140   IF RIGHT$(NAME$,3) = FILE.TYPE$ THEN GOSUB GET.DATA
150   WEND
160   END
170   GET.DATA: PRINT NAME$
180   INPUT "SPECIES NAME"; SPECIES.NAME$
190   INPUT "NAME OK (Y/N)"; ANSWER$
200   IF NOT ANSWER$ = "Y" THEN GOTO GET.DATA
210   WRITE £1, GENUS$
220   WRITE £1, SPECIES.NAME$
230   OPEN "I", £3, NAME$
240   FOR X = 1 TO 69
250   INPUT £3, SPEC.DAT!
260   WRITE £1, SPEC.DAT!
270   NEXT X
280   CLOSE £3
290   RETURN
```

List of SIMILAR.BAS

```
10    REM -------------------------------------------------------------------
20    REM ************************  DISK DIRECTORY  **************************
30    REM -------------------------------------------------------------------
40    REM CHARTYPE.DAT    = £1 = CHARACTER TYPES
50    REM [FILE NAME]     = £2 = DATA FILE
60    REM MINMAX.DAT      = £4 = MINIMUM AND MAXIMUM VALUES
70    REM SIMCALC.DAT     = £6 = SIMILARITY VALUES
80    REM ===================================================================
90    OPTION BASE 1
100   NO.OF.CHAR% = 69
110   LINE INPUT "ENTER NAME OF FILE -- ", NAME.OF.FILE$
120   OPEN "I", £2, NAME.OF.FILE$
130   INPUT £2,NO.OF.SPEC%
140   REM -------------------------------------------------------------------
150   REM *************  PUT DATA FOR EACH SPECIES INTO ARRAY  ***************
160   REM -------------------------------------------------------------------
170   DIM SIMDAT!(NO.OF.SPEC%, NO.OF.CHAR%)
180   NO.OF.SPEC% = 0
190   WHILE NOT EOF(2)
200   LPRINT NO.OF.SPEC% + 1;" = ";
210   INPUT £2,NAME$
220   LPRINT NAME$;" ";
230   INPUT £2,NAME$
240   LPRINT NAME$
250   GOSUB GET.DATA
260   WEND
270   CLOSE £2
280   LPRINT
```

List of SIMILAR.BAS

```
  290   REM ------------------------------------------------------------------
  300   REM *******  PUT CHARACTER TYPES AND MIN/MAX VALUES INTO ARRAYS  *******
  310   REM ------------------------------------------------------------------
  320   DIM MINMAX!(NO.OF.CHAR%,2)
  330   DIM TYPE$(NO.OF.CHAR%)
  340   OPEN "I", £4, "MINMAX.DAT"
  350   FOR X = 1 TO 2
  360   OPEN "I", £1, "CHARTYPE.DAT"
  370   FOR CHARACTER% = 1 TO NO.OF.CHAR%
  380   INPUT £4, MINMAX!(CHARACTER%, X)
  390   INPUT £1, TYPE$(CHARACTER%)
  400   NEXT CHARACTER%
  410   CLOSE £1
  420   NEXT X
  430   CLOSE £4
  440   REM ------------------------------------------------------------------
  450   REM ************  CALCULATE QUANTITATIVE CHARACTER RANGES  *************
  460   REM ------------------------------------------------------------------
  470   FOR CHARACTER% = 1 TO NO.OF.CHAR%
  480   IF TYPE$(CHARACTER%) = "Q" THEN MINMAX!(CHARACTER%,1) = MINMAX!(CHARACTE
%,2) - MINMAX!(CHARACTER%,1)
  490   NEXT CHARACTER%
  500   REM ------------------------------------------------------------------
  510   REM ***********  CALCULATE SIMILARITY COEFFICIENTS BETWEEN  ************
  520   REM ***********             ALL PAIRS OF SPECIES            ************
  530   REM ------------------------------------------------------------------
  540   INPUT "FIRST CHARACTER NUMBER";FIRST%
  550   INPUT "LAST CHARACTER NUMBER ";LAST%
```

List of SIMILAR.BAS

```
560   OPEN "O", £6, "SIMCALC.DAT"

570   WRITE £6, NO.OF.SPEC%

580   LPRINT "SPEC X","SPEC Y","MATCHES","COMPARISONS","SIMILARITY"

590   FOR X = 1 TO NO.OF.SPEC% - 1

600   FOR Y = X + 1 TO NO.OF.SPEC%

610   LPRINT X,Y,

620   GOSUB CALC.SIMILARITY

630   LPRINT NO.OF.MATCHES, NO.OF.COMPARISONS, SIMILARITY.VALUE

640   NEXT Y

650   NEXT X

660   END

670   REM -------------------------------------------------------------------

680   REM *************  GET DATA FOR EACH SPECIES INTO ARRAY  **************

690   REM -------------------------------------------------------------------

700   GET.DATA: NO.OF.SPEC% = NO.OF.SPEC% + 1

710   FOR CHARACTER% = 1 TO NO.OF.CHAR%

720   INPUT £2, SIMDAT!(NO.OF.SPEC%, CHARACTER%)

730   NEXT CHARACTER%

740   RETURN

750   REM ===================================================================

760   REM ****************  SIMILARITY CALCULATION ROUTINES  ****************

770   REM ===================================================================

780   CALC.SIMILARITY: NO.OF.COMPARISONS! = 0

790   NO.OF.MATCHES! = 0

800   FOR CHARACTER% = FIRST% TO LAST%

810   IF TYPE$(CHARACTER%) = "B" THEN GOSUB CALC.BINARY

820   IF TYPE$(CHARACTER%) = "R" THEN GOSUB CALC.RANGE

830   IF TYPE$(CHARACTER%) = "Q" THEN GOSUB CALC.QUANTITATIVE

840   NEXT CHARACTER%
```

List of SIMILAR.BAS

```
   850   SIMILARITY.VALUE! = NO.OF.MATCHES!/NO.OF.COMPARISONS!

