A GLOBAL TAXONOMIC INVESTIGATION OF SCUTELLARIA L. AND ITS ALLIES (LABIATAE)

BY

ALAN J. PATON

A THESIS PRESENTED IN FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF EDINBURGH
1989

ACKNOWLEDGEMENTS

I would like to express my deep gratitude to the following:

my supervisors, Dr Philip Smith, Mr Ian Hedge and Dr David Mann for their interest, help and encouragement throughout this work;
the S.E.R.C. for funding this project;
the Regius Keeper and the staff of the Royal Botanic Garden, Edinburgh, for the use of herbarium and library facilities and the kind advice and friendship offered to me;
the keepers and staff of the following herbaria for the loan of specimens: K, MO, LE, W, PE, TI, US, GH, RSA, KUN, BG, MEXU, P, GB;
Colin McFarland and John Findlay for advice and help in electron microscopy and photography;
Helen Talbot for assistance in computing;
Hervé Burdet for information concerning Arthur Hamilton;
Gladys Millar for typing the manuscript;
the members of the Botany department of Edinburgh University for making postgraduate life completely tranquil and serene;
my mother and Margaret for being as they are.

"To study history one must know in advance that one is attempting something fundamentally impossible, yet necessary and highly important. To study history means submitting to chaos and nevertheless retaining faith in order and meaning."

Herman Hesse

CONTENTS

ABSTRACT

A global taxonomic review of the Labiatae genera *Scutellaria* L., *Perilomia* Kunth, *Harlanlewisia* Epling and *Salazaria* Torrey is presented. It is based on a study of a representative selection of species from throughout the world covering all known aspects of morphological and geographical variation. A detailed investigation of available practical characters showed that features of the inflorescence, calyx, corolla and nutlets were the most important and taxonomically most reliable. Macromorphology and micromorphology via scanning electron microscopy and anatomy were the principle sources of data.

Three classification methods were used: intuitive, numerical phenetic and cladistic. These classifications are compared, conclusions drawn and a new integrated classification proposed.

All the taxa studied are included in one genus, *Scutellaria*. Two subgenera are delimited and redefined: Subgenus *Scutellaria* and Subgenus *Apeltanthus*. (Nevski ex Juz.) Juz. Within the type subgenus, five sections are recognised: Sections *Scutellaria*, *Anaspis* (Rech. f.) Paton *Salviifoliae* (Boiss.) Edmondson, *Salazaria* (Torrey) Paton and *Perilomia* (Kunth) Epling. Subgenus *Apeltanthus* is divided into two sections: Sections *Apeltanthus* and *Lupulinaria* A. Hamilton, the latter further subdivided into Subsections *Lupulinaria* and *Cystaspis* (Juz.) Paton. A large number of informally designated species groups are also recognised. The higher infrageneric taxa are described, typified and keyed out.

The new classification, the first global review of a major cosmopolitan Labiate genus this century, provides a framework for future monographic studies.

Patterns of distribution in the infra-generic taxa were studied and an isoflor map for the whole genus provided. The main centre of diversity appears to be in the Hindu Kush and the Pamir-Alay mountains of Central Asia, with secondary centres in the area of the eastern Mediterranean and the Andes. The likely migratory history of the genus is reviewed.

Some aspects of fruit dispersal were considered -in particular the role played by the calyx and the possible functions of various ornamentations on the surface of the nutlets.

CHAPTER 1

Introduction

The aim of this work is to investigate the global infrageneric variation of *Scutellaria* L. and its allied genera, *Perilomia* Kunth, *Salazaria* Torrey and *Harlanlewisia* Epling and to produce a classification which reflects as far as possible the evolution undergone within these taxa.

Scutellaria is a large genus in the Labiatae of around 350 species. There are 420 published species names but a large number of species are microspecies doubtfully meriting specific status. *Scutellaria* is found throughout the northern hemisphere south of the Arctic Circle and in the temperate mountains of the southern continents, though absent as a native in the Cape of Africa. *Perilomia*, an Andean genus, differing from *Scutellaria* mainly in corolla form, contains up to 8 species, the number depending on taxonomic treatment. *Perilomia* was considered to be a section of *Scutellaria* by Epling (1942). The Andean monotypic genus *Harlanlewisia* differs from *Scutellaria* in corolla form. The monotypic *Salazaria*, which differs from *Scutellaria* in having a large membranous-inflated, bladder-like calyx in fruit, is found in the south-western United States and north Mexico.

No previous treatment of any large Labiate genus this century has considered the infrageneric variation on a global scale. This is important because if a classification is to represent accurately the variation within a genus it must be based on the total infrageneric variation rather than just a narrow geographical sample of it. At present there is little similarity between the classification of New and Old World species; there are also discrepancies between the treatment in individual Floras of the Old World. If the evolution and phytogeography of *Scutellaria* are to be studied and understood it is necessary to have a classification which is consistent throughout the world.

Due to the number of species involved and the limited time available, a sample of 109 species had to be studied rather than every one in the genus. However, the sample covers every aspect of morphological and geographical variation within the genera investigated, as far as I am aware.

Inflorescences, flowers, nutlets together with leaf surfaces and sections were examined for new or neglected taxonomic evidence. Features noted by earlier workers were also analysed. The time available did not permit study of cytology or chemotaxonomy.

Three methods of classification were employed in this work: intuitive, which uses a few characters subjectively assessed to be important; numerical phenetic, which is based on all available characters, equally weighted; and cladistic, which utilises parsimony to produce a classification which reflects ancestry. Parsimony is the assumption that evolution has proceeded by the shortest route, i.e. the number of character state changes is minimised throughout the phylogeny and hence in the construction of a 'phylogenetic tree'. The three classification methods were used to enable me to study and evaluate the assumptions, and the results of these assumptions, made in these methods. An integrated classification based on the results of all three methods could then be presented by assessing these assumptions and drawing conclusions as to which were likely to be valid and which were not. Pragmatic properties were also considered.

The phytogeography of Scutellaria and its allies could then, it was hoped, be studied using this final classification and by interpreting the distributions of all the species.

During this work, species previously placed in Perilomia will be considered and referred to as members of Scutellaria following Epling (1942). Salazaria and Harlanlewisia will be considered as separate genera until they are demonstrated to be infrageneric taxa of Scutellaria. (Chapter 7: Taxonomic Conclusions). Thenceforth they will be considered and referred to as species of Scutellaria, i.e. Scutellaria mexicana and Scutellaria sarmentosa respectively.

CHAPTER 2

Taxonomic History

There are three parts to this chapter. Firstly the position of *Scutellaria* and allied genera within the Labiatae is discussed. Secondly the four genera *Scutellaria*, *Perilomia*, *Harlanlewisia* and *Salazaria* are described and their taxonomic histories detailed. Finally some taxonomic problems regarding the delimitation of these four genera are summarised.

1. Scutellaria and allied genera within the Labiatae

The genera *Scutellaria* L., *Salazaria* Torrey, *Perilomia* Kunth, and *Harlanlewisia* Epling, seem to form a natural group recognised by the following characters: the entire-lipped, bilabiate calyx which closes at the mouth in fruit; a peg-like gynophore; the abaxial or anterior pair of stamens have unilocular thecae due to a bortion of the upper locule, often referred to as dimidiate stamens; and an embryo which is curved, or bent so that the radicle forms a right angle with the cotyledons, or is incumbent. These characters, although individually rare in the family, are known in other genera. *Tinnea* Kotschy & Peyritsch and *Prostanthera* Labill. possess entire-lipped calyces which close in fruit. Dimidiate anthers occur in several genera, *e.g.* *Sideritis* L.. *Catopheria* (Benth.) Benth. has a bent embryo, though accumbent rather than incumbent. However, it is the combination of these characters that clearly isolates *Scutellaria* and its allies from the rest of the Labiatae.

Bentham (1834) reflected this isolation, placing *Scutellaria* and *Perilomia* in the separate tribe Scutellarineae, along with *Prunella* L. and *Cleonia* L. (Tables 2.1, 2.2). The latter two genera were included because of their superficial calyx resemblance even though Bentham (1834) stated that: "this tribe, if confined to *Scutellaria* and *Perilomia*, would have been more natural". Visiani (1847) removed *Cleonia* and *Prunella* from the tribe, which seems more sensible. But, in his later treatments (1848 and 1876), Bentham kept these genera together and merged them into Tribe Stachydeae (Table 2.1, 2.2). This group does not

Table 2.1 Summary of the Subclassification of the Labiatae

Bentham 1832-1836	Bentham 1876	Briquet 1895-97	Melchior 1964	Erdtman 1945	Wunderlich 1967
Tribe Ajugoideae	Tribe Ajugoideae	Subfamily Ajugoideae	Subfamily Ajugoideae	Subfamily Lamioideae	Subfamily Ajugoideae
			Subfamily Rosmarinoideae		
Tribe Prostanthereae	Tribe Prostanthereae	Subfamily Prostantheroideae	Subfamily Prostantheroideae		Subfamily Prostantheroideae
Tribe Prasieae	Tribe Prasieae	Subfamily Prasoideae	Subfamily Prasoideae		
Tribe Scutellarineae	Tribe Stachydeae Subtribes: Scutellarieae Melliteae Marrubieae Balloteae	Subfamily Scutellarioideae	Subfamily Scutellarioideae		Subfamily Scutellarioideae
Tribe Stachydeae		Subfamily Stachyoideae Tribes: Marrubieae Perilomeae Nepeteae Stachydeae Glechomeae	Subfamily Stachyoideae Tribes: Marrubieae Perilomieae Nepeteae Stachydeae Glechomeae		Subfamily Stachyoideae Tribes: Prasieae Marrubieae Stachydeae Laminae Pogostemoneae
Tribe Nepeteae	Tribe Nepeteae	Salvieae	Salvieae	Subfamily Nepetoideae	Subfamily Saturejeae (a) Nepeteae Prunelleae Glechoneae Saturejeae (b) Rosmarineae Lavanduleae Hormineae Monardeae Salvieae Meriandreae Lepechineae Elsholtzieae (c) Ocimoideae
Tribe Monardeae	Tribe Monardeae	Meriandreae Monardeae	Meriandreae Monardeae		
Tribe Satureineae	Tribe Satureineae Subtribes: Pogostemoneae Menthoideae	Hormineae Lepechinieae	Hormineae Lepechineae		
Tribe Melissineae	Melisseae Lepechineae	Saturejeae Pogostemoneae	Saturejeae Pogostemoneae		
Tribe Ocimoideae	Tribe Ocimoideae	Subfamily Ocimoideae	Subfamily Ocimoideae		
		Subfamily Lavanduloideae	Subfamily Lavanduloideae		
		Subfamily Catopherioideae	Subfamily Catopherioideae		Subfamily Catopherioideae

Table 2.2 Summary of some taxonomic treatments of <u>Scutellaria</u> and related genera

Bentham 1834	Bentham 1848	Bentham 1876	Briquet 1896	Erdtman 1945	Wunderlich 1967
Tribe Scutellarineae Included genera: Scutellaria; Perilomia; Cleonia; Prunella	Tribe Stachydeae Subtribe Scutellarieae Included genera: Scutellaria; Perilomia; Cleonia; Prunella	Tribe Stachydeae Subtribe Scutellarieae Included genera: Salazaria; Scutellaria; Perilomia; Cleonia; Prunella	Subfamily Scutellarioideae Included genera: Scutellaria; Salazaria	Subfamily Lamioideae Many genera including: Perilomia; Scutellaria; Salazaria	Subfamily Scutellarioideae Including genera: Scutellaria; Salazaria; Perilomia
			Subfamily Stachyoideae Tribe Perilomeae Included genera: Perilomia		

seem natural and does not reflect the isolated position of *Scutellaria* within the Labiatae.

Caruel (1886), emphasising the character of the curved or bent embryo, placed *Scutellaria*, *Perilomia* and *Salazaria* in a new family - Scutellariaceae. Although correctly drawing attention to the relative isolation of the group, such a classification obscures the vegetative and floral affinities of *Scutellaria* to the rest of Labiatae.

Gray (1872) suggested that *Perilomia* with a spatulate embryo and *Scutellaria* with a bent embryo (Terms from Martin 1946) do not form a natural group. Briquet (1896), using this character and also the position of the seed in fruit, (transverse in *Scutellaria*, erect in *Perilomia*) placed the two genera in entirely different subfamilies. (Tables 2.1, 2.2). Although I have examined only a few embryos of *Scutellaria* and *Perilomia*, there seems to be no sharp discontinuity between the incumbent radicle of, *e.g.* *S. galericulata* L.: the short-radicled, right angled embryo of, *e.g.* *Salazaria*; and the short radicled, slightly curved embryo of *Scutellaria nummulariifolia* Hook. f. or *Perilomia ocymoides* Kunth. I am unsure of the meanings of 'seed transverse' and 'seed upright' (Briquet 1896). If the hilum is regarded as the base of the seed, then the seed of *Scutellaria* is transverse because the hilum is halfway along the fruit ("*hilo ventralis*" Bentham 1876). In *Perilomia* the seed may be considered upright if the hilum is near the base of the fruit. However, the fruits of *Scutellaria* attach to the gynophore halfway along their length, *i.e.* opposite the hilum. *Perilomia* fruits may attach to the gynophore near their base, again perhaps opposite the hilum. Thus, with reference to the gynophore and hilum, the seeds have the same orientation. Further examination of living *Perilomia* material is needed.
But even if the seeds do have different orientation, Penland (1924) points out "Undoubtedly the position of the seed [in *Scutellaria*] is important in classification, but its infallibility is questionable when it separates such closely related forms". Perhaps this is not a very good character.

Thus in my view, Briquet's (1896) and Melchior's (1964) similar classification, obscure the resemblances between these genera. However, it is Briquet's subfamilial system which is most commonly used today, e.g. Flora URSS (Juzepczuk 1954), Flora Reipublicae Popularis Sinicae (Wu & Li 1977) and The Flora of the British Isles (Clapham et al. 1987).

Erdtman (1945) proposed a new division of the Labiatae based on pollen morphology. He placed Scutellaria and Perilomia, with tricolpate pollen, in subfamily Lamioideae. (Tables 2.1, 2.2). Of the characters supporting this classification, which are listed by Cantino & Sanders (1986), the few species of Scutellaria studied are similar to the rest of the Lamioideae in having iridoid glycosides (Kooiman 1972), but being poor in volatile terpenoids (El Gazzar & Watson 1970), rosmarinic acid (Zoz & Litvinenko 1979) and linolenic acid (Hagemann et al. 1967). However, Scutellaria differs from the rest of the Lamioideae in lacking endosperm, at least in the species I have examined.

Wunderlich's (1967) classification, based on pollen seed and embryo characters is consistent with Erdtman's, none of her subfamilies having both tri- and hexa-colpate pollen. (Tables 2.1, 2.2). By placing Scutellaria, Perilomia and Salazaria in the same subfamily, Scutellarioideae, her classification accurately reflects the position of Scutellaria and allied genera, because these two are morphologically similar to each other, but isolated from the rest of the Labiatae.

2. Description and Taxonomic History of the Genera

A: Scutellaria

Scutellaria with about 400 currently recognised species is one of the largest genera of Labiatae. Its species occur naturally throughout the world except north of the Arctic Circle, the Amazon basin and Southern Africa.* (See Fig.8.1 in Chapter 8).

---

* S. racemosa, an introduced S. American species, is naturalised in Transvaal and Cape Province (South Africa).

Most of the species native to tropical areas grow at altitudes where the climate is relatively temperate. Globally, the species are found in a remarkable wide range of habitats: woods, damp meadows, waterside, dry rocky steppe, semi-desert, high alpine screes, and grow at altitudes from sea-level to 5000m. In habit they vary from herbaceous annuals and perennials to scrambling or erect shrubs. In Central Asia there are cushion-forming, cliff-dwelling chasmophytes.

Although there is a high degree of morphological similarity throughout the genus, there is an intriguing range of variation in floral, inflorescence and nutlet characters. These features have dominated historical debate about the taxonomy of *Scutellaria*. It is therefore appropriate to begin by giving a brief review of the characters which have attracted attention, including those of high taxonomic value and those of lesser use in classification.

(i) *Leaf and petiole*. Leaves usually petiolate, entire or variously dentate. Lower leaves similar to upper, or rarely brown, scale-like and clasping the stem, *e.g*. *S. leptosiphon* Nevski.

(ii) *Indumentum*. Hairs usually simple, multicellular, may bear capitate glands, rarely hairs are branched (dendroid), *e.g*. *S.flocculosa* Epling & Mathias. Abaxial leaf surface, calyx and occasionally inflorescence axis with sessile glands, adaxial leaf surface either with sessile glands or not.

(iii) *Inflorescence*. This is an important source of taxonomic characters. There are three types:
(a) The flowers of the inflorescence are opposite and secund, subtended by leaves similar in size to cauline leaves, or by smaller leaf-like bracts. This type of inflorescence is similar to that found in many genera of Labiatae, (*e.g*. *Teucrium* L. Sect. *Scorodonia*) and is found in species throughout the geographical range of *Scutellaria*.
(b) Inflorescence four-sided. Flowers opposite and decussate, subtended by cucullate bracts; pedicels strongly flattened. This type of inflorescence is found in species from the mountainous regions of the Old World, from the Pyrenees and the Atlas Mts. of N. Africa to the Altai Mts. and Western Himalaya. It is reminiscent of the inflorescence of

Prunella L. or species of Sideritis L. except that each bract subtends a single flower rather than a verticillaster.

(c) Flowers not oppositely but spirally inserted: either secund, e.g. S. inflata Epling, or pointing in all directions, radiating out from the inflorescence axis, e.g. S. costaricana H. Wendl. Species with such inflorescences are found mainly in Central America and the Andes, but also disjunctly in S.E. Asia, (S. discolor Wallich). It should be noted that non-opposite flower insertion is rare in the Labiatae, but Lavandula burmanni Benth. is another example.

(iv) Calyx. This is another source of important characters, and again there are three types:

(a) Upper lip folded midway along its length into an erect sail-like appendage called a scutellum. Found throughout the geographical range of Scutellaria, e.g. S. galericulata.

(b) Scutellum is inflated and membranous in fruit. Found in a few high alpine scree plants, e.g. S. heydei Hook. f.

(c) Upper lip is testudinate.* Found in chasmophytes of Central Asia and some plants of South America.

(v) Corolla. Corolla form is more or less constant throughout the world through variations occur in South America. The tube is straight though it may be bent upward at its base where it emerges from the calyx. The corolla is clearly bilabiate with short unequal lobes or lips, the lower being the larger; the upper is galeate, enclosing the stamens: lateral lobes are short, more substantially connected to the upper lobe than the lower. The tube interior is glabrous or may contain a broad or narrow annulus of hairs. Colour varies from white to pink, red, violet, blue and yellow, often in various combinations on a flower. In South and Central America there is additionally a range of other forms: the tube may be bent downwards in the middle to appear sigmoid or arcuate; lobes may be equal and spreading,

---

* I have adopted this adjective for an arched or vaulted upper calyx lobe which resembles a tortoise shell. A scutellum is absent.

anthers exserted or situated half-way down the tube, the interior of the tube may be densely hairy, or have hairs only at the base of the anterior stamens, or be folded into teeth or corrugations at the base; corolla is often scarlet.

(vi) *Stamens*. Stamens are uniform in structure. Anthers are short in comparison to the filaments. The anterior stamens are dimidiate. Filaments are inserted about half-way up the corolla tube. The pollen is ellipsoid and tricolpate.

(vii) *Gynophore*. This is variously formed and may be brightly coloured.

(viii) *Nutlets*. These vary in colour from grey to black, brown, orange brown or yellow, with a smooth, papillate or ridged surface with or without a wing, hairs, hooks or glands.

Pre-Linnaean History of Scutellaria

The name "*Scutellaria*" was apparently first used by Cortuso (1591). I have been unable to see this reference but Bauhin (1596) describes a *Teucrium*-like plant and refers it to *Scutellaria* "*Teucria* similis *Scutellaria* dicta" and states that this name was given by Cortuso, "Scutellaria ... quo nominae eam Cortusus donauit". Bauhin (1623, 1671) refers *Scutellaria* to *Lamium*: "*Lamium peregrina* sive *Scutellaria*". Morison (1669) first describes the new genus *Scutellaria*, "*Lamium peregrina* *Scutellaria* C.B. Pin ..... A forma capsulae seminalis, aprime referertis imaginem aut formam tali vulgaris, qui mulierum calceis subjicitur quae exsiccata & aperta scutellam exprimit, unde ille nomen, novem genus Scutellaria". This can be translated as follows:

"*Lamium peregrinum* C. B[auhin] Pin[ax] [= *Scutellaria peregrina* L. 1753] the form of the seed capsule reminds one immediately of such a common shape as a Ladies slipper, which on drying and opening is forced into a dish, from which the new genus *Scutellaria* takes its name". The dish refers to the concave scutellum of this plant. Morison lists five other plants which belong to this genus.

The English common name Skullcap, the French La toque and the Russian Shlemnik refer to the name *Cassida*, meaning

a metal helmet, given by Colonna (1606 and 1616, earlier edition not seen). He states: "Quam a singulari & priutata fructas sive pericarpii, in aliis nondum visa, militaris galae iconem exprimente. Cassidam appellare libuit, sic enim Latine illam appellant". This can be translated as follows:
"due to the pericarp /calyx/ raised into the form of a military helmet, a structure not yet seen in others, it enjoys a singular and peculiar position. It is pleasing to name it after a metal helmet, in fact it should be called that in Latin. /Cassida/". Tournefort (1700) and also Seguier (1754) use this name but Linnaeus (1735) used the older name Scutellaria. This is the name he uses in Species Plantarum (1753) where he lists twelve species, one of which, S. cretica, is now placed in Teucrium.

Post-Linnaean generic synonyms are discussed at the end of the next section - The infrageneric taxonomic history of Scutellaria.

Infrageneric Taxonomic History of Scutellaria

A. Hamilton (1832)*first divided Scutellaria into three sections: Sect. Lupulinaria, Sect. Galericularia and Sect. Stachymacris, on the basis of inflorescence characters. (Tables 2.3, 2.4). Later that year Bentham (1832) also used that character to divide the genus into five groups, but as they "run so much into one another ..... I /Bentham/ had not thought it worth while to give them distinct names". (Tables 2.3, 2.4). But later Bentham (1834) then adopted Hamilton's corresponding names for three of his sections and added Sect. Maschalostachys and Sect. Heteranthesia (Tables 2.3, 2.4). In Bentham's (1848) third treatment, in De Candolle's Prodromus, he again comments on the uncertain limits of his sections. Sect. Maschalostachys was merged into Sect. Galericularia and he split Sect. Stachymacris into two subsections, suggesting Subsection Angustifoliae was intermediate between this section and Section Galericularia. (Tables 2.3, 2.5). In Bentham's fourth treatment (1876), he stated that the species of Scutellaria are distributed in 3 or 4 overlapping groups, rather than distinct sections, and combined Sect. Galericularia and

---

* See Appendix 4.

Table 2.3 Summary of the Infrageneric Classification of *Scutellaria*

Hamilton 1832	Bentham 1832	Bentham 1834	Bentham 1848	Bentham 1876	Briquet 1896	Kudo 1929	Epling 1942	Juzepczuk 1954	Wu & Li 1977	Rechinger 1982	Edmondson 1982
Sect. Lupulinaria	Spicatae	Sect. lupulinaria	Sect. Lupulinaria	Sect. Lupulinaria	Subgenus Euscutellaria Sect. Lupulinaria	Sect. Lupulinaria	Sect. Galericularia Sect. Antarctica Sect. Lateriflorae Sect. Mixtae Sect. Resinosae Sect. Saxicolae Sect. Annulatae Sect. Uliginosae Sect. Spinosae Sect. Crassipeda Sect. Pallidiflorae Sect. Speciosae Sect. Cardinales Sect. Coccinae Sect. Lutea Sect. Perilomioidae Sect. Perilomia Sect. Theresa	Subgenus Euscutellaria Sect. Lupulinaria Sect. Nevskinthe	Subgenus Euscutellaria Sect. Lupulinaria	Subgenus Euscutellaria Sect. Lupulinaria	Sect. Lupulinaria
	Racemosae Floribus Sparsis	Sect. Heteranthesia	Sect. Heteranthesia	Sect. Heteranthesia	Sect. Heteranthesia	Sect. Heteranthesia			Sect. Heteranthesia		
Sect. Stachymacris	Racemosae Floribus oppositis	Sect. Stachymacris	Sect. Stachymacris	Sect. Vulgares	Sect. Vulgares	Sect. Vulgares Series Stachymacris		Sect. Stachymacris	Sect. Stachymacris	Sect. Stachymacris	Sect. Salviifoliae Sect. Stachymacris
Sect. Galericularia	Axillares	Sect. Galericularia	Sect. Galericularia Subsection: Genuinae Perilomioidae Lateriflorae			Series Galericularia		Sect. Galericularia	Sect. Galericularia	Sect. Galericularia	Sect. Galericularia
	Lateriflorae	Sect. Maschalostachys				Series Lateriflorae			Sect. Maschalostachys		
					Subgenus Scutellariopsis				Subgenus Scutellariopsis		
								Subgenus Cystaspis		Subgenus Cystaspis	
								Subgenus Anaspis		Subgenus Anaspis	
								Subgenus Apeltanthus		Subgenus Apeltanthus	

Table 2.4 Detail of the Infrageneric Classification of Scutellaria 1832-1834

Hamilton 1832	Bentham 1832	Bentham 1834
Sect. Lupulinaria A. Ham. Flowers disposed in a terminal spike, singly in the axils of overlapping, entire, bracts. Leaves ovate, cordate, dentate or crenate.	Spicatae Benth. Leaves subtending flowers membranous. Flowers in a four-sided spike.	Sect. Lupulinaria A. Ham. Leaves subtending flowers often membranous. Flowers in a four-sided spike, or similarly subracemose, not secund.
Sect. Stachymacris A. Ham. All flowers secund in a terminal raceme, single in the axils of entire, herbaceous bracts. Leaves usually cordate and crenate.	Racemosae Benth. b) Opposite flowers Leaves subtending flowers herbaceous, small, differing from cauline leaves.	Sect. Stachymacris A. Ham. Leaves subtending flowers herbaceous, small, differing from cauline leaves. Inflorescence with flowers secund, opposite, racemose.
Sect. Galericularia A. Ham. Bracts similar to leaves which diminish in size from the base to the top of the plant. Flowers axillary, secund. Leaves lanceolate to linear. Petioles short.	Axillares Benth. Leaves subtending flowers herbaceous, grade into cauline leaves. Flowers secund in a raceme.	Sect. Galericularia A. Ham. Leaves subtending, flowers herbaceous, similar to cauline or slightly smaller. Flowers axillary or subracemose above.
	Racemosae Benth. a) Flowers sparse. Leaves subtending flowers herbaceous, small differing from cauline leaves.	Sect. Heteranthesia Benth. Leaves subtending flowers small, herbaceous. Flowers racemose, secund, all, or at least the upper, sparse.
	Lateriflorae Benth. Leaves subtending flowers herbaceous, lower ones conforming with cauline leaves. Flowers opposite and secund, placed in axillary and terminal racemes.	Sect. Maschalostachys Benth. Leaves subtending flowers herbaceous, the lower conform to the cauline. Flowers opposite, secund, most disposed in axillary and terminal racemes.

Table 2.5 The infrageneric classification of <u>Scutellaria</u> (continued)

Bentham. 1848	Bentham. 1876	Kudo 1929
Sect. Lupulinaria A. Ham.	Sect. Lupulinaria A. Ham.	Sect. Lupulinaria A. Ham.
Sect. Heteranthesia Benth.	Sect. Heteranthesia Benth.	Sect. Heteranthesia Benth.
Sect. Stachymacris A. Ham. 1 Cauline leaves ovate, petiolate. All flowers borne in the axils of small entire leaves. 2 Angustifoliae Leaves shortly petiolate, lanceolate or linear. Subentire. Floral leaves grade into cauline.	Sect. Vulgares Benth. Flowers opposite, often secund above.	Sect. Vulgares Benth. **Series** Stachymacris
Sect. Galericularia A. Ham. 1 Genuinae Flowers blue or violet, all axillary or subracemose above. 2 Lateriflorae Herbs extremely laxly branched. Flowers blue or violet, mostly in small axillary racemes. = Sect. Maschalostachys Benth. 3 Perilomoideae Herbs lax on fruticose. Flowers irregular in axillary or terminal racemes. Flowers scarlet or red.		**Series** Galericularia **Series** Maschalostachys

Sect. *Stachymacris* into Sect. *Vulgares*. This classification was followed by Kudo (1929) although he divided Sect. *Vulgaris* into series. (Tables 2.3, 2.5).

Briquet (1896) attaching more weight to the presence of a nutlet band or wing, than to characters of the inflorescence, divided the genus into Subgenus *Euscutellaria* and Subgenus *Scutellariopsis* (Tables 2.3, 2.6). Subgen. *Euscutellaria* was divided into three sections of Bentham (1876). Sect. *Vulgares* was divided into seven subsections on the basis of floral, inflorescence and habit characters. Briquet's account in *Die natürlichen Pflanzenfamilien* was the last global treatment of *Scutellaria* and it is on this that most of the later regional classifications are based.

In the *Flora URSS*, where 148 species are dealt with, Juzepczuk (1954), emphasising the character of the conformation of the upper lip of the calyx, divided the genus into four subgenera, maintaining *Euscutellaria* Briq. and adding *Cystaspis*, *Anaspis* and *Apeltanthus*. Subgen. *Euscutellaria* is again divided by inflorescence characters into four sections. The new section *Nevskinthe* Juz. is very similar to Sect. *Lupulinaria*. (Tables 2.3, 2.6). Rechinger (1982) follows Juzepczuk classification but Sect. *Nevskinthe* is not present in the *Flora Iranica* region. (Tables 2.3,2.6).

Wu & Li (1977) maintain *Euscutellaria* and *Scutellariopsis* Briq. but follow Bentham (1834) in dividing *Euscutellaria* into sections on the basis of inflorescence characters. (Tables 2.3, 2.7).

Edmondson (1982), in his *Flora of Turkey* account, abandoned Briquet's subgenera, dividing the genus into sections similarly to Hamilton and Bentham on the basis of inflorescence characters. (Tables 2.3, 2.7).

Epling's 1942 account is the only revision of New World *Scutellaria* since Briquet (1896). The genus is divided into 18 sections, based on floral, inflorescence, rhizome and habit characters. Only three of his sections, Sect. *Galericularia*, Sect. *Lateriflorae* and Sect. *Perilomoideae* are common to any other subclassification of *Scutellaria*. (Table 2.3). This demonstrates the fact that modern infrageneric classifications of *Scutellaria* are mostly not comparable with one another, as their authors

Table 2.6 The infrageneric classification of Scutellaria (continued)

Briquet 1896	Juzepczuk 1954	Rechinger 1982
Subgenus Euscutellaria Briq. Nutlets without a membranous band.	Subgenus Euscutellaria Briq. Calyx with a scutellum	Subgenus Scutellaria = Euscutellaria Briq.
Sect. Heteranthesia Benth.		
Sect. Lupulinaria A. Ham.	Sect. Lupulinaria A. Ham. Subsects: Fruticosae Juz. Ramosissimae Juz. Orientales Juz. Alpinae Juz.	Sect. Lupulinaria A. Ham.
	Sect. Nevskinthe Juz.	
Sect. Vulgares Benth. Subsects: Salviifoliae Boiss. Peregrinae Boiss. Cuneatae Briq. Coccinae Briq. Angustifoliae(Benth.) Briq. Galericulatae Boiss. Laterifoliae(Benth.) Briq.	Sect. Galericularia A. Ham.	Sect. Galericularia A. Ham.
	Sect. Stachymacris A. Ham. Subsects: Angustifoliae Benth. Peregrinae Boiss. Salviifolae Boiss.	Sect. Stachymacris A. Ham.
Subgenus Scutellariopsis Nutlets with an evident encircling band		
	Subgenus Cystaspis(Juz.) Juz. Like Sect. Lupulinaria but scutellum very large, membranous-inflated	Subgenus Cystaspis(Juz.) Juz.
	Subgenus Anaspis (Rech.f.) Juz. Inflorescence secund, upper lip of calyx testudinate.	Subgenus Anaspis (Rech.f.) Juz.
	Subgenus Apeltanthus (Nevski ex Juz.) Juz. Upper lip of calyx testudinate.	Subgenus Apeltanthus (Nevski ex Juz.) Juz.

Table 2.7 Infrageneric classification of *Scutellaria* (continued)

Wu & Li 1977	Edmondson 1982
Subgenus Scutellaria = Euscutellaria Briq. Section Lupulinaria A. Ham Subsections: Orientales Już. Alpinae Juz.	Section Lupulinaria A. Ham.
Section Stachymacris A. Ham. Subsections: Angustifoliae Benth. Peregrinae Boiss.	Section Salviifoliae (Boiss.) Edmondson
	Section Stachymacris A. Ham.
Section Galericularia A. Ham.	Section Galericularia A.Ham.
Section Heteranthesia Benth.	
Section Maschalostachys Benth.	
Subgenus Scutellariopsis Briq.	

have not considered the global variation of the genus.

Some of the infrageneric taxa described above have been raised to the rank of genus in the past, e.g. *Anaspis* Rechinger (1941) and *Apeltanthus* as a generic *nomen nudum* by Nevski (1935). Grossheim (1945) suggested too that *Heteranthesia* should be elevated to generic rank. Some species were placed in monotypic genera when first described: *S. nummulariifolia* in *Cruzia* (Philippi 1895) and *S. valdiviana* Epling in *Theresa* (Clos 1849). These treatments have not been followed by subsequent authors, the general view clearly being that *Scutellaria* is a natural genus.

B: *Perilomia*

Two species of *Perilomia*, *P. ocymoides* and *P. scutellariodes*, were collected by Humboldt and Bonpland from Ecuador, probably in 1802 when they visited this area (Stearn 1968). Kunth (1818) described the species and stated, "Plantam nostram a Scutellariis distinxi ob formam corollae et praesertim ob fructum marginatum". "I distinguished our plants from *Scutellaria* by the form of their corolla [which is red, tube bent distally and has equal, spreading lips] and especially by the border of the fruit [which is winged]".

The generic name *Perilomia* is derived from the Greek words - peri meaning around and loma meaning border which refers to the winged border of the fruit.

Perilomia consists of up to eight species (Briquet 1896) though the number depends on taxonomic treatment. Its species are found in the mountains of Colombia, Ecuador and Peru, at altitudes of around 3500m. They occur in a range of habitats: woods, steep slopes and open shrubby areas.

They can be scrambling or erect shrubs up to 1.5m tall. The inflorescence consists of opposite and secund flowers, borne singly in the axils of upper leaves or reduced leaf-like bracts. The corolla is red or sulphurous yellow, the tube is bent downward distally and the lobes are equal and spreading. The interior of the corolla tube can be glabrous or have hairs only at the base of the anterior anther. The tube may also have teeth or folds at its base. Anthers

Table 2.8 Briquet's Infrageneric Classification of Perilomia with his descriptions of sections

Section Euperilomia

Nutlet with a membranous, unequally cut band; surface tuberculate.

Section Holocraspeda Briq.

Nutlet, with a protruding but not jagged or cut band, surface not ornamented.

Section Aprosphyla Briq.

Nutlets with a more or less sharp but unwinged edge.

are situated below the free lobes of the corolla. But Briquet (1896) however, included some plants with unequal corolla lobes, the upper being galeate and housing the anthers. The upper lip of calyx is testudinate or folded into a scutellum. Nutlets are smooth or papillate, with or without a wing, hairs or hooks. The embryo is slightly curved. All over the plant, the indumentum consists of multicellular, unbranched, eglandular hairs.

Infrageneric and Generic Taxonomic History

Briquet (1896) is the only author to have subclassified Perilomia. He lists the three sections based on the presence and type of wing on the nutlet (Table 2.8). Sect. Aprosphylla consists wholly of species which Bentham (1848) included in Scutellaria. Epling (1942) incorporated Perilomia into Scutellaria stating: "some of the species may preferably be segregated as the genus Perilomia, primarily on the basis of corolla structure. The data are as yet insufficient, and I have retained all in Scutellaria".

C: Harlanlewisia

The monotypic genus Harlanlewisia was described by Epling in 1955. The genus takes its name from Prof. F.Harlan Lewis of California whose first contribution to taxonomy was a revision of the N. American Labiate genus Trichostema. Epling states that in Harlanlewisia the "bivalved calyx, conformation of the gynobase, and the line of attachment of the nutlets clearly relates this genus to Scutellaria ..... But the specimen differs from all other Scutellarias by the exserted stamens .... Also each of the upper stamens, rather than the lower, as is generally the case, has an aborted theca". I have managed to examine four specimens of H. sarmentosa, kindly sent on loan from Göteburg (GB) and Kew (K). The upper (anterior) stamen has indeed an aborted theca, but this is the case in all other Scutellaria studied.

H. sarmentosa is a woody shrub growing to 4m. Inflorescences have flowers secund in opposite pairs borne singly in the axils of upper leaves. The corolla is rose-red or reddish violet; the tube is straight at its base, but bent downward distally, appearing pendulous; the lobes are equal and spreading. Upper lip of the calyx is testudinate, similar in form to the lower lip. The indumentum, all over the plant, consists of short branched hairs, similar to that of S. flocculosa. The nutlets appear to be papillate from the description, but I have not been able to examine any personally.

The field notes indicate that Harlanlewisia grows in open spaces, in woods in mountains, and on slopes along road in cloud forest.

It has a very limited geographical range, growing only in the Canar and Cotopaxi provinces of Ecuador.

Taxonomic History

Epling (1955) originally described Harlanlewisia with one species, H. murex. Epling & Jativa (1968) then created the new combination H. sarmentosa (Epling) Epling et Jativa as H. murex Epling and Scutellaria sarmentosa Epling were regarded as synonyms.

D: Salazaria

This monotypic genus was first described by Torrey (1858) from a gathering made in Ravines, Chihuahua, North Mexico. Although the plant had been previously collected in 1844 by Col. Frémont in New Mexico, this specimen was badly damaged. The generic name commemorates Don José Salazar. Mexican Commissioner of the United States Boundary Survey (1857-59).

Torrey gave an accurate description of S. mexicana and concluded, "It is evident that Salazaria makes a near approach to Scutellaria, but its nearly regular and bladder-like inappendiculate fructiferous calyx in which there is scarcely any distinction of upper and lower lip, distinguishes it sufficiently from that genus". Although Salazaria does look different from North American Scutellaria on account of the shrubby habit and inflated calyx, examination of more than 70 specimens kindly sent on loan from Rancho Santa Ana (RSA) and Kew (K), and Scutellaria on a global scale, reveals the differences to be slight.

S. mexicana is an intricately branched shrub up to 1m high. Its inflorescence has opposite and secund flowers single in the axils of leaves similar in size to cauline leaves. In flower, the two lips of the calyx are equal and about 6-7mm long, in fruit the calyx greatly expands and becomes membranous. The corolla is not significantly different from any of the N.American species of Scutellaria: the tube is straight, though bent slightly upward at its base; the upper (posterior) lobe is galeate enclosing the anthers, and the lower (anterior) lobe has a large, median lip with small laterals united with the upper lobe. Nutlets are papillate and without hooks, glands or hairs, and embryo is bent, the radicle forming a right angle with the cotyledons. The plant's indumentum consists of short, mostly unicellular, eglandular hairs.

The field notes indicate that Salazaria grows in the following types of habitats: dry washes, sub-desert, Joshua Tree (Yucca brevifolia Engelm.) wood and Creosote bush (Larrea Cav.) scrub, and below 450m. It has a limited geographical range, growing in California, S. Utah, Arizona, New Mexico,. Baja California and Mexico.

Taxonomic History

Salazaria has since its recognition been considered a distinct genus from Scutellaria, although closely allied to it. However, Barkley (1975) recently created the new family Salazariaceae to accommodate Salazaria. He did not give a critical assessment of the taxon, merely observing that: "the writer considers /this taxon/ to be sufficiently distinctive to be considered as a family". This classification obscures the relationship to Scutellaria and other Labiatae. It has not been followed in any modern Floras or family systems, e.g. Cantino & Sanders (1986).

3: Problems of Generic Delimitation

The first problem concerns the delimitation of Scutellaria, Perilomia and Harlanlewisia. The distinction between Scutellaria and Perilomia has been a matter for dispute in the past: Briquet (1896), using seed and embryo characters, included in Perilomia some species, e.g.

P.volubilis, which Bentham, using corolla and nutlet characters, placed in *Scutellaria*. Epling (1942) resolved this conflict by merging the two genera, placing *Perilomia*, *sensu* Bentham (1848-1872) and Kunth (1818) in *Scutellaria* Sect. *Perilomia* and most of the debated species in *Scutellaria* Sect. *Perilomoideae*. However, Epling has been inconsistent in his treatment of these taxa by giving *Harlanlewisia* generic rank (Epling 1955). *Harlanlewisia* is no more distinct from the rest of *Scutellaria* than are Sect. *Perilomia* and Sect. *Theresa*, the latter of which has a similar corolla to *Harlanlewisia*. These sections were not given generic rank.

Thus one of the aims of the present investigation was to identify the discontinuities between *Scutellaria*, *Harlanlewisia* and *Perilomia*, if any exist.

The second problem concerns *Salazaria* and *Scutellaria*. *Salazaria*, since its original description, has been considered generally separate from *Scutellaria* on the basis of its inflated calyx and shrubby habit. But *Scutellaria utriculata* Labill. from Lebanon and Syria has a similar inflated calyx, and several South American *Scutellarias* are shrubby, *e.g.* *S. gardoquioides* Benth. Therefore, when viewed on a global basis, there must be doubt as to whether *Salazaria* merits generic delimitation, purely on the basis of its two differentiating characters.

CHAPTER 3

Material and Methods

This chapter deals with four topics:
A. The selection of species studied; B. The sources of material used; C. Methods of data collection and observations; D. Methods and materials for cladistic and numerical phenetic classifications.

A. Selection of species studied.

A sample of species was taken to represent the total taxonomic variation and geographical distribution of Harlanlewisia, Perilomia, Salazaria and Scutellaria. This was because there was not enough time to study every species. The monotypic genera Salazaria and Harlanlewisia were both examined. In Perilomia, one species from each of Briquet's sections and subsections were studied (Briquet 1896). In Scutellaria, the overall variation was sampled by choosing one species from every previously published section and subsection. Where an author had recognised series, one member from each series was chosen, wherever material permitted. Juzepczuk's (1954) and Wu & Li's (1977) Section Lupulinaria, Subsections Alpinae and Orientales were exceptions to this sampling procedure because these taxa seem to consist of many very closely related species which the authors divide into several series. An in-depth study of such critical groups was outwith the scope of this study because it would necessitate the study of a very large number of individuals and their phenotypic plasticity. Unfortunately there was not enough time to do this. The diversity within Subsection Orientales was sampled by studying one species from each of Juzepczuk's main groups, Oxystegia and Platystegia, (S. araxensis and S. platystegia respectively) (Juzepczuk 1954). Subsection Alpinae was represented by S. alpina. The geographical spread of these two subsections was represented by S. kotkaiensis, S. glechomoides and S. pinnatifida from the Flora Iranica region (Rechinger 1982) and S. orientalis ssp. alpina from the Flora of Turkey region (Edmondson 1982).

For geographical areas where no infrageneric divisions of Scutellaria have hitherto been recognised, so far as can be determined from the literature, representative species were chosen using the Index Kewensis and regional Floras. Also some recently described species were selected.

In this way, 109 species were selected to represent the total variation in these four genera which collectively consist of about 400 species. However, a substantial number of those in Scutellaria Section Lupulinaria A. Ham. are microspecies doubtfully meriting specific status. As far as I am aware, this sample fairly covers every aspect of taxonomic variation and geographical distribution in this group. The species sampled are listed in Appendix 1.

B. Sources of material

Most observations were made from herbarium material. Some material was also grown. A complete list of the c.650 specimens examined, housed at E, K, LE, MO, W, GB, US, BR, P, TI, BG, GH, RSA, KUN, PE and MEXU, (codes following Index Herbariorum), with details of their study and sources of living material is given in Appendix 1.

If only a few specimens of a particular species were available, an attempt was made to see the type specimen. If a large number of specimens was available a sample was taken to represent every facet of morphological and geographical variation detected in the herbarium collection.

C. Methods of data collection and observation

(1) Macromorphological characters

Wherever possible for each species, observations were made from at least four herbarium specimens covering a maximum geographical spread. Extremes of variation were identified and sampled appropriately. Characters were recorded with the aid of a x10 or x20 magnification binocular microscope.

(2) Floral characters

Wherever possible flowers of two individuals per species were examined. Flowers were removed from herbarium sheets, boiled in water with one drop of detergent (R.B.S. 25. Chemical Concentrates Ltd. (R.B.S.) London) until soft, then dissected and examined with the aid of a binocular microscope. (Mag.x10 or x20).

(3) Leaf anatomy: Sections

Initially, leaves from three individuals of each species were sectioned. However, because little intraspecific variation was found, usually only one leaf was subsequently used. Leaves from a standard position on a plant, i.e. one or two nodes below the lowest flower, were always used.

The following procedure was followed based on the method of Johansen (1940):

(a) Preparation

Standard leaves were removed from a herbarium sheet and boiled in water with one drop of detergent (R.B.S. 25) for one minute.

(b) Dehydration

Boiled leaves were placed in 25% ethanol overnight. Specimens were then put through the following tertiarybutyl alcohol (TBA) dehydration sequence:

Solution	1	2	3	4	5
Distilled H_2O	50%	30%	15%		
Methylated Spirits	40%	50%	50%	45%	
TBA	10%	20%	35%	55%	75%
Ethanol	-	-	-	-	25%
Total alcohol	50%	70%	85%	95%	100%

Leaves were placed in each solution for at least two hours. Specimens were then put through three changes of 100% TBA, one of which was overnight.

(c) Infiltration

Dehydrated specimens were placed in 50/50 TBA/ liquid paraffin for two hours. They were then poured onto the surface of some Paraplast (Oxford Laboratories International Corp.) which had been melted and allowed to cool. Specimens were heated to 59°C and left for three hours. (Paraplast melts at 57°C and degrades under temperatures of more than 61°C). The Paraplast was changed thrice with pure molten Paraplast, each change lasting at least three hours.

(d) Embedding

Specimens were embedded in paper embedding trays (Johansen 1940).

(e) Sectioning

10μm sections were cut with a rotary microtome and attached to slides using glycerin albumen.

(f) Staining

The following schedule was followed:

(i) 100% Xylene, 10 minutes
(ii) 50/50 Xylene/Ethanol 5 minutes
(iii) 100% Ethanol 5 minutes
(iv) Fast Green (Johansen 1940) 20 minutes
(v) Wash in Ethanol thrice 5 minutes
(vi) Mount in Euparal (Raymond Lamb Lab. London Refractive index = 1.485) and allowed to harden on a warming tray overnight. Photographs of sections were taken on Kodak Technical Pan Film with a Reichert Polyvar Photomicroscope. Chemicals were supplied by BDH Ltd. Poole, U.K. unless otherwise stated.

(4) Leaf anatomy: Leaf surface

Pieces of leaf tissue were mounted on aluminium stubs using double sided adhesive tape. The specimen was earthed to the stub using quick drying silver paint. (Agar Scientific Ltd. Stanstead Essex U.K.). Stubs were coated with gold using an Emscope (Emscope Laboratories Ashford, Kent U.K.). Sputter coater (3-5 minutes, 20 mA 0.08 Torr flushed with argon). Stubs were viewed using Cambridge Stereoscan

250 and 90B Scanning Electron Microscopes (SEM), at an accelerating voltage of 5-10 KV. Electron micrographs were recorded on Ilford FP4 and Kodak Plus-x Pan 120 film. Stubs were stored in a container with silica gel to keep the air dry.

(5) Pollen anatomy

Pollen from dissected flowers was dried down onto aluminium stubs, coated and viewed in the same way as leaf surfaces.

(6) Nutlet anatomy: Mature nutlet surface

Nutlets were mounted onto aluminium stubs using quick drying silver paint to ensure good conductivity. They were coated and viewed as with the leaf surfaces except that the accelerating voltage used was lower, (3-5kV), to prevent charging.

(7) Nutlet anatomy: Developing nutlet surface

The method used was based on Jeffree et al. (1987)

Developing nutlets were mounted on to copper specimen stubs, within one minute of excision, using Tissue Tek 11 O.C.T. compound (Miles Laboratories) as an adhesive. Imbibed nutlets were attached by their radicle only to prevent the nutlet surface becoming covered in Tissue Tek. Specimens were cryo-fixed by plunging into melting nitrogen at -210°C under an atmosphere of dry argon in an Emscope SP 2000 cryo-preparation system. Specimens were covered and transferred under vacuum to the cryo-stage of a Cambridge Stereoscan 250 SEM, fitted with a 'top hat anode', and viewed uncoated. Surface water was etched away by raising the SEM stage temperature to -70°C. Specimens were then transferred back to the work chamber of the SP2000 and sputter coated with gold in an argon atmosphere (2-3 mins., 20 mA, 0.08 Torr). Coated specimens were then transferred back to the cryo-stage of the SEM and examined at an accelerating voltage of 3kV which prevents heating and charging. Electron micrographs were recorded on Kodak Plus-X Pan 120 film.

(8) Nutlet anatomy: Sections

Scutellaria nutlets proved extremely hard to infiltrate. The following technique was developed.

(i) Nutlets were cut in half randomly to allow the fixatives to penetrate fully.

(ii) Fixation

Specimens were placed in 10% buffered acrolein (O'Brien and McCully 1981) for 48 hours, rinsed twice with distilled water, then post-fixed in 1% OSO_4 for 1½ hours (O'Brien and McCully 1981).

(iii) Dehydration

Specimens were washed twice in distilled water, placed on a carousel, and put through a dehydration sequence of acetone: 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 100%, 100%, 100%. Specimens were kept in each solution for at least one hour and in 100% acetone overnight.

(iv) Infiltration

Acetone was first replaced using polypropylene oxide (PPO) using the following sequence of solutions:

Solution	Parts acetone	Parts PPO
1	3	1
2	2	2
3	1	3
4	-	100% PPO

Specimens were left in each solution for one hour. The PPO was then replaced by Spurr's resin (Spurr 1969). The following sequence was used.

Solution	% PPO	% Spurr resin
	90	10
	80	20
	70	30
	60	40
	50	50
	40	60
	30	70
	20	80
	10	90
		100%

Specimens were kept in each solution for 24 hours, on a carousel. They were then kept in 100% resin solution for one week, the resin being changed every one or two days.

(v) Embedding

Specimens were embedded in silicone rubber blocks at 70°C for three days.

(vi) Sectioning

1 μm sections were cut with glass knives on a Reichert OMU 4 ultramicrotome.

(vii) Staining

The sections were dried down onto glass slides and stained with ½% Toluidine blue in 1% Borax ($Na_2 B_4 O_7 10 H_2O$). (Adapted from Richardson et al. 1960). Sections were mounted in Spurr's resin and hardened for three days at 70°C. Photographs of sections were taken with a Reichert Polyvar Photomicroscope.

All chemicals were supplied from Agar Scientific Ltd. Stanstead, Essex, U.K.

D. Methods and materials for cladistic and numerical phenetic classifications

The philosophies used in the construction of intuitive, numerical phenetic and cladistic classifications will be detailed in a separate chapter. However, it is appropriate here to list the materials and methods used to create the dendrogram and consensus tree on which the numerical phenetic and cladistic classifications respectively are based.

The dendrogram

A dendrogram was constructed using the hierarchical cluster analysis methods provided in Genstat, a general statistical programme (Release 4.04 1983, Rothamstead Experimental Station) mounted on an Amdahl V7 mainframe computer.

Firstly a data file for all 109 species was created using the coded characters states listed in chapter 4. Then a similarity matrix was constructed using the general similarity coefficient SG, of Gower (1971) provided in Genstat.

The coefficient is obtained for two individuals i and j by assigning a score $0 \leqslant \text{Sijk} \leqslant 1$ and a weight, Wijk, for character k.

The coefficient is defined as:

$$\text{SG} = \frac{\left(\sum_{K=1}^{n} \text{Wijk Sijk} \right)}{\sum_{K=1}^{n} \text{Wijk}}$$

By designating each character as Type 2 qualitative in the programme (Rothamstead Experimental Station 1983), the weight (Wijk) is set either to 1, when a comparison is considered valid for character k, or to 0 when the value of the state of character k is unknown for one or both operational taxonomic units (OTU). The score (Sijk) is then 1 if character k is of similar state in both OTUS and 0 when character k differs in state between the two taxa.

Using the directive, "Hierarchy", average linkage cluster analysis was carried out with the unweighted pair group method using arithmetic averages, (UPGMA).

The cluster threshold which determines the interval between the levels at which clusters are presented in the dendogram were set to 2.5% and 1% (CM = 4, CT = 2.5 or 1 Rothamstead Experimental Station 1983). The Genstat programme is given in Appendix 3. For 6 species two individuals were used to see how the programme dealt with taxa which differ only in one or two characters.

Equally parsimonious trees and consensus trees

50 equally parsimonious trees were produced using the computerised parsimony programme PAUP (Phylogenetic Analysis Using Parsimony version 2.4) written by D.L. Swofford, (Illinois Hatural History Survey, Champaign, Illinois), and

implemented on a Digital Equipment VAX 850 computer running under the VMS operating system. The data was coded as for the Genstat programme. PAUP was run with the following options specified: Unordered all, Missing = 9, Addseq = Closest, Swap = Global, Mulpars, Maxtree = 50, Root = Lundberg (Swofford 1985). Finally a strict consensus tree was calculated using the programme CONTREE, the version (1/3/86) distributed with PAUP.
See Appendix 2 for PAUP programme.

CHAPTER 4

The Taxonomic Characters

In this chapter all characters of potential taxonomic use are listed and briefly discussed. Characters are dealt with in the following suites:
(A) Leaf and Petiole; (B) Indumentum of the Stem and Inflorescence Axis; (C) Habit; (D) Inflorescence; (E) Floral Characters; (F) Nutlet Characters; (G) Pollen. (H) Embryo Morphology.

Within these suites, specific characters are indicated by Arabic numbers, and character states by Roman numerals. The code used to represent each state in the numerical phenetic and cladistic computer programmes, (see Appendices 2 & 3) is given in parenthesis following the description of each state.

In addition to characters which are useful in classification, characters of little or no use are discussed in so far as it is necessary to show why they are discounted.

A: Leaf and Petiole

It is important to record all observations using a standard part or organ of the plant. For instance, the leaf morphology of S. minor was examined to see if it varied with age. Hair length and distribution, sessile glands and stomata were all found to vary. I chose the leaf arising one or two nodes below the lowest flower or fruiting calyx. Leaf section and leaf surface characters were all observed from this standard leaf.

(A1) Leaf Shape

All leaf shapes observed are illustrated in Fig. 4.1. States of this character are based on the ratio of leaf length and breadth, whether the sides are parallel or not, and on the position of the widest part of the leaf. However, because the leaves usually taper at the tip, there is often a problem in deciding if the sides are parallel or not, e.g. S. colpodea. Further, the position of the widest part of the leaf can vary between the standard leaves of one plant, e.g. S. schugnanica can have both rhomboid and ovate standard leaves on any one plant. Therefore, for the delimitation

Fig. 4.1 LEAF SHAPES

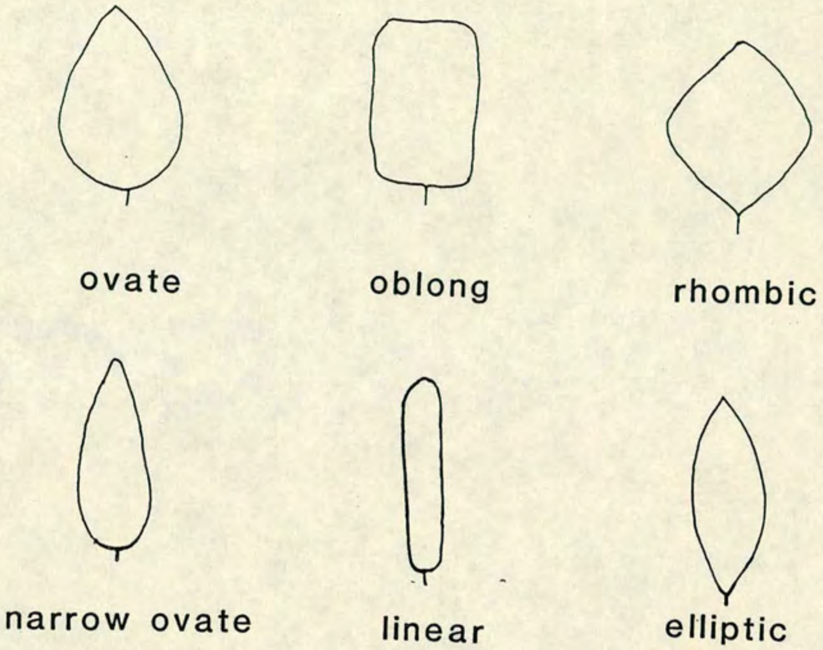
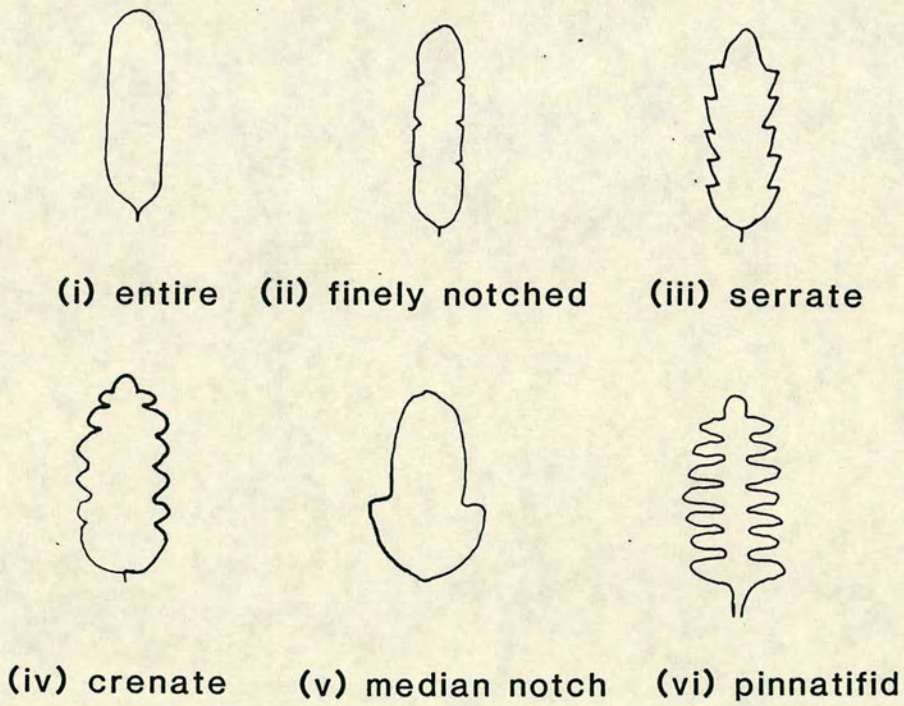


Fig. 4.2 LEAF MARGINS



of taxa, only the following states were used:

(i) Leaf breadth greater than half leaf length (0).

(ii) Leaf breadth less than or greater to half leaf length (3).

Naturally the leaf shape character in general (Fig. 4.1) was useful in description.

(A2) Leaf Margin

All character states shown in Fig. 4.2 were observed.

(i) Entire (0)

(ii) Finely notched (1)

(iii) Serrate (3)

(iv) Crenate (4)

(v) Medium notch (2)

(vi) Pinnatifid (5).

(A3) Leaf Base

Plants with truncate, round, cuneate or cordate leaf bases frequently display more than one sort of leaf base. e.g. S. splendens can have both cuneate and cordate leaf bases, and S. churchilliana can have round, cordate or intermediate leaf bases. Plants with hastate leaf bases do not show this variation. The states recognised here are therefore restricted to:

(i) Leaf bases hastate (3).

(ii) Leaf bases not hastate (0).

(A4) Lower Leaf Type

Some plants, e.g. S. leptosiphon have brown, scale-like lower leaves, which clasp the stem and covered with long white hairs, (Fig. 4.3).

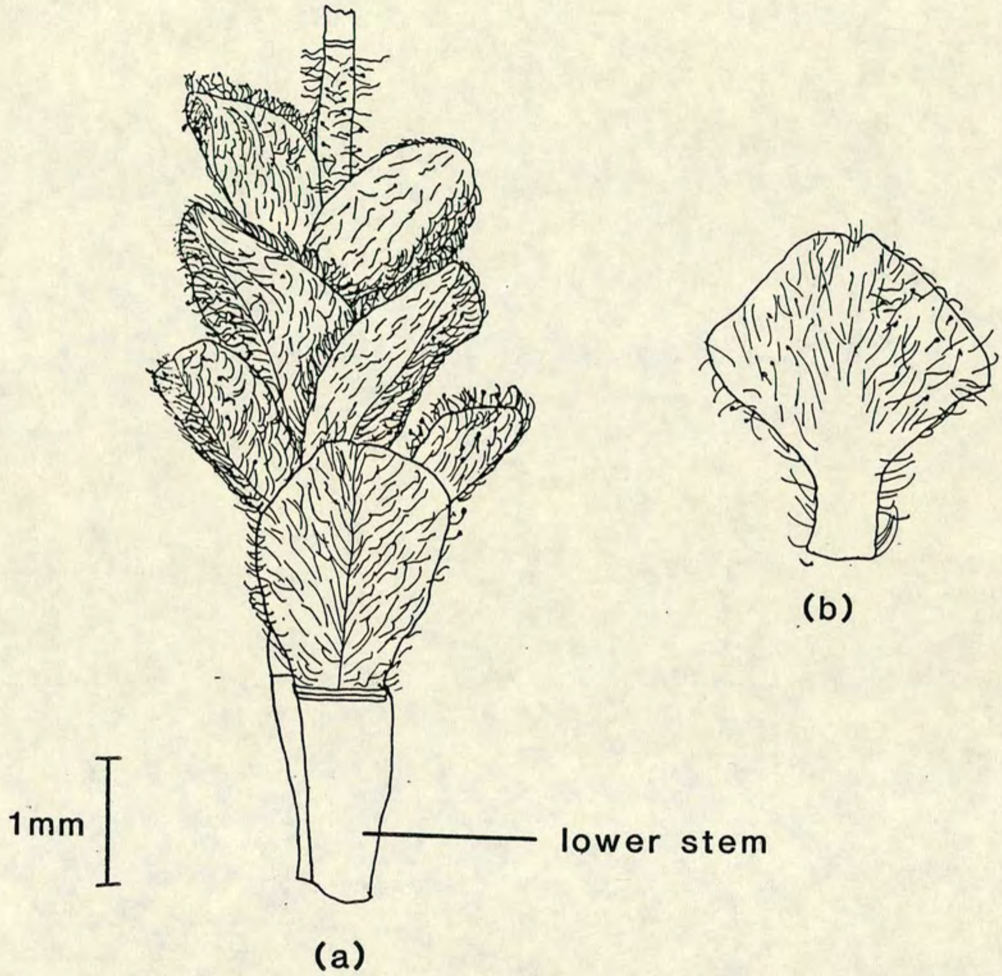
(i) Lower leaves scale-like, different from the upper leaves (0).

(ii) Lower leaves not scale-like, similar to the upper leaves (3).

(A5) Adaxial Cuticle Thickness

The cuticle varies in thickness across the leaf, being thicker above the veins and at the margins. Cuticle thickness was measured between the veins, using an eyepiece graticule in a light-microscope, at 400x magnification. A discontinuity in the variation of thickness was found at 4.34×10^{-3} mm. There was little intraspecific variation using this measurement to delimit states, thick and thin.

Fig. 4.3 SCALE-LIKE LEAVES



(a) Scale-like leaves of S.leptosiphon

(b) Single scale-like leaf

(i) Thick cuticle (Fig. 4.4i) (3).
(ii) Thin cuticle (Fig. 4.4ii)(0).

The following characters, A6-A13, were observed from the leaf surface with the S.E.M. Results were recorded from the areas of the leaf lamina shown in Fig. 4.5.

The middle of the leaf was chosen because this area was usually undamaged in herbarium sheets. The adaxial surface of the main vein was not examined. Characters were often present in different states on the vein and adaxial lamina. There was not time to study both characters. The adaxial lamina was chosen as this area had a more diverse indumentum than the vein.

(A6) Presence of Adaxial Stomata

Some taxa have stomata only on the abaxial surface, *e.g.* S. *balearica*. Others have stomata on both surfaces, *e.g.* *S. bolanderi*.

(i) Adaxial stomata present (3).
(ii) Adaxial stomata absent (0).

(A7) Adaxial Hair Density

(i) Leaf glabrous, 0 hairs in the area examined (0).
(ii) 1-74 hairs in the area examined (2).
(iii) 75 or more hairs in the area examined (4).

(A8) Adaxial Hair Cell Length

The hairs were measured in micrometers using a electron-microscope scale.

(i) Hairs less than or equal to 300 μm (0).
(ii) Hairs longer than 300 μm (3).

(A9) Adaxial Hair Cell Number

If there were no adaxial hairs, cell number was based on abaxial hairs.

(i) Most hairs 1-3 celled (0).
(ii) Most hairs 3 or more celled (3).

(A10) Branched Hairs

Plants with branched hairs on the leaves also have them on the stem, *e.g.* *S. flocculosa*. These plants ~~now~~ never

Fig. 4.4 Cuticle thickness

(i) Thick cuticle of *S. nana* Mag. x 90.

(ii) Thin cuticle of *S. zaprjagaevii* Mag. x 90.

Fig. 4.5 Leaf area studied with S.E.M.

(a) Abaxial surface.

(b) Adaxial surface.

The area studied is represented by □
This measures 1.2 x 1mm in both cases.

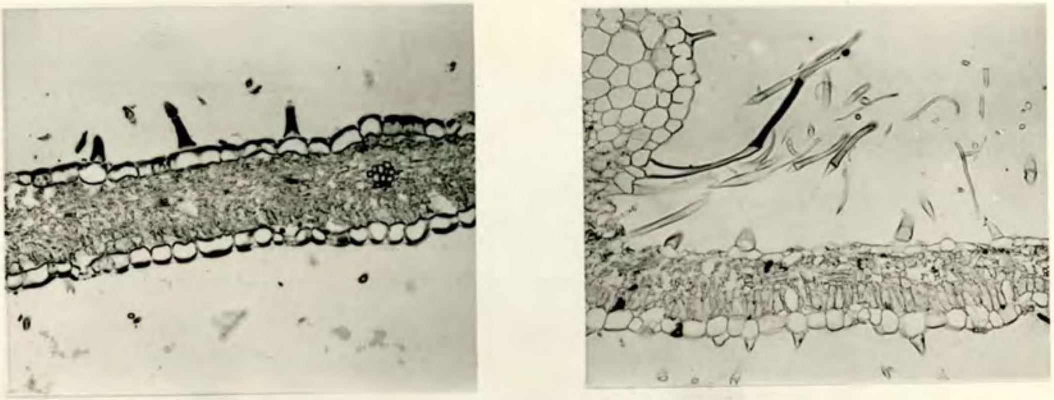


Fig. 4.4 CUTICLE THICKNESS

(i) Thick

(ii) Thin

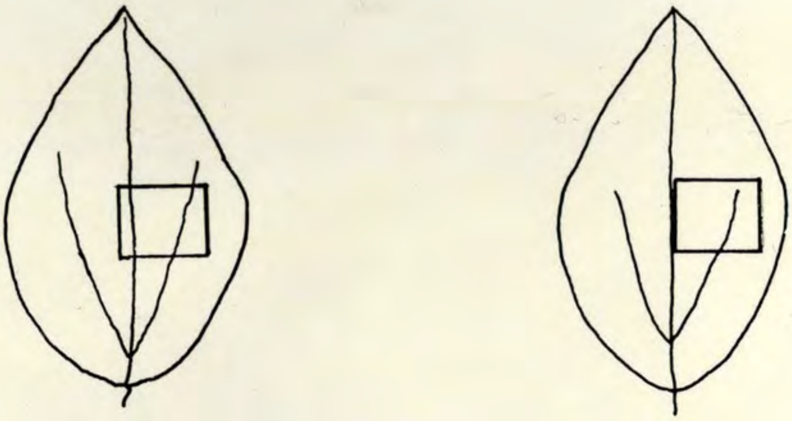


Fig. 4.5 AREA STUDIED WITH SEM

(a) abaxial surface

(b) adaxial surface

have unbranched hairs on the leaf and stem, so there are clear presence and absence states. These dendroid hairs are the only type of branched hairs seen in the genus.

(i) Branched hairs present on leaf (Fig. 4.6) (3).

(ii) Branched hairs absent on leaf (0).

(A11) Abaxial Hair Distribution

(i) Hairs all over the abaxial surface (0).

(ii) Hairs only on the veins of the abaxial surface (3).

(iii) Abaxial surface glabrous (5).

(A12) Sessile Glands on the Adaxial Surface

The size of these glands varies continuously between taxa, Fig. 4.7a and 4.7b.

(i) Adaxial sessile glands absent (0).

(ii) Adaxial sessile glands present (3).

(A13) Sessile Glands on the Abaxial Surface

Very few species lack these glands, e.g. *S. indica*.

(i) Abaxial sessile glands present (0).

(ii) Abaxial sessile glands absent (3).

The following characters, A14-A19, describe and discuss features of leaf anatomy which cannot, I believe, be used to delimit taxa, for the reasons given.