   860   WRITE £6, SIMILARITY.VALUE!

   870   RETURN

   880   REM ----------------------------------------------------------------

   890   REM ************  COMPARE BINARY OR TWO-STATE CHARACTERS  **************

   900   REM ----------------------------------------------------------------

   910   CALC.BINARY: IF SIMDAT!(X,CHARACTER%) = 0 OR SIMDAT!(Y,CHARACTER%) = 0 TH

EN RETURN

   920   IF SIMDAT!(X,CHARACTER%)=SIMDAT!(Y,CHARACTER%) THEN NO.OF.MATCHES! = NO.O

F.MATCHES! + 1

   930   NO.OF.COMPARISONS! = NO.OF.COMPARISONS! + 1

   940   RETURN

   950   REM ----------------------------------------------------------------

   960   REM ****************  COMPARE QUANTITATIVE CHARACTERS  *****************

   970   REM ----------------------------------------------------------------

   980   CALC.QUANTITATIVE: IF SIMDAT!(X,CHARACTER%) < 0 OR SIMDAT!(Y,CHARACTER%)

< 0 THEN RETURN

   990   NO.OF.MATCHES! = NO.OF.MATCHES! - (ABS(SIMDAT!(X,CHARACTER%) - SIMDAT!(Y,

CHARACTER%))/MINMAX!(CHARACTER%,1)) + 1

   1000  NO.OF.COMPARISONS! = NO.OF.COMPARISONS! + 1

   1010  RETURN

   1020  REM ----------------------------------------------------------------

   1030  REM ********  COMPARE CHARACTERS WHICH HAVE A RANGE OF STATES  *********

   1040  REM ----------------------------------------------------------------

   1050  CALC.RANGE: IF SIMDAT!(X,CHARACTER%) = 0 OR SIMDAT!(Y,CHARACTER%) = 0 THE

N RETURN

   1060  IF (SIMDAT!(X,CHARACTER%) AND SIMDAT!(Y,CHARACTER%)) > 0 THEN NO.OF.MATCH

ES! = NO.OF.MATCHES! + 1

   1070  NO.OF.COMPARISONS! = NO.OF.COMPARISONS! + 1

   1080  RETURN
```

List of PAIRSORT.BAS

```
10     REM -------------------------------------------------------------------
20     REM                CLUSTER ANALYSIS BY GROUP PAIRS SORTING
30     REM -------------------------------------------------------------------
40     REM                         by A. M. Doroszenko
50     REM -------------------------------------------------------------------
60     REM
70     REM
80     REM -------------------------------------------------------------------
90     REM *************  PUT SIMILARITY COEFFICIENTS INTO ARRAY  ***********
100    REM -------------------------------------------------------------------
110    OPTION BASE 1
120    OPEN "I", £6, "SIMCALC.DAT"
130    INPUT £6,NO.OF.SPEC%
140    DIM SIM.VALUES!(2*NO.OF.SPEC%-1,NO.OF.SPEC%-1)
150    FOR X = 1 TO NO.OF.SPEC% - 1
160    FOR Y = X + 1 TO NO.OF.SPEC%
170    INPUT £6, SIM.VALUES!(X,Y-1)
180    NEXT Y
190    NEXT X
200    CLOSE £6
210    REM -------------------------------------------------------------------
220    REM **********************  SET UP LINK TABLE  ************************
230    REM -------------------------------------------------------------------
240    DIM LINK.TABLE%(2*NO.OF.SPEC%,3)
250    LEFT% = 1                          : REM POINTER TO LEFT BRANCH
260    RIGHT% = 2                         : REM POINTER TO RIGHT BRANCH
270    UP% = 3                            : REM POINTER TO HIGHER BRANCH ORDER
280    FOR X = 1 TO 2*NO.OF.SPEC%
290    FOR Y = 1 TO 3: LINK.TABLE%(X,Y) = 0: NEXT Y
300    NEXT X
```

List of PAIRSORT.BAS

```
310   REM *****************************************************************
320   REM ********************  DO CLUSTER ANALYSIS  **********************
330   REM *****************************************************************
340   BOTTOM% = 1
350   TOP% = NO.OF.SPEC%
360   LPRINT "CLUSTER NO.","LEFT","RIGHT","SIMILARITY VALUE"
370   WHILE TOP% <> 0
380   GOSUB CLUSTER
390   IF MAX.SIM.VALUE! = 0 THEN END
400   LPRINT TOP%+1,SPECIES.NO.X%,SPECIES.NO.Y%,MAX.SIM.VALUE!
410   TOP% = TOP% + 1
420   LINK.TABLE%(SPECIES.NO.X%,UP%) = TOP%
430   LINK.TABLE%(SPECIES.NO.Y%,UP%) = TOP%
440   LINK.TABLE%(TOP%, LEFT%) = SPECIES.NO.X%
450   LINK.TABLE%(TOP%, RIGHT%) = SPECIES.NO.Y%
460   REM -----------------------------------------------------------------
470   REM *********************  CALCULATE AVERAGES  **********************
480   REM -----------------------------------------------------------------
490   FOR X = BOTTOM% TO TOP% - 1
500   V3 = LINK.TABLE%(TOP%,LEFT%)
510   V4 = LINK.TABLE%(TOP%,RIGHT%)
520   IF LINK.TABLE%(X, UP%) = 0 THEN GOSUB CALC.AVERAGES
530   NEXT X
540   WEND
550   END
560   REM -----------------------------------------------------------------
570   REM *********************  INITIALISE VARIABLES  ********************
580   REM -----------------------------------------------------------------
590   CLUSTER: MAX.SIM.VALUE! = 0
```

List of PAIRSORT.BAS

```
600   SPECIES.NO.X% = 0
610   SPECIES.NO.Y% = 0
620   REM ------------------------------------------------------------------
630   REM ************  SCAN TABLE FOR MAXIMUM SIMILARITY VALUE  ***********
640   REM ------------------------------------------------------------------
650   FOR X = BOTTOM% TO TOP% - 1
660   IF LINK.TABLE%(X,UP%) = 0 THEN GOSUB FIND.MAX
670   NEXT X
680   RETURN
690   REM ------------------------------------------------------------------
700   REM *********************  FIND MAXIMUM VALUE  ***********************
710   REM ------------------------------------------------------------------
720   FIND.MAX: FOR Y = X + 1 TO TOP%
730   IF LINK.TABLE%(Y,UP%)=0 THEN GOSUB CHECK
740   NEXT Y
750   RETURN
760   CHECK: IF (X<=NO.OF.SPEC% AND Y<=NO.OF.SPEC%) THEN GOSUB COMPARE.VALUES
770   IF (X>NO.OF.SPEC% OR Y>NO.OF.SPEC%) THEN GOSUB CHECK.VALUES
780   RETURN
790   REM ------------------------------------------------------------------
800   REM ****************  COMPARE TWO SIMILARITY VALUES  *****************
810   REM ------------------------------------------------------------------
820   COMPARE.VALUES: IF SIM.VALUES!(X,Y-1) <= MAX.SIM.VALUE! THEN RETURN
830   MAX.SIM.VALUE! = SIM.VALUES!(X,Y-1)
840   SPECIES.NO.X% = X
850   SPECIES.NO.Y% = Y
860   RETURN
870   CHECK.VALUES: GOSUB TRANSFORM.X.Y
880   IF SIM.VALUES!(C1,C2-1) <= MAX.SIM.VALUE! THEN RETURN
```

List of PAIRSORT.BAS

```
890   MAX.SIM.VALUE! = SIM.VALUES!(C1,C2-1)

900   SPECIES.NO.X% = X

910   SPECIES.NO.Y% = Y

920   RETURN

930   REM ------------------------------------------------------------------

940   REM **************  CALCULATE AVERAGE SIMILARITY VALUES  *************

950   REM ------------------------------------------------------------------

960   CALC.AVERAGES: V1 = X

970   V2 = X

980   IF V1 > V3 THEN SWAP V1,V3

990   IF V2 > V4 THEN SWAP V2,V4

1000  V5=V1: V6=V2: V7=V3: V8=V4

1010  IF (V1>NO.OF.SPEC% OR V3>NO.OF.SPEC%) THEN GOSUB TRANSFORM.V1.V3

1020  IF (V2>NO.OF.SPEC% OR V4>NO.OF.SPEC%) THEN GOSUB TRANSFORM.V2.V4

1030  Y = TOP%: GOSUB TRANSFORM.X.Y

1040  SIM.VALUES!(C1,C2-1)=(SIM.VALUES!(V5,V7-1)+SIM.VALUES!(V6,V8-1))/2

1050  RETURN

1060  REM ------------------------------------------------------------------

1070  REM ***********  CALCULATE COORDINATES IN SIM.VALUES ARRAY  ***********

1080  REM ------------------------------------------------------------------

1090  TRANSFORM.X.Y: C1 = 2*NO.OF.SPEC%-Y+X

1100  C2 = 2*NO.OF.SPEC%-Y+1

1110  RETURN

1120  TRANSFORM.V1.V3: V5=2*NO.OF.SPEC%-V3+V1

1130  V7=2*NO.OF.SPEC%-V3+1

1140  RETURN

1150  TRANSFORM.V2.V4: V6=2*NO.OF.SPEC%-V4+V2

1160  V8=2*NO.OF.SPEC%-V4+1

1170  RETURN
```

Abrams, L. (1951). *Illustrated Flora of the Pacific States* 3:646.

Adams, C. D. (1972). *Flowering Plants of Jamaica* p. 640.

Babu, C. R. (1969). Proposal to conserve the generic name *Micromeria* Benth. against *Xenopoma* Willd. and *Zygis* Desv. *Taxon* 18:733-734.

Ball, P. W. (1972). Variation in *Acinos alpinus* (L.) Moench. *Bot. J. Linn. Soc.* 65:342-344.

----- (1972). The *Calamintha officinalis* - *nepeta* complex. *Bot. J. Linn. Soc.* 65:344-348.

----- (1972). The *Satureja montana* group. *Bot. J. Linn. Soc.* 65:350-352.

Barthlott, W. & Capesius, I. (1974). Wasserabsorption durch Blatt- und Sprossorgane einiger Xerophyten. *Z. Pflanzenphysiol.* 72:443-455.

Baum, B. R. (1968). The problem of typifying certain names in Linnaeus' Systema Naturae ed. 10. *Taxon* 17:507-513.

Bawa, K. S. (1980). Evolution of dioecy in flowering plants. *Ann. Rev. Ecol. Syst.* 11:15-39.

Bentham, G. (1832-36). *Labiatarum Genera et Species.* London. 783 pp.

Bentham, G. in De Candolle, A. (1848). *Prodromus Systematis Naturalis Regni Vegetabilis*, vol 12. Paris. 707 pp.

Binns, B. (1968). *A first checklist of the herbaceous flora of Malawi*.

Bir, S. S. & Saggoo, M. I. S. (1981). Cytopalynology of certain Acanthaceae and Labiatae. *J. Palynol*. 17:93-102.

Blakelock, R. A. (1950). The Rustam Herbarium, Iraq. Part III. *Kew Bull*. 1949:517-553.

Boissier, E. (1879). *Flora Orientalis* 4:562-583. Geneva.

Borissova, A. (1953). Labiatarum genus novum ex Asia media. *Not. Syst. (Leningrad)* 15:321-324.

----- (1953). De tribu Satureineae Benth. labiatarum florae USSR notae systematicae. *Not. Syst. (Leningrad)* 15:325-331.

Bothmer, R. (1967). Infraspecific variation in *Clinopodium vulgare* L. (Labiatae). *Bot. Not.* 120:202-208.

Brenan, P. M. (1954). Plants collected in Nyasaland. *Mem. N.Y. Bot. Gard.* 9:45-53.

Briquet, J. (1893-95). *Les Labiées des Alpes Maritimes*, part 2, 393-407; part 3, 411-457.

Briquet, J. in Engler, A. & Prantl, K. (1897). *Natürlichen Pflanzenfamilien* 4,3a:296-303.

Brizicky, G. K. (1969). Sub-generic and sectional names: their starting points and early sources. *Taxon* 18:643-660.

Brullo, S. & Furnari, F. (1979). *Euhesperida linearifolia* gen. et sp. nov. of Labiatae of Cyrenaica. *Webbia* 34:433-437.

Caballero, A., Jimenez, M. S. & Perez de Paz, P. L. (1978). Contribucion al estudio anatomico del gen. *Micromeria* Benth. (Lamiaceae) en la region Macaronesica. 1. Estructura foliar. *Anal. Inst. Bot. Cavanilles* 34:467-483.

Caballero-Ruano, A. & Ramos, I. S. (1980). Contribucion al estudio anatomico del genero *Bystropogon* L'Her. I. Estructura foliar. *Bol. Soc. Brot.* ser. 2, 54:121-132.

Camerik, A. M. & Werger, M. J. A. (1981). Leaf characteristics of the flora of the high plateau of Itatiacia, Brasil. *Biotropica* 13:39-48.