(A14) Leaf Petiole Length

This was measured in millimetres. The characters varied continuously between taxa and I was unable to divide it up into discrete states. However it is still a useful descriptive character in some taxa.

(A15) Leaf Epidermis Relief

There are two extreme forms of this character: smooth and rugose. (see Fig. 4.8). However many intermediates occur which make it difficult to divide this character into states. Also, if the epidermis is thin, it can be difficult to see clearly and determine the character state. The epidermis can also vary from being smooth to rugose across the width of the individual leaf.

Fig. 4.6 BRANCHED HAIRS

Branched hairs of S.flocculosa

Mag.X750

Fig. 4.7 Adaxial sessile glands.

(a) Adaxial leaf surface of S. resinosa Mag. x 50 showing smallish sessile glands.

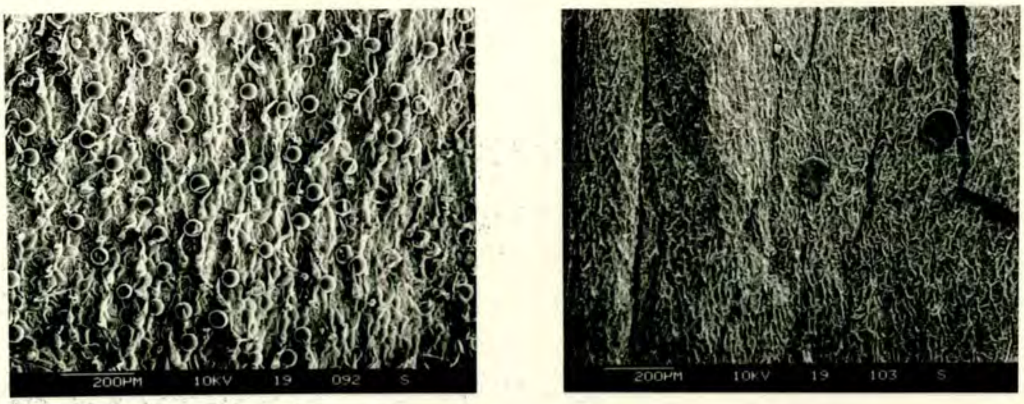
(b) Adaxial leaf surface of S. barbata Mag. x 50 showing longer sessile glands.

Fig. 4.8 Leaf epidermis relief.

(a) Rugose leaf epidermis Mag. x 500.

(b) Smooth leaf epidermis Mag. x 500

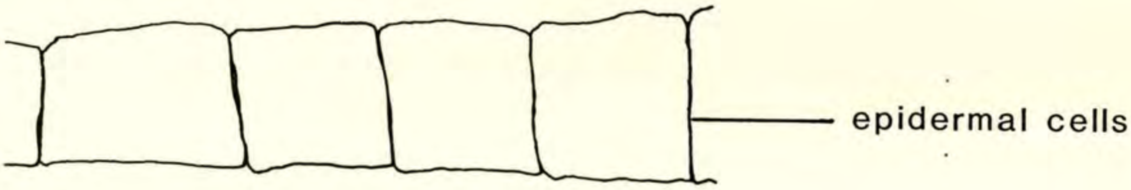
Fig. 4.7 ADAXIAL SESSILE GLANDS



(a) (b)

Fig.4.8 LEAF EPIDERMIS RELIEF

(a) rugose



(b) smooth

(A16) Thickness of the Epidermis

The thickness of the epidermis varies across the width of the leaf so the character could not be delimited into states. Also, because this variation in inconsistent, no standard position for recording the character could be found.

(A17) Abaxial Hair Density

Hairs are more densely crowded on the veins than on the rest of the lamina. As a percentage of the standard leaf area taken up by vein tissue varies from leaf to leaf, no standard area could be found from which meaningful comparisons between taxa could be made.

(A18) Abaxial Hair Length

The abaxial hairs on the veins are usually longer than those on the rest of the lamina. The character was not used because of this inconsistent variation in length.

(A19) Capitate Leaf Hairs

The area investigated with the S.E.M. is very small. The number of capitate hairs on the leaf also tends to be small. The recording of this character was hence prone to sampling error and thus did not give repeatable, accurate results. This character could have been investigated by hand lens but unfortunately there was not enough time to do this.

B: Indumentum Characters of the Stem and Inflorescence Axis

Stem indumentum characters were observed on the first or second internode below the lowest flower. The inflorescence axis indumentum characters were observed on the internode above the lowest flower at anthesis. Lower flowers were not consistently available.

(B1) Stem Indumentum: Hair Length

(i) Most hairs less than 0.5mm long (0).
(ii) Most hairs at least 0.5mm long (3).

(B2) Stem Indumentum: Hair Orientation

(i) Hairs patent (0).
(ii) Hairs retrorse (4).
(iii) Hairs antrorse (2).

(B3) Stem Indumentum: Capitate Glandular Hairs

(i) Capitate glands present (3).
(ii) Capitate glands absent (0).

Capitate glands are always patent in orientation. If a stem bears capitate glands the hair orientation characters, (B2), refers to any eglandular hairs present.

(B4) Stem Indumentum: Hair Distribution

(i) Hairs on angles only (2).
(ii) Hairs all over (0).
(iii) Glabrous (4).

The indumentum of the inflorescence axis is often the same as the indumentum of the stem. However, in a few cases they are different. Therefore the two character suites are considered separately.

(B5) Inflorescence Axis Indumentum: Hair Length

The hairs of the stem indumentum of, for instance, *S. pontica*, are less than 0.5mm long, whereas the hairs of the inflorescence axis indumentum are mostly 1mm long. Hence this is a different character from (B1) - the two are not correlated.

(i) Hairs less then 0.5mm long (0).
(ii) Hairs longer than or equal to 0.5mm long (3).

(B6) Inflorescence Axis Indumentum: Hair Orientation

On some species, *e.g.* *S. ventenatii*, the stem hairs are retrorse whereas the hairs of the indumentum axis are patent.

(i) Hairs patent (0).
(ii) Hair retrorse (4).
(iii) Hairs antrorse (2).

(B7) Inflorescence Axis Indumentum: Hair Distribution

This character is deemed to be independent from (B4), because some species, *e.g.* *S. polyadena* have hairs only on the stem angles but all over the inflorescence axis.

(i) Hairs on angles only.(2).

(ii) Hairs all over axis.(0).

(iii) Glabrous.(4).

(B8) Inflorescence Axis Indumentum: Capitate Glandular Hairs

In several species, e.g. S. violascens, there are multicellular glandular hairs on the inflorescence axis, but these are absent on the rest of the stem. Hence this is a different character from.(B3).

(i) Capitate glands present.(3).

(ii) Capitate glands absent. (0).

C: Habit Characters

(C1) General Facies:

(i) Erect herb; one or two stems emerging from the ground, e.g. S. altissima.(0).

(ii) Prostrate herb, mat forming, e.g. S. balearica.(1).

(iii) Erect suffruticose herb; several slender woody stems emerging from the ground, e.g. S. multicaulis . (2).

(iv) Prostrate, woody or suffruticose plant; mat or cushion forming, e.g. S. leptosiphon. (3).

(v) Shrub; scrambling or erect, greater than 1 m tall, e.g. S. gardoquioides. (5).

(C2) Life Duration

Most species are perennial, though some annuals are known, e.g. S. guilielmi.. From herbarium specimens it is often hard to decide if a plant is annual or a short-lived perennial, e.g. S. drummondii. If such plants had rhizomes they were recorded as perennials. If not they were recorded as annual.

(i) Plant annual;perennating organs never present. (3).

(ii) Plant perennial;perennating organs usually present. (0).

(C3) Rhizome Tubers

In a few species there is a rhizome which terminates in a small tuber, e.g. S. tuberosa.

(i) Tuber present.(3).

(ii) Tuber absent. (0).

(C4) Rhizome Form

(i) Rhizome slender moniliform, creeping, not woody, e.g. S. galericulata. (0).

(ii) Rhizome short, woody, more or less vertical. May form a small caudex. e.g. S. albida. (3).

(iii) Rhizome large, woody, creeping or not, e.g. S. multicaules. (5).

D: Inflorescence Characters

(D1) Floral Arrangement

(i) Flowers with opposite insertion. (0)

(ii) Flowers not opposite but spirally inserted. (3).

(D2) Floral Orientation

(i) Inflorescence with secund flowers, all flowers point the same way, e.g. S. altissima. (Fig. 4.9a) (0).

(ii) Inflorescence four-sided; flowers opposite and decussate, e.g. S. alpina. (Fig. 4.9b). (4).

(iii) Inflorescence spiral; flowers radiating out in all directions, e.g. S. costaricana (Fig. 4.9c). (2).

(D3) Bract Form

Flowers can be subtended by: leaves similar in size and margin to cauline leaves, e.g. S. galericulata; by leaf-like bracts much smaller than cauline leaves; or by cucullate bracts which are roughly the same size as cauline leaves or not. Strictly speaking all these structures are bracts, i.e. leaf homologues which subtend a flower. In several taxa, e.g. S. barbata, S. altissima, flowers are subtended by leaves and small leaf-like bracts in the same inflorescence, but generally there is a discontinuity between these states. Hamilton (1832), Bentham (1834), Juzepczuk (1954) and Wu & Li (1977) all use these states to separate Sect. Galericularia and Sect. Stachymacris.

(i) Flowers in the axils of leaves; there is a graduation in size between these leaves and the cauline leaves. (0)

(ii) Flowers mostly in axils of leaf-like bracts which are less than one third the length and breadth of the

Fig. 4.9a.

Inflorescence of *S. altissima* composed of secund flowers in a one-sided inflorescence. Flowers in the axils of leaf-like bracts. Mag. x $\frac{1}{3}$.

Fig. 4.9b.

Inflorescence of *S. alpina*. Flowers opposite and decussate in a four-sided inflorescence, subtended by cucullate bracts. Mag. x $1\frac{1}{2}$.

Fig. 4.9 (a) inflorescence of S.altissima

(b) inflorescence of S.alpina

Fig. 4.9(cont) (c) infloresence of S.costaricana

Flowers inserted spirally, radiating out in all directions from the inflorescence axis.

Mag. X 0.75

standard leaf. There is no gradation in size between the cauline leaves and leaf-like bracts. (Fig. 4.9a).(3).

(iii) Flowers in the axils of cucullate bracts. (Fig. 4.9b) (5).

(D4) Inflorescence Axillary/Terminal

(i) The majority of flowers are carried on short, unbranched, axillary branches where axis is roughly half the thickness of the main stem, e.g. S. repens. (3).

(ii) The majority of flowers are carried on the tip of the branches whose axis is roughly the same width as the main stem, and/or the flowers are borne on the tip of the main stem itself. (0).

(D5) Pedicel Scales

These structures, shown in Fig. 4.10, may be bracteoles but their homology has not been investigated.

(i) Scales present. (0).

(ii) Scales absent. (3).

The following inflorescence characters, D6-D9, could not be used for the delimitation of taxa for the reasons cited.

(D6) Pedicel Length

This character is hard to divide up into states as it varies continuously, but it may still be informative in some taxa.

(D7) Number of Flowers per Flowering Stem

This varied between different flowering stems of one plant.

(D8) Inflorescence Condensed or Lax

Though extremes are detectable, I could not find an objective way of classifying inflorescence as condensed or lax. It cannot be done by measuring the amount of overlap between bracts on adjacent nodes as this varies according to the age of the inflorescence. Taxonomic variation is thereby compounded with developmental variation.

Fig. 4.10 PEDICEL SCALES

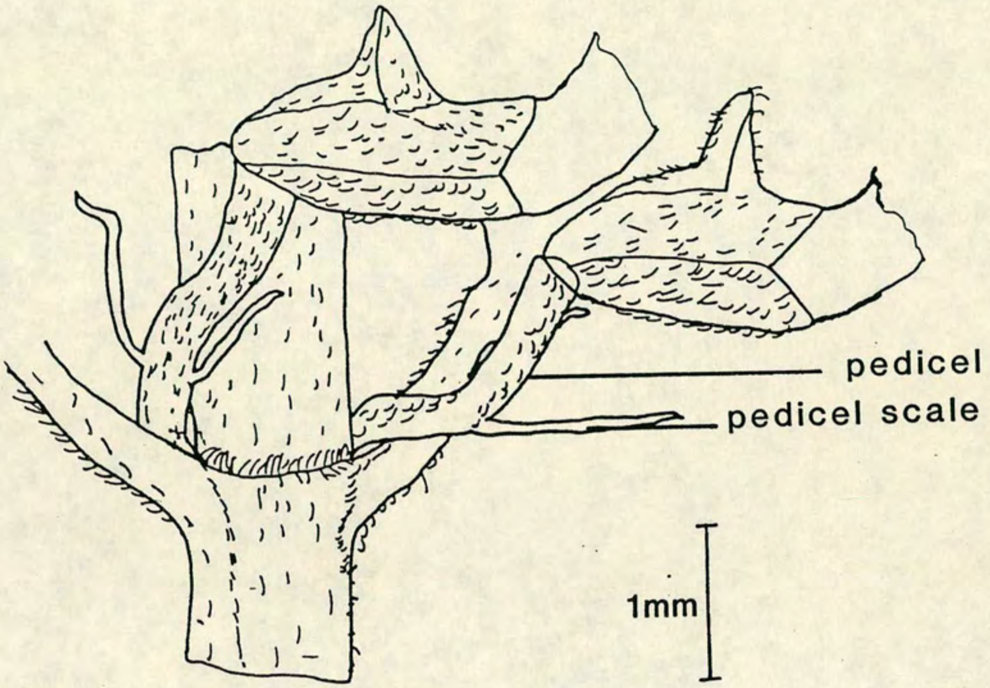


Fig. 4.10. Pedicel scales

The pedicel scales of S. galericulata.

(D9) Pedicel Form

Some plants, *e.g.* *S. linearis* have a strongly flattened pedicel. However this character could not be used as the range of pedicel forms could not be divided into discrete states. The variation is continuous.

E: Floral Characters

(E1) Configuration of the Calyx

(i) Calyx with scutellum: the upper lip of the calyx is folded midway along its length to form a small, rigid erect structure, known as a scutellum. The scutellum is thus sail-like. The scutellum enlarges in fruit but is not membranous - inflated and is less than 7mm high and wide. The sides of the fold forming the scutellum may be tightly pressed together or not. *e.g.* *S. albida* Fig. 4.11. (0).

(ii) Calyx with expanded scutellum: Calyx has a small scutellum at anthesis which becomes membranous-inflated and greater than 7mm high and wide in fruit. *e.g.* *S. heydei*. (Fig. 4.12). (1).

(iii) Calyx long, with testudinate upper lip: upper lip of calyx lacks a scutellum, though there may be a slight ridge midway along anthesis; becomes testudinate in fruit; calyx 4-6mm long. *e.g.* *S. ariana*, (Fig. 4.13) (2).

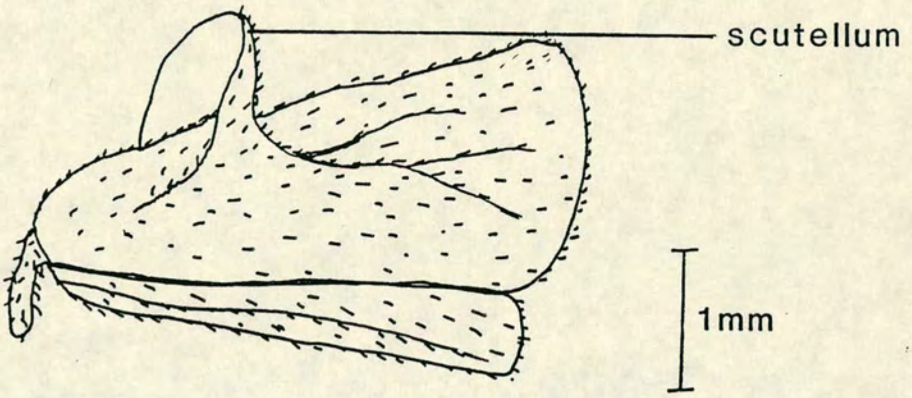
(iv) Calyx short, with testudinate upper lip: upper lip of calyx lacks a scutellum though there may be a slight ridge midway along at anthesis; becomes testudinate in fruit; calyx ± 3mm long. *e.g.* *S. zaprjagaevii*. (Fig. 4.14). (3).

(v) Calyx bladder-like: there is no scutellum though there may be a slight ridge on the upper lip of the calyx at anthesis; clearly inflated and papery in fruit, forming a bladder 1-1.5cm in diameter, *e.g.* *Salazaria mexicana* (Fig. 4.15). (4).

The following characters, E2-E19, were observed from flowers at anthesis.

Fig. 4.11 CALYX OF S.ALBIDA

(a) calyx at anthesis



(b) inflorescence with fruiting calyces

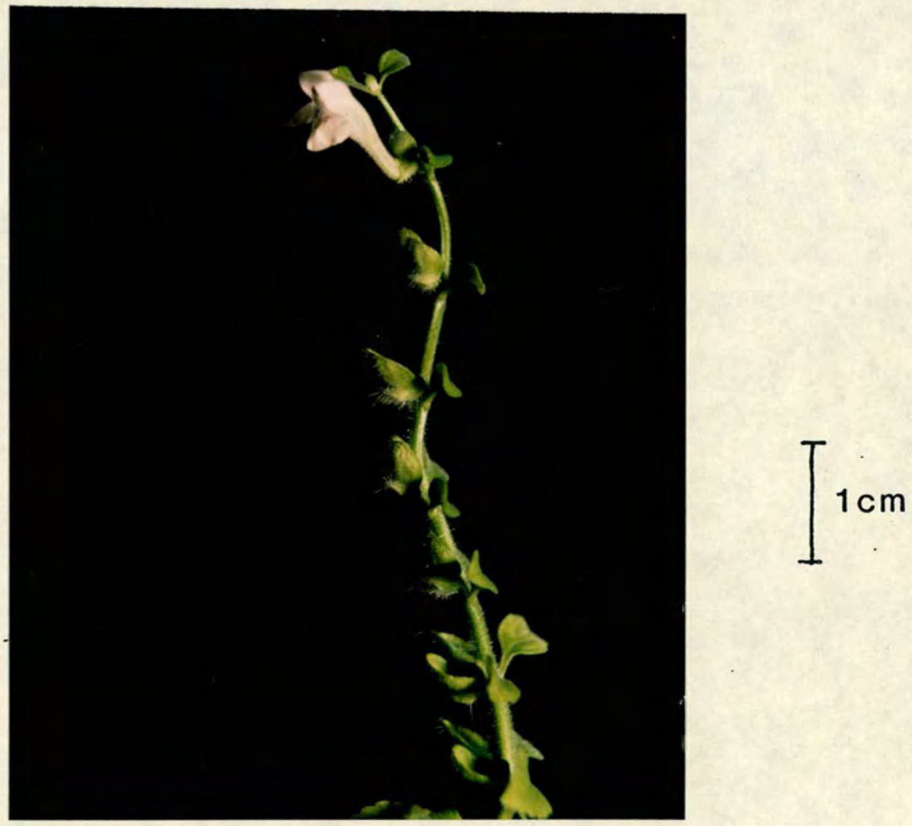


Fig. 4.12 Membranous expanded calyx of S.heydei

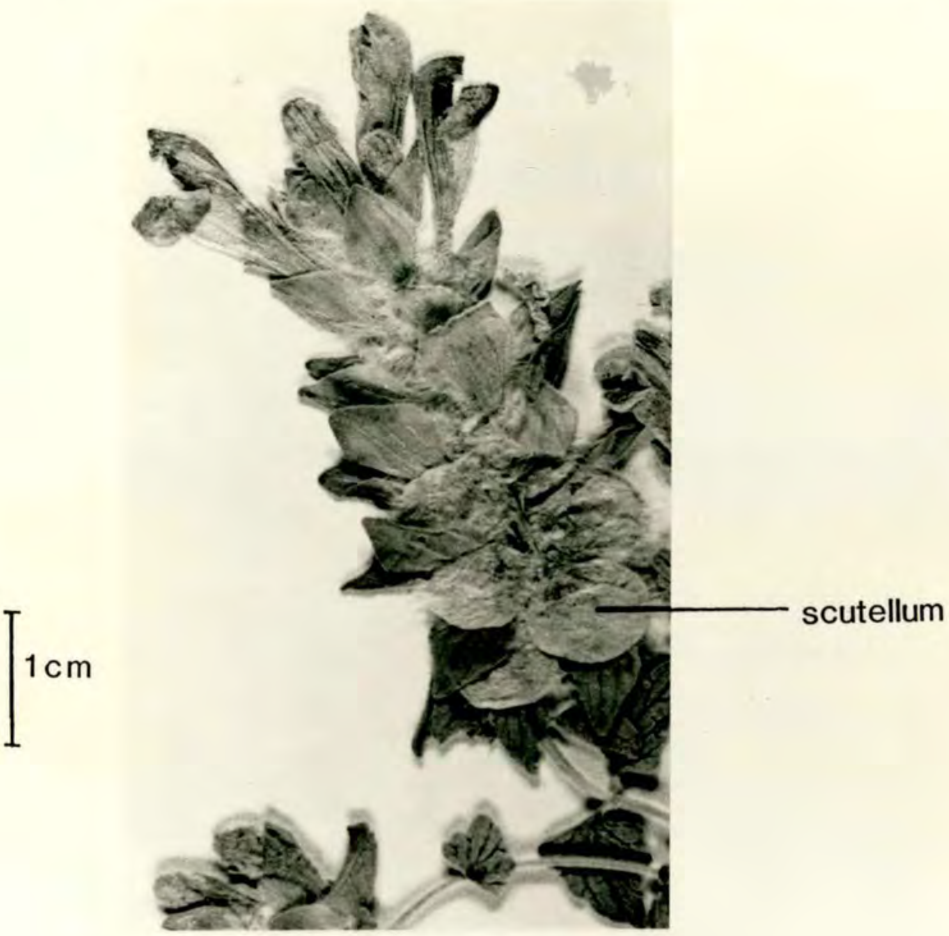


Fig.4.13 Testudinate calyx of S.ariana

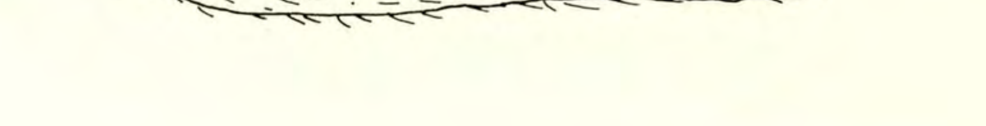


Fig. 4.14 CALYX OF S.ZAPRJAGAEVII

(a)calyx at anthesis

(b) mature calyx

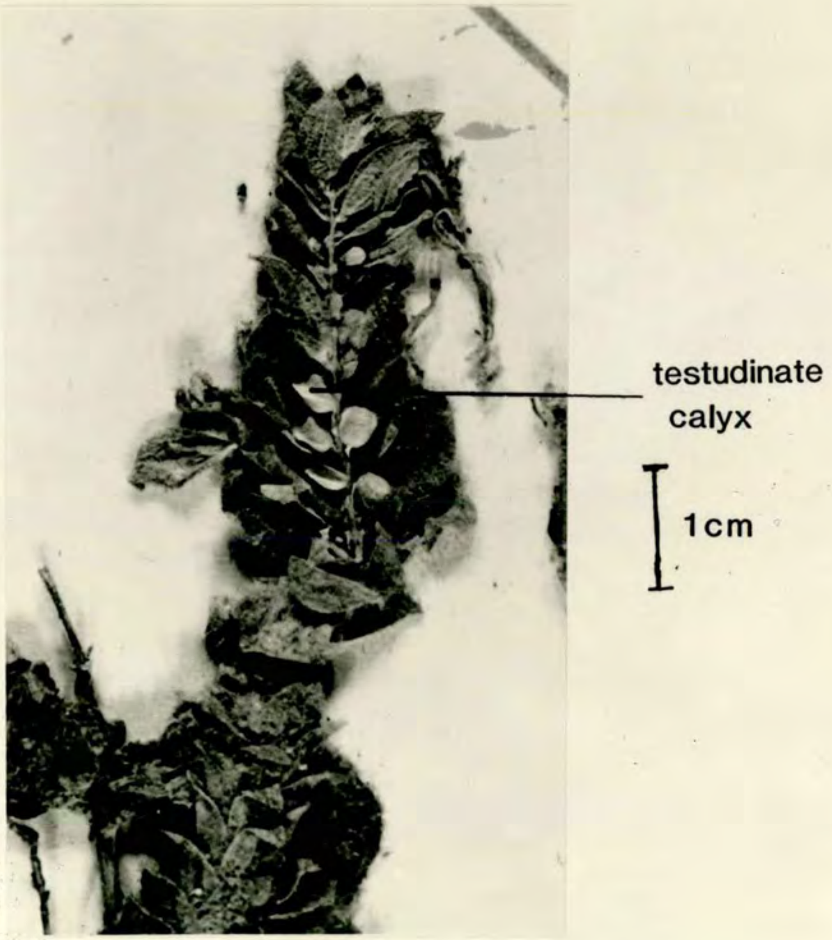
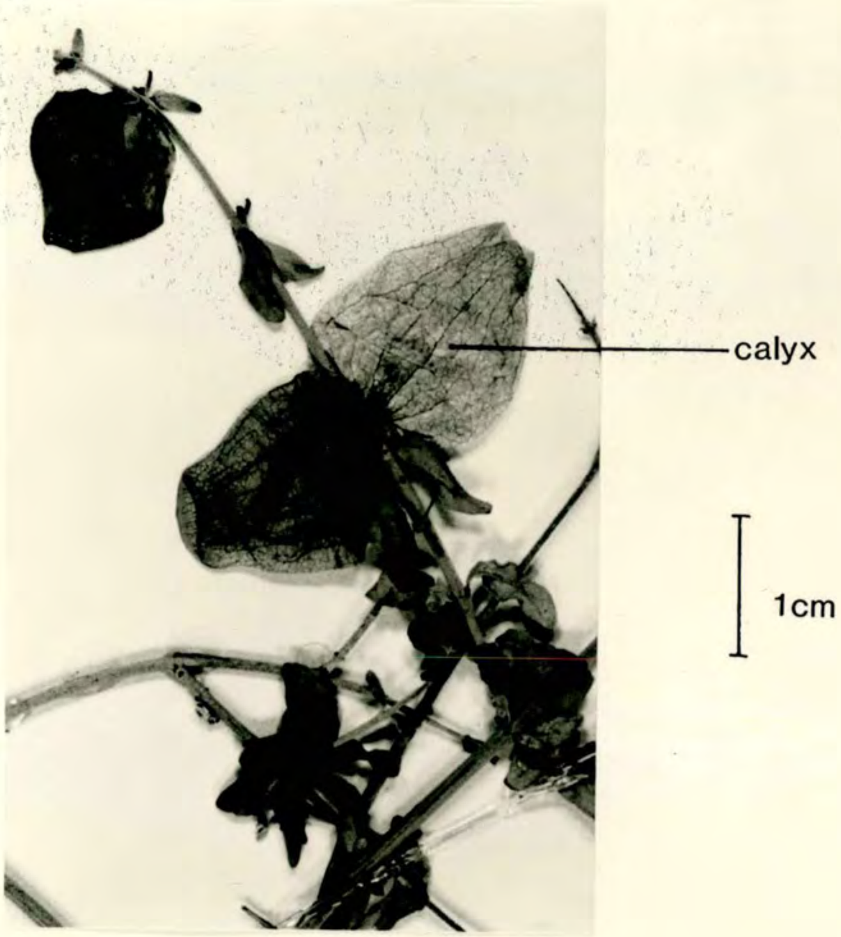


Fig. 4.15 CALYX OF SALAZARIA MEXICANA



(E2) Calyx Indumentum: Hair Length

(i) Most hairs less than 0.5mm long. (0).

(ii) Most hairs more than 0.5mm long. (3).

(iii) Most hairs on lower lip less than 0.5mm, most hairs on upper lip more than 0.5mm. (5). *e.g.* *S. heydei*.

(E3) Calyx Indumentum: Hair Distribution

(i) Hairs all over calyx. (0).

(ii) Hair only on vein, margin and scutellum of calyx. (3).

(E4) Calyx Indumentum: Hair Type

(i) Calyx hairs patent. (3).

(ii) Calyx hairs adpressed. (0).

(E5) Calyx Indumentum: Capitate Glands

(i) Capitate glands present. (3).

(ii) Capitate glands absent. (0).

The capitate glands of the calyx are always patent. Thus the hair type character, (E4) refers to the eglandular hairs of the indumentum.

(E6) Corolla Colour

Because there is difficulty in accurately classifying colours and in determining colour from herbarium specimens, general terms are used to describe the predominant corolla colour. Collectors' field notes on colour are generally inprecise and different collectors are likely to use different terms for the same colour.

(i) Blue. (0).

(ii) White. (1).

(iii) Pink. (2).

(iv) Yellow. (3).

(v) Scarlet. (4).

The following two characters, E8-E9, define the shape of the corolla. The term 'sigmoid' has previously been frequently used, *e.g.* Edmondson (1982). However, this term lacks the precision to describe the total global variation in corolla tube form.

(E7) Angle at the Base of the Corolla Tube

See Fig. 4.16.

(i) Angle less than or equal to 45°. (0).

(ii) Angle greater then 45°. (3).

Fig. 4.16. Corolla Form.

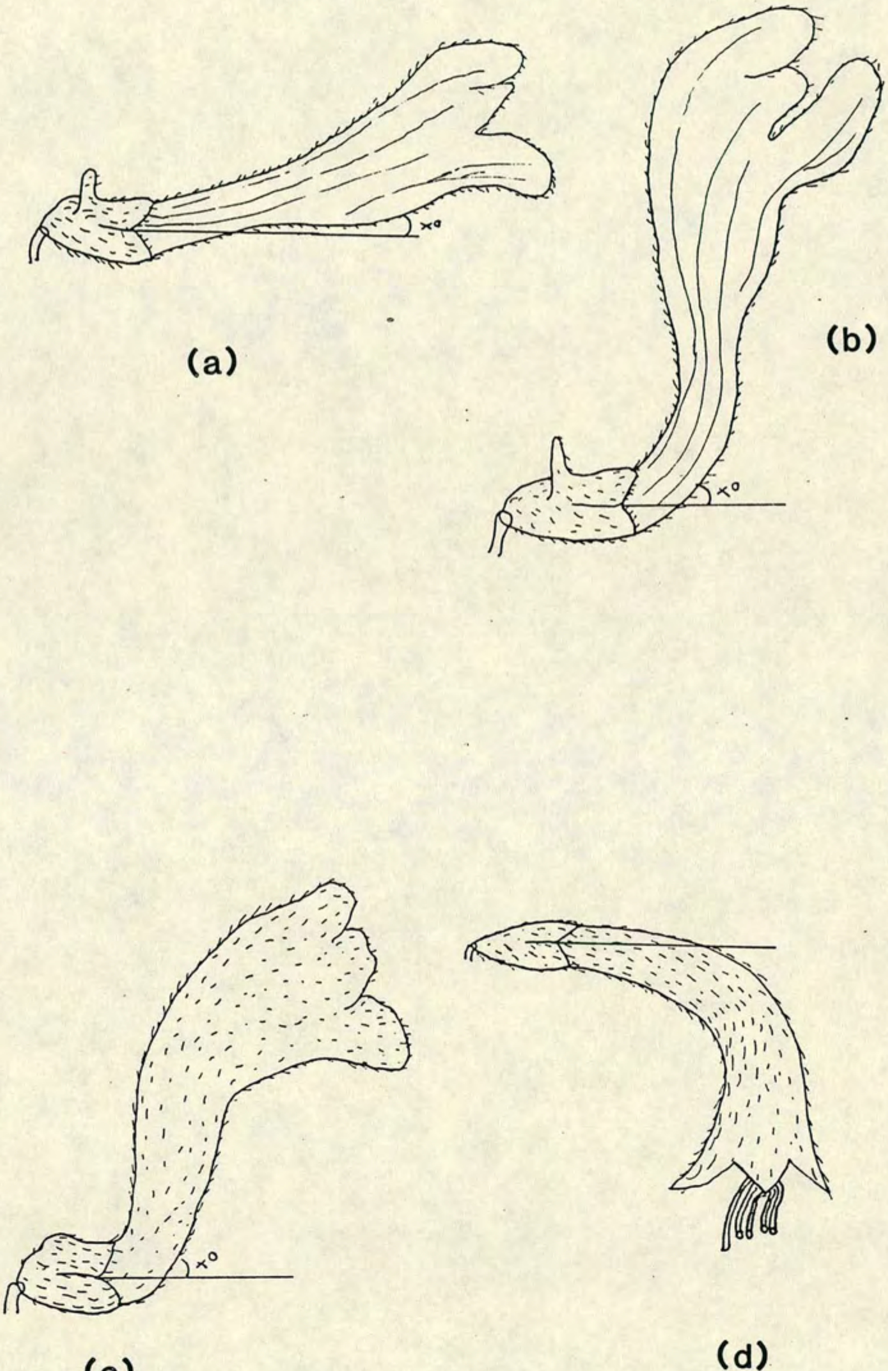
(a) Flower of S. minor Mag. x 7. Angle at the base of the corolla, x^{o}, is less than 45^{o}. Corolla tube is straight distally. Lower corolla lobe is larger than the other lobes. Upper lip forms a galea.

(b) Flower of S. altissima Mag. x 5. Angle at the base of the corolla, x^{o}, is greater than 45^{o}. Corolla tube is straight distally. Lower corolla lobe is larger than the other lobes. Upper lip forms a galea.

(c) Flower of S. ocymoides Mag. x 6. Angle at the base of the corolla, x^{o}, is greater than 45^{o}. Tube is bent distally. Corolla lobes are equal in size and shape.

(d) Flower of Harlanlewisia sarmentosa Mag. x 1½. Angle at the base of the corolla less than 45^{o}. Tube bent distally. Corolla lobes equal in size and shape. Anthers exserted.

Fig. 4.16 COROLLA FORM



(E8) Curved Corolla Tube   See Fig. 4.16.

(i) Corolla tube bent distally. (3).

(ii) Corolla tube straight distally, not bent. (0).

(E9) Conformation of Corolla Lobes   See Fig. 4.16

(i) The upper, lateral and lower corolla lobes are all roughly equal in size. Upper lobe does not form galea. (3).

(ii) The lower corolla lobe is much larger than other lobes. Upper lobe forms galea. (0).

(E10) Indumentum on the Lower Corolla Lobe

(i) Hairs absent or few. (0).

(ii) Lower lobe clearly hairy, e.g. S. nummulariifolia. (3).

(E11) Internal Indumentum of the Corolla Tube

(i) Inner surface of corolla tube with hairs all over, e.g. S. costaricana. (1).

(ii) Inner surface of corolla tube with a broad annulate band of hairs at base, e.g. S. discolor. (Fig. 4.17b). (4).

(iii) Inner surface of corolla tube with a narrow, slightly raised, hairy annulus at base, e.g. S. bushii. (Fig. 4.17a). (3).