Castri, F., Goodall, D. W., & Specht, R. L. (eds.) (1972). *Mediterranean-type shrublands*. Ecosystems of the World, vol. 11.

Charlesworth, B. & Charlesworth, D. (1978). A model for the evolution of dioecy and gynodioecy. *Amer. Natur*. 112:975-997.

Cheng, W. T. (1977). A numerical taxonomic study of Formosan Labiatae. *Taiwania* 22:113-122.

Correns, C. (1904). Experimentelle Untersuchungen über die Gynodoecie. *Ber. Deutsch. Bot. Ges.* 22:506-517.

Darwin, C. (1877). *The different forms of flowers of the same species*. London. 352 pp.

Davis, P. H. (1949). Additamenta ad floram Anatoliae I. *Kew Bull*. 1949:393-426.

DeWolf, G. P. (1954). Notes on cultivated Labiates 4. *Satureja* and some related genera. *Baileya* 2:142-150.

----- (1955). A note on the name *Calamintha*. Rhodora 57:73-78.

Druce, G. C. (1914). The abridgement of Miller's Gardener's Dictionary of 1754. *Bot. Exch. Club Brit. Isles* 3:426-436.

Duncan, T. (1980). Cladistics for the practicing taxonomist - An eclectic view. *Syst. Bot.* 5:136-148.

Eberhardt, P.H. (1903). Influence de l'air sec et de l'air humide sur la forme et sur la structure des vegetaux. *Ann. Sci. Nat. Bot.* ser. 8, 18:61-152.

El-Gazzar, A. & Watson, L. (1970). A taxonomic study of Labiatae and related genera. *New Phytol.* 69:451-486.

Epling, C. C. (1927). Studies on South American Labiatae, III. Synopsis of the genus *Satureja* L. *Ann. Missouri Bot. Gard*. 14:47-86.

----- (1936). Synopsis of the South American Labiatae. *Fedde, Repert. Sp. Nov. Beih.* 85:1-341.

----- (1937). The Labiatae of Northern South America: Colombia, Ecuador and Venezuela. *Fedde, Repert. Sp. Nov. Beih*. 95:5-144.

----- (1938). The Labiatae of Peru. *Fedde, Repert. Sp. Nov. Beih.* 105:1-93.

----- (1940). Supplementary notes on American Labiatae, I. *Bull.*

Torrey Bot. Club 67:512.

----- (1941). Supplementary Notes on American Labiatae, II. Bull. Torrey Bot. Club 68:553-554.

----- (1950). Supplementary notes on American Labiatae, V. Brittonia 7:139.

----- (1957). Supplementary notes on American Labiatae, VII. Brittonia 12:145-146.

Epling, C. & Játiva, C. (1964). Revision del genero *Satureja* en America del sur. Brittonia 16:393-416.

----- (1966). A descriptive key to the species of *Satureja* indigenous to North Aerica. Brittonia 18:244-248.

Epling, C. C. & Mathias, M. E. (1957). Supplementary notes on American Labiatae, VI. Brittonia 8:304-305.

Epling, C. C. & Stewart, W. S. (1939). A revision of *Hedeoma* with a review of allied genera. Fedde Rep. Beih. 115:1-49.

Esau, K. (1965). Plant anatomy. Ed. 2. New York.

Ettiene, R. (1930). Contribution a l'etude structurale des labiées endemiques des Iles Canaries. Univ. Paris Fac. Pharm. no. 16:1-159.

Fabre, G. & Nicoli, R. M. (1965). Sur la morphologie des akenes de quelques Labiées de la flore de France. Bull. Soc. Bot. Fr. 112:267-271.

Feoli, E. & Poldini, L. (1979). Biometria di "*Satureja montana*" L. s.l. in Italia. Webbia 33:205-216.

Fuller, P. J. & Hay, M. E. (1983). Is glue production by seeds of *Salvia columbariae* a deterrent to desert granivores? Ecology 64(4):960-963.

Galinat, M. (1950). Observations sur le Tegument des Graines. II. Dissemination des Graines. Bull. Mus. Nat. Hist. Nat. (ser. 2) 22:379-387.

Genova, E. M. (1980). On essential oil dynamics in some Bulgarian representatives of the genus *Satureja* L. Phytology (Sofia) 14:51-59.

Gill, L. S. (1981). Taxonomy, distribution, and ecology of Canadian Labiatae. Fedde, Repert. Sp. Nov. 92:33-93.

Grant, E. & Epling, C. C. (1943). A study of *Pycnanthemum* (Labiatae). Univ. Calif. Publ. Bot. 20:195-240.

Grant, K. A. & Grant, V. (1968). Hummingbirds and their flowers.

Gray, A. (1886). Synoptical Flora of North America, ed. 2, 2(1):341-388.

Gregorius, H.-R., Ross, M. D. & Gillet, E. (1982). Selection in plant population of effectively infinite size. III. The maintenance of females among hermaphrodites for a biallelic model. Heredity 48:329-343.

Grisebach, H. R. A. (1861). Flora of the British West Indian

Islands 4-5:489.