(iv) Inner surface of corolla tube with hairs only at the base of the anterior stamens where they become adnate to the corolla, e.g. S. volubilis (Fig. 4.17c). (5).

(v) Inner surface of the corolla tube glabrous, e.g. S. galericulata. (0).

(E12) Teeth or Folds present at the Base of the Corolla Tube.

(i) Teeth or folds present, e.g. S. gardoquioides. (Fig. 4.17c). (3).

(ii) Teeth or folds absent (0).

The next two characters, E13-E14, describe the relationship of staminal filaments to the corolla tube. Epling (1942) measured the length that the filament was adnate to the corolla. I found this absolute length to vary inconsistently within species and to be difficult to divide into discrete states.

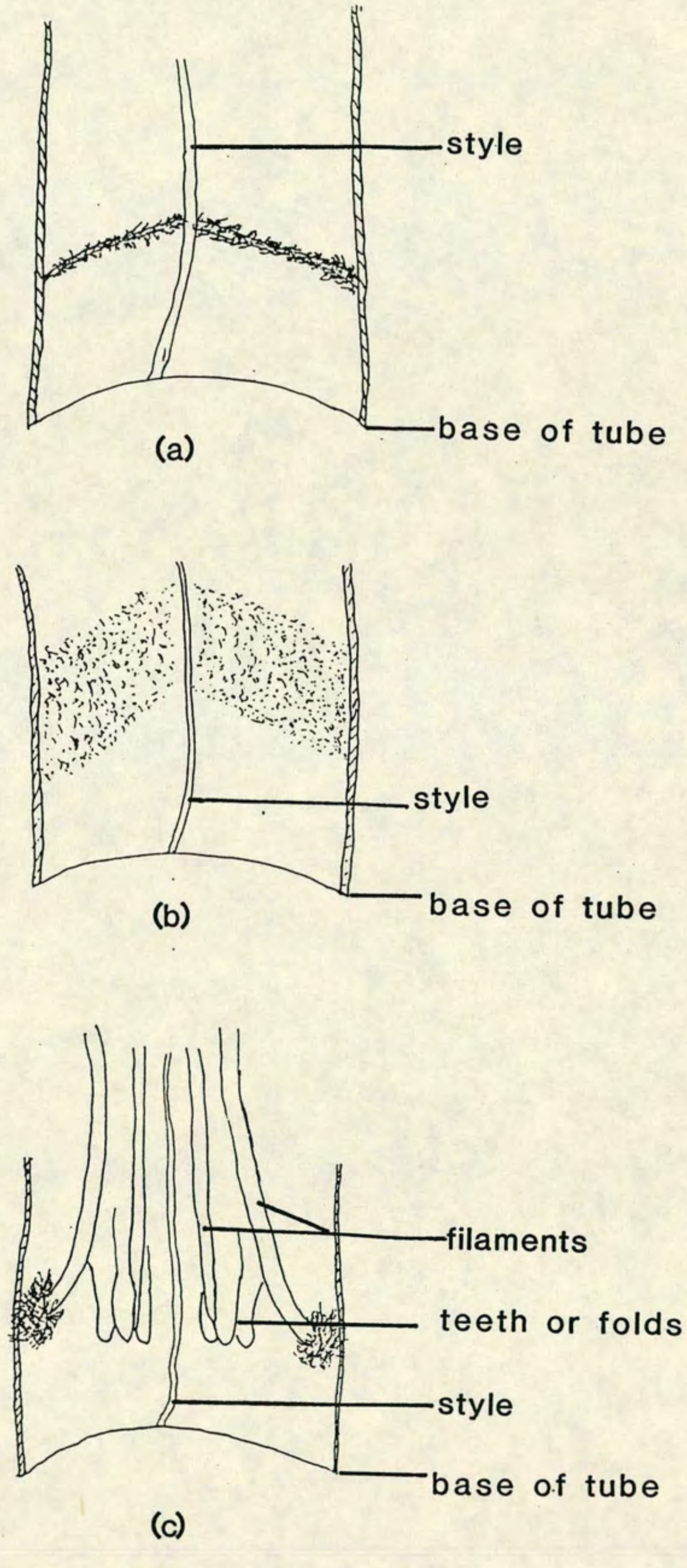
Fig. 4.17. <u>Interior of the Corolla Tube</u>.

(a) Corolla tube with a narrow, slightly raised hairy annulus at the base.

(b) Corolla tube with a broad annulate band of hairs at the base.

(c) Corolla tube with hairs only at the base of the anterior stamens where they become adnate to the corolla, and with teeth or folds.

Fig. 4.17 INTERIOR OF THE COROLLA TUBE



(E13) Point of Insertion of Anterior Stamen

(i) Stamen adnate to corolla for more than half the length of the stamen. (3).

(ii) Stamen adnate to corolla for less than half the length of the stamen. (0).

(E14) Point of Insertion of Posterior Stamen

(i) Stamen adnate to corolla for more than half the length of the stamen. (0).

(ii) Stamen adnate to corolla for less than half the length of the stamen. (3).

(E15) Position of Anthers Related to the Corolla Lobes

(i) Anthers exserted. (Fig. 4.16d). (2).

(ii) Anthers within the upper lobe of corolla (Fig. 4.18a). (0).

(iii) All anthers within the corolla tube, below the free corolla lobes. (Fig. 4.18b). (4).

The following characters, E16-E19, describe features of floral morphology which, although important diagnostically, could not be used for the delimitation of taxa for the reasons cited.

(E16) Corolla length

This character varied continuously and could not be expressed in distinct states. However it can still be a useful character at species level.

(E17) Form of Gynophore See Fig. 4.19

There is considerable variation in the structure of the gynophore, however the variation is continuous and the character is difficult to observe from herbarium specimens Therefore, I could not distinguish any discrete states.

(E18) Colour of Gynophore

The gynophore may be brightly coloured, e.g. in S. minor it is scarlet; however in dried specimens the colour is lost.

Fig. 4.18. Position of Anthers

(a) Dissection of the flower of S. altissima showing anthers within the upper lobe of the corolla. Mag. x 5.

(b) Dissection of the flower of S. scutellarioides showing anthers within the corolla tube. Mag. x 5.

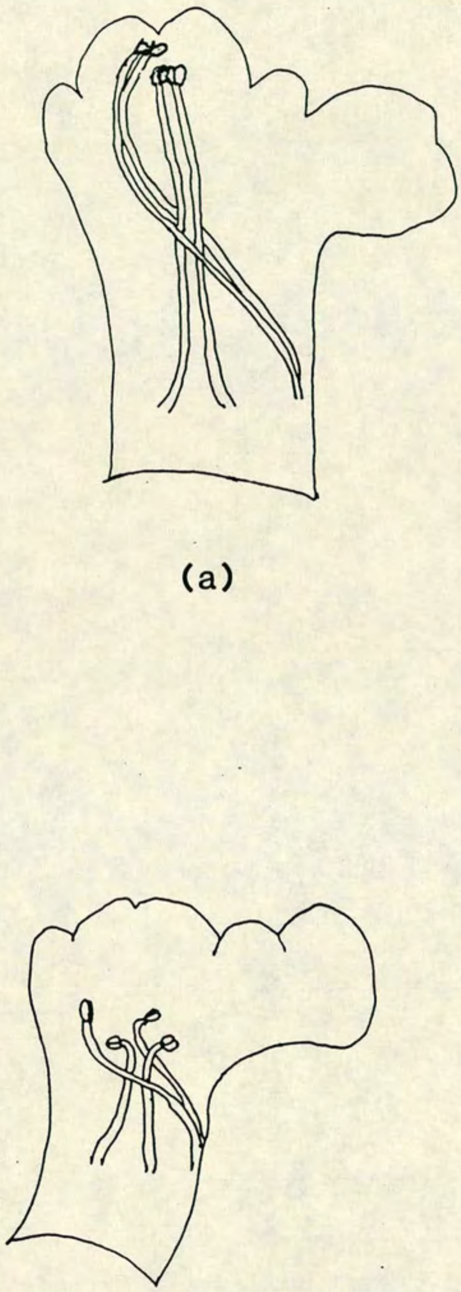


Fig. 4.18 POSITION OF ANTHERS

(a)

(b)

Fig. 19. Form of Gynophore

(a) Gynophore of S. alpina.

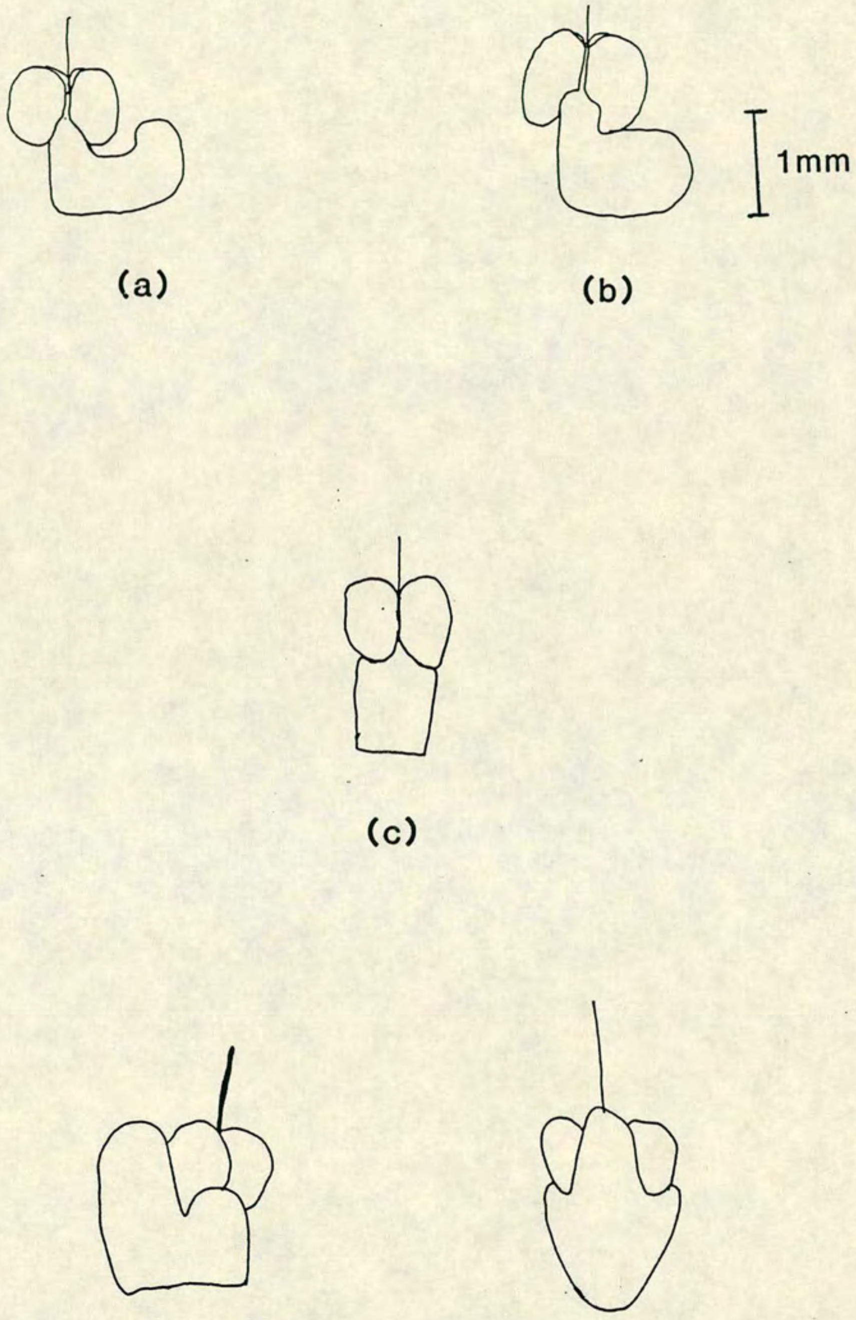
(b) Gynophore of S. galericulata.

(c) Gynophore of S. caerulea.

(d) Gynophore of S. scutellarioides (side view).

(e) Gynophore of S. scutellarioides (back view).

Fig. 4.19 FORM OF GYNOPHORE



(a)

(b)

(c)

(d)

(e)

(E19) Bosses on Corolla Lobes

The lateral and lower corolla lobes of some species, *e.g.* *S. californica*, have bosses on them indicating that the throat of the corolla is closed like that of an *Antirrhinum*, but this character was hard to observe from dried specimens and thus was not used.

F: Nutlet Characters

(F1) Nutlet Colour

There is considerable variation in nutlet colour from black, grey, brown, orange-brown to yellow. However, as in the case of corolla colour, character E6, this character is difficult to communicate accurately so general terms were used.

(i) Brown. (0).
(ii) Orange-brown. (1).
(iii) Yellow. (2).
(iv) Black. (3).
(v) Grey. (4).

The following characters, F2-F11, were observed with the S.E.M.

(F2) Nutlet Size

See Fig. 4.20.

(i) Axial length of nutlet not more than 1mm. (0).
(ii) Axial length of nutlet more than 1mm. (3).

(F3) Nutlet Bands

See Fig. 4.21.

(i) No nutlet band present. (0).
(ii) Nutlet band positioned midway radially. (3).
(iii) Nutlet band positioned basally with respect to the radial dimension. (5).

(F4) Nutlet Ornamentation

(i) Nutlet smooth with no projections (Fig. 4.22a). (0).
(ii) Nutlet covered with papillae. (3).
(iii) Nutlet covered with ridges. (Fig. 4.22b). (5).

(F5) Form of Nutlet Papillae

(i) Subpapillate. (Fig. 23b) (0).
(ii) Dactyloid. (Fig. 4.21a). (2).
(iii) Flattened dactyloid. (Fig. 4.21b) (1).
(iv) Hair-like. (Fig. 4.23a). (3).

Fig. 4.20 NUTLET DIMENSIONS

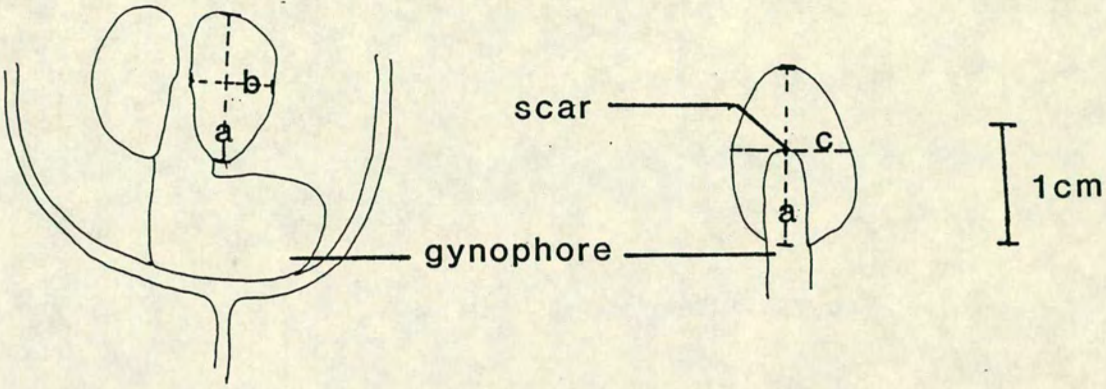


Fig. 4.20. Nutlet Dimensions

a = axial dimension.

b = radial dimension.

c = tangential dimension.

Fig. 4.21. Nutlet Bands.

(a) Nutlet of S. hastifolia with a band situated midway radially and with patent, dactyloid papillae. Mag. x 50.

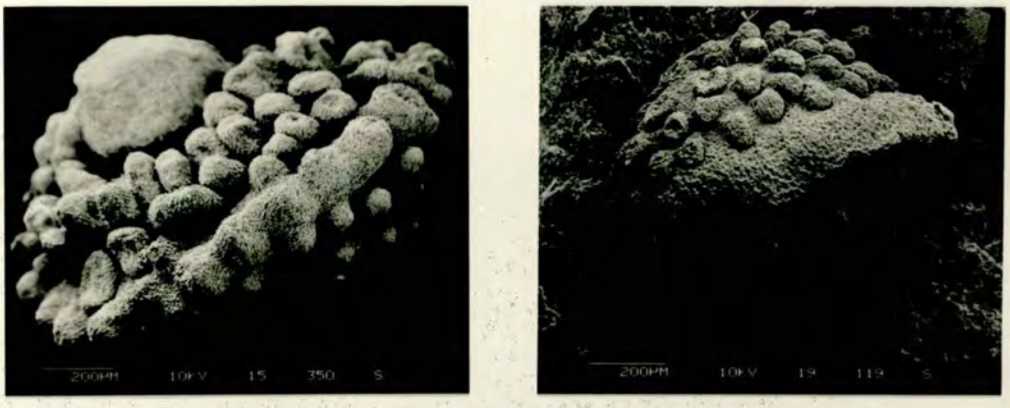
(b) Nutlet of S. parvula with a basal band and adpressed, flattened, dactyloid papillae. Mag. x 50.

Fig. 4.22. Nutlet Ornamentation.

(a) Smooth nutlet of S. volubilis Mag. x 20.

(b) Nutlet of S. drummondii with ridges. Mag. x 40.

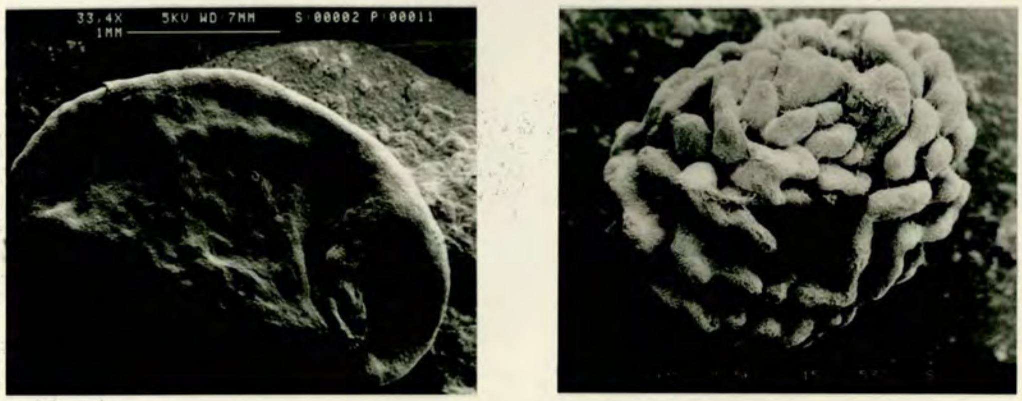
Fig. 4.21 NUTLET BANDS



(a) midway radially

(b) basal

Fig. 4.22 NUTLET ORNAMENTATION



(a) smooth

(b) ridges

Fig. 4.23. Form of Nutlet Papillae

(a) Nutlet of S. guilielmi showing hair-like papillae. Mag. x 60.

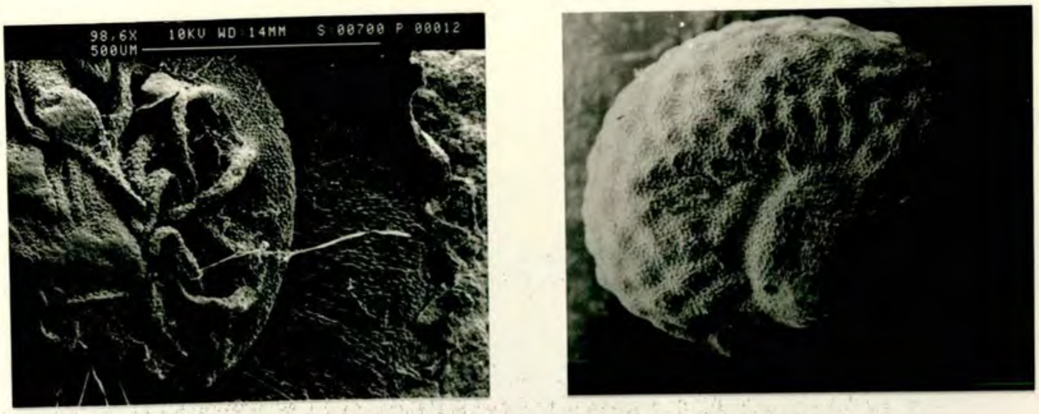
(b) Nutlet of S. barbata showing subpapillate surface. Mag. x 60.

Fig. 4.24. Nutlet Surface Hairs.

(a) Nutlet of S. albida showing hairs which do not totally obscure the nutlet surface. Mag. x 300.

(b) Nutlet of S. alpina with hairs completely covering the nutlet surface. Mag. x 125.

Fig. 4.23 FORM OF NUTLET PAPILLAE



(a) (b)

Fig. 4.24 NUTLET SURFACE HAIRS

(a) (b)

(F6) Arrangement of Papillae

(i) Papillae adpressed. (Fig. 4.21b). (3).
(ii) Papillae patent. (Fig. 4.21a). (0).

(F7) Nutlet Surface Hairs

(i) Surface without hairs. (0).
(ii) Hairs do not totally obscure the nutlet surface, often patent, borne on the tip of papillae. (Fig. 4.24a). (3).
(iii) Hairs completely obscure the nutlet surface, never patent. (Fig. 4.24b). (5).

(F8) Nutlet Papillae with Hooks

(i) Hooks present. (Fig. 4.25). (3).
(ii) Hooks absent. (0).

(F9) Conformation of the Periclinal Walls of the Nutlet Surface Cells

(i) Convex. (Fig. 4.26a). (0).
(ii) Concave. (Fig. 4.26b). (1).
(iii). Periclinal tubercule. (Fig. 4.26c). (3).

(F10) Papillae with an Apical Pore

(i) Apical pore present. (Fig. 4.27). (3).
(ii) Apical pore absent. (0).

(F11) Glands on Nutlet Surface

(i) Glands present. (Figs. 4.26a and 4.28b). (3).
(ii) Glands absent. (0).

The following characters, F12-F13, were observed from sections of the nutlet wall.

(F12) Glands on the Interior Surface of the Pericarp Wall.

(i) Present. (Figs. 4.28a, c and d). (0).
(ii) Absent. (Fig. 4.28b). (3).

Fig. 4.25. Nutlet Papillae with Hooks.

Nutlet of S. ocymoides Mag. x 200.

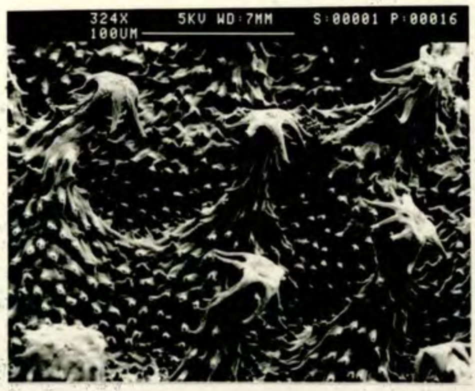
Fig. 4.26. Conformation of the Periclinal Walls of the Nutlet Surface Cells.

(a) Surface of the nutlet of S. galericulata showing glands and convex surface cells. Mag. x 150.

(b) Surface of the nutlet of S. minor showing concave surface cells. Mag. x 220.

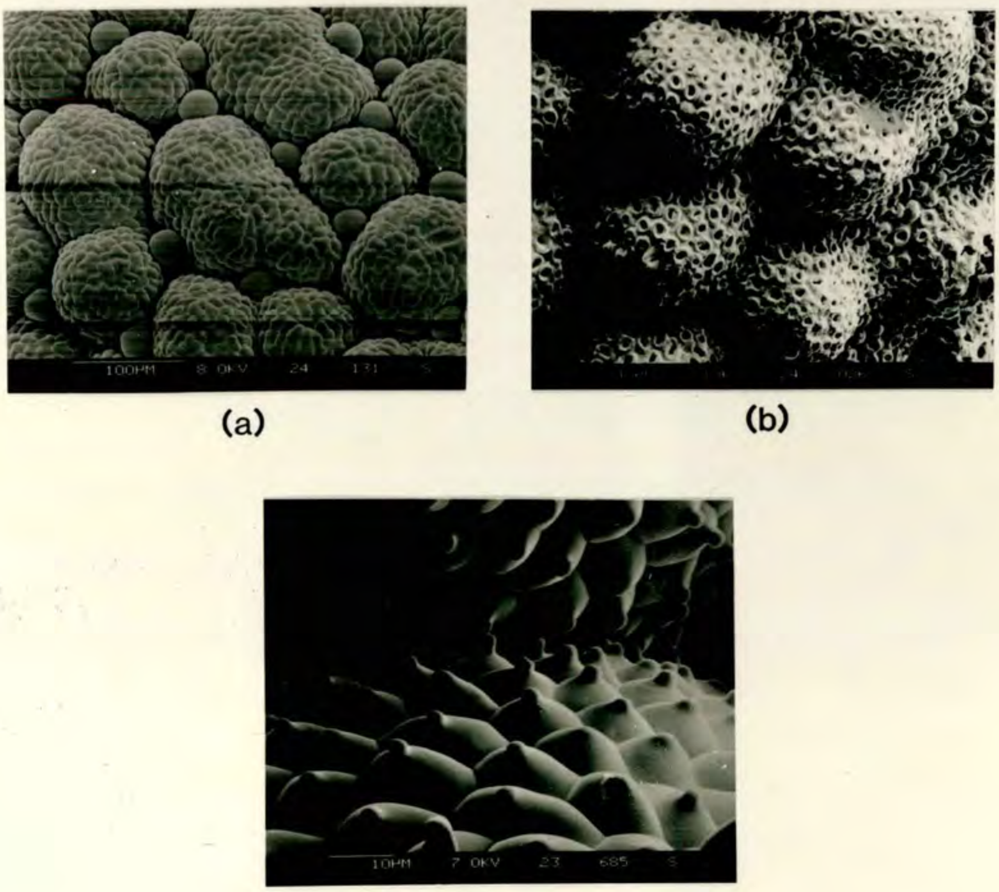
(c) Surface of the nutlet of S. albida showing the surface cells with periclinal tubercules. Mag. x 800.

Fig.4.25 NUTLET PAPILLAE WITH HOOKS



(a)

Fig. 4.26 CONFORMATION OF THE PERICLINAL WALLS OF THE NUTLET SURFACE CELLS



(a)

(b)

(c)

Fig. 4.27. Papillal Pores

(a) Nutlet of S. dependens showing papillae with an apical pore. Mag. x 225 .

Fig. 4.28. Sections through the Nutlet Wall.

(a) S. speciosa. Section through the pericarp wall showing glands on the interior and exterior surface. Papillae are composed of mostly large, thin-walled cells. Mag. x 112.

(b) S. albida. Section through the pericarp wall showing papillae composed of large thin-walled cells, with air spaces. Pericarp lacks interior glands. Mag. x 112

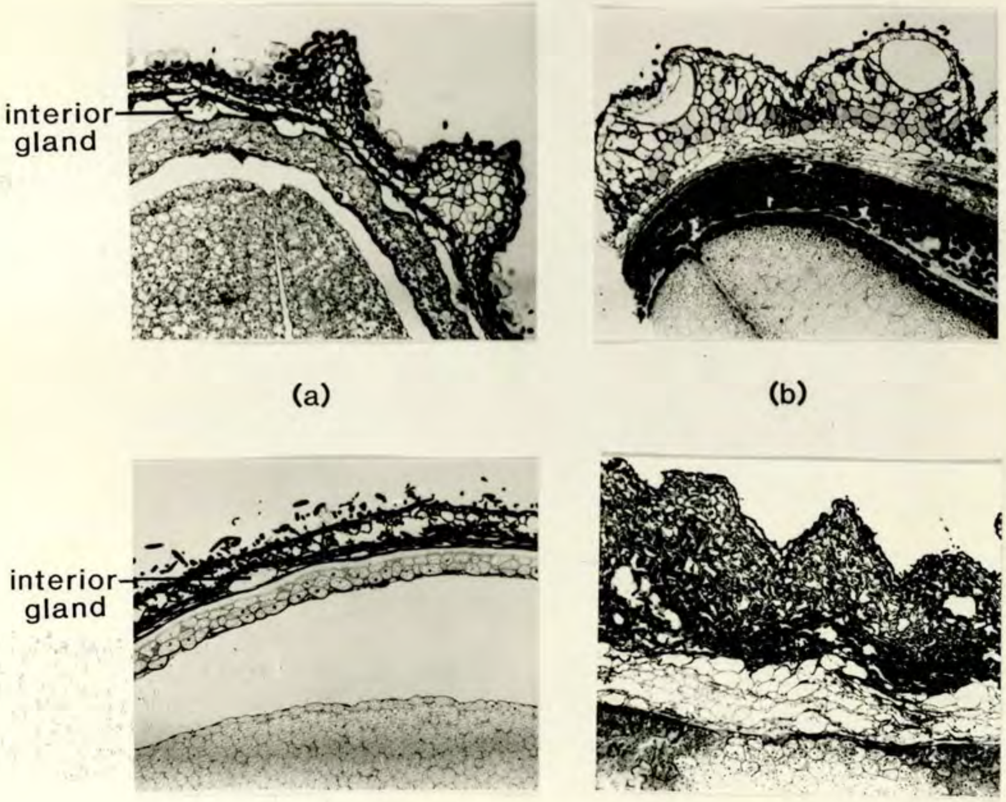
(c) S. alpina. Section through the thin pericarp wall. Internal pericarp glands are present. Mag. x 112.

(d) S. nummulariifolia. Section through the pericarp wall showing papillae composed of small thick-walled cells. Internal pericarp glands are present. Mag. x 112.

Fig. 4.27 PAPILLAL PORES

(a)

Fig.4.28 SECTIONS THROUGH THE NUTLET WALL



(a) (b)

(c) (d)

(F13) Air Space within the Larger Papillae

(i) Present. (Fig. 4.28b). (0).
(ii) Absent. (3).

The following characters, F14-F15, were observed from nutlet sections, but were not useful in the delimitation of taxa for the reasons cited.

(F14) Thickness of the Fruit Wall

There is considerable variation in the thickness of the fruit wall, *e.g.* *S. alpina* possesses a thin wall (Fig. 4.28c) whereas *S. albida* possesses a thick wall. However, due to the small number of taxa investigated and due to the variation being continuous, this character was not used.

(F15) The Density of the Fruit Wall

b, d /

The density of the fruit wall varies between taxa, *e.g.* *S. albida* has mostly large, thin-walled cells (Figs. 4.28a and b), and *S. nummulariifolia* has small thick walled cells (Fig. 4.28d). But the variation is continuous so the character cannot be used as it is impossible to define discrete states.

G: Pollen

No useful characters could be found from pollen shape and surface. Although there is some variation in pollen shape and size, this could not be described in discrete character states, (Figs. 4.29a, b and c).

H: Embryo

(H1) Embryo Shape

(i) Embryo has an incumbent radicle, or at least the embryo is bent, with the radicle forming a right angle with the cotyledons. (Fig. 4.30a).
(ii) Embryo is straight or slightly curved. (Fig. 4.30b).

This character was not used in the computer and

Fig. 4.29. Pollen

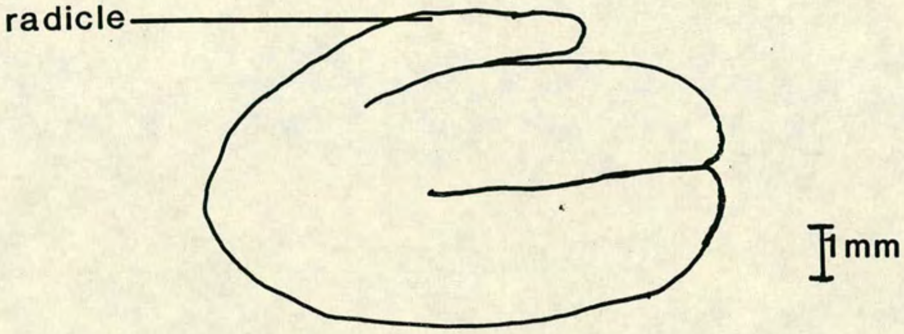
a. Pollen of S. saxatilis. Mag. x 560.

b. Pollen of Harlanlewisia sarmentosa. Mag. x 310.

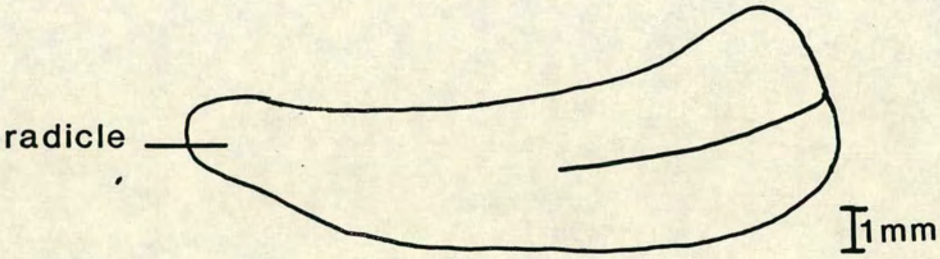
c. Pollen of S. multicaulis. Mag. x 750.

Fig. 4.29 POLLEN

Fig.4.30 EMBRYO SHAPE



(a) bent embryo of S.galericulata



(b) straight embryo of S.ocymoides

intuitive classification because material allowed this character to be studied in only a few species.

Summary

The inflorescence, flower, leaf surface and morphology, and nutlets provide the most taxonomic variation and thus the most character states. Leaflet sections and pollen provide the least taxonomic variation. Embryo morphology requires further investigation as only 15 taxa were studied.

CHAPTER 5

Taxonomic Philosophy

This chapter describes the methods and philosophies used in constructing intuitive, cladistic and numerical phenetic classifications.

Three philosophies of classification were employed: (A), intuitive, which classifies on the basis of similarity or difference in a few characters subjectively assessed to be important. These characters are assumed to reflect the evolution undergone in the group; (B), numerical phenetic, which employs phenetic similarity based on all, equally weighted characters; and (C), cladistic which uses parsimony to classify purely on the basis of assumed phylogenetic relationship. Parsimony is the assumption that evolution has proceeded by the shortest route, i.e. the number of character state changes is minimised throughout the phylogenetic tree.

A. Intuitive Classification

The aim of intuitive classification is to create a hierarchical arrangement of groups, the members of which are phenetically similar, but also more closely related to each other than to members of any other group. To this end, certain characters which vary little throughout the group, are given greater weight than more variable characters. These characters are conservative, e.g. inflorescence structure, and are assumed to be better indicators of evolutionary change than highly variable characters, e.g. hair glands. This is a valid assumption because closely related taxa may share a conservative character state when differing in a character which is prone to change. A character can be considered conservative in one area but variable in another. For example, in the Old World the interior of the corolla tube is usually glabrous. Thus it can be considered an important conservative character. However, in S. American Scutellaria there is diverse ornamentation of the interior corolla tube. Therefore, the character would be given less weight in S. America than elsewhere.

Once characters have been studied and decisions as to their importance made, the species studied can be grouped into a hierarchical system. Within each rank, the members of each group must be more similar to each other than to members of other groups, on the basis of characters considered important at that rank. Each group of taxa is thus circumscribed by a discontinuity. The size of the discontinuity should reflect the rank, being larger at a higher rank. There is no absolute size of discontinuity which separates different ranks. All that can be said is that discontinuities separating species should be smaller than discontinuities separating sections, which should be smaller than those circumscribing genera, and so on.