Grubert, M. (1974). Studies on the distribution of myxospermy among seeds and fruits of the Angiospermae and its ecological importance. *Acta Biol. Venez.* 8 (3-4):315-551.

Gupta, M. L. & Bhambbie, S. (1980). Studies in Lamiaceae VII. Trends of specialisation in the petiole. *Fedde, Repert. Sp. Nov.* 91:109-114.

Halácsy, E. (1902). *Conspectus Florae Graecae* 2:546.

Hara, H. (1935). Observationes ad plantas Asiae orientalis (IV). *Clinopodium*. *Journ. Jap. Bot*. 11:101-111.

Hedge, I. C. & Feinbrun, N. (1969). *Satureja thymbrifolia* Hedge & Feinbrun, sp. nov. *Israel J. Bot.* 17(1968):213-216.

Hegi, G. (1927). *Illustrierte Flora von Mitteleuropa* 5(4).

Heinrichter, E. (1884). Über isolateralen Blattbau mit besonderer Berücksichtigung der europäischen, speciell der deutschen Flora. *Bot. Jahrb.* 15:502-567.

Hillson, C. J. (1959). Comparative studies of floral morphology of the Labiatae. *Amer. J. Bot.* 46:451-459.

Hitchcock, C. L., Cronquist, A., Ownbey, M. & Thompson, J. W. (1959). *Vascular Plants of the Pacific Northwest* 4:270-272.

Hooker, W. J. (1838). *Flora Boreali-Americana* 2:113-114.

Howell, J. T. (1931). The genus *Pogogyne*. *Proc. Calif. Acad. Sci.* 20:105-128.

Ietswaart, J. H. (1980). A taxonomic revision of *Origanum* (Labiatae). Leiden Univ. Press. (*Leiden Bot. Ser. No.4*). 153 pp.

Inamdar, J. A. & Bhatt, D. C. (1972). Structure and development of stomata in some Labiatae. *Ann. Bot.* 36:335-344.

Irving, R. S. (1972). A revision of the genus *Poliomintha* (Labiatae). *Sida* 5:8-22.

----- (1980). The systematics of *Hedeoma* (Labiatae). *Sida* 8:218-295.

IUCN Threatened Plants Committee Secretariat (1982). The rare, threatened and endemic plants of Greece. *Ann. Mus. Goulandris* 5:69-105.

Janchen, E. (1943). Zur Nomenklatur der Gattungsnamen, II. *Fedde, Repert. Sp. Nov.* 52:144-161.

Jaramillo, J. & Coello, F. (1982). Reporte del trabajo de Campo Ecuador 1977-81. *Rep. Bot. Inst. Univ. Aarhus* 6:28.

Jepson, W. L. (1925). *A Manual of the Flowering Plants of California* 874-875.

----- (1943). *Flora of California* 3(2):421-422.

Junell, S. (1934). Gynaeceummorphologie und Systematik der Verbenaceen und Labiaten. *Symb. Bot. Upsal.* 4:1-219. (1934).

Keng, H. (1969). A revision of Malesian Labiatae. *Gard. Bull.*

(Singapore) 24:41-45.

Killick, D. J. B. (1961). South African species of Satureia. Bothalia 7:435-437.

Knobloch, I. W. (1972). Intergeneric hybridisation in flowering plants. Taxon 21:97-103.

Knuth, P. (1899). Handbuch der Blutenbiologie 2(2):214-294.

Kumari, D. S. (1977). A note on monadelphy in some Lamiaceae (Labiatae). Current Science 46(1):22-23.

----- (1980). Origin of gynobasic style in Lamiaceae. Indian J. Bot. 3:166-169.

----- (1982). Evolution of calyx in Lamiaceae. J. Ind. Bot. Soc. 61:129-137.

Kunth, C. S. in Bonpland, A. & Humboldt, A. (1817). Nova Genera et Species Plantarum 2:311-315.

Legendre, P. (1971). Circumscribing the concept of the genus. Taxon 20:137-139.

----- (1972). The definition of systematic categories in biology. Taxon 21:381-406.

Lemée, G. (1946). Recherches sur l'economie d'eau chez les sous-arbrisseaux xeromorphes des landes. Ann. Sci. Nat. Bot., ser. 11, 7:53-85.

Leon, H. & Alain, H. (1957). Flora de Cuba 4:332-333.

Lewis, D. (1941). Male sterility in natural populations of hermaphrodite plants. The equilibrium between females and hermaphrodites to be expected with different types of inheritance. New Phytol. 40:56-63.

----- & Crowe, L. K. (1956). The genetics and evolution of gynodioecy. Evolution 10:115-125.

Linnaeus, C. (1725). Ortabok. Reprint (1957)

----- (1753). Species Plantarum, ed. 1.

Lloyd, D. G. (1974, a). Theoretical sex ratios of dioecious and gynodioecious angiosperms. Heredity 32:11-34.

----- (1974, b). Female-predominant sex-ratios in angiosperms. Heredity 32:35-44.

Löve, A. (1963). Cytotaxonomy and generic delimitation. Reg. Veg. 27:45-51.

Lundkvist, L. O. (1956). Xeromorphose in Beziehung zu Wasser- und Stickstoffmangel. Svensk. Bot. Tidskr. 50:361-384.

Macoun, J. M. (1889). Checklist of Canadian Plants 45-46.