The process is divisive: the species are studied, largest discontinuities found, and the species are divided into groups of a certain rank. The process is then continued within each subgroup, the new subgroup being placed in the next lowest rank of the system. Rank attribution and nomenclatural research are considered in detail later.

This method is often criticised for not being objective because it is personal opinion that decides which characters are important at each rank of classification. This objection can be countered somewhat by making it clear exactly how the species are classified, which characters are used at each rank, and discussing the reasons underlying the choice of particular characters.

B. Cladistic Analysis

The aim of cladistic analysis is to produce a classification based on ancestry rather than phenetic divergence. There are two methods for doing this: (a) character compatibility and (b) parsimony. (See Funk & Stuessy 1978, Felsenstein 1982).

Character compatibility methods demand that characters are polarised, that is assumptions are made as to which character states are advanced and which are primitive. These decisions are based on outgroup analysis, i.e. comparing the characters with those present in another taxon which is assumed to have evolved from the same ancestor as the group being studied (Maddison et al. 1984). Ontogeny and fossil evidence can also be used for polarisation of characters (Crisci & Stuessy 1980).

Once the characters have been polarised they can be portrayed in the form of character state trees. These trees show the direction of evolution for individual characters. By comparing them, sets of compatible characters can be found so that a phylogenetic tree of taxa can be drawn, based on which of the states of each character seem to have evolved only once. Characters which are not compatible and not included in the set employed to make the tree can be used to examine similarities due to character reversals and parallelisms.

This method was not used because of the difficulty in deciding which are the primitive and advanced states of each character. The most common way of determining primitive states is outgroup analysis (Donoghue & Cantino 1984, Maddison et al 1984). However as Scutellaria is isolated from the rest of the Labiatae, there is no obvious outgroup. One way around this problem would be to use every other subfamily in the Labiatae as outgroups and assign primitive states by outgroup substitution methods (Donoghue & Cantino 1984). But this is a time-consuming process and may not be very informative because, as each subfamily contains many genera, there would be a great problem in deciding which was the typical character state for each character in each of the subfamilies. Other methods used in polarising characters such as the assumption "common is primitive", require that suppositions about phylogeny are made. Since the phylogeny is supposed to be inferred from the tree produced, this is a circular argument. As the fossil record for Scutellaria is non-existent, there is no objective way of determining which character states are primitive and which advanced.

The second technique of cladistic analysis is based on parsimony. This method assumes that evolution proceeds by the shortest route, i.e. the number of character state changes are minimised throughout the phylogenetic tree. The programme PAUP (Phylogenetic Analysis Using Parsimony) employs the criterion of Wagner Parsimony. (See Felsenstein 1982). Wagner Parsimony assumes that characters can change state by evolving in any direction, i.e. there are no a priori restrictions on the nature of character state changes permitted. All characters are weighted equally.

With PAUP, by specifying the option 'closest', the most similar OTUs (operational taxonomic units, species in this case) are joined via a hypothetical ancestor. Then each currently unplaced OTU is added in turn to every possible position on the tree. The length of the tree, i.e. the number of character state changes, is then calculated. The OTU whose connection adds the least length to the tree is joined via a hypothetical ancestor and the process continues (Swofford 1985). Once all OTUs have been added the final tree may be shortened by specifying "Swap = Global". This removes and reinserts all possible subtrees at all other positions on the tree. Any shorter trees that are found are then subjected to "branch swapping". The process stops when no shorter tree can be found.

The trees computed by PAUP are undirected, that is they require the same length regardless of the position of the root. This allows the tree to be rooted using a hypothetical ancestor, without any assumptions about the nature of the ancestor affecting ingroup parsimony. With this method the shortest unrooted tree is found for ingroup taxa and the resulting tree is rooted at the position where a hypothetical ancestor would join (Lundberg 1972).

However, because there is no fossil evidence the nature of this hypothesised ancestor must be subjectively derived. The criteria which were used to choose the primitive state of the characters are as follows:

(a) Character states which are widespread throughout the global distribution of Scutellaria are assumed to be more primitive than character states which only occur in geographically localised taxa, e.g. character E10: conformation of corolla lobes (See Chapter 4). Unequal corolla lobes are found in Scutellaria from around the world. Equal corolla lobes are found only in S. American Scutellaria. Therefore unequal corolla lobes are assumed primitive.

(b) If a character exists in a simple and a structurally complicated state, the structurally simple state is assumed primitive. e.g. character D2: Floral Orientation (See Chapter 4). A four-sided inflorescence is a more complicated structure in Scutellaria than a one-sided inflorescence, as it involves the close association of bract and calyx unlike the one-sided inflorescence. The other character state of this character, flowers radiating out in all directions, is found only in Central American Scutellaria. Therefore the one-sided inflorescence is assumed primitive.

(c) Character states which are common are assumed more primitive than ones which are rare. For example, character D1: Flower Arrangement. (See Chapter 4). The character state flowers opposite is considered more primitive than having flowers not opposite which occur in only a few species of S.E. Asia and S. America.

Appendix 2 lists the character states of the hypothetical ancestor used to root the tree.

To summarise so far, the parsimony method of phylogenetic analysis is used rather than the character compatibility method because of the difficulty in polarising characters. The resultant undirected tree produced by PAUP was rooted where a hypothetical ancestor would join. Using this method, the subjectively derived nature of this ancestor does not effect the parsimonious relationships of the OTUs actually studied. The advantages of the parsimony method of cladistic analysis are as follows:

(a) All characters can be used, not just those which can be polarised, so all taxonomic evidence available can be utilised.

(b) By declaring all characters as 'unordered' in PAUP, any character state is deemed to be potentially capable of changing, i.e. evolving, into any other state. Thus there is no need to create character state trees or assume which character states are derived.

Problems and limitations of cladistic analysis based on parsimony.

(1) It is unlikely that the shortest most parsimonious tree will be found. An algorithm is considered to be effective if it can guarantee to solve any instance of the problem for which it was designed by performing a number of

computational steps and if the number of these steps can be limited by a polynomial function of the size of the problem. There are problems which have effective, i.e. polymonially bounded, algorithms and ones which have not (Graham & Foulds 1982). The problem of construction of maximally parsimonious trees belong to a third class of problems, nondeterministic polynomial-complete (NP-complete). This means that an effective polynomial-bounded time algorithm probably does not exist. These problems are so difficult that no one has yet succeeded in designing an efficient algorithm to solve any known NP-complete problem (Day 1983).

The consequence of this is that finding the shortest tree requires an enormous amount of computer time. Hence an approximate or heuristic answer, such as that outlined below, is more realistic. Until faster, better computers are available this is the best that can be done.

(2) It is possible that several trees of equal length exist. Some countering of this problem is possible using the 'Mulpars' and 'Maxtree' options provided in PAUP which allow up to 100 equally parsimonious trees to be found. However, to reduce computer running time in this investigation, the number was limited to 50. After 11 hours of computer running time, the programme was halted with 50 trees, each equally parsimonious with 585 character state changes. The information from each of these trees can be represented on a strict consensus tree. A consensus tree is one tree which summarises all the information contained in the constituent trees. A strict consensus tree is a tree which consists only of those subsets of taxa that are found in all the constituent trees being compared.

To recap, the strict consensus tree produced summarises information from 50 equally parsimonious trees of length 585 character state changes. Two restraints on the programme have been introduced:

(a), a shorter length of tree probably exists, but longer computer running time was not possible;

(b), only 50 constituent trees were used rather than 100 to reduce computer running time.

Fig. 5.1 See text for explanation

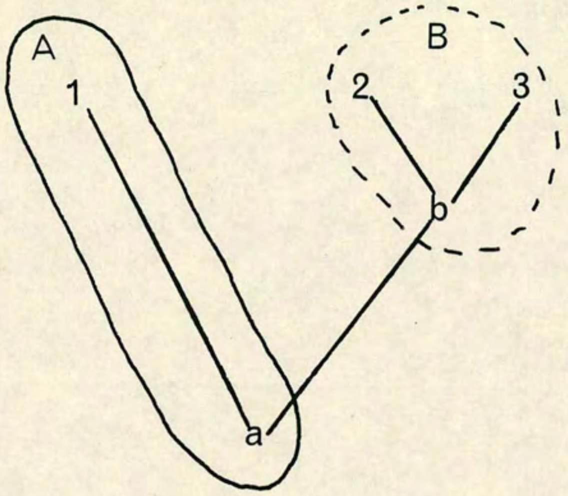
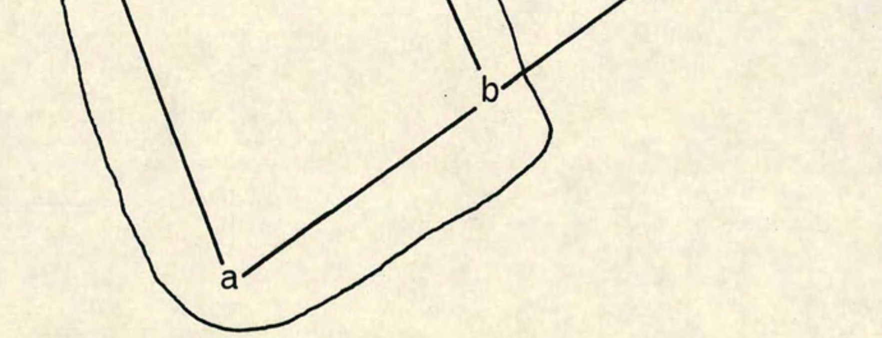


Fig. 5.2 See text for explanation

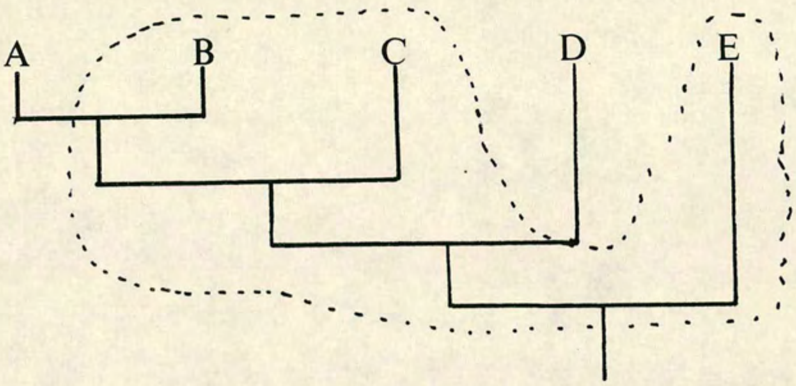


(3) How can one convert the eventual consensus tree into a hierarchical system of ranked taxa?

The first part of the problem concerns the nature of the taxa to be ranked: should they be holophyletic or convex? (See Ashlock 1971, Meacham & Duncan 1987). A holophyletic taxon includes all the descendants of an ancestor and nothing else. Meacham and Duncan (1987) define a convex taxon thus: "A taxon is said to be convex on a phylogenetic tree if, for every pair of species, X and Y, that are members of the taxon, all species on the path from X to Y are also members of the taxon. Thus, all taxa that are holophyletic on a phylogenetic tree are also convex. But taxa that are convex on a particular tree are not necessarily holophyletic.

If only holophyletic groups are allowed no extant taxon can be ancestral to another extant taxon. Consider the phylogenetic tree in figure 5.1. All taxa 1, 2, 3 and A and B are extant. Taxon B (broken line) is holophyletic. It includes all, and only all the descendants of b. Taxon A (solid line) is not permitted because it is paraphyletic, i.e. it includes only some of the descendants of a. This tree can only be divided into holophyletic groups if a is ignored. But a must have existed at some time and may still exist. By delimiting a holophyletic group on a phylogenetic tree, a paraphyletic group is automatically created because some of the descendants of the taxon which is ancestral to all taxa studied, have been removed. Therefore a classification made up of purely holophyletic groups is illogical. It is easily conceivable that paraphyletic groups exist in nature. For example, a widespread ancestral taxon may give rise to several new taxa in different areas and still exist. Both holophyletic and paraphyletic taxa are convex. Consider the phylogenetic tree in Fig. 5.2. Taxon A (broken line) is holophyletic, it contains all and only all the descendants of c. It is also convex as it contains all taxa on the path between 1 and 2, i.e. it is composed of 1, 2 and c. Taxon B (solid lines) is paraphyletic: it contains only some of the descendants of a. However, taxon B is also convex

Fig. 5.3 See text for explanation



as it contains all taxa on the path from 3 to 4. i.e. it is composed of 3 and 4, and a and b.

Convexity is the criterion used in this work to divide the phylogenetic tree into taxa. However, convex groups are not completely satisfactory because any collection of OTUs on the consensus tree generated by PAUP can be convex as they can be connected by hypothetical ancestors. However any convex taxon delimited on the tree reduces the number of other convex taxa possible, and thus increases the likelihood that any other combination of OTUs will be polyphyletic, thus not convex. Consider the tree shown in Fig. 5.3. If a convex taxon is delimited to include B, C and E (shown by the broken line), A and D cannot be placed in the same convex taxon as each other. This is because all taxa on the path between A and D have been placed in the taxon containing B, C and E. Thus if the taxon containing B, C and E is accepted, any taxon containing both A and D will be polyphyletic, not convex and cannot be accepted.

So far a method for splitting up the phylogenetic continuum has been determined: a strict consensus tree is created by PAUP and divided up into convex groups. The next problem is to decide where on the continuum convex taxa should be delimited. Because there is no objective way of deciding this, distribution of conservative characters, used in the intuitive classification, can reasonably be employed to divide up the phylogenetic tree into convex taxa. By comparing these taxa with those of the intuitive classification it can be seen to what extent the intuitive classification is consistent with phylogeny, assuming of course that evolution has indeed proceeded in the most parsimonious fashion.

C. Numerical Phenetic Classification

The aim of this method is to classify purely on the basis of phenetic similarity. All characters are given equal weight. Its advocates believe that if enough characters are studied this classification should also represent the phylogenetic relationships of the taxa because there will be more characters whose changes in state are consistent with phylogeny than otherwise.

Firstly, a measure of similarity between each species and every other species is calculated. In this case, for any two taxa, a similarity was scored, if for any character, the states were similar. This method gives an unbiased account of similarity irrespective of which character states are similar. (See Chapter 3).

Using the calculated similarity coefficients, the species are grouped together. Some clustering methods, e.g. single linkage clustering (Sneath & Sokal 1973) produce clusters which are long and straggly. Such techniques are said to be 'space contracting', as the space around a group of OTUs shrinks as the clustering process goes on, and the clusters are said to 'chain'. Discontinuities which exist in the data are hard to find and it is difficult to divide the OTUs into subgroups. With other strategies, e.g. complete linkage, the clusters formed are compact and discrete (Sneath & Sokal 1972). Such methods are said to be 'space dilating'. The space around the clusters is dilated as clustering proceeds. There are two problems with this method (Clifford & Stephenson 1975). First, OTUs which have little affinity with other OTUs can be lumped together in a 'ragbag' cluster. Second, as more OTUs fuse with a cluster, the cluster becomes harder to join and it is more likely that a separate cluster will form. Thus clusters are affected by the factors other than OTU similarity and this is undesirable. The third group of methods are said to be 'space conserving' e.g. UPGMA (Sneath & Sokal 1973). It is this method that is employed here. The space around the group of OTUs is conserved as clustering proceeds and the discontinuities in the resultant dendogram reflects those in the data. First, the most similar OTUs are grouped to form clusters. Similarity coefficients between each cluster and each remaining OTU are calculated by averaging the similarity coefficients between each remaining OTU and each component of each cluster. The similarities between clusters are calculated by averaging the similarity coefficients between each component of each cluster and every component of every other cluster. Thus for five taxa a, b, c, d, e, the similarity coefficient, S, between a cluster a, b and an OTU e would be:

$S(a, b)\ e = \frac{1}{2}(S(a, e) + S(b, e)$; and the similarity coefficient between two clusters a, b and c, d would be: $S(a, b)\ (c, d) = \frac{1}{4}\ (S(a, c) + S(a, d) + S(b, c) + S(b, d)$. The most similar taxa, whether OTUs or clusters are then grouped together and the process continues.

The arrangement of clusters is presented as a branching structure known as a dendrogram. The interval between the levels of which clusters are listed on the dendrogram can be controlled. i.e. The components of each cluster can be listed at any level of similarity desired. By requesting clusters to be shown at every 1% and 2.5% level of similarity there is a complete list of the members of each cluster at each of these levels which allows more freedom to decide which levels to use for ranking.

Although UPGMA analysis is objective and repeatable, the division of the dendrogram into groups of differing rank, i.e. rank distribution, is naturally more subjective. The line delimiting a given rank must be a straight line drawn across the dendrogram at one similarity level. (Sneath & Sokal 1973). Groups limited in this way have been called phenons. For example a 62.5% phenon group indicates a group whose members are affiliated at no less than 62.5% similarity. However, exactly where these lines are drawn is subjective. I have divided the dendrogram into phenon groups using the distribution of conservative characters employed in the intuitive classification, so that the members of these groups have close, presumed phylogenetic, relationships. The dendrogram is divided by using all the phenon levels available and the resultant taxa are examined in each case. The phenon levels chosen for rank attribution are the ones which divide the dendrogram up into taxa which are supported by the most conservative characters. Phenon levels separating taxa of high rank are supported by more conservative characters than are phenon levels separating taxa of lower rank.

CHAPTER 6

Taxonomic Results: discussion of the results of the three classification methods employed.

This chapter details the results of the different classification methods used. There are three sections:

A: Results of the intuitive classification
B: Results of the cladistic classification
C: Results of the numerical phenetic classification.

A. Results of the Intuitive Classification

My assessment of the similarity between all the taxa studied, requires that all be placed in one genus Scutellaria. The following characters reflect this similarity: non-aromatic; cross-sectional leaf anatomy; flowers single in the axil of a leaf, leaf-like bract or bract; calyx lips entire and close together in fruit; anterior stamens longer than the posterior; anthers ciliate and the anterior always dimidiate due to the aborted development of the upper theca; pollen shape and sculpturing; peg-like gynophore; anatomy of seed and pericarp; there is no discontinuity in chromosome number. Unfortunately the chromosomes are too small for detailed study in the time available to me.

The largest discontinuity in variation within the taxa studied rests on differences in inflorescence structure, nutlet anatomy and geography. I have called the resulting groups subgenera and divided them into sections rather than calling the higher ranks sections and their subgroups, subsections. The former better describes the degrees of discontinuity which exist and is more consistent with previous classifications of Scutellaria and also of other large, widespread, labiate genera such as Salvia L. The 'intuitive' infrageneric taxa are listed below with their diagnostic characters.

Subgenus IA Suffruticose herbs usually with thick woody rhizomes. Flowers opposite and decussate in a four-sided inflorescence, subtended by cucullate bracts, clearly differentiated from leaves, which clasp the calyx. Pedicels

strongly flattened, lacking scales. Nutlets grey-black with hairs usually completely covering the nutlet surface.
Distribution: Upland and mountainous areas of North Africa and Eurasia, from the Atlas Mts in the west to the Himalaya and Altai in the east. Usually over 1000m.

Subgenus IB. Perennial, rarely annual herbs or shrubs, with thick woody rhizomes or not. Flowers in the axils of leaves or reduced leaf-like bracts, opposite, or rarely spirally inserted. Secund in a one-sided inflorescence or rarely radiating out from the inflorescence axis in all directions. Pedicels rarely strongly flattened, often with scales. Nutlets brown, yellow or grey-black, with hairs or glabrous, but hairs rarely completely covering the nutlet surface.
Distribution: Throughout the natural range of *Scutellaria*.

Subgenus IA is split into two sections on the basis of differences in calyx, leaf and nutlet characters.

Section 1. Suffruticose, prostrate or cushion-forming, chasmophytes. Lower leaves brown, scale-like, clasping the stem. Calyx less than 4 mm long in fruit, upper lip testudinate, indumentum longer on upper lip than lower. Nutlet hairs partially covering the nutlet surface.
Distribution: Pakistan, Afghanistan, Kashmir, Pamir Mts. and Tien Shan Mts.
Included species: *S. stocksii*, *S. leptosiphon*, *S. orbicularis* and *S. zaprjagaevii*.

Section 2. Prostrate or erect suffruticose herbs, not chasmophytic. Lower leaves similar in form to upper. Upper lip of calyx formed into a compressed sail-like scutellum, half-way along its length. Nutlet hairs completely covering the surface.
Distribution: Atlas Mts, Pyrenees Mts to Himalaya and Altai Mts.

There are two subsections based on the form of the scutellum.

Section 2, *Subsection 1*. High alpine, prostrate, scree-

dwelling plants; scutellum expanded, greater than 5mm high and wide, membranous. Hairs on upper lip of calyx longer than on lower.
Distribution: Kashmir, Pakistan, Afghanistan, Pamir Mts.
Included species: *S. heydei* and the doubtfully distinct *S. macrochlamys*.

Section 2, *Subsection 2*. Scutellum small, less than 5 mm tall and wide, not membranous. Calyx indumentum ± uniform.
Distribution: Atlas Mts., Pyrenees Mts to the Himalaya and Altai Mts.

The species of this group differ from each other only in leaf size, shape and margin, habit and density of inflorescence. These characters are difficult to divide into discrete states and may also be affected by phenotypic plasticity. Study of the colour and lip conformation of the corolla may illuminate relationships but such study is not possible from herbarium specimens. Hence I have not formally divided this subsection. The included species are listed below, seemingly similar species are grouped together in species-groups, *i.e.* an informal group without nomenclatural status which is loosely equivalent to Epling's sections (Epling 1942) or Juzepczuk's subsections (Juzepczuk 1954). These groups are described in Chapter 7: Taxonomic conclusions.

S. linearis

S. glechomoides

S. orientalis
S. pinnatifida
S. platystegia
S. kotkaiensis

S. intermedia
S. glabrata
S. litwinowii
S. multicaulis
S. araxensis

S. colpodea

S. alpina

Subgenus IB. This subgenus is further divided on the basis of habit, calyx, corolla and nutlet characters into four sections.

Section 1. Chasmophytes with few or many slender ascending stems arising from a thick woody rhizome. Corolla with unequal lips, galeate, anthers included in the upper lobe. Upper lip of calyx testudinate in fruit, differing

from that of Subgenus IA Section 1 by being longer than 5mm. Nutlets grey-black with extremely long hairs (0.5-1mm), papillae with internal air spaces ; pericarp lacking glands on the internal surface.
Distribution: Xizang (Tibet), Pamir Mts, Afghanistan and S. Iran.
Included species: S. ariana, S. ghorana, S. schugnanica, S. tibetica.

Subgenus IB Section 2. Xerophytic shrub, to 1m; stems round. Corolla lips unequal, galeate, anthers included within the upper lobe. Calyx inflated to form a membranous bladder, 1-1.5cm in diameter.
Distribution: S. Arizona, S. Utah, New Mexico, Texas, California, Baja California, Chihuahua

Salazaria mexicana is the only species included in this taxon. Scutellaria utriculata Labill. from Syria has a similar calyx though not as enlarged. The shrubby habit of Salazaria is also found in some South American Scutellaria.

Subgenus IB Section 3. Shrubs to 4m tall. Corolla red, occasionally yellow, bent distally downward; lobes equal and spreading.
Distribution: The Andes from Colombia to Chile.

The relationship of taxa within this group are complex. There is striking floral variation within the group but there is no morphological discontinuity between the members. This makes it difficult to subdivide. The species are listed below, with aspects of their floral morphology.

S. flocculosa. Flowers small, 6-8mm, interior of tube glabrous; anthers positioned below corolla lips. Calyx with scutellum. Nutlets unknown. All-over indumentum of branched hairs.

Harlanlewisia sarmentosa. Flowers large 34-39mm; interior of corolla tube with hairs at the base of the anterior anthers; anthers exserted. Upper lip of calyx testudinate. Nutlets papillate? All-over indumentum of branched hairs.

S. valdiviana. Flowers 19-22mm; interior of corolla tube not seen; anthers exserted. Calyx with scutellum. Nutlets not seen. Indumentum of unbranched hairs.

S. volubilis. Flowers 22-24mm; interior of corolla tube with hairs at the base of the anterior anther and teeth at the base of the posterior; anthers level with corolla lips. Upper lip of calyx testudinate. Nutlets smooth. Indumentum of unbranched hairs.

S. gardoquioides. Flowers 13-19mm, yellow; interior of corolla tube with hairs at the base of the anterior anther and folds at the base of the posterior; anthers level with the lips of the corolla. Calyx with a scutellum. Nutlets with papillae and hairs. Indumentum with unbranched hairs.

S. ocymoides. Flowers 17-18mm; interior of corolla tube glabrous; anthers below corolla lips. Calyx with very small scutellum at anthesis, testudinate in fruit. Nutlets with papillae ending with hooks, some fusion of papillae to form a partial band midway radially. Indumentum with unbranched hairs.

S. scutellarioides. Flowers small, 8-10mm; interior of corolla tube glabrous. Anthers situated below the corolla lips. Calyx with very small scutellum at anthesis becoming testudinate in fruit. Nutlets with small papillae terminating in hooks and a large median band.

Subgenus IB Section 4. Herbs, suffruticose or not. Corolla lips unequal, galeate, anthers within the upper lobe. Upper lip of calyx with a small, non-membranous, sail-like scutellum. This section can be broken up into informal species groups on the basis of geography and one or two characters which appear to have evolved more than once as they are not consistently correlated with any other characters. Distribution: Throughout the natural range of Scutellaria.

Section 4, Species-Group 1. Suffruticose herbs, with prostrate and erect slender stems arising from a thick woody rhizome. Nutlets grey-black, with hairs which completely cover the nutlet surface. Similar to Subgenus IA, Section 2, Subsection 2, except the flowers are secund in a one-sided inflorescence and subtended by leaves. The group is perhaps intermediate between the two subgenera.
Distribution: Turkey-Caucasus.
Included species: *S. pontica*.

This is the only species group described here in detail because the taxonomic position of this group is different in the cladistic and numerical phenetic classifications. For reasons outlined later, the remaining species groups are maintained in my final classification in Chapter 8: Taxonomic Conclusions, and are described there.

Species-Group II
S. albida
S. tournefortii
S. arabica
S. sieberi
S. altissima
S. sciaphila
S. shweliensis

Species-Group III
S. schweinfurthii
S. polyadena
S. pauciflora
S. violascens

Species-Group IV
S. ovata
S. saxatilis
S. cardiophylla
S. pallidiflora
S. havanensis

Species-Group V
S. incana
S. integrifolia
S. bushii

Species-Group VI
S. violacea
S. tenax
S. indica
S. forrestii

Species-Group VII
S. discolor

Species-Group VIII
S. purpurascens

Species-Group IX
S. atriplicifolia

Species-Group X
S. splendens
S. speciosa
S. ventenatii
S. inflata

Species-Group XI
S. costaricana

Species-Group XII
S. lindeniana
S. hintoniana

Species-Group XIII

S. suffrutescens

Species-Group XIV

S. lutea

Species-Group XV

S. caerulea

Species-Group XVI

S. repens
S. sessiliflora
S. franchetiana

Species-Group XVII

S. lateriflora
S. churchilliana

Species-Group XVIII

S. parvula
S. leonardi
S. nervosa

Species-Group XIX

S. bolanderi
S. californica
S. antirrhinoides
S. nana
S. brittonii
S. angustifolia
S. simphocampyloides
S. austinae

Species-Group XX

S. tuberosa

Species-Group XXI

S. stigillosa
S. scordifolia
S. regeliana
S. moniliorrhiza
S. baicalensis

Species-Group XXII

S. hastifolia

Species-Group XXIII

S. humilis
S. mollis
S. javanica
S. novae-zealandiae

Species-Group XXIV

S. tubifera
S. guilielmi

Species-Group XXV

S. drummondii
S. resinosa

Species-Group XXVI

S. galericulata
S. barbata
S. minor
S. komarovii
S. xhybrida
S. cavaleriei
S. dependens

Species-Group XXVII

S. racemosa
S. platensis

Species-Group XXVIII

S. balearica

Species-Group XXIX

S. nummulariifolia

B. Results of the Cladistic Classification

Fig. 6.1 shows a strict consensus tree produced by the programme CONTREE and based on 50 trees of length 585 generated by PAUP. 108 species were studied. Two variants from each of S. tuberosa and S. nervosa were used to study how the programme dealt with infraspecific variations. These variants differed in 3 characters in the case of S. tuberosa and only 1 in S. nervosa. In both cases, the variants were grouped together in all trees produced. The relationships shown on the consensus tree can thus be assumed not to be affected by small amounts of infraspecific variation. The data from all 110 taxa entered in to PAUP is given in Appendix 2.

The consensus tree can be divided into convex groups in numerous ways. The only rationale that can be used and defended is to divide the consensus tree into convex taxa using the distribution of conservative character states. Therefore it is meaningful to compare the intuitive classification, which is based on these conservative characters, with the consensus tree to see if the intuitive taxa are consistent with the phylogeny, assuming evolution has proceeded in the most parsimonious manner.

Comparison of the Intuitive Classification with the Consensus Tree generated by PAUP.

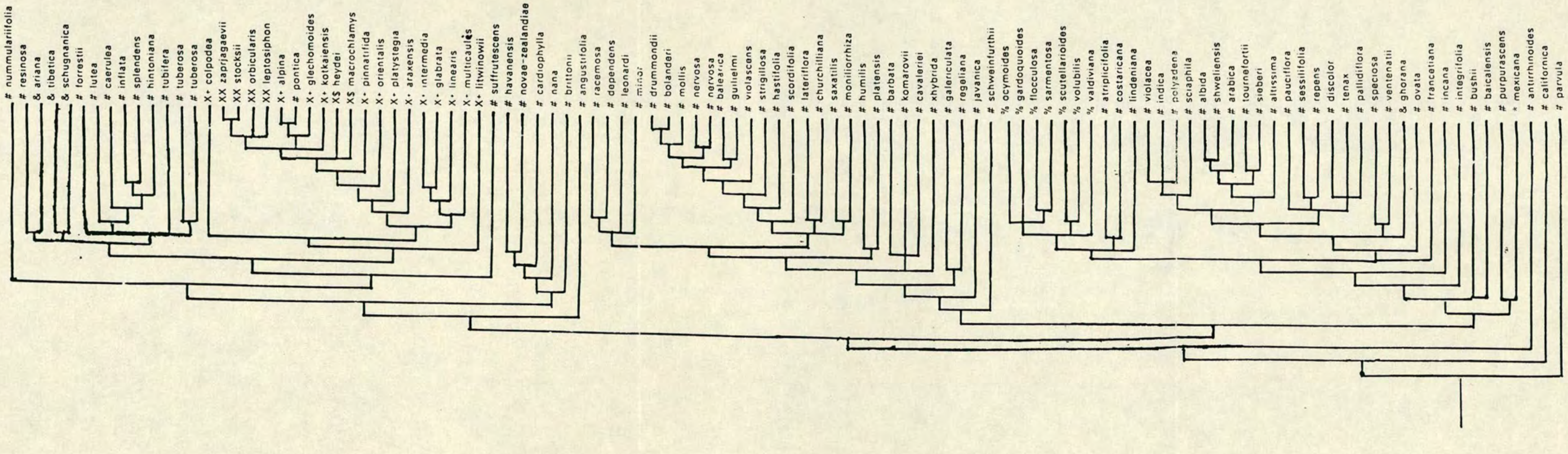
The two intuitive subgenera IA and IB are only both convex if S. pontica (Subgen. IB, Sect. 4, Species Group 1) is placed in Subgenus IA. (See Fig. 6.1). Then Subgenus IA is holophyletic and Subgenus IB is paraphyletic. Within Subgenus IA, Section 1 is holophyletic as is Section 2, Subsection 1. Section 2 Subsection 2, which includes S. pontica, is paraphyletic.

Within Subgenus IB, Section 3 is holophyletic as is of course Section 2, which contains only one species Salazaria mexicana. Section 1 and 4 cannot both be convex. Of the species included in Section 1, S. ghorana is situated far from S. schugnanica, S. ariana and S. tibetica on the consensus tree. The nutlets of S. ghorana were unseen so

Fig. 6.1 STRICT CONSENSUS TREE

KEY TO SYMBOLS PRECEDING SPECIES NAMES

XX species placed in Subgenus IA Section 1
X$ " " Subgenus IA Section 2 Subsection 1
X+ " " Subgenus IA Section 2 Subsection 2
& " " Subgenus IB Section 1
* " " Subgenus IB Section 2
% " " Subgenus IB Section 3
# " " Subgenus IB Section 4



all its nutlet characters were coded as 'missing' in PAUP. The effect of this is that PAUP 'fills in' the character states according to what the most parsimonious state would be had it not been missing. Even if S. ghorana is ignored because this treatment is unsatisfactory, Section 1 and Section 4 can only both be convex if S. resinosa is placed in Section 1 rather than in Section 4.

Within Section 4 all species groups containing one species are convex. All that can be said of the other species groups is that they cannot all be convex. The large number of equally defendable combinations of convex and not convex groups within Section 4 makes any further analysis of whether a species group is consistent with assumed phylogeny or not, meaningless. The maximum number of species groups consistent with the consensus tree could be found by trying to fit every possible combination of the species groups of Section 4 to the consensus tree. However, this would be a time consuming and pointless process as the species groups in Section 4 may have to be changed due to the existence of unstudied, intermediate species.

C. Results of the Numerical Phenetic Classification

In some species I was unable to assign states of some characters because material was insufficient or the character was inapplicable, e.g. Character B2 - stem hair orientation is inapplicable if the stem is glabrous. Such characters are coded as * in the Genstat data file. (See Appendix 3). Calculation of similarity coefficients ignores characters where there is a missing value recorded from either of the taxa being compared. To find the effects of missing values and intraspecific variation the following sets of intraspecific variants were incorporated in the study. The differences in character states between the variants of each species are expressed in the computer code used by Genstat. See Chapter 4: The Taxonomic Characters.

Character	B1	B2	B3	E7
S. tournefortii	0	2	0	3
S. tournefortii	*	*	*	*

Character	B1	B2	B4
S. baicalensis	*	*	4
S. baicalensis	0	4	2

Character	A1	B2	B3
S. speciosa	3	2	0
S. speciosa	0	0	3

Character	B5	B6	D5	E5
S. suffrutescens	0	4	0	0
S. suffrutescens	3	0	3	3

Character	B3
S. nervosa	0
S. nervosa	3

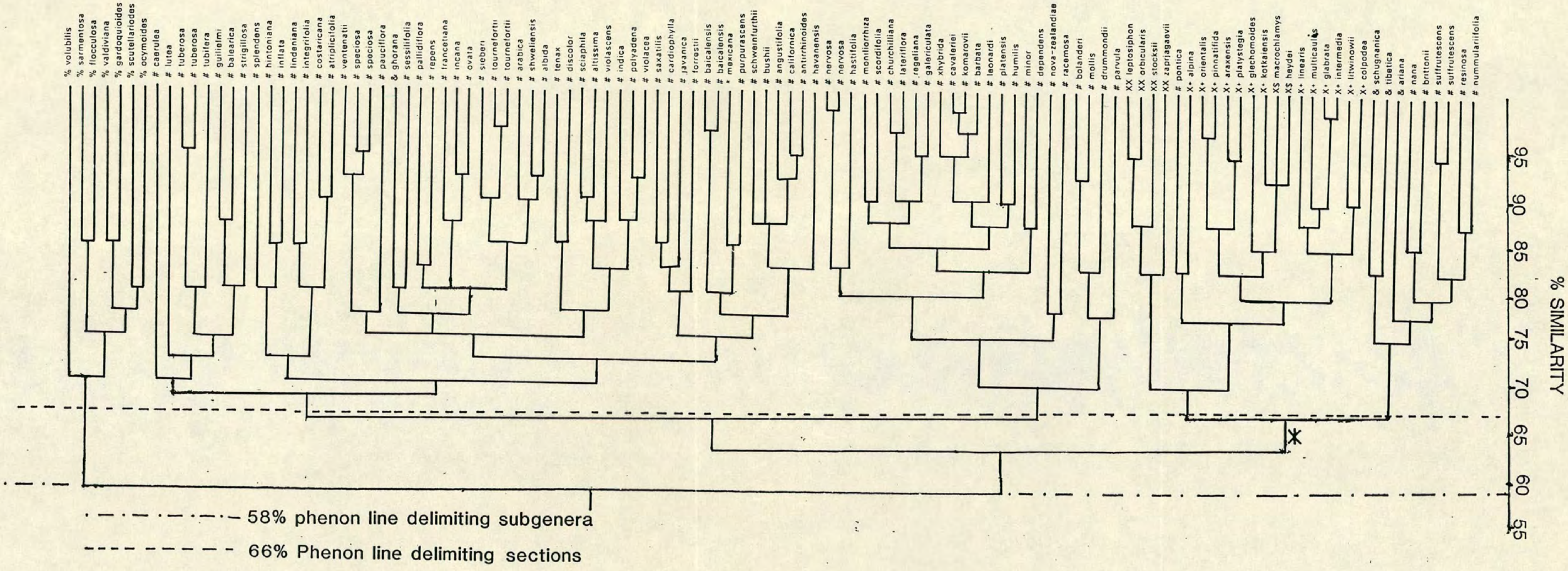
Character	A2	A7	A8
S. tuberosa	3	0	0
S. tuberosa	0	3	3

In the dendrograms produced and discussed below, intraspecific variants were always grouped together. Thus it can be assumed the dendrograms are not affected by a small amount of intraspecific variation and a few missing values.

As nutlets were absent for about a third of the species, two dendrograms were constructed, the second omitting nutlet data from all species. The data used to construct these two dendrograms are given in Appendix 3. The two dendrograms are similar, (compare Fig. 6.2 and 6.3), but important discrepancies are described below. The discussion is primarily based on Fig. 6.2 as more taxonomic evidence was used to construct this dendrogram than the other, (Fig. 6.3), which ignored nutlet evidence.

The largest discontinuity shown on the dendrograms is at the 58% phenon level. There are two 58% phenon groups which I have called Subgenera. This discontinuity does not merit generic rank because the two taxa can only be

Fig. 6.2 DENDROGRAM BASED ON ALL AVAILABLE CHARACTERS



* 65% phenon group referred to in text

KEY TO SYMBOLS PRECEDING SPECIES NAMES

XX species placed in Subgenus IA Section 1

X$ " " Subgenus IA Section 2 Subsection 1

X+ " " Subgenus IA Section 2 Subsection 2

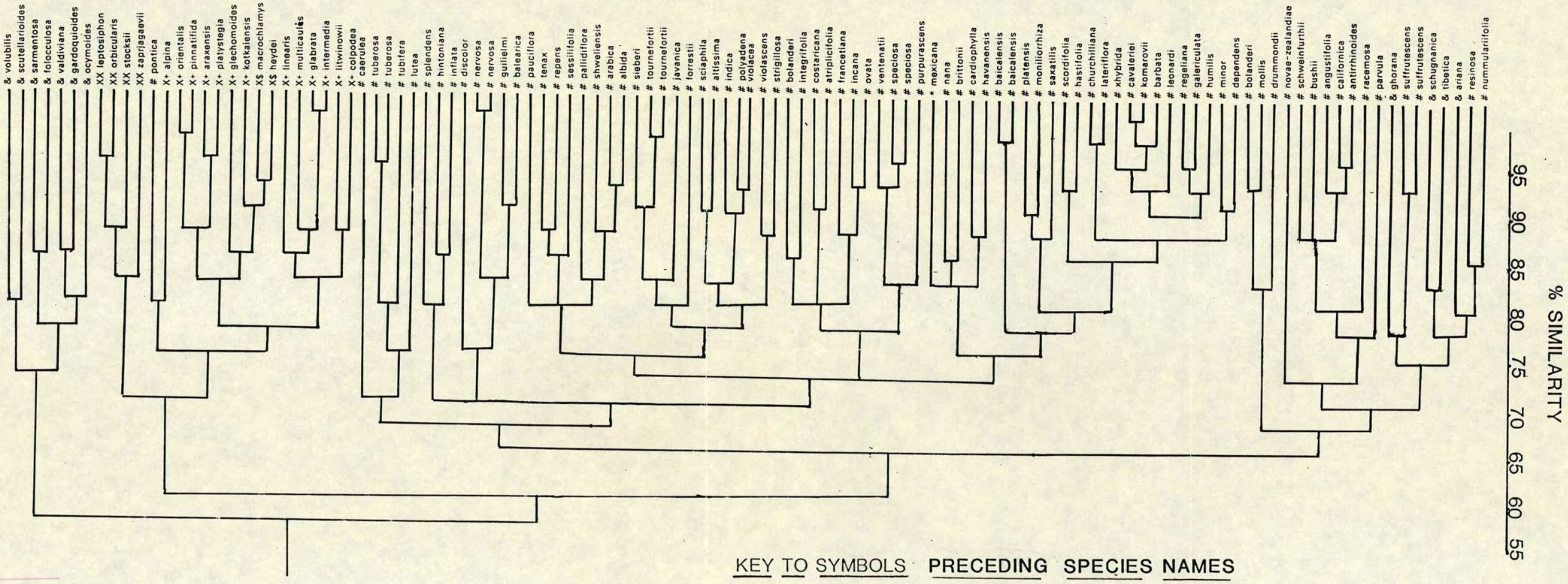
& " " Subgenus IB Section 1

* " " Subgenus IB Section 2

% " " Subgenus IB Section 3

" " Subgenus IB Section 4

FIG. 6.3 DENDROGRAM PRODUCED WHEN NUTLET CHARACTERS ARE OMITTED



KEY TO SYMBOLS PRECEDING SPECIES NAMES

XX	species placed	in	Subgenus IA Section 1
X $	"	"	Subgenus IA Section 2 Subsection 1
X +	"	"	Subgenus IA Section 2 Subsection 2
&	"	"	Subgenus IB Section 1
*	"	"	Subgenus IB Section 2
%	"	"	Subgenus IB Section 3
#	"	"	Subgenus IB Section 4

separated on the basis of whether the corolla lobes are spreading and equal, or unequal. I have used the rank, Subgenus, for the same reasons given in the intuitive classification of this chapter.

Subgenus NA consists of South American shrubs with equal and spreading corolla lobes. This group is identical with Subgenus IB, Section 3 of the intuitive classification. The species are *S. ocymoides*, *S. scutellarioides*, *S. valdiviana*, *S. flocculosa*, *S. sarmentosa*, *S. volubilis* and *S. gardoquioides*.

Subgenus NB consists of the remainder of the genus. This is an unsatisfactory group because there are no characters common to every species except unequal corolla lobes; the lower lip larger and the upper galeate.

I have chosen the 66% phenon level to separate sections within these Subgenera. Taxa delimited between 58% and 66% are difficult to describe. This is because as all characters are weighted equally, constituent species of taxa delimited by a certain phenon level, may not uniquely share any one character state or any combination of character states. For example, the 65% phenon group denoted by * on Fig. 6.2 consists of species belonging to Subgenus IA, Sections 1 and 2 and Subgenus IB Sections 1 and 4 of the intuitive classification. This group of species do not uniquely share any combination of character states so the group cannot be described and communicated. The 66% phenon level was used to delimit sections because taxa delimited by this level are supported by the distribution of more conservative characters than are taxa delimited by any other phenon level.

I tried to divide these sections into species groups but I could find no phenon level which consistently delimited taxa which were supported by the distribution of character states.

Thus Subgenus NA consists of only one section and Subgenus NB of four (See Fig. 6.2). The classification of Subgenus NB is summarised below.

Subgenus NB, Section 1 consists of the following species: *S. nummulariifolia*, *S. resinosa*, *S. suffrutescens*,

S. brittonii, S. nana, S. ariana, S. tibetica, S. schugnanica.

All species of this section have a suffruticose habit and occupy dry or exposed habitats. If nutlet characters are omitted, S. ghorana clusters along with the species listed above. (See Fig. 6.3).
S. ghorana, S. ariana, S. tibetica and S. schugnanica are the constituent species of Subgenus IB Section 1, of the intuitive classification.

Subgenus NB, Section 2 consists of the following species: S. colpodea, S. litwinowii, S. intermedia, S. glabrata, S. multicaules, S. linearis, S. heydei, S. macrochlamys, S. kotkaiensis, S. glechomoides, S. platystegia, S. araxansis, S. pinnatifida, S. orientalis, ssp. alpina, S. alpina, S. pontica, S. zaprjagaevii, S. stocksii, S. orbicularis and S. leptosiphon.

This section is the same as Subgenus IA of the intuitive classification, plus S. pontica. The dendrogram also supports sections 1 and 2 of Subgenus IA. The largest discontinuity in this section is at the 70% phenon level. (See Fig. 6.2). One 70% phenon group contains the constituent species of Subgenus IA Section 1: S. zaprjagaevii, S. stocksii, S. leptosiphon and S. orbicularis. The other 70% phenon group contains Subgenus IA Section 2 plus S. pontica. The division of Subgenus IA Section 2 into two subsections, one containing S. heydei and S. macrochlamys and the other remaining species, is not supported by the dendrogram.

The remaining sections, Section 3 and 4 of Subgenus NB correspond to Subgenus IB Section 2 and 4 of the intuitive classification. Section 3 and 4 of Subgenus NB are unsatisfactory as they connot be distinguished on the basis of any character or combination of characters.
Section 3 consists of the following species: S. parvula, S. drummondii, S. mollis, S. bolanderi, S. racemosa, S. novae-zealandiae, S. dependens, S. minor, S. humilis, S. platensis, S. leonardi, S. barbata, S. komarovii, S. cavalieriei, S. x hybrida, S. galericulata, S. regeliana,

S. lateriflora, *S. churchilliana*, *S. scordifolia*, *S. monilliorrhiza*, *S. hastifolia* and *S. nervosa*. Section 4 consists of the following species: *S. havanensis*, *S. antirrhinoides*, *S. californica*, *S. angustifolia*, *S. bushii*, and *S. schweinfurthii* ,*S. purpurascens*, *Salazaria mexicana*, *S. baicalensis*, *S. forrestii*, *S. javanica*, *S. cardiophylla*, *S. saxatilis*, *S. violascea*, *S. polyadena*, *S. indica*, *S. violascens*, *S. altissima*, *S. sciaphila*, *S. discolor*, *S. tenax*, *S. albida*, *S. shweliensis*, *S. arabica*, *S. tournefortii*, *S. sieberi*, *S. ovata*, *S. incana*, *S. francetiana*, *S. repens*, *S. pallidiflora* *S. sessiliflora*, *S. ghorana*, *S. pauciflora*, *S. speciosa*, *S. ventenatii*, *S. atriplicifolia*, *S. costaricana*, *S. integrifolia*, *S. lindeniana*, *S. inflata*, *S. hintoniana*, *S. splendens*, *S. strigillosa*, *S. balearica*, *S. guilielmi* *S. tubifera*, *S. tuberosa*, *S. lutea*, and *S. caerulea*.

The philosophy of the classification methods employed, and their results are further discussed in the next chapter. Conclusions are drawn and a classification based on the integrated results of the intuitive, cladistic and numerical phenetic classifications is proposed.

CHAPTER 7

Taxonomic Conclusions

This chapter includes A: a comparison of the classification philosophies employed in this work. A procedure is outlined for resolving the discrepancies between the various classification methods. This leads to B: a comparison of classification results and taxonomic and nomenclatural conclusions. All taxa are placed in Scutellaria L. Two subgenera are delimited and redefined: Subgenus Apeltanthus (Nevski ex Juz.) Juz. emend. Paton and Subgenus Scutellaria. Subgenus Apeltanthus is divided into two sections: Section Lupulinaria A. Hamilton and Section Apeltanthus. Section Lupulinaria is further split into two subsections: Subsection Cystaspis (Juz.) Paton and Subsection Lupulinaria. Subgenus Scutellaria is composed of five sections: Section Salviifoliae (Boiss.) Edmondson, Section Anaspis (Rech.f.) Paton, Section Perilomia (Kunth) Epling emend. Paton, Section Salazaria (Torrey) Paton and Section Scutellaria. This part of the chapter concludes with a summary of this classification which indicates the cladistic and numerical status of each of these infrageneric taxa.

A formal taxonomic account of Scutellaria with keys to the infrageneric taxa is given in part C and the chapter ends with D: a comparison of the present classification with those of previous authors.

A. Comparison of Classification Philosophies

The aim of an infrageneric classification of Scutellaria is to produce a system which describes the present phenetic similarities and discontinuties caused by the differing rates of evolutionary divergence and extinction within the genus. How evolution proceeded in the past is unknown. The three classification methods make different assumptions about how to infer this evolution from its results, i.e. the distribution of character states. These assumptions and their effects will now be discussed.

Intuitive classification assumes that certain conservative characters are the best indicators of evolutionary divergence and thus that similarity indicated by these characters is more significant than similarity based on more variable characters. As there is no record of the course of evolution within Scutellaria, it is unknown whether this assumption is correct. But it seems reasonable to suppose that closely related taxa would be likely to share a conservative character state while differing in one which is prone to change. Using conservative characters to delimit taxa means that these same conservative charaters can be used to describe the taxa. As taxa can be described, the resultant classification can easily communicate the assumed pattern of evolutionary divergence.

The decision as to which conservative characters should be used to delimit each rank of the classification is subjective. However I have tried to ensure that higher ranking is indicated by differences in a larger number of conservative characters than in lower ranking. Some taxonomists dislike the subjectivity of this method and dismiss it as unscientific. This was the driving force behind the development of numerical phenetic and cladistic methods. Their advocates claim that these methods are objective and repeatable and, because classifications can be tested against a set of rules, they are scientific.

The method of cladistic analysis used here assumes that evolution proceeds in the most parsimonious manner. This may not always be a valid assumption. In places where colonisation of new niches and habitats occur it is possible that a radically different form will evolve and be selected from an ancestor, rather than a series of forms each differing slightly from its predecessor. Evolution may then continue in the opposite direction, creating a range of intermediate forms.

Both cladistic analysis using parsimony and numerical phenetic classification avoid subjective character weighting by assuming that every character is equally important in recognising evolutionary divergence. This leads to difficulties in recognising similarity due to convergence from similarity due to direct relationship. For example, S. ariana and S. resinosa were both placed in Subgenus NB Section 1 in the numerical phenetic classification. This is consistent with the consensus tree generated by PAUP. However in the intuitive classification S. resinosa was placed in Subgenus IB Section 4 and S. ariana in Subgenus IB Section 1. Both S. resinosa from SW. USA and S. ariana from Afghanistan are suffruticose herbs which occupy dry xerophytic habitats so it is possible that they are similar in many characters due to convergence or it may be due to direct relationship. A further difficulty arising from treating all characters with equal weight is that taxa thus delimited may be difficult to describe and hard to communicate or key out. This is because no easily perceivable character or combination of such characters may be common to all members of the taxon.

It has been shown that cladistic analysis and numerical phenetic study try to limit subjectivity, but to what extent are they objective, i.e. uncoloured by the taxonomists own senses? A classification can only be objective if the taxonomist does not have to make decisions. However, there are always elements of subjectivity: which characters to use, which specimens to study, which model of parsimony to employ and which clustering strategy to apply to the data? These are all subjective decisions.

As a truly objective classification is unobtainable it is important that the methods of the subjective classification are repeatable and their assumptions made clear. It is only by studying the assumptions on which classifications are based, that a rational decision can be made as to which classification best presents the variation seen today. This rational decision is of course, subjective.

If classifications are examined and found to be consistent, then there is no rational reason for not following this classification proposed by all the methods used. However, if the intuitive, numerical phenetic and cladistic classifications are not consistent and there is discrepancy, as, in this study, in the case of some infrageneric taxa of

Scutellaria, which classifications should be rejected? An integrated classification which describes the phenetic similarities and discontinuities caused by differing rates of evolutionary divergence and extinction can be produced in the following way:

(i) Identify the discrepancy between the various classifications.

(ii) Identify the assumptions used in each classification which lead to the discrepancy.

(iii) Make a subjective decision on which assumption, and therefore which classification is most likely to reflect the true evolutionary relationships within the genus.

The last decision is unfortunately, but necessarily, always intuitive because there is no physical record of evolutionary divergence and extinction in Scutellaria, only its present-day results are known. Thus, by necessity, discrepancies must be resolved intuitively, i.e. subjectively, rather by an objective method.

B: Comparison of Classification Results and Taxonomic and Nomenclatural Conclusions

(i) Generic level.

There is no discontinuity within the taxa studied which can be used as the basis of generic delimitation. Salazaria, Perilomia and Harlanlewisia cannot be considered distinct from Scutellaria. This is because there is no combination of characters which can be used for division, as there is, for example, between the closely related Eremostachys Bunge and Phlomis L. which can be separated on the combination of leaf division, flower colour and nutlet indumentum characters. Salazaria differs from Scutellaria only in calyx form. All other characters fall within the range of variation present in Scutellaria. Even the inflated calyx is not unique - that of Scutellaria urtriculata Labill. from Syria and Lebanon is similar, though not as inflated. A similar philosophy was employed by Hedge (1982) in retaining Salvia pterocalyx Hedge, which has a strikingly inflated calyx, in Salvia L.

Perilomia and Harlanlewisia differ from Scutellaria in corolla characters only. In my view differences in corolla form cannot outweigh the similarity of the taxa based on all other characters.

I have placed all the taxa studied in the genus Scutellaria L.

(ii) The Subgeneric Level

The subgenera proposed by intuitive and numerical phenetic classifications differ. Subgenera NA and NB are distinguished only by corolla characters. Subgenera IA and IB differ in inflorescence structure and nutlet anatomy. The reason for this discrepancy is that Subgenera IA and IB are founded on a few conservative characters, whereas Subgenera NA and NB are supported by more numerous, equally weighted, mainly floral characters.

It is likely that Scutellaria invaded South America from North America. (See Chapter 8: Phytogeographical and evolutionary conclusions, for discussion of this point). This floral diversity and evolution, which occurs only in South America, may thus have been recent and rapid. Equally weighting all characters has emphasised this evolution in flower form but obscured more ancient evolutionary divergence. This, plus the fact that (1) the members of Subgenus NB form a continuous spectrum of variation when all characters are weighted equally, (2) the only character common to all, and which can be used to describe and communicate this taxon, is that of unequal corolla lobes, the lower lip being larger and the upper galeate, lead me to reject the numerical phenetic subgenera NA and NB as Subgenera of Scutellaria. Subgenera IA and IB are more likely to reflect a more significant evolutionary divergence than Subgenera NA and NB because they are delimited using conservative characters from several parts of the plant: inflorescence, bracts, petioles and nutlets. As Subgenus IA is recognised in the numerical phenetic classification but at selection rank (Subgenus NB, Section 2); and both Subgenera IA and IB are convex on the consensus tree generated by PAUP, (with the exception of the position of

S. pontica), these subgenera are accepted here. S. pontica was placed in Subgenus IB (Section 4) because of its one-sided inflorescence, although it was suggested that it may be intermediate between the two subgenera. Both numerical phenetic and the cladistic analysis place S. pontica alongside members of Subgenus IA. This species is found in the same kind of habitats as are members of Subgenus IA, Section 2, Subsection 2, and it is morphologically similar to them. Hence the two taxa are classified together when all characters are weighted equally. It is possible that this similarity is due to convergence but it is unlikely because the two taxa are similar in all characters except inflorescence structure, because they are sympatric, and further, there is no obvious ancestor from which S. pontica might be deemed to have evolved by convergence.

S. pontica and Subgenus IA, Section 2, Subsection 2 are probably directly related but it is unknown which is ancestral. It is possible for a plant with opposite and decussate flowers to produce a mutation with secund flowers, the cucullate bracts then becoming leaves subtending the flowers. This is the option supported by the consensus tree (Fig. 6.1). However, if only conservative characters are considered it is equally possible for a plant with secund flowers to produce a mutant with opposite and decussate flowers. I have seen individuals of S. albida like this. Large bracts could then become cucullate. If the first scenario is correct, S. pontica should be placed in Subgenus IA, if the second is correct, it should be placed in Subgenus IB. The botanical evidence is inadequate for me to decide between the two possibilities.

How then is the classification to describe the relationship of Subgenus IA and S. pontica? One possibility is to place S. pontica and its near relatives in a separate subgenus of their own. Although this subgenus would be easy to describe, such an arrangement would obscure the possible relationships of S. pontica to either Subgenus IA or IB. Placing S. pontica in Subgenus IA would make that taxon very difficult to describe. As one of the purposes of classification is to communicate the phenetic and assumed evolutionary discontinuities which exist in nature, this is undesirable. No such difficulties exist if *S. pontica* and its near relatives are placed in Subgenus IB. Hence it is this pragmatic solution which is followed here. Perhaps further botanical evidence will be forthcoming one day. Further consideration of the intermediate nature of *S. pontica* is given later in this chapter.

The correct name for Subgenus IA is Subgenus *Apeltanthus* (Nevski ex Juz.) Juz. *emend* Paton. The basionym *Apeltanthus* Nevski was published as a section by Nevski in Juzepczuk (1951).
The correct name for Subgenus IB is Subgenus *Scutellaria*.

(iii) Sectional Level and Below

(a) Sections of Subgenus *Apeltanthus*

Subgenus *Apeltanthus* is divided in the intuitive classification into Subgenus IA, Section 1 and Section 2. Both these sections are convex on the consensus tree computed by PAUP. The two taxa also compromise the 70% phenon groups within Subgenus NB Section 2 of the numerical phenetic classification (equivalent to Subgenus *Apeltanthus* plus *S. pontica*). These two sections are defined by all the classifications and they are maintained here. The correct rank and name for Subgenus *Apeltanthus*, Section 1 is Section *Apeltanthus*. The correct rank and name for for Subgenus *Apeltanthus*, Section 2 is Section *Lupulinaria* A. Ham.

Section *Lupulinaria* is split into two subsections in the intuitive classification. These subsections are convex on the consensus tree. The section is undivided in the numerical phenetic classification because by weighting all characters equally there is no defensible discontinuity which can be used as the basis of subsectional delimitation. In the intuitive classification, scutellum form is considered an important character. Subsection 1 is defined by a large, membranous, slightly inflated scutellum, whereas Subsection 2 is delimited by having a small, thick textured, membranous-inflated scutellum. This division is supported by corolla, calyx indumentum and habitat differences.

There are no intermediates and the subsections are easy to describe. A classification should draw attention to this important, (and conspicuous), discontinuity so the intuitive classification is followed here. The correct rank and name for Section Lupulinaria Subsection 1 is Subsection Cystaspis (Juz.) Paton. stat. nov.; the basionym Cystaspis was published as a section (Juzepczuk 1951). The correct rank and name for Section Lupulinaria Subsection 2 is Subsection Lupulinaria.

Subsection Lupulinaria is split into six informal, easily described species groups in the intuitive classification. These species groups are all convex on the consensus tree computed by PAUP. These species groups are maintained here in order to draw attention to different aspects of variation within Subsection Lupulinaria. The species groups are described informally because there may be intermediate species outwith my sample and because the groups are delimited by relatively variable characters.

(b) Sections of Subgenus Scutellaria

This subgenus is split into four sections in the intuitive classification and into Subgenus NA and Subgenus NB, sections 1, 3 and 4 in the numerical phenetic classification. Neither of these classifications is consistent with the phenetic similarity and assumed direct relationship of S. pontica and Subgenus Apeltanthus (Nevski ex Juz.) Juz. emend. Paton.

Placing S. pontica and its relatives into a separate section of Subgenus Scutellaria draws attention to the discontinuity which separates the taxon from the rest of the subgenus and to its intermediate position. The correct rank and name of this section is Section Salviifoliae (Boiss.) Edmondson; the basionym Salviifoliae was published as a subsection. (Boissier 1879).

Subgenus IB, Section 3 of the intuitive classification is supported by the consensus tree and is the same as Subgenus NA of the numerical phenetic classification. The latter method, as discussed before, over-emphasises the floral evolution of this group due to equal weighting of relatively minor characters. Hence the taxon is given subgeneric rank in the numerical phenetic classification, but sectional rank in the intuitive classification. The taxon is presented here as a section which, as it has a one-sided inflorescence, belongs in Subgenus Scutellaria. The correct rank and name for this section is Section Perilomia (Kunth) Epling emend. Paton. The basionym Perilomia was published as a genus (Kunth 1818).

As there is no morphological discontinuity which can be used to divide this section, no species groups are listed.

There is little agreement between the numerical phenetic and the intuitive classification on the further sub-division of Subgenus Scutellaria. The most similar taxa are Subgenus IB, Section 1 and Subgenus NB, Section 1. Subgenus IB Section 1 consists of Central Asiatic, suffruticose chasmophytes with testudinate calyces. Subgenus NB, Section 1 contains these plants plus other suffruticose xerophytes from S.W. USA, Mexico and southern S. America. The reason for this discrepancy is that when all characters are weighted equally, characters probably related to physiological stress became more important because there are a lot of them, e.g. leaf surface and indumentum characters. Thus numerical phenetic classification lumps together suffruticose xerophytes from all over the world which endure similar physiological conditions. If this morphological similarity is due to convergence, then the intuitive classification should be followed; if it is due to direct relationship then the numerical classification should prevail. Direct relationship is unlikely because no conservative characters can be used to describe Subgenus NB Section 1. However the delimitation of Subgenus IB, Section 1 from the rest of Subgenus Scutellaria is supported by conservative characters of the calyx and nutlets.

Subgenus IB, Section 1 and the remaining taxa of Subgenus Scutellaria can only all be convex on the consensus tree if (1), the position of S. ghorana is ignored and (2), S. resinosa is included in Subgenus IB, Section 1 (See Fig. 6.1). It is possible to ignore the position of S. ghorana as it may have been misclassified due to having several characters coded as 'missing'. However, the inclusion of S. resinosa into Subgenus IB, Section 1 is not supported by any conservative character and it would make the section impossible to describe exclusively. Hence Subgenus IB, Section 1 as proposed in the intuitive classification is retained unaltered.

The correct rank and name for this section is Section Anaspis (Rech. f.) Paton stat. nov.; the basionym Anaspis was published as a genus (Rechinger 1941).

The numerical phenetic classification divides the remainder of Subgenus Scutellaria into two sections, each difficult to describe. (Subgenus NB, Section 3 and 4). The intuitive classification also separates these species into two sections - one distinguished by a small sail-like scutellum (Subgenus IB, Section 4) and another containing only Salazaria mexicana, distinguished by an inflated bladder-like calyx (Subgenus IB, Section 2). The cause of this discrepancy is that if all characters are weighted equally there is no discontinuity in variation between the taxa. The numerical phenetic classification divides their continuous spectrum of variation into two arbitrary groups at the 66% phenon level. Thus the numerical phenetic classification does not communicate what I believe to be evolutionarily significant discontinuities in variation and is not followed here.

Salazaria differs from the rest of Scutellaria only in having an inflated calyx. However, this calyx form is a conservative character and the classification should draw attention to this evolutionarily divergent taxon.

Subgenus IB, Section 2 and 4 of the intuitive classification are both convex on the consensus tree generated by PAUP with the exception of the position of S. resinosa as discussed previously. Section 2 is holophyletic, Section 4 is polyphyletic if S. resinosa is included in it, but paraphyletic if it is ignored. As S. resinosa forms a convergent group with S. ariana, due to equal character weighting, it is justifiable to ignore the position of S. resinosa. The intuitive classification is then consistent with the cladistic analysis and is followed here.

The correct rank and name for Subgenus IB, Section 2 is Section Salazaria (Torrey) Paton stat. nov.; the basionym Salazaria was published as a genus (Torrey 1858).

S. utriculata Labill. is not included in this section. Although its calyx is membranous and inflated, the upper lip is folded into a scutellum. The species therefore belongs to Subgenus IB, Section 4.

The correct rank and name for Subgenus IB, Section 4 is Section Scutellaria.

It is impossible to divide Section Scutellaria if all characters are weighted equally. Few of the species groups which can be delimited by phenon lines on the dendrogram, or groups convex on the consensus tree, can be described exclusively. This is because these methods arbitrarily divide up a continuous spectrum of variation. Also within this wide-spread section, convergent taxa are likely to be grouped together by cladistic and numerical methods, because of equal weighting of characters. e.g. S. balearica, a Balearic Island endemic and S. guilielmi from China and Japan are clustered together on the dendrogram and consensus tree.

It is desirable for a classification to highlight separate paths of evolutionary devergence within this section. This can only be done when characters are not all weighted equally. Therefore the intuitive classification is followed generally. The species groups are described informally because there may be unstudied intermediates, and because the decision as to which characters best reflect evolutionary divergence is highly subjective at this level of the classification.

Table 7.1 presents a summary of the classification outlined above, and indicates the status of each taxon on the consensus tree (Fig. 6.1) and dendrogram (Fig. 6.2).

Table 7.1 Summary of Classification

Taxon	Status of the taxon on the consensus tree	Status of the taxon on the numerical phenetic dendrogram
Subgenus *Apeltanthus*. (Nevski ex Juz.) Juz. *emend*. Paton	Holophyletic	66% phenon group. Equivalent to Subgenus NB, Section 2.
Section *Apeltanthus*	Holophyletic	70% phenon group within Subgenus NB, Section 2
Section *Lupulinaria* A. Hamilton	Paraphyletic	70% phenon group, including *S. pontica*, within Subgenus NB Section 2
Subsection *Lupulinaria*	Paraphyletic	Not delimited at any phenon level within Subgenus NB Section 2
Subsection *Cystaspis* (Juz.) Paton	Holophyletic	92% phenon group within Subgenus NB Section 2
Subgenus *Scutellaria*	Paraphyletic if *S. pontica* is omitted	Not supported by any phenon level. Equivalent to Subgenus NA together with Subgenus NB Sections 1, 3 and 4
Section *Scutellaria*	Paraphyletic if *S. resinosa* is omitted	Mainly supported by a 61% phenon level, equivalent to Subgenus NB, Section 3 and 4. However this group omits six suffruticose xerophytes classified along with Section *Anaspis* and includes Section Salazaria.
Section *Anaspis* (Rech. f.) Paton	Holophyletic if *S. ghorana* is omitted	Part of 66% phenon group (Part of Subgenus NB Section 1)
Section *Perilomia* (Kunth)Epling *emend*. Paton	Holophyletic	58% phenon group. Equivalent to Subgenus NA

Table 7.1 contd.

Taxon	Status of the taxon on the consensus tree	Status of the taxon on the numerical phenetic dendrogram
Section *Salazaria* (Torrey) Paton	Holophyletic	85% phenon group with *S. purpurascens* within Subgenus NB Section 4
Section *Salviifoliae* (Boiss.) Edmondson	Holophyletic	81% phenon group with ***S. alpina***, within Subgenus NB Section 2

C: Taxonomic Account of Scutellaria

Scutellaria L. *Species Plantarum* 2: 598-600. 1753.

Literature: Hamilton, A. *Esquise d'une monographie du genre Scutellaria ou Toque*. Lyon. 1832. Bentham, G. *Scutellaria* in *Labiatarum Genera et Species*: 416-445. 1834. Bentham, G. Scutellaria in Candolle, A.P. de. *Prodromus systematis naturalis* 12: 412-431. 1848. Bentham, G. *Scutellaria* in Bentham, G. & Hooker, J.D. *Genera Plantarum* 2: 1201-1202. 1876. Briquet, J. *Scutellaria* in Engler, A. & Prantl, K.A.E. *Die natürlichen Pflanzenfamilien* Ed. 1, 4.3a: 225-227. 1896. Epling, C. American Species of *Scutellaria*. *Univ. Cal. Publ. Botany* 20: 1-146. 1942. Juzepczuk, S.V. *Scutellaria* in Komarov, *Flora URSS* 20: 73-150. 1954. Rechinger, K.H. *Scutellaria* in *Flora Iranica* 150: 44-84. 1982.

Synonyms: *Cassida* Tournefort *Institutiones rei herbariae* ed. 1, 1: 181. 1700.

Cassida Seguier *Pl. Veron* 3: 130. 1754.

Type species: *S. galericulata* L. (cf. Hitchcock & Green 1929). The earlier lectotype, *S. peregrina* (Britton & Brown 1913) should be superseded according to Article 8 of the *Internation Code of Botanical Nomenclature* as this choice was based on a mechanical method of selection.

Perennial, rarely annual herbs, suffruticose herbs or shrubs, not aromatic. Stems prostrate or erect; indumentum glandular or not. Leaves petiolate. Flowers single, opposite or spirally inserted, in the axils of leaves or small leaf-like bracts, secund in a one-sided inflorescence or rarely radiating out in all directions from the inflorescence axis; or opposite and decussate, subtended by cucullate bracts in a four-sided spike. Pedicels short. Calyx tube short, upper and lower lips equal, rounded and entire; upper lip folded into a sail-like scutellum or testudinate, or both lips expanded to form a membranous bladder. Corolla white, blue, pink, violet, yellow, brown, red or scarlet; lips unequal, lateral lobes more closely joined to upper lip than lower, upper, (posterior), lip galeate, lower lip large, rounded bearded or not, or corolla lobes ± equal in size and shape and spreading, upper lip not galeate; tube bent upward at base or bent distally, or both (sigmoid), dilated above. Interior of corolla tube glabrous, annulate, variously hairy or with folds at the base of the posterior lobe. Anterior stamens longer than the posterior; staminal filaments often ciliate; anther slits surrounded by a ring of cilia; anterior anther dimidiate due to aborted development of upper theca. Pollen ovoid and tricolpate. Ovary on a short, peg-like gynophore; gynophore with a variously swollen base which produces nectar. Nutlets ovoid, with a small scar, 1-1½mm, usually 4; yellow, orange, brown, black or grey-black, smooth, ridged or papillate, with hooks, hairs or glands or not. Seeds exalbuminous. Embryo curved, bent at right angles or incumbent.