Mandenova, I. & Schengelia, E. (1953). Novum genus labiatarum antasiacum. Not. Syst. (Leningrad) 15:332-337.

Markgraf, V. (1980) Palaeoclimatic reconstruction of the last 15000 years in sub-antarctic and temperate regions of Argentina. Mem. Mus. Nat. Hist. Natur. ser. B, 27:87-97.

Marticorena, C. & Quezada, M. (1977). Sinopsis del genero Satureja

L. (Labiatae) en Chile. Bol. Soc. Biol. Concepcion 51:141-147.

Maximov, N. A. (1929). The Plant in Relation to Water. 451 pp. London. English translation by R.H. Yapp.

Mayr, E. (1969). Principles of Systematic Zoology. pp. 403.

McDougall, W. B. & Penfound, W. T. (1928). Ecological anatomy of some deciduous forest plants. Ecology 9:349-353.

McVaugh, R. & Schmid, R. (1967). Novelties in Satureja sect. Gardoquia (Labiatae). Brittonia 19:261-267.

Merrill, E. D. (1935). A commentary on Loureiro's "Flora Cochinchinensis". Trans. Amer. Phil. Soc. n.s. 24:1-445.

----- (1949). Index Rafinesquianus.

Metcalfe, C. R. & Chalk, L. (1979). Anatomy of the Dicotyledons. ed. 2. 1:201-204.

Miller, P. (1754). The Gardener's Dictionary, abridged 4th. ed. (Reprint 1969).

Moench, C. (1794). Methodas Plantas. (Reprint 1966).

Montenegro, G., Hoffman, A. J., Aljaro, M. E. & Hoffmann, A. E. (1979). Satureja gilliesii, a poikilohydric shrub from the Chilean mediterranean vegetation. Can. J. Bot. 57:1206-1213.

Moscoso, R. M. (1943). Catalogus Florae Domingensis 1:549-550, 555.

Natarajan, A. T. (1974). Pollen morphology of Indian Labiatae. I. Tribes Ocimoideae and Satureineae. J. Palynol. 10:89-105.

Nius, E. (1931). Untersuchungen über den Einfluss des Interzellularvolumens und der Offnungsweite der Stomata auf die Luftwegigkeit der Laubblätter. Jahrb. Wiss. Bot. 74:33-126.

Novruzova, Z. A. & Zeinalova, C. A. (1969). Morphological anatomical analysis of species of the genus Satureja represented in Azerbajdzhan. Izv. Akad. Nauk Azerb. SSR 1969(2):14-17.

Nyman, C. F. (1855). Sylloge Florae Europaeae 88-105.

----- (1881). Conspectus Florae Europaeae 563-597.

Oppenheimer, H. R. (1960). Adaptation to drought: xerophytism. UNESCO: Arid Zone Research 15:105-138.

Oyster, J. H. (1885). Catalogue of the Phanerogamous and Vascular Cryptogamous Plants of North America. 76 pp.

Parker, J. (1968). Drought-resistance mechanisms, in Kozlowski, T. T. Water Deficits and Plant Growth, vol. 1, Development, Control, and Measurement: 195-234. Academic Press. London.

Pellecuer, J. et al. (1980). Therapeutic value of the cultivated Mountain Savoury (Satureja montana L.: Labiatae). Acta Hortic. 96:35-39.

Perez de Paz, P. L. (1978). Revision del Genero Micromeria Benth. (Lamiaceae - Stachyoideae) en la Region Macaronesica. Inst. Est. Can. Univ. La Laguna. Monografias 16. 306 pp.

Picci, V. (1980). The exploration of medicinal plants of the Mediterranean area. *J. Ethnopharmacology* 2:81-89.

Pignatti, S. (1979). Plant geographical and morphological evidences in the evolution of the Mediterranean flora (with particular reference to the Italian representatives). *Webbia* 34:243-255.

Pijl, L. (1972). Functional considerations and observations on the flowers of some Labiatae. *Blumea* 20:93-103.

Pittier, H., Lasser, T., Schnee, L. & Badillo, Z. L. (1947). *Catalogo de la Flora Venezolana* 2:346-347.

Privat, G., Pellecuer, J., & Motte, M.-E. (1976). Etude ecologique de Satureja montana L. (Labiees). *Nat. Monspel.*, ser. Bot. 26:55-72.

Pyke, G. H. & Waser, N. M. (1981). The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* 13:260-270.

Pyykkö, M. (1966). The leaf anatomy of East Patagonian xeromorphic plants. *Ann. Bot. Fenn.* 3:453-622.

Raulin, V. (1858). *Description Physique de l'Ile de Crete*: 828; also in *Acta Soc. Linn. Bord.* 24:524 (1869).

Raven, P. H. & Axelrod, D. I. (1978). Origin and relationships of the Californian flora. *Univ. Calif. Publ. Bot.* 72.

Rechinger, K. H. (1943). *Flora Aegaea* p.530.

----- (1949). Grundzüge der Pflanzenverbreitung in der Aegäis. *Vegetatio* 2:81-85, 285 (table 3).

----- (1982). *Flora Iranica* vol. 150.