I have seen no sign of structural gynodioecism or gynomonoecism in any <u>Scutellaria</u> studied. However, some form of genetic incompatibility may operate in the breeding system of <u>Scutellaria</u>. The reported 5% of unfertilised seed reported by Gams in <u>S. galericulata</u> may be due to such a phenomenon (Gams 1927). Bothmer observed strong protandry and self incompatibility in populations of <u>S. rupestris</u> Boiss. & Heldr. (Bothmer 1987). However, this is not the case in all <u>Scutellaria</u>: self pollination prevails in <u>S. sporadum</u> Bothmer. (Bothmer 1985).

Another feature of the breeding system of <u>Scutellaria</u> may be the production of sterile pollen. I have seen misshapen pollen with the scanning electron microscope. However I cannot be sure if this reflects sterility or is merely due to studying immature pollen.

Distribution: A genus of c.350 species (420 published names) found in most parts of the world except the Amazon basin, lowland tropical Africa, South Africa*, the

---

* <u>S. racemosa</u>, a South American species is widely naturalised in South Africa.

pacific islands and north of the arctic circle. (See Fig. 8.1 in Chapter 8: Phytogeographical and evolutionary conclusions).

Key to the Subgenera of Scutellaria

(1) Inflorescence one-sided, or rarely spiral, flowers opposite or not, subtended by leaves or leaf-like bracts .... 1. Subgenus Scutellaria

\+ Inflorescence four-sided with flowers opposite and decussate subtended by cucullate bracts .... 2. Subgenus Apeltanthus (Nevski ex Juz.) Juz. emend. Paton

1. Subgenus Scutellaria

Type species: S. galericulata.

Perennial, rarely annual herbs or shrubs, with slender or thick woody rhizomes or not. Flowers in the axils of leaves or reduced leaf-like bracts; opposite and solitary or rarely spirally inserted in a one-sided inflorescence; rarely flowers radiating out from the inflorescence axis in all directions. Pedicels rarely strongly flattened, with scales or not. Calyx tube short, upper and lower lips equal, rounded and entire; upper lip folded into a sail-like scutellum or testudinate, or both lips expanded to form a membranous bladder. Corolla white, blue, pink, violet, yellow, red or scarlet; lips unequal, lateral lobes more closely joined to upper lip than lower, upper (posterior) lip galeate, lower lip large, rounded, bearded or not, or corolla lobes ± equal in size and shape and spreading, upper lip not galeate; tube bent upward at base or bent distally or both (sigmoid), dilated above. Interior of corolla tube glabrous, annulate or variously hairy or with folds at the base of the posterior lobe. Nutlet smooth, variously papillate or ridged; yellow, orange, brown, black or grey-black with glands or hooks or not, with or without hairs, but hairs rarely completely covering the nutlet surface. Embryo curved, bent at right angles or incumbent.

Distribution: Around 275 species, found throughout the natural range of Scutellaria. See Fig. 8.2 in Chapter 8: Phytogeographical and evolutionary conclusions.

Key to the sections of Subgenus Scutellaria

(1) Corolla lips ± equal in size and shape, spreading; upper lip not galeate .... 3. Section Perilomia (Kunth) Epling emend. Paton

\+ Corolla lips unequal, lateral lips more closely joined to upper lip than lower; upper lip galeate .... (2)

(2) Intricately branched shrub to 1m. Calyx forming a membranous bladder in fruit, longer than 1 cm .... 5. Section Salazaria (Torrey) Paton

\+ Herbaceous or suffruticose. Calyx not membranous in fruit, less than 1cm long, upper lip testudinate or with a scutellum .... (3)

(3) Chasmophyte. Upper lip of calyx testudinate in fruit. Nutlets grey-black with hairs longer than ½mm .... 4. Section Anaspis (Rech.f.) Paton

\+ Upper lip of calyx with a sail-like scutellum. Nutlets grey-black or not, with hairs less than ½mm or glabrous .... (4)

(4) Suffruticose, mat- or cushion-forming herbs. Nutlets subpapillate grey-black with hairs obscuring the nutlet surface. A Turkish, E. Mediterranean-Caucasian group .... 2. Section <u>Salviifoliae</u> (Boiss.) Edmondson

\+ Erect or prostrate herb, suffruticose or not. Nutlets rarely subpapillate, smooth or ridged, usually papillate, yellow, orange, brown black or grey-black, glabrous or with hairs only partially covering the nutlet surface. (If the nutlet surface is obscured by hairs, then a scandent plant of 2m, never suffruticose, mat- or cushion-forming herbs) .... 1. Section <u>Scutellaria</u>

1. Section Scutellaria

Syn. <u>Cruzia</u> Phillipi <u>Anal. Univ. Chil</u>. 90: 558. 1895.

Subgenus <u>Euscutellaria</u> Briq. <u>Die natürlichen Pflanzenfamilien</u> ed. 1, 4.3a: 225-227. 1896.

Subgenus <u>Scutellariopsis</u> Briq. <u>l.c</u>.: 227. 1896.

Section <u>Stachymacris</u> A. Hamilton. <u>Esquisse d'une monographie du genre Scutellaria ou toque</u>. Lyon: 17-31. 1832.

Section <u>Galericularia</u> A. Hamilton. <u>l.c</u>.: 31-40. 1832.

Section <u>Racemosae floribus sparsis</u> Benth. <u>Edward's Bot. Reg</u>. 18: <u>t</u> 1493. 1832.

Section <u>Racemosae floribus oppositis</u> Benth. <u>l.c</u>. 1832.

Section <u>Axillares</u> Benth. <u>l.c</u>. 1832.

Section <u>Lateriflorae</u> Benth. <u>l.c</u>. 1832.

Section Heteranthesia Benth. Labiatarum Genera et Species: 425-428. 1834.

Section Maschalostachys Benth. l.c.: 443-445. 1834.

Section Vulgares Benth. in Bentham, G. & Hooker, J.D. Genera Plantarum: 1201. 1876.

Section Antarctica Epling Lilloa 4: 232. 1939.

Section Uliginosa Epling l.c.: 232-251. 1939.

Section Spinosae Epling l.c.: 254. 1939.

Section Crassipedes Epling l.c. 255-256. 1939.

Section Pallidiflora Epling l.c. 256-258. 1939.

Section Speciosae Epling l.c. 258-263. 1939.

Section Cardinales Epling l.c. 263-270. 1939.

Section Coccinae Epling l.c. 270-271. 1939.

Section Luteae Epling l.c. 271-272. 1939.

Section Mixtae Epling Univ. Cal. Publ. Botany 20: 43-57. 1942.

Section Resinosae Epling l.c. 57-69. 1942.

Section Saxicolae Epling l.c. 69-70. 1942.

Section Annulatae Epling l.c. 70-96. 1942.

Section Galericularia Subsection Genuinae Benth. in Candolle, A.P. de, Prodromus systematis naturalis 12: 424-429. 1848.

Section Galericularia Subsection Lateriflorae Benth. l.c.: 429-430. 1848.

Section Stachymacris Subsection Folia cauline ovata petiolata crenata, floralia fere omnia parva integerrima. Benth. l.c. 417-423. 1848.

Section *Stachymacris* Subsection *Angustifoliae* Benth. *l.c.*: 423-424. 1848.

Section *Heteranthesia* Subsection *Uliginosa* Epling *Repert. Spec. Nov. Regni. Veg. Beih.* 85: 173-174. 1936.

Section *Heteranthesia* Subsection *Speciosa* Epling *l.c.*: 174-178. 1936.

Some of these synonyms are more or less equivalent to species groups presented within this section. However, there are always sufficient differences to make it misleading to list these synonyms under the relevant species groups. Further discussion of the similarities between the species groups and the sections and subsections of previous authors can be found in part D of this chapter: comparison of this classification with those of previous authors.

This section is equivalent to Section *Stachymacris* A. Hamilton together with Section *Galericularia* A. Hamilton, Section *Heteranthesia* Benth. and Section *Maschalostachys* Benth. of previous classifications.

Type species: *S. galericulata*.

Annual or perennial herbs or subshrubs. Flowers opposite or spirally inserted, in the axils of leaves or reduced leaf-like bracts, forming a one-sided inflorescence or rarely radiating out from the inflorescence axis in all directions. Upper lip of calyx folded into an erect sail-like scutellum halfway along its length. The sides of the scutellum may be pressed together, *e.g. S. altissima* or not, *e.g. S. galericulata*. Corolla lips unequal, galeate. Anthers included within the upper lip of the corolla. Nutlets yellow, orange, brown, black or grey-black; with or without bands, hooks, hairs or glands. Embryos curved or incumbent.

Distribution: Around 240 species found throughout the natural range of *Scutellaria* with around equal numbers in the Old and New World. See Fig. 8.2 in Chapter 8: Phytogeographical and evolutionary conclusions.

The members of species-groups(i-v) are erect herbs with a few thickish stems and a short woody rhizome. Flowers are opposite and subtended by small leaf-like bracts, and dispersed in a one-sided inflorescence. Corollas are bent basally upwards at an angle greater than 45°. The scutella are large and dish-like in fruit. The species-groupsare separated mainly on nutlet characters and geography. These species-groups are roughly equivalent to Section Stachymacris A. Hamilton.

(i) "S. albida species-group": Nutlets grey-black, rarely brown; papillae with interior air space and hairs which do not completely cover the nutlet surface. Interior surface of pericarp lacking glands.

Distribution: S. Europe-Iran, Pakistan, S. China.

Affinities and relationships: The interior papillal air space and lack of glands on the inner surface of the pericarp relates this species-group to Section Anaspis (Rech. f.) Paton.

S. altissima L. differs from other species in this group in having brown, glabrous nutlets. It is otherwise very similar to other members of this group especially S. tournefortii Benth.

S. sciaphila S. Moore and S. shweliensis W.W. Smith may also belong here, being very similar in nutlet surface, inflorescence and flower characters. However their nutlets have not been sectioned and being Chinese they are geographically disjunct.

In preparing an account of Scutellaria for the Flora of Pakistan /In press/ it was found that S. grossa Wall. ex Benth. is very similar to S. albida and should be placed in this species group. S. rubicunda Hornem. from the eastern Mediterranean also belongs here.

Species studied: S. albida L., S. altissima L., S. arabica Jaub. & Spach , S. sciaphila S. Moore, S. shweliensis W.W. Smith, S. sieberi Benth and S. tournefortii Benth.

(ii) "S. violascens species-group": An African group, similar to the previous group but the nutlets lacking hairs.

Distribution: East Africa, Congo, Senegal, Guinea, Sierra Leone, China and Camerouns.

Affinities and relationships: S. violascens Gürke is very similar to S. altissima L. but the pericarp lacks papillal air space and has glands on its internal surface. I have not sectioned the nutlets of any other members of this group.

Species Studied: S. pauciflora Baker, S. polyadena Briq., S. schweinfurthii Briq. and S. violascens Gürke.

(iii) "S. ovata species-group": A similar American group. Nutlets lack hairs.

Distribution: East and south-central USA, Mexico and West Indies.

Affinities and relationships: S. ovata Hill. is very similar to S. altissima L. Unfortunately there was no time to section the nutlets of S. ovata.

S. cardiophylla Engelm. & Gray is an annual but otherwise very similar to other members of this group.

Species studied: S. cardiophylla Engelm. & Gray, S. havanensis Jacq., S. ovata Hill., S. pallidiflora Epling and S. saxatilis Riddell.

(iv) "S. incana species-group": This group is extremely similar to the previous one, differing only in the possession of a narrow hairy annulus at the base of the corolla tube.

Distribution: East and south central USA.

Affinities and relationships: S. incana Spreng. is particularly similar to S. ovata of group (iii).

S. bushii Britton differs from the other members of this group in having several, more slender stems, and flowers in the axils of leaves rather than leaf-like bracts. It is otherwise very similar to S. integrifolia L.

Species studied: S. bushii Britton, S. incana Spreg. and S. integrifolia L.

(v) "S. violacea species-group": An Indian-Himalayan group.

Distribution: South India, Sri Lanka, Nepal, Burma, Thailand, Laos, Vietnam, south and central China, Indonesia.

Affinities and relationships: S. tenax W.W. Smith and S. violacea Heyne ex Wall. are the most similar species, both having a basally annulate corolla and nutlets with papillal hooks. S. indica L. which lacks an annulus and has less sharply hooked nutlets, (Fig. 7.1), and S. forrestii Diels. which lacks an annulus and papillal hooks are otherwise very similar to these two species.

Species studied: S. forrestii Diels, S. indica L., S. tenax W.W. Smith and S. violacea Heyne ex Wall.

(vi) "S. discolor species-group": Inflorescence one-sided with flowers inserted spirally. Corolla with a broad basal annulus. Nutlets with hooks. (Fig. 7.1).

Distribution: South-west India, north-east India, south-east Asia, south China and Indonesia.

Affinities and relationships: S. discolor Wallich is the only species from the Old World with spirally inserted flowers. However the nutlet hooks and annulate corolla relate S. discolor to the previous group.

Species studied: S. discolor Wallich.

The next few South and Central American groups - Groups (vii-xiv) are similar and probably related. The groups differ mainly in combinations of the following

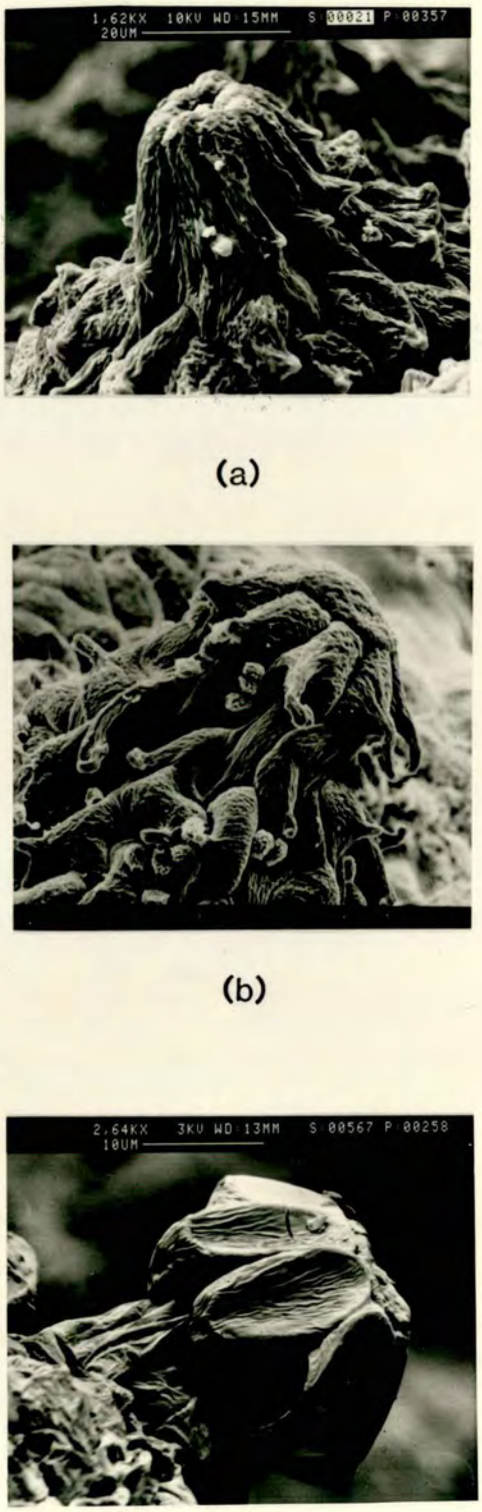
Fig. 7.1 Nutlet Hooks.

(a) Nutlet hooks of S. indica mag. x 1000.

(b) Nutlet hooks of S. violacea mag. x 1300.

(c) Nutlet hooks of S. discolor mag. x 1600.

Fig. 7.1 NUTLET HOOKS



(a)

(b)

(c)

characters: corolla red, yellow or blue; corolla tube bent distally or not; and whether the flowers are opposite or not.

(vii) "S. purpurascens species-group":

Short herbs. Flowers inserted spirally in a one-sided inflorescence. Corolla purple, straight. Nutlet surface without glands.

Distribution: West Indies, Colombia, Venezuela and Panama.

Species studied: S. purpurascens Sw.

(viii) "S. atriplicifolia species-group":

Tall herbs. Flowers inserted spirally in a one-sided inflorescence. Corolla red; tube straight. Nutlet surface without glands.

Distribution: Ecuador and Peru.

Species studied: S. atriplicifolia Benth.

(ix) "S. speciosa species-group":

Tall herbs. Flowers inserted spirally in a one-sided inflorescence. Corolla red; tube bent distally. Nutlets of S. speciosa with surface glands, other species not examined.

Distribution: Mexico, Peru, Ecuador, Colombia, Venezuela, West Indies.

Species studied: S. inflata Epling, S. speciosa Epling, S. splendens Link. ex Klotysh & Otto and S. ventenatii Hook. f.

(x) "S.costaricana species-group":

Tall herbs. Flowers inserted spirally and radiating out in all directions from the inflorescence axis. Corolla scarlet, tube bent distally. Nutlets not seen.

Distribution: Costa Rica.

Species studied: *S. costaricana* H. Wendl.

Groups (xi), (xii) and (xiii) are the most similar members of this section to Section *Perilomia* (Kunth) Epling *emend*. Paton.

(xi) "*S. hintoniana* species-group":

Tall herbs. Flowers opposite in a one-sided inflorescence. Corolla red, tube bent distally. Nutlets not seen.

Distribution: Mexico, Venezuela.

Species studied: *S. hintoniana* Epling and *S. lindeniana* Benth.

(xii) "*S. suffrutescens* species-group":

Densely branched suffritucose herbs. Flowers opposite in a one-sided inflorescence. Corolla red, tube bent distally. Nutlets not seen.

Distribution: Mexico.

Species studied: *S. suffrutescens* Wats.

(xiii) "*S. lutea* species-group":

Tall herb, subshrub. Flowers opposite in a one-sided inflorescence. Corolla yellow; tube bent distally. Nutlets without surface glands.

Distribution: Guatemala.

Species studied: *S. lutea* J.D. Smith

(xiv) "*S. caerulea* species-group":

Tall herbs. Flowers opposite in a one-sided inflorescence. Corolla blue; tube bent distally. Nutlets not seen.

Distribution: Central America, Mexico.

Species studied: S. caerulea Mocino & Sesse

(xv) "S. repens species-group":
Himalayan scandent herbs. Up to 1.5m tall.

Distribution: Pakistan, Kashmir, Nepal, Sikkim, Bhutan, Yunnan, Sichuan, Guizhou and Guanxi.

Affinities and relationships: A group of morphologically very similar species, but nutlets show tremendous variation: S. repens Buch.-Ham. ex D. Don has grey-black subpapillate nutlets, with hairs which completely cover the nutlet surface; identical to the nutlets of Section Lupulinaria. On the other hand, S. scandens Buch.-Ham. ex D. Don and S. sessilifolia Hemsley have brown, papillate glabrous nutlets.

Species studied: S. franchetiana A. Lévl., S. repens Buch.-Ham. ex D. Don, S. scandens Buch.-Ham. ex D. Don, S. sessilifolia Hemsley.

(xvi) "S. lateriflora species-group":
North American erect herbs, to 0.5m tall. Similar inflorescence structure to the previous group. Nutlets yellow-brown, papillate and glabrous.

Distribution: S. Canada, east and central USA.

Affinities and relationships: This group may be related to the previous group, however the differences in habit, nutlets and the geographical disjunction make this unlikely. The S. lateriflora and S. repens species-group are equivalent to Section Maschalostachys Benth. S. churchilliana Fern. is a putative hybrid of S. galericulata L. and S. lateriflora L. (Gill & Morton 1978).

All the remaining species-groups, (xvii)-(xxvii) have their flowers in the axils of leaves. Differences are based on geography, habit, floral and nutlet characters. These species-groups together are equivalent to Section Galericularia A. Hamilton.

(xvii) "*S. parvula* species-group":

Erect herbs with slender or moniliform rhizomes. Flowers small, less than 2cm. Basal corolla angle less than 45°. Nutlets with basal band.

Distribution: East and central USA.

Affinities and relationships: Similar to *S. galericulata* L., group (xxv).

Species studied: *S. leonardi* Epling, *S. nervosa* Pursh. and *S. parvula* Michaux f.

(xviii) "*S. angustifolia* species-group":

Erect or prostrate herbs with slender or moniliform rhizomes. Flowers longer than 2 cm. Corolla blue; basal corolla angle usually greater than 45°. Nutlets usually with basal band, but absent in *S. brittonii* Porter. Nutlets of *S. nana* A. Gray not seen.

Distribution: Western USA.

Affinities and relationships: *S. angustifolia* Pursh., *S. austinae* Eastw. and *S. siphocampyloides* Vatke form a morphological continuum and are probably conspecific. They are very similar to the *S. strigillosa* Hemsley species-group (xx) of east Asia.

S. californica A. Gray and *S. antirrhinoides* Benth. may also form a morphological continuum but there is enough difference in corolla form to maintain the two species separately: *S. californica* with white flowers and *S. antirrhinoides* with blue.

S. bolanderi A. Gray, a species from western USA, is included in this group. However it has small flowers and may be intermediate between this group and the previous eastern United States group (xviii).

(xix) "*S. tuberosa* species-group":

Similar to the members of the previous group but with the rhizome terminating in a tuber and an extremely small scutellum at anthesis.

Distribution: California.

Affinities and relationships: A somewhat isolated group.

Species studied: *S. tuberosa* Benth.

(xx) "*S. strigillosa* species-group":

East Asian erect or weakly ascending herb with a slender or moniliform rhizome. Flowers longer than 2cm. Corolla blue; basal corolla angle greater than 45°. Nutlets brown, papillate not banded, although papillae of *S. strigillosa* show some fusion.

Distribution: Sakhalin to the Ob and Quinghai.

Affinities and relationships: *S. strigillosa* Hemsley, *S. scordifolia* Fischer, *S. moniliorrhiza* V. Komarov and *S. regeliana* Nakai are very similar to the *S. angustifolia* species group of W. USA except their leaves tend to have dentate margins rather than being entire and their nutlets are unbanded.

S. regeliana Nakai is also similar to *S. galericulata*. *S. baicalensis*, a northern Asian species probably also belongs to this group. It differs from the other members of this group only in having black nutlets.

Species studied: *S. baicalensis* Georgi, *S. moniliorrhiza* V. Komarov, *S. regeliana* Nakai, *S. scordiifolia* Fisch., *S. strigillosa* Hemsley.

(xxi) "*S. hastifolia* species-group":

Erect herbs with slender rhizomes. Flowers longer than 2cm. Corolla blue; basal angle of corolla usually greater than 45°. Nutlets with a prominant median band.

Distribution: Western Europe.

Affinities and relationships: A somewhat isolated group, perhaps related to the *S. strigillosa* species group (xx).

Species studied: *S. hastifolia* L.

(xxii) "S. humilis species-group":

Herbs with slender ascending or weakly ascending stems. Flowers small, less than 2cm.

Distribution: S.E. Australia, New Zealand, New Guinea, Indonesia.

Affinities and relationships: An isolated group.

Species studied: S. humilis R. Br., S. javanica Junghuhn, S. mollis R. Br., S. novae-zealandiae Hook. f.

(xxiii) "S. guilielmi species-group":

Plants with prostrate slender stems. Flowers small. Nutlets banded.

Distribution: Japan to Shaanxi and Zhejiang.

Affinities and relationships: An isolated group.

S. tubifera is the only Old World species to have rhizomes terminating in tubers. S. guilielmi differs otherwise from S. tubifera in being an annual with an annulate corolla.

Species studied: S. guilielmi A. Gray, S. tubifera Wu & Li.

(xxiv) "S. resinosa species-group:

Erect suffruticose xerophytes with many branched stems arising from a thick woody rhizome.

Distribution: S.W. USA and N. Mexico.

Affinities and relationships: Similar to S. bushii Britton of the S. incana species-group (v) and the S. suffrutescens species-group (xii). This is the species group most similar to Section Salazaria (Torrey) Paton.
S. drummondii is unique in the genus in having ridged nutlets.

Species studied: S. drummondii Benth. and S. resinosa Pers.

(xxv) "S. galericulata species-group":

Weakly ascending herb with slender rhizomes. Flowers small less than 2cm. Found in waterside or damp habitats.

Distribution: Northern and upland Eurasia.

Affinities and relationships: S. galericulata is the only species of Scutellaria present in the Old and New World. It is most similar to members of the following species-groups: (xvi) S. lateriflora species-group, (xvii) S. parvula species-group, S. bolanderi of (xviii) S. angustifolia species-group, S. regeliana of (xx) S. strigillosa species-group and (xxvi) S. racemosa species-group.

Species studied: S. barbata D. Don and the conspécific S. cavaleriei A. Lévl. and S. komarovii A. Lévl., S. dependens Maxim, S. xhybrida Strail, S. minor L. and S. galericulata.

(xxvi) "S. racemosa species-group":

Prostrate or weakly ascending herbs with slender stems. Flowers small, less than 2cm. Waterside and damp habitats.

Distribution: S. Mexico, Andes, N. Argentina and E. Brazil.

Affinities and relationships: Similar to the S. galericulata species-group (xxv) but geographically disjunct.

Species studied: S. platensis Speg. and S. racemosa Pers.

(xxvii) "S. balearica species-group":

Slender prostrate herbs. Flowers small.

Distribution: Majorca.

Affinities and relationships: An isolated group, probably monotypic.

Species studied: S. balearica Barcelo.

(xxviii) "S. nummulariifolia species group":

Prostrate suffruticose herbs. Flowers small; lower lip of corolla hairy. Nutlets large. Embryo slightly curved.

Distribution: S. Argentina, S. Chile and the Falkland Islands.

Affinities and relationships: An isolated group.

Species studied: S. nummulariifolia Hook. f.

The following 2 species have not been studied in detail. However they represent important aspects of variation of this section and should be placed in their own separate species groups.

(xxix) "S. utriculata species-group":

Weakly ascending herbs. Calyx membranous-inflated in fruit.

Distribution: Lebanon and Syria.

Affinities and relationships: An isolated group. The calyx shows a superficial resemblance to that of S. mexicana of Section Salazaria but differs in having a scutellum.

Species studied: S. utriculata Labill.

(xxx) "S. longituba species-group":

Tall herb. Flowers large. Corolla white; tube bent distally.

Distribution: Bonin Islands.

Affinities and relationships: An isolated group. S. longituba is the only species in the Old World having a tube which is bent distally.

Species studied: S. longituba Koidz.

2. Section Salviifoliae (Boiss.) Edmondson in Davis, P.H. ed. Flora of Turkey 7: 87-89.

Syn. Subsection Salviifoliae Boiss. Flora Orientalis 4: 686-687. 1879.

Lectotype species: S. salviifolia Benth. chosen here because it seems to best fit the description of Subsection Salviifoliae given by Boissier, and all the other species, listed as members of this taxon by Boissier (1879) have their closest affinity to S. salviifolia.

Suffruticose, prostrate, mat- or cushion-forming perennial herbs. Inflorescence condensed; flowers opposite and secund in the axils of leaves. Anthers closed within the upper lip of the corolla. Upper lip of calyx folded into a scutellum. Nutlets grey-black, subpapillate, with hairs completely covering the nutlet surface. Embryos incumbent in all species examined.

Distribution: 5 species found from Turkey, E. Mediterranean-Caucasus. See Fig. 8.2 in Chapter 8: Phytogeographical and evolutionary conclusions.

Affinities: Intermediate between Subgenus Scutellaria and Subgenus Apeltanthus.

This section includes all species included in Section Salviifoliae by Edmondson (1982) and in Subsection Salviifoliae (Boiss.) by Juzepczuk (1954).

Species studied: S. pontica C. Koch.

3. Section Perilomia (Kunth) Epling emend. Paton.

Syn.: Perilomia Kunth in Humboldt. A., Bonpland, A. & Kunth, C.A. Nova genera et species plantarum 2: 326-328. 1818.

Harlanlewisia Epling Am. J. Bot. 42: 436. 1955.

Theresa Clos. in Gray, C. ed., *Historia fisica de Chile botanica* 4: 497-498. 1849.

Perilomia Section *Euperilomia* Briq. *Die natürlichen Pflanzenfamilien* Ed. 1, 4.3a: 233. 1896.

Perilomia Section *Holocraspeda* Briq. *l.c.*

Perilomia Section *Aprosphylla* Briq. *l.c.*

Scutellaria Section *Perilomia* (Kunth) Epling *Repert Spec. Nov. Regni. Veg.* Beih. 85: 178. 1936.

Scutellaria Section *Perilomioideae* (Benth.) Epling. *l.c.*: 178-180. 1936.

Scutellaria Section *Theresa* ((Clos.) Epling *l.c.*: 180. 1936.

Scutellaria Section *Galericularia*, Subsection *Perilomioideae* Benth. in Candolle, A.P. de, *Prodromus systematis naturalis* 12: 431-432. 1848.

Lectotype species: *S. scutellarioides* (Kunth) R. Harley The species best fitting the description of *Perilomia* Kunth (Epling 1936).

Shrubs to 4m tall. Flowers opposite and secund in the axils of leaves on smaller leaf-like bracts. Corolla red or scarlet; tube straight or bent at base, bent distally; Lips equal. Anthers exserted, within the tube, or level with the corolla lips. Embryo curved in all species examined.

Distribution: Around 11 species found in the Andes from Colombia to Chile. See Fig. 8.2 Chapter 8: Phytogeographical and evolutionary conclusions.

Species studied: *S. flocculosa* Epling & Mathias, *S. gardoquioides* Benth., *S. ocymoides* (Kunth) Epling, *S. sarmentosa* Epling, *S. scutellarioides* (Kunth) R.Harley.

4. Section *Anaspis* (Rech. f.) Paton, *stat. nov.*

Syn.: *Anaspis* Rech. f. *Notizbl. bot. Gart. Berlin* 15: 630-632. 1941.

Subgenus *Anaspis* (Rech. f.) Juz. in Komarov, *Flora URSS* 20: 207-217. 1954.

Type species: *S. fedtschenkoi* Bornm. The only species listed as a member of the genus *Anaspis* by Rechinger 1941.

Suffruticose chasmophytes with few or several slender ascending stems arising from a thick, woody rhizome. Flowers opposite in the axils of reduced leaf-like bracts. Corolla with unequal lips, galeate. Anthers included within the upper lobe. Calyx longer than 5mm in fruit; upper lip testudinate. Nutlets grey-black papillate with very long hairs which do not obscure the nutlet surface. Papillae with internal air spaces. Internal surface of pericarp lacking glands. Embryo incumbent.

Distribution: Around 15 species found in S. Iran, Central Asia and Xizang (Tibet). See Fig. 8.2 in Chapter 8: Phytogeographical and evolutionary conclusions.

This section includes all species placed in Subgenus *Anaspis* by Juzepczuk (1954), Wu & Li (1977) and Rechinger (1982). It also includes *S. fragillima* Rech. f., *S. nuristanica* Rech. f., *S. neubaueri* Rech. f., *S. petiolata* Hemsley & Lace and *S. poliochlora* Rech. f. & Edelb. placed in Subgenus *Scutellaria*, Section *Stachymacris* by Rechinger (1982).

Species studied: *S. ariana* Hedge, *S. ghorana* Hedge, *S. schugnanica* B. Fedtsh, and *S. tibetica* Wu & Li - a probable synonym of *S. kingiana* Prain.

5. Section *Salazaria* (Torrey) Paton, *stat. nov.*

Syn.: *Salazaria* Torrey ~~1858~~, in Emory, W.H. *Rep. U.S. Mex. Bound* 2(1), Botany of the boundary: 133-135. 1858

A monotypic section; type species: S. mexicana (Torrey) Paton, comb. nov.

Dense shrub to 1m high. Stems round or square. Flowers opposite in the axils of leaves or leaf-like bracts. Corolla lips unequal, galeate. Anthers included within the upper lobe of corolla. Calyx 6-8mm long at anthesis; upper lip without a scutellum; forming a membranous, inflated bladder in fruit, with upper lip similar to lower. Nutlets black, papillate, embryo with cotyledons and radicle forming a right angle.

Distribution: S. Utah, S. Arizona, New Mexico, Texas, California, Baja California and Chihuahua. See Fig. 8.2 in Chapter 8: Phytogeographical evolutionary conclusions.

Species studied: S. mexicana (Torrey) Paton.

2. Subgenus Apeltanthus (Nevski ex Juz.)Juz. emend. Paton.

Synonym: Section Apeltanthus Nevski ex Juz. Bot. Mater. Gerb. Bot. Inst. Komarov Akad. Nauk SSSR 14: 427-435. 1951.

Lectotype species: S. orbicularis Bunge: chosen here because it was the only species placed in the genus Apeltanthus by Nevski (1935) and it was referred to in the protologue of Section Apeltanthus Nevski by Juzepczuk (1951).

Suffruticose, perennial herbs with several stems arising from a thick,rarely slender, woody rhizome. Flowers subtended by clearly differentiated cucullate bracts which clasp the calyx; arranged in an opposite and decussate manner forming a four-sided inflorescence. Pedicels strongly flattened, lacking scales. Calyx tube short, upper and lower lips equal, rounded and entire; upper lip folded into a sail-like scutellum or testudinate. Corolla yellow, cream, brown or pink or combinations of these in one flower, rarely blue; lips unequal, lateral lobes more closely joined to upper lip than lower, upper, (posterior) lip galeate, lower lip large rounded, never bearded; tube bent upward at base, more or less straight, distally dilated. Interior of corolla tube glabrous. Nutlets subpapillate, grey-black with hairs. Embryo incumbent.

Distribution: Around 140 species found in the mountains and upland areas of North Africa and Eurasia, (usually over 1000m), from the Atlas and Pyrenees mountains in the west to the Altai and Himalaya in the east. Absent in the New World. See Fig. 8.3 and 8.4 in Chapter 8: Phytogeographical evolutionary conclusions.

Key to the sections of Subgenus Apeltanthus

(1) Chasmophytes, lower leaves brown, scale-like, clasping the stem. Upper lip of calyx testudinate. Nutlet hairs only partially covering the nutlet surface .... 1. Section Apeltanthus

\+ Lower leaves similar in form to the upper leaves, petiolate. Upper lobe of calyx folded half way along its length to form a scutellum. Nutlet hairs completely covering the nutlet surface .... 2. Section Lupulinaria A. Hamilton

1. Section Apeltanthus

Synonyms: Apeltanthus Nevski ex Pavlov Trudy Sredne-Aziatsk. Gosud. Univ. Ser. 8b. Bot. 19: 35. 1935. (nomen nudum)

Section Apeltanthus Nevski ex Juz. Bot. Mater. Gerb. Bot. Inst. Komarov Akad. Nauk. SSSR 14: 427-435. 1951.

Subgenus Apeltanthus (Nevski ex Juz) Juz. in Komarov, Flora URSS 20: 217-225. 1954.