Reveal, J. L. & Strachan, J. L. (1980). Proposal for the conservation of the generic name *Cunila* D. Royen ex L. (1759) against *Cunila* L. ex P. Miller (1754) (Lamiaceae). *Taxon* 29:332-334.

Risch, C. (1956). Die Pollenkorner der Labiaten. *Willdenowia* 1:617-641.

Ross, M. D. (1978). The evolution of gynodioecy and subdioecy. *Evolution* 32:174-188.

----- (1982). Five evolutionary pathways to subdioecy. *Amer. Natur.* 119:297-318.

Rudall, P. (1980). Leaf anatomy of the subtribe Hyptidinae. *Bot. J. Linn. Soc.* 80:319-340.

Russell, M. W. (1895). Influence du climat Mediterranean sur la structure des plantes communes en France. *Ann. Sci. Nat., Bot.* ser. 8, 1:323-353.

Schenk, H. (1877). Zur Kenntnis des Baues der Fruchte der Compositen und Labiaten. *Bot. Zeit.* 35:409-415.

Schermann, S. (1966). *Magismeret*. Budapest.

Schroder, J. (1938). Über natürliche und kunstliche Änderungen des Interzellularvolumens bei Laubblättern. *Beitr. Biol. Pflanzen* 25:75-124.

Scoggan, H. J. (1979). *The Flora of Canada* 4:1317-1319.

Seddon, G. (1974). Xerophytes, xeromorphs and sclerophylls; the history of some concepts in ecology. *Biol. J. Linn. Soc.* 6:65-87.

Sharma, M. & Singh, V. (1980). Procambial development in some Labiatae in relation to vascular conservation. *Ann. Bot.* 46:119-123.

----- (1982). Morphology of the gynoecium in Labiatae. *Blumea* 28:61-75.

Sherff, E. E. (1940). The delimitation of genera from the conservative point of view, in Symp. The Concept of the Genus. *Bull. Torrey Bot. Club* 67:349-389.

Shetler, S. G. & Skog, L. E. (1978). *A Provisional Checklist of Species for Flora North America (Revised).*

Shields, L. M. (1950). Leaf xeromorphy as related to physiological and structural influences. *Bot. Rev.* 16:399-447.

Shinners, L. H. (1962). *Calamintha* (Labiatae) in the southern United States. *Sida* 1:69-75.

Šilić, C. (1978). Horologia i ekologija vrsta roda *Micromeria* Bentham u Flori Jugoslavije. *God. Biol. Ist. Univ. Sarajevu* 31:169-182.

Simpson, B. B. (1973). Contrasting modes of evolution in two groups of *Perezia* (Mutisieae, Compositae) of southern South America. *Taxon* 22:525-536.

Small, J. K. (1903). *Flora of the Southeastern United States* 1042-1044.

Special Committee for Pteridophyta and Phanerogamae (1954). *Taxon* 3:120.

Spira, T. P. (1980). Floral parameters, breeding system and pollinator type in *Trichostema* (Labiatae). *Amer. J. Bot.* 67:278-284.

Sprengel, C. K. (1793). *Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen*. 444 col. Berlin.

Stålfelt, M. G. (1956). Morphologie und Anatomie des Blattes als Transpirationsorgan. *Handb. Pflanzenphysiologie* 3:324-341.

Starr, A. M. (1912). Comparative anatomy of dune plants. *Bot. Gaz.* 54:265-305.

Stebbins, G. L. (1971). Relationships between adaptive radiation, speciation and major evolutionary trends. *Taxon* 20:3-16.

Stocker, O. (1957). Grundlagen, Methoden und Probleme der Ökologie. *Ber. Deutsch. Bot. Ges.* 70:411-423.

----- (1960). Physiological and morphological changes in plants due to water deficiency. *UNESCO: Arid Zone Research* 15:63-104.

Swarbrick, J. T. (1971). External mucilage production by the seeds of British plants. *Bot. J. Linn. Soc.* 64:157-162.

Valdeyron, G., Dommée, B. & Valdeyron, A. (1973). Gynodioecy: another computer simulation model. Amer. Natur. 107:454-459.

Velenovsky, J. (1899). Über Micromeria frivaldskyana Deg. und M. balcanica Vel. Oest. Bot. Zeitschr. 49:291-292.

Walther, E. & Walther, K. (1957). Systematische Studien an Micromeria biflora Benth. aus Afrika. Mitt. Thür. Bot. Ges. 1:1-12.

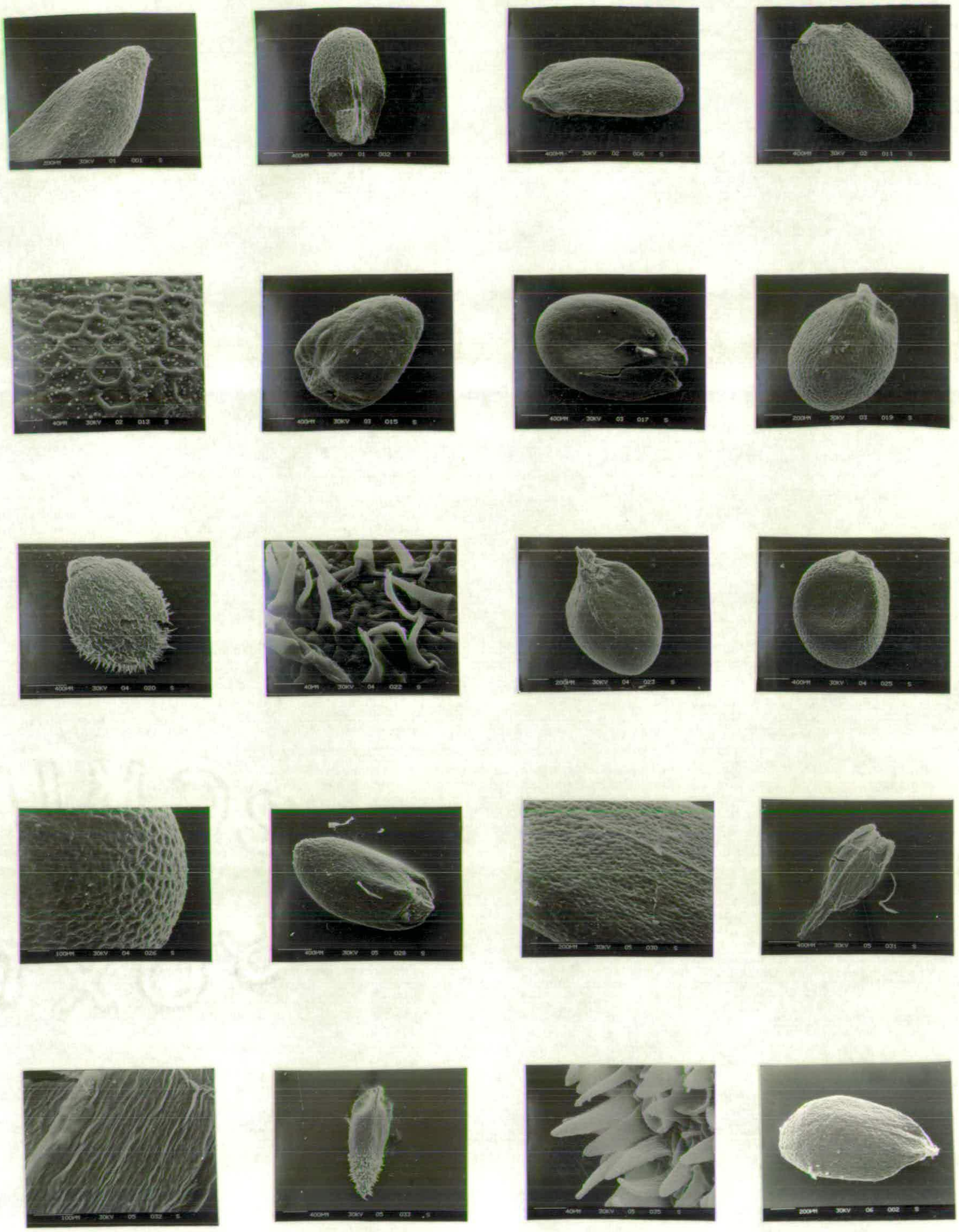
Wilkinson, H. P. (1979). The plant surface (mainly leaf). Part 1: Stomata, in Metcalfe, C. R. & Chalk, L. Anatomy of the Dicotyledons. ed. 2, 1:97-117.

Wojciechowska, B. (1961, a). Fruits of the Middle European species of the genus Prunella L., their morphology and anatomy. Monog. Bot. 12:49-88.

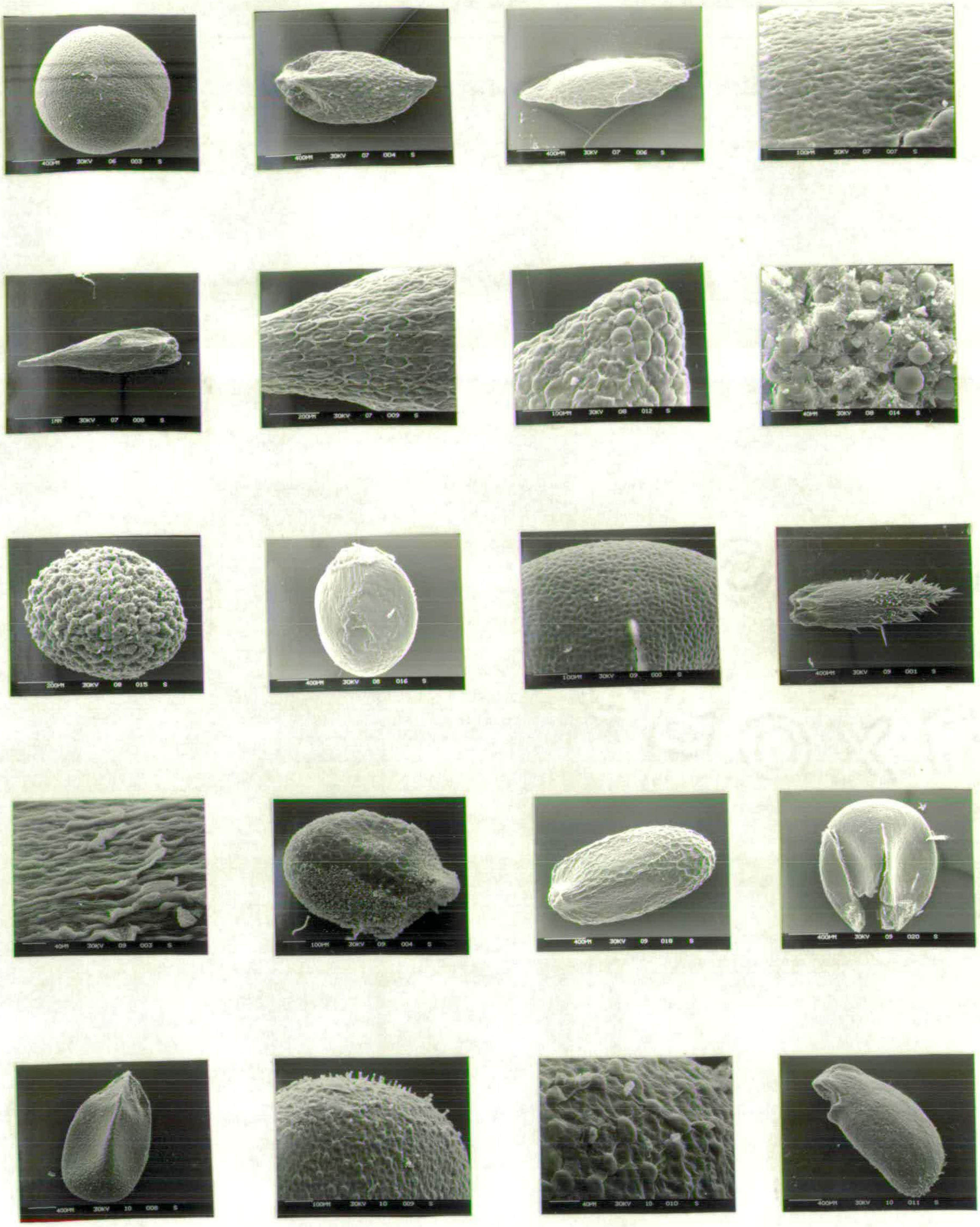
----- (1961, b). Fruits of the Middle European species of some genera of the sub-family Stachyoideae. Monog. Bot. 12:89-120.

----- (1966). Morphology and anatomy of fruits and seeds in the family Labiatae with particular respect to medicinal species. Monog. Bot. 21:3-244.

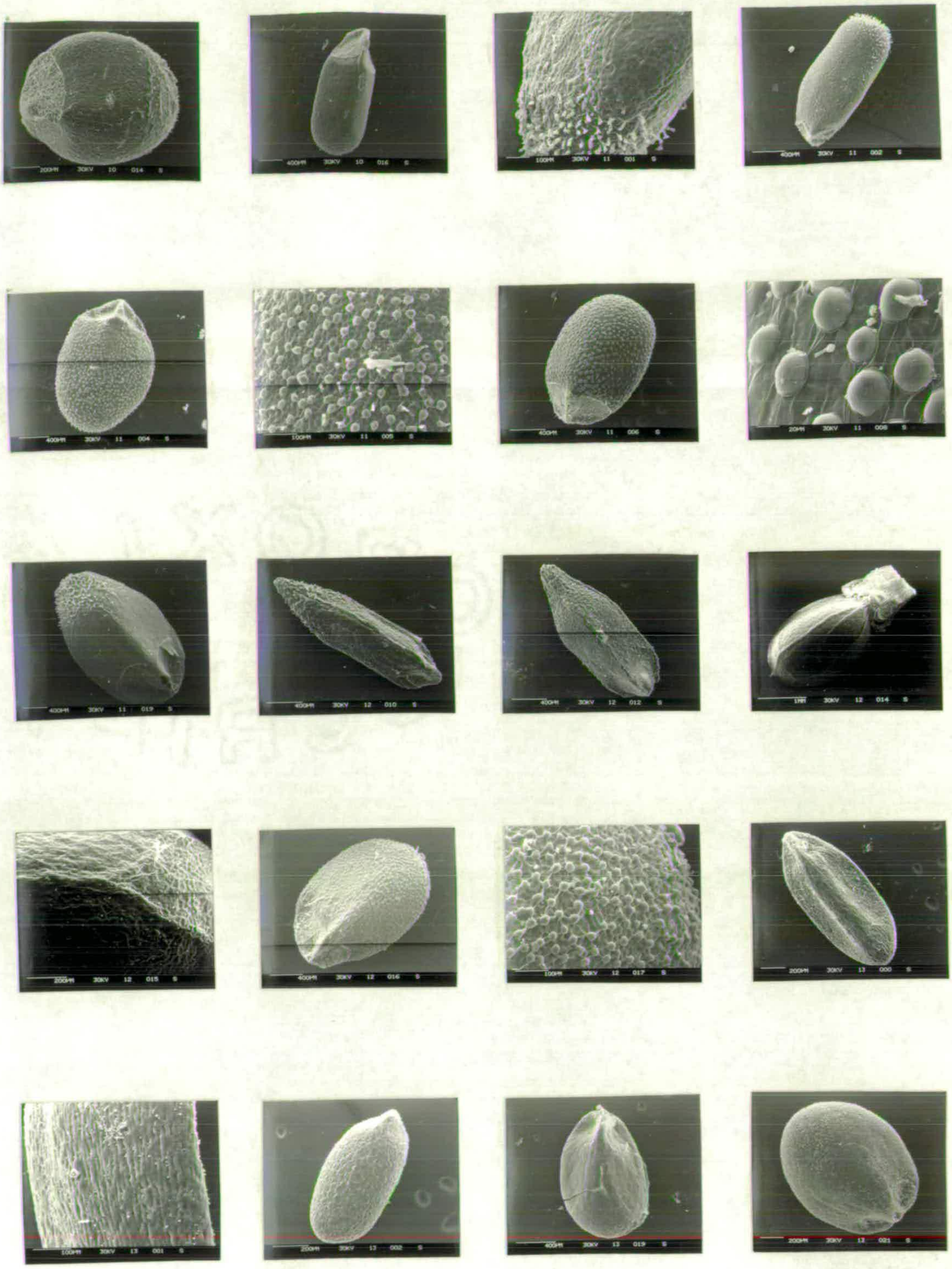
Zohary, M. (1937). Die verbreitungsökologischen Verhältnisse der Pflanzen Palästinas. I. Die antitelechorischen Erscheinungen. Beih. Bot. Centralbl. 56(A):1-155.



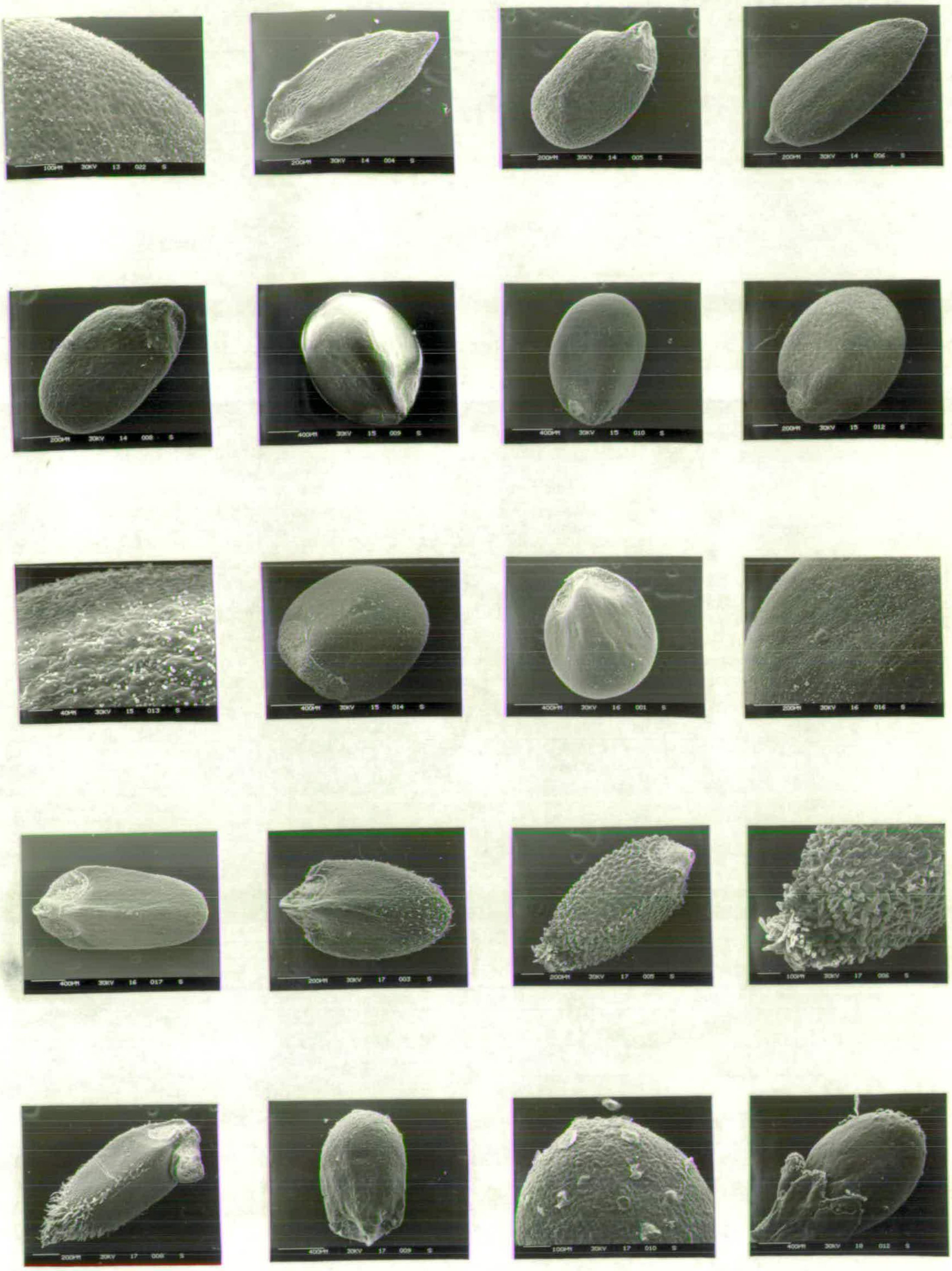
Pl. 1.1 Gardoquia cercocarpoides, abaxial apex; Pl. 1.2 G. tomentosa, adaxial; Pl. 2.6 G. impressa, abaxial; Pl. 2.11 G. multiflora, adaxial; Pl. 2.13 G. impressa, abaxial surface; Pl. 3.15 G. seleriana, adaxial; Pl. 3.17 G. macrostema, adaxial; Pl. 3.19 Piloblephis rigida, adaxial; Pl. 4.20 Xenopoma brevicalyx, abaxial; Pl. 4.22 X. brevicalyx, hairs; Pl. 4.23 X. nubigena, adaxial; Pl. 4.25 Diodeilis coccinea, adaxial; Pl. 4.26 D. coccinea, adaxial apex; Pl. 5.28 X. gilliesii, adaxial; Pl. 5.30 X. gilliesii, abaxial surface; Pl. 5.31 X. schusteri, adaxial; Pl. 5.32 X. schusteri, adaxial surface; Pl. 5.33 X. viminea, adaxial; Pl. 5.35 X. viminea, hairs; Pl. 6.2 X. mutabilis, abaxial.



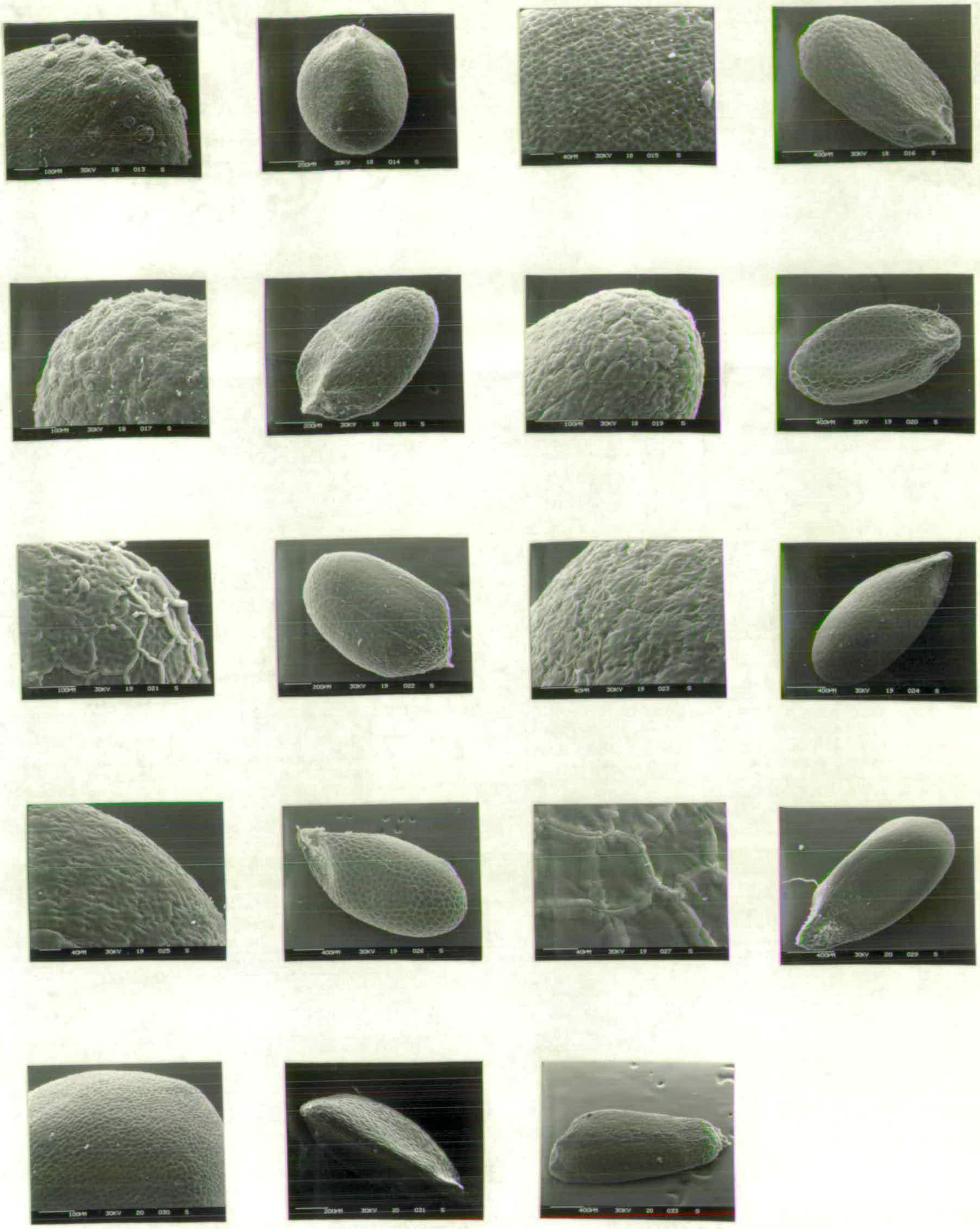
Pl. 6.3 Diodeilis georgiana, abaxial; Pl. 7.4 Xenopoma odora, adaxial; Pl. 7.6 X. axillaris, abaxial; Pl. 7.7 X. axillaris, abaxial surface; Pl. 7.8 Gardoquia sphenophylla, adaxial; Pl. 7.9 G. sphenophylla, adaxial near apex; Pl. 8.12 X. cylindristachys, adaxial apex; Pl. 8.14 Hesperothymus brownei, surface; Pl. 8.15 H. brownei, abaxial; Pl. 8.16 H. douglasii, adaxial; Pl. 9.0 D. procumbens, surface; Pl. 9.1 X. alpestris, adaxial; Pl. 9.3 X. alpestris, surface; Pl. 9.4 D. amissa, adaxial; Pl. 9.18 X. chandleri, adaxial; Pl. 9.20 D. procumbens, adaxial; Pl. 10.8 Satureja montana, adaxial; Pl. 10.9 S. montana, abaxial apex; Pl. 10.10 S. montana, glands; Pl. 10.11 S. bachtiarica, abaxial.



Pl. 10.14 Satureja spinosa, adaxial; Pl. 10.16 S. macrantha, adaxial; Pl. 11.1 S. thymbra, abaxial apex; Pl. 11.2 S. coerulea, adaxial; Pl. 11.4 S. spicigera, adaxial; Pl. 11.5 S. spicigera, glands; Pl. 11.6 S. hortensis, adaxial; Pl. 11.8 S. hortensis, glands; Pl. 11.19 S. thymbra, adaxial; Pl. 12.10 Nanbrea cacondensis, adaxial; Pl. 12.12 N. myriantha var. myriantha, adaxial; Pl. 12.14 Killickia compacta, adaxial; Pl. 12.15 K. compacta, adaxial surface; Pl. 12.16 S. bzybica, adaxial; Pl. 12.17 S. bzybica, near apex; Pl. 13.0 Micromeria graeca ssp. graeca, adaxial; Pl. 13.1 M. graeca ssp. graeca, abaxial; Pl. 13.2 M. nervosa, adaxial; Pl. 13.19 M. abyssinica, adaxial; Pl. 13.21 Calamintha kilimandschari, adaxial.



Pl. 13.22 Calamintha kilimandschari, adaxial surface; Pl. 14.4 Micromeria juliana, adaxial; Pl. 14.5 M. inodora, adaxial; Pl. 14.6 M. marginata, abaxial; Pl. 14.8 M. lanata, adaxial; Pl. 15.9 C. grandiflora, adaxial; Pl. 15.10 C. debilis, adaxial; Pl. 15.12 C. nepeta ssp. glandulosa, adaxial; Pl. 15.13 C. nepeta ssp. glandulosa, near apex; Pl. 15.14 C. pamphylica, adaxial; Pl. 16.1 Clinopodium atlanticum, adaxial; Pl. 16.16 Cl. vulgare, surface; Pl. 16.17 M. barosma, adaxial; Pl. 17.3 M. mollis, adaxial; Pl. 17.5 M. thymifolia, adaxial; Pl. 17.6 M. thymifolia, adaxial apex; Pl. 17.8 M. pulegium, adaxial; Pl. 17.9 M. nepalensis, adaxial; Pl. 17.10 M. nepalensis, adaxial apex; Pl. 18.12 M. euosma, adaxial.



Pl. 18.13 Micromeria euosma, adaxial apex; Pl. 18.14 M. cymuligera, adaxial; Pl. 18.15 M. cymuligera, surface; Pl. 18.16 M. hydaspidis, adaxial; Pl. 18.17 M. hydaspidis, adaxial apex; Pl. 18.18 M. capitellata, adaxial; Pl. 18.19 M. capitellata, adaxial apex; Pl. 19.20 Acinos nanus, adaxial; Pl. 19.21 A. nanus, apex; Pl. 19.22 A. pseudosimensis, abaxial; Pl. 19.23 A. pseudosimensis, surface; Pl. 19.24 A. suaveolens, adaxial; Pl. 19.25 A. suaveolens, surface; Pl. 19.26 A. rotundifolius, adaxial; Pl. 19.27 A. rotundifolius, surface; Pl. 20.29 Cyclotrichium origanifolium, adaxial; Pl. 20.30 C. origanifolium, adaxial apex; Pl. 20.31 M. cinerea, adaxial; Pl. 20.33 Gontscharovia popovii, abaxial.