Type species S. orbicularis Bunge

Prostrate, suffruticose, brittle-stemmed chasmophytes. Lower leaves brown, scale-like, clasping the stem. Inflorescence dense, the bracts on successive nodes overlapping. Calyx less than 4mm in fruit; upper lip testudinate; indumentum of upper lip longer than the lower. Corolla white, pink or yellow; tube slender, bent upwards at base. Nutlet hairs incompletely covering the nutlet surface.

Distribution: Around 12 species found in Pakistan, Afghanistan and Soviet Central Asia. See Fig. 8.4 in Chapter 8: Phytogeographical and evolutionary conclusions.

This section contains all species placed in Subgenus *Apeltanthus* (Nevski *ex* Juz.) Juz. by Juzepczuk (1954) and Rechinger (1982).

Species studied: *S. leptosiphon* Nevski, *S. orbicularis* Bunge, *S. stocksii* Boiss. and *S.zaprjagaevii* Koczk. & Zhogoleva.

2. Section *Lupulinaria* A. Ham. *Esquisse d'une monographie du genre Scutellaria ou Toque* Lyon: 11-17. 1832.

Lectotype species: From Hamilton's account (1832) of Section *Lupulinaria* the type species should be *S. caucasica* A. Hamilton: "Cette plante, par ses large bractées meriterait plus qu'aucune autre le nom *Lupulina*, car se sont le plus larges du genre". (This plant by its large bracts, would merit more than any other the name *Lupulina*, because they are the largest of the genus).

According to Hamilton (1832) his description of *S. caucasica* ~~and~~ was based on a specimen in De Candolle's herbarium, but no such authenticated specimen has been traced at Geneva. The best candidate for a Lectotype for *S. caucasica* is apparently a specimen of *S. orientalis* L., *ann.* 1808, *Wilmsen* *s.n.* from the Caucasus (Georgia). The microfiche of this specimen (G-DC) shows a plant that agrees well with Hamilton's description of *S. caucasica* on account of its large membranous bracts and triangular, crenate leaves which are white below. In the absence of an authentic type specimen of S. caucasica and because Hamilton states that S. caucasica is very similar to S. orientalis, an opinion which I share, S. orientalis is proposed as the lectotype species of Section Lupulinaria.

Prostrate or erect suffruticose herbs; not chasmophytic. Lower leaves similar in form to the upper. Inflorescence dense or lax. Calyx around 5mm long in fruit, upper lip folded halfway along its length into a scutellum. Corolla white, yellow, pink or brown, or combinations of these, often with purple lips, or rarely blue; tube bent sharply upwards at base. Nutlet hairs completely cover the nutlet surface.

Distribution: Around 130 species found in the upland and mountainous areas of North Africa and Eurasia, from the Atlas Mts and Pyrenees in the west to the Altai and Himalaya in the east.

Key to the subsections of Section Lupulinaria.

(1) Scutellum membranous-inflated, more than 6 mm high and wide. Indumentum on the upper lip of the calyx longer than on lower. Corolla tube thickish. High alpine, scree-dwelling plants .... 2. Subsection Cystaspis (Juz.) Paton

\+ Scutellum thick textured, not membranous, less than 6 mm high and wide. Calyx indumentum uniform. Corolla tube slender ,................. 1. Subsection Lupulinaria

1. Subsection Lupulinaria

Synonyms: Section Spicatae Benth. in Edward's Bot. Reg. 18: t 1493. 1832.

Section *Nevskinthe* Juz. in Komarov, *Flora URSS* 20: 115-118. 1954.

Type species: *S. orientalis* L.

Prostrate or erect suffruticose herbs. Upper lip of calyx with a small scutellum less than 5mm wide and tall, not membranous-inflated; calyx indumentum ± uniform. Corolla tube slender.

Distribution: About 119 species found in the upland and mountainous areas of North Africa and Eurasia, usually over 1000m. Many of these species are microspecies which doubtfully merit specific status. See Fig. 8.3 in Chapter 8: Phytogeographical and evolutionary conclusions.

This subsection contains all species previously placed in Section *Lupulinaria* A. Hamilton by Bentham (1848) except *S. stocksii* Boiss., Juzepczuk (1954), Wu & Li (1977), Rechinger (1982) and Edmondson (1982). It also includes *S. linearis* placed by previous authors in Section *Stachymacris* A. Hamilton. This species has a four-sided inflorescence and grey-black, subpapillate nutlets with hairs which totally cover the nutlet surface, so it belongs in this taxon.

The species studied in this subsection are split into six informal species-groups.

(i) "*S. linearis* species-group":

Suffruticose herb with thick woody rhizome. Stems ascending. Leaves linear, entire.

Species studied: *S. linearis* Benth.

Distribution: West Pakistan-Himalaya

Affinities and relationships: A monotypic group.

(ii) "*S. glechomoides* species-group":

Weakly suffruticose herbs with a filiform subterranean rhizome. Stems weakly ascending.

Species studied: *S. glechomoides* Boiss.

Distribution: N. Iran.

Affinities and relationships: A monotypic group.

(iii) "*S. orientalis* species-group":

Suffruticose, prostrate herbs with a thick woody rhizome; stems several, slender. Cauline leaves small.

Species studied: *S. kotkaiensis* Rech. f., *S. orientalis* L. subsp. *alpina* O. Schwarz, *S. pinnatifida* A. Hamilton, *S. platystegia* Juz.

Distribution: Atlas Mts., Balkan Mts - Himalaya.

Affinities and relationships: The numerous segregates of *S. orientalis* recognised in Komarov, *Flora URSS* 20, species numbers 37-93, come within this species-group.

(iv) "*S. multicaulis* species-group":

Suffruticose, erect herbs with a thick woody rhizome; stems several, slender. Cauline leaves small.

Species studied: *S. araxensis* Grossh., *S. glabrata* Vved., *S. intermedia* M. Pop., *S. litwinowii* Bornm. & Sint. and *S. multicaulis* Boiss.

Affinities and relationships: *S. edelbergii* Rech. f. (Iran, Afghanistan, Pakistan) is intermediate between the *S. orientalis* species-group and the *S. multicaulis* species-group.

(v) "*S. colpodea* species-group":

As the *S. multicaulis* species-group but the bracts do not clasp the calyx at anthesis. In this respect the group is unique in the subsection.

Species studied: S. colpodea Nevski

Distribution: Pamir-Alay Mts.

Affinities and relationships: This species group is equivalent to Section Nevskinthe Juz. (Juzepczuk 1954) and includes S. striatella Gontsch. and S. cristata M. Pop.

(VI) "S. alpina species-group":

Suffruticose erect herbs with a thick woody rhizome; stems few, thick. Cauline leaves large.

Species studied: S. alpina L.

Distribution: Alps - Caucasus.

Affinities and relationships: Very close to the S. orientalis species-group.

The S. orientalis, S. multicaulis, S. colpodea and S. alpina species-group probably form a continuous spectrum of variation.

2. Subsection Cystaspis (Juz.) Paton stat. nov.

Synonyms: Section Cystaspis Juz. Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR. 14: 413-420. 1951.

Subgenus Cystaspis (Juz.) Juz. in Komarov, Flora URSS 20: 199-207. 1954.

Lectotype species: S. physocalyx Rgl. & Schmalh. chosen here because its characteristics concur best with Section Cystaspis described by Juzepczuk 1951.

High alpine, prostrate, scree-dwelling, suffruticose plants. Inflorescence condensed. Upper lip of calyx folded into a large membranous-inflated scutellum, which is more than 6mm wide and tall. Calyx indumentum longer on the upper lip than lower. Corolla white, yellow, pink or combinations of these; tube thickish.

Species studied: *S. heydei* Hook. f. and *S. macrochlamys* Rech. f. & Fitz.

Distribution: Around 11 species found up to 4500m in the Himalaya, Hindu Kush and Pamir-Alay Mts. See Fig. 8.4 in Chapter 8: Phytogeographical and evolutionary conclusions.

This subsection contains all species previously placed in Subgenus *Cystaspis* (Juz.) Juz. by Juzepczuk (1954) and Rechinger (1982).

D. Comparison of the present classification with those of previous authors.

(i) The generic level.

No previous classifications have included *Scutellaria*, *Salazaria* and *Perilomia* within one genus. My generic concept of *Scutellaria* is thus appreciably broader than those of previous authors. This is the first taxonomic assesment which considers the global variation of *Scutellaria* since Briquet's account of 1896. Since then the variation represented by Sect. *Apeltanthus*, Sect. *Anaspis* and Sect. *Cystaspis*, as well as many new species has been discovered and described. By broadening the concept of *Scutellaria* to allow for this variation, the discontinuities which separate *Salazaria*, *Perilomia* and *Harlanlewisia* from *Scutellaria* no longer merit recognition at generic level.

Salazaria and *Scutellaria* have always been treated as separate genera because the inflated calyx and shrubby habit of *Salazaria* were given great weight. This is understandable because where *Salazaria* grows in the USA and N. Mexico, all other *Scutellaria* have a small sail-like scutellum and are herbaceous or suffruticose. However when calyx form and habit are considered on a global scale and variation in Sect. *Apeltanthus*, Sect. *Anaspis*, Sect. *Perilomia* and *S. utriculata* are considered it can be seen that these characters of *Salazaria* do not

Fig. 7.2 Summary of the Infrageneric Classification of Scutellaria

Hamilton 1832	Bentham 1832	Bentham 1834	Bentham 1848	Bentham 1876	Briquet 1896	Kudo 1929	Epling 1942	Juzepczuk 1954	Wu & Li 1977	Rechinger 1982	Edmondson 1982
Sect. Lupulinaria	Spicatae	Sect. lupulinaria	Sect. Lupulinaria	Sect. Lupulinaria	Subgenus Euscutellaria Sect. Lupulinaria	Sect. Lupulinaria	Sect. Galericularia Sect. Antarctica Sect. Lateriflorae Sect. Mixtae Sect. Resinosae Sect. Saxicolae Sect. Annulatae Sect. Uliginosae Sect. Spinosae Sect. Crassipeda Sect. Pallidiflorae Sect. Speciosae Sect. Cardinales Sect. Coccinae Sect. Lutea Sect. Perilomioidae Sect. Perilomia Sect. Theresa	Subgenus Euscutellaria Sect. Lupulinaria Sect. Nevskinthe	Subgenus Euscutellaria Sect. Lupulinaria	Subgenus Euscutellaria Sect. Lupulinaria	Sect. Lupulinaria
	Racemosae Floribus Sparsis	Sect. Heteranthesia	Sect. Heteranthesia	Sect. Heteranthesia	Sect. Heteranthesia	Sect. Heteranthesia			Sect. Heteranthesia		
Sect. Stachymacris	Racemosae Floribus oppositis	Sect. Stachymacris	Sect. Stachymacris	Sect. Vulgares	Sect. Vulgares	Sect. Vulgares Series Stachymacris Series Galericularia Series Lateriflorae		Sect. Stachymacris	Sect. Stachymacris	Sect. Stachymacris	Sect. Salviifoliae Sect. Stachymacris
Sect. Galericularia	Axillares	Sect. Galericularia	Sect. Galericularia Subsection: Genuinae Perilomioidae Lateriflorae					Sect. Galericularia	Sect. Galericularia	Sect. Galericularia	Sect. Galericularia
	Lateriflorae	Sect. Maschalostachys							Sect. Maschalostachys		
					Subgenus Scutellariopsis				Subgenus Scutellariopsis		
								Subgenus Cystaspis		Subgenus Cystaspis	
								Subgenus Anaspis		Subgenus Anaspis	
								Subgenus Apeltanthus		Subgenus Apeltanthus	

merit generic distinction. As there are no other morphological discontinuities between *Salazaria* and *Scutellaria*, *Salazaria* cannot be considered a separate genus.

Epling (1942), working on American *Scutellaria*, is the only other author to have fused *Perilomia* into *Scutellaria*. He listed the species of *Perilomia* (Kunth) Epling *emend*. Paton in three sections: Sect. *Perilomia* Epling, Sect. *Perilomiodeae* Epling and Sect. *Theresa* Epling (Fig. 7.2). The discontinuities between *Harlanlewisia* Epling and *Scutellaria* L. and between Epling's Sections *Perilomia*, *Perilomoideae* and *Theresa* are based on similar characters. Thus the division of *Harlanlewisia* as a separate genus is inappropriate. There is no discontinuity which separates *Harlanlewisia* from *Perilomia* nor *Perilomia* from *Scutellaria*.

(ii) The infrageneric level.

The present classification differs from all previous classifications by dividing *Scutellaria* into two subgenera on the basis of inflorescence structure. Previous classifications which have considered Old World plants, have all drawn attention to this discontinuity by placing species with four-sided inflorescences and with a small scutellum in Section *Lupulinaria* A. Ham. (Fig. 7.2) Juzepczuk (1954) also describes Sect. *Nevskinthe* Juz. which differs from Sect. *Lupulinaria* by having bracts which do not clasp the calyx at anthesis. Placing such plants, e.g. *S. colpodea* in a separate section obscures their clear relationship and similarity to plants of Sect. *Lupulinaria*. Juzepczuk (1954) and Wu & Li (1977) split Section *Lupulinaria* into several subsections (Fig. 7.2). All these taxa, previously placed within Section *Lupulinaria* plus Section *Nevskinthe* are placed in Sect. *Lupulinaria* Subsect. *Lupulinaria* in the present classification. The difference in rank is due to Section *Lupulinaria* being enlarged in the present classification to accommodate Juzepczuk's (1954) and Rechinger's (1982) Subgenus *Cystaspis* Juz. The members of Sect. *Lupulinaria*

Subsect. Lupulinaria are very similar. I have studied one species from each of Juzepczuk's (1954) subsections, but can find no discontinuity above the level of species which merits formal description. Both Rechinger (1982) and Juzepczuk (1954), who are the only other authors to consider the variation present in Subgenus Apeltanthus, Section Apeltanthus and Section Lupulinaria, Subsection Cystaspis, place these taxa in separate subgenera from other species with four-sided inflorescences, i.e. Section Lupulinaria. Their subgenera are Subgenus Apeltanthus and Subgenus Cystaspis respectively. However, all these taxa are more similar to each other than to any other infrageneric taxon of Scutellaria. A classification should communicate this relationship.

The present classification places all plants with a four-sided inflorescence, cucullate bracts and flattened petioles in Subgenus Apeltanthus. The discontinuity between Section Apeltanthus and Section Lupulinaria is larger, being based on leaf, nutlet and calyx characters, than the discontinuity between Section Lupulinaria Subsection Lupulinaria and Subsection Cystaspis which is only based on calyx characters. Thus the present classification communicates the discontinuities which exist and their magnitude.

The remainder of the genus, here classified as Subgenus Scutellaria has been variously divided in the past. (Fig. 7.2). Juzepczuk (1954) in the Flora URSS and Rechinger in Flora Iranica (1982) the only previous authors to include the variation of Section Anaspis in their study, both considered this taxon as a separate subgenus because of the testudinate upper lip of the calyx. (Fig. 8.2). But some members of Section Perilomia also have a testudinate calyx. When the global variation of Scutellaria is taken into account both Section Anaspis and Section Perilomia can be seen to be similar to Section Scutellaria. Hence it is best to view these taxa as separate sections of Subgenus Scutellaria. Epling's (1942) classification differs from the others because he only worked on American Scutellaria. (omitting Salazaria). The New World species show less of a range of variation than do Old World species: only one subgenus and three sections are present here. Epling divided this narrow range of variation represented in my classification by Section Scutellaria and Section Perilomia, into 18 sections. Some of these are equivalent to my species groups: Sections Saxicolae and Annulatae are equivalent to (iv) S. incana species-group. This fusion is supported by Collins (1976); Section Laterifolae is equivalent to (xvi) S. lateriflora species-group; Section Galericularia is equivalent to (xvii) S. parvula, (xviii) S. angustifolia, (xxv) S. galericulata and (xxvi) S. racemosa species-groups; Section Resinosae is equivalent to (xxiv) S. resinosa species group; and Section Antarctica is equivalent to (xxviii) S. nummularifolia species-group. I cannot comment to great extent on Epling's classification as I have studied relatively few American Scutellaria in detail, but many of his sections are hard to define and appear to overlap.

All other authors divide the continuum of variation, represented in the present classification by Section Scutellaria, into 2, 3 or 4 sections (Fig. 7.2). Section Stachymacris A. Ham. with flowers in the axils of reduced leaf-like bracts is equivalent to my species-groups (i)-(v). Section Galericularia A. Ham., with flowers in the axils of leaves is equivalent to my species-groups (xvii)-(xxviii). Section Maschalostachys Benth., with flowers in axillary racemes is equivalent to species-group (xv) and (xvi). Section Heteranthesia Benth., with flowers dispersed spirally is equivalent to species-groups (vi)-(x). When all the other species groups of Scutellaria are considered there is no discontinuity which warrants sectional rank. These large sections including species from large geographical areas do not communicate the different pathways of divergent evolution represented here by the species groups of Section Scutellaria.

Briquet (1896) in Die natürlichen Pflanzenfamilien divides the continuum of Section Scutellaria into two subgenera on the basis of whether the nutlet is banded or not. This is unsatisfactory because banded nutlets are present in several species groups, e.g. (xvii),

(xviii) and (xxi), and have probably evolved more than once. Penland (1924) also came to this conclusion. However, Briquet divided his large Section *Vulgares* into subsections or species-groups. Five of the seven groups have equivalents in my classification. *Galericulatae* Boiss. is equivalent to species-groups (xvii)-(xxviii); *Peregrinae* Boiss. is more or less equivalent to species-groups (i)-(v); *Lateriflorae* (Benth.) Briq. is equivalent to species-groups (xv) and (xvi); *Coccineae* Briq. is equivalent to species-group (xi) and (xii); and *Salviaefoliae* Boiss. is equivalent to Section *Salviifoliae*. Edmondson's account in the *Flora of Turkey* (1982) is the only other classification to acknowledge the intermediate position of Section *Salviifoliae* by giving it sectional rank.

The broadening of the concept of *Scutellaria* to embrace *Salazaria*, *Perilomia*, *Harlanlewisia* as well as the more recently described taxa such as Section *Apeltanthus* and *Anaspis*, frustrates comparison of this infrageneric classification with those of previous authors. However, Bentham's treatment is probably most similar to mine (Fig. 7.2). His Sections *Lupulinaria* and *Vulgares* correspond to Subgenus *Apeltanthus* and *Scutellaria* respectively. Bentham over-emphasised the spiral arrangement of flowers in Section *Heteranthesia*. This taxon is represented by several species groups of Section *Scutellaria* in my classification. I believe spirally disposed flowers may have evolved more than once. *S. discolor* (species-group (vi)), is more similar to *S. violascens* (species-group (v)), from India and China, than to any South American plant with spirally disposed flowers, (species-groups(vii)-(x)). There is no discontinuity within Section *Scutellaria* which supports the delimitation of Section *Heteranthesia*.

Bentham, to his credit, realised that the infrageneric taxa of *Scutellaria* were similar and that intermediates existed. He stated "Species numerosae quoad, floram structuram conformes, non nisi ex inflorescentia in series 3 vel 4 intermediis pluribus conexas potius quam sectiones distinctas distribuendae" : (Numerous species which conform in flower structure, must be placed in 3 or 4 series with many intermediates rather than distinct sections, only by using inflorescence [characters]. The broadening of the concept of *Scutellaria* to include more recently described species, and *Perilomia* and *Salazaria*, justified when the global variation of *Scutellaria* is examined, allows the division of *Scutellaria* into distinct subgenera and sections. However, intermediates still exist, *e.g.* Section *Salviifoliae*. The present classification is consistent with that of Bentham (1876). Considering that Bentham knew of only 90 species and the variation represented by Section *Anaspis*, Section *Apeltanthus* and Section *Cystaspis* was unknown to him, his classification should be highly regarded.

CHAPTER 8

Phytogeographical and Evolutionary Conclusions

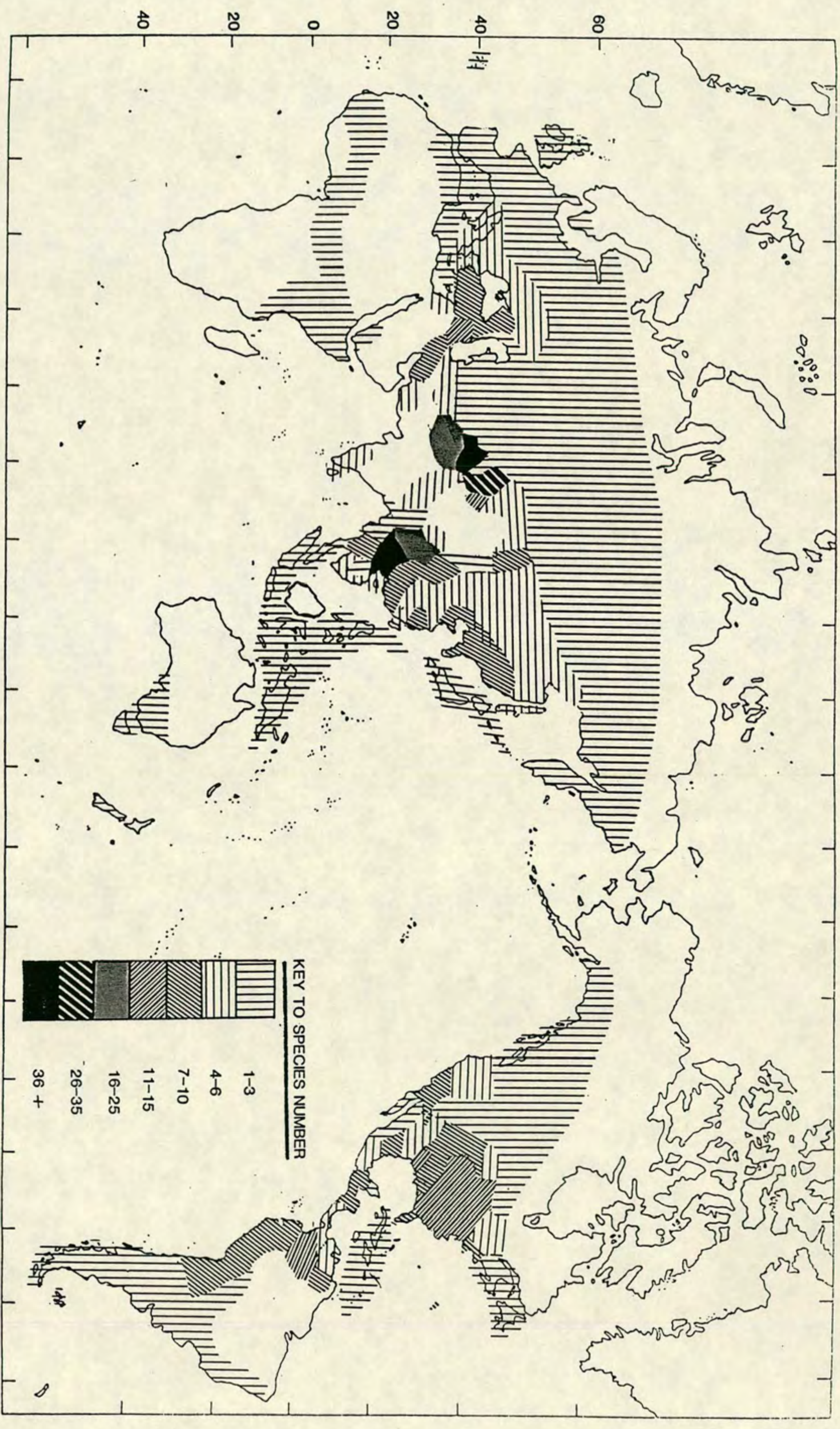
This chapter has two aims: first, to describe and analyse the present-day distribution of Scutellaria in order to indicate the centres of diversity; and second, to use the results of this phytogeographical survey and the taxonomic conclusions of the preceding chapter to illuminate the history and adaptive radiation of Scutellaria.

The present-day distribution of Scutellaria

An isoflor map, based on the number of species inhabiting particular areas, was compiled using numerous Floras, Epling's monograph of the New World species, (Epling 1942) and data from herbarium specimens. (Fig. 8.1).

This map is, in part, misleading as an indicator of diversity in different areas. The number of species recorded from the areas of Flora Reipublicae Popularis Sinicae (Wu & Li 1977) and Flora URSS (Juzepczuk 1954) are apparently both much inflated because of the very narrow species concepts of the authors. For example, Juzepczuk (1954) lists 53 species which are "equivalent to Scutellaria orientalis L. sensu latissimo of previous authors", whereas Edmondson in dealing with the S. orientalis complex in Turkey, (Edmondson 1982) recognises one species with 16 subspecies. Another source of difficulty concerning species number is that the same taxon may be given different specific epithets or treated differently in different areas. For example S. orientalis L. is recognised in the Flora of Turkey (Edmondson 1982) and S. pinnatifida A. Hamilton in Flora Iranica (Rechinger 1982) yet these taxa are probably conspecific. This problem also occurs in Nepeta L. and Phlomis L. (Hedge 1968). Thus mere species number may not necessarily reflect true variation within the genus. However, the map reveals the following facts. Scutellaria is absent or very poorly represented in the arctic, in deserts, in low-land tropical areas such as the Amazon

Fig. 8.1 Isoflor map of Scutellaria



basin and in the Pacific Islands. In the tropics and Southern Hemisphere, it is present mainly on the temperate mountains. Species number is greatest in the mountains of Central Asia and China: 50 species are found in the Pamir-Alay region, (as delimited in Komarov *et al*., 1934-64, *Flora URSS*); 41 in Yunnan; 35 in Tien Shan (as recognised in Komarov *et al*., *Flora URSS*, but extended to include the range in Xinjiang); 22 in Sichuan and 18 in the mountains of Afghanistan and Pakistan.

Figs. 8.2, 8.3 and 8.4 show the distributions of all the sections and subsections of *Scutellaria* described in the previous chapter.

The number of sections in a particular area gives a more accurate measure of diversity than species number, particularly as, in this study, only one philosophy of classification was used throughout the range of *Scutellaria*. Table 8.1 combines the information of Figs. 8.2, 8.3 and 8.4 giving the number of species and the number of which are endemic in each section and also the total number of species and endemics in each of Takhtajan's (1986) floristic regions of the world.

It can be seen that the major centre of diversity is in the Irano-Turanian region. Both subgenera are present here: Sections *Scutellaria*, *Anaspis* and *Salviifoliae* of Subgenus *Scutellaria* and both Subsections of Section *Lupulinaria* and Section *Apeltanthus* of Subgenus *Apeltanthus*. Smaller centres are in the Mediterranean region, particularly in the East Mediterranean Province with Sections *Lupulinaria*, *Scutellaria* and *Salviifoliae* all being present and in the Andean Region where Section *Scutellaria* is most variable and Section *Perilomia* is present. Generally, there appears to be less diversity in the New World than in the Old. The large number of species in Yunnan and Sichuan all belong to Section *Scutellaria* while in Tien Shan most of the 35 species belong to Section *Lupulinaria*.

The diversity of the Irano-Turanian Region is examined in more detail in Table 8.2. Takhtajan's (1986) Provinces are used for the west of the region but individual mountain ranges are used in the east for better resolution. The

Fig. 8.2 Distribution of Sections Scutellaria (✳✳✳), Anaspis (●●●), Salviifoliae (⬢⬢⬢), Perilomia (◆◆◆) and Salazaria (▼▼▼)

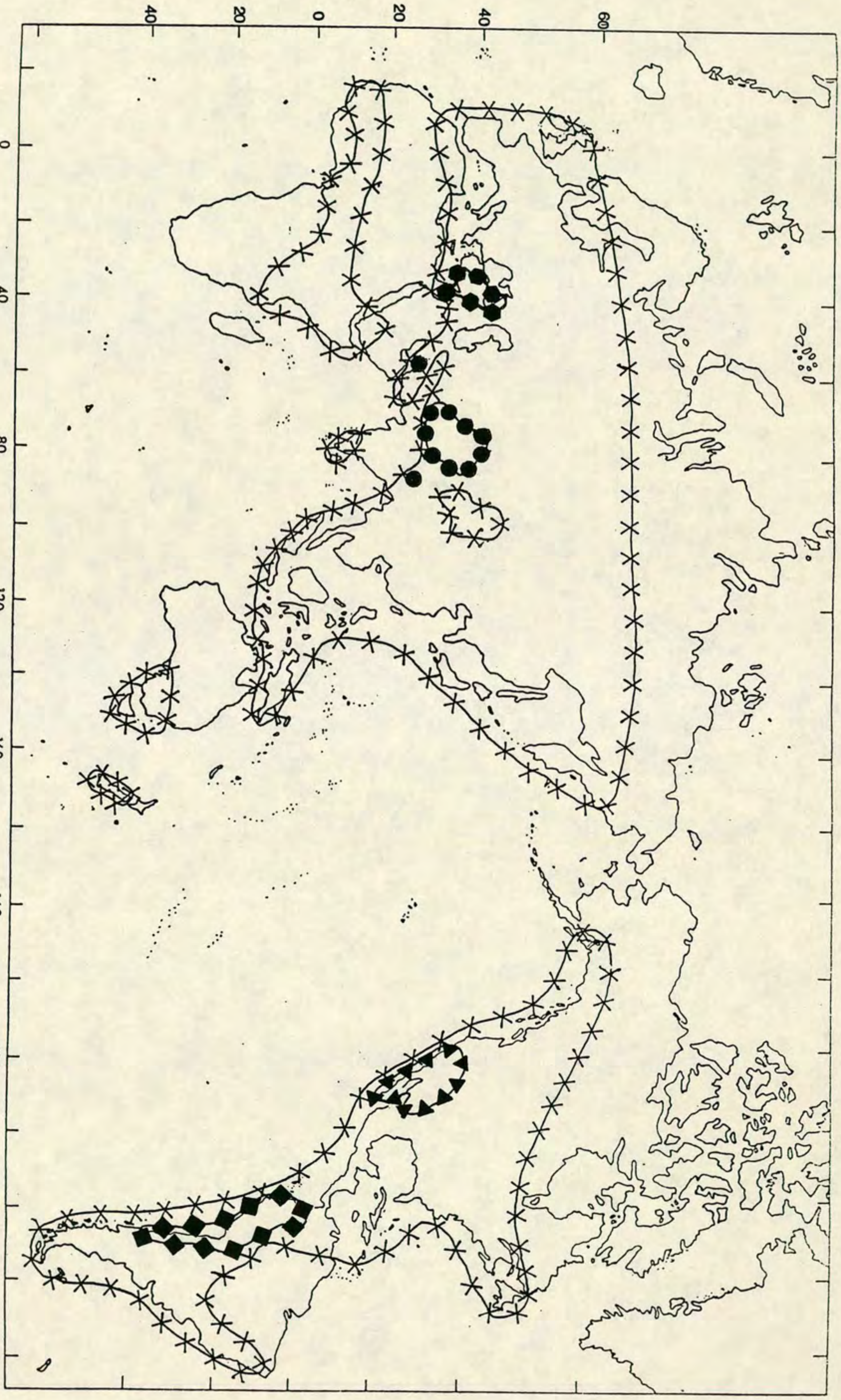


Fig. 8.3 Distribution of Section *Lupulinaria* Subsection *Lupulinaria*

(●—●—●)

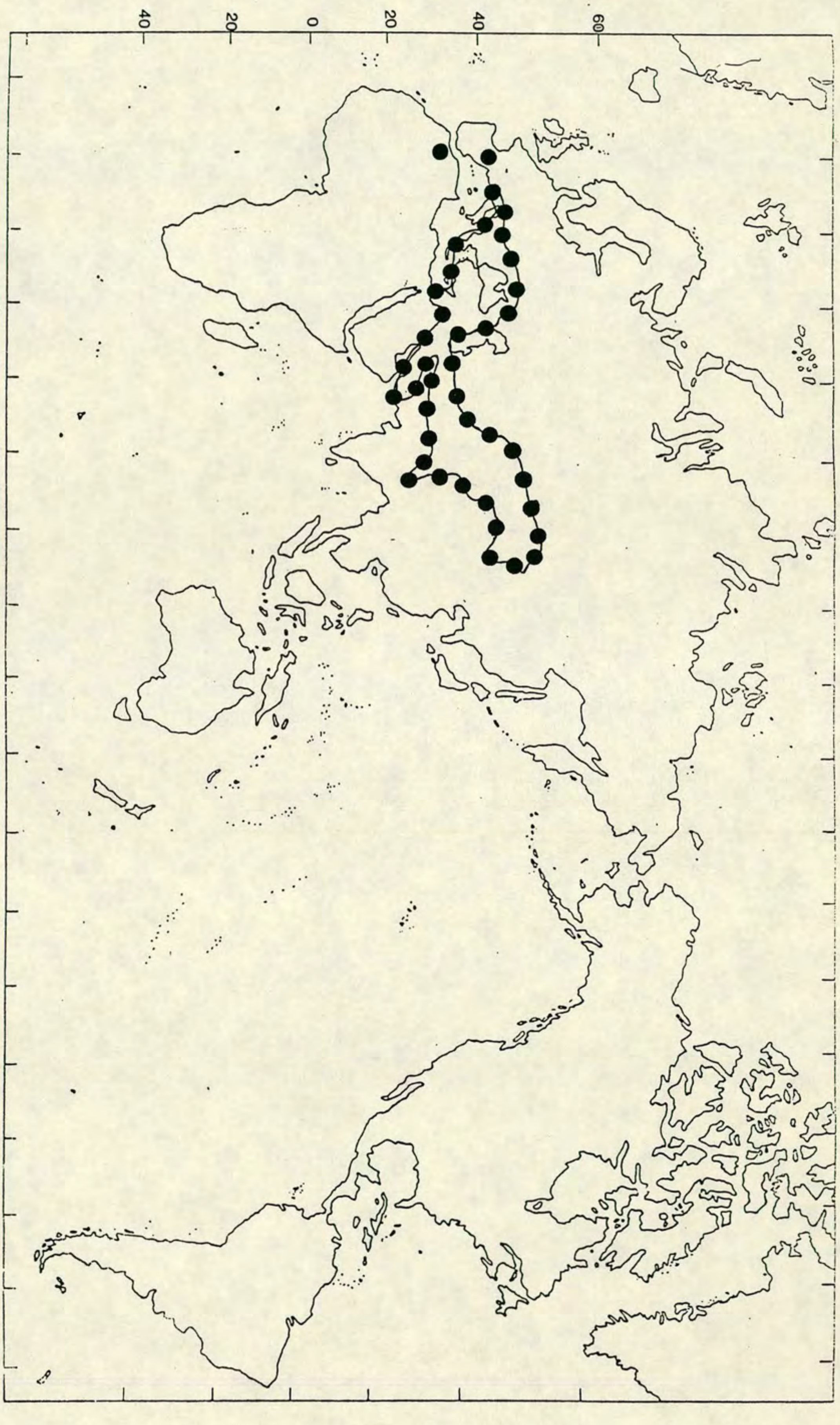


Fig.8.4 Distributions of Sections *Anaspis* (●), *Apeltanthus* (▼) and Subsection *Cystaspis* (■)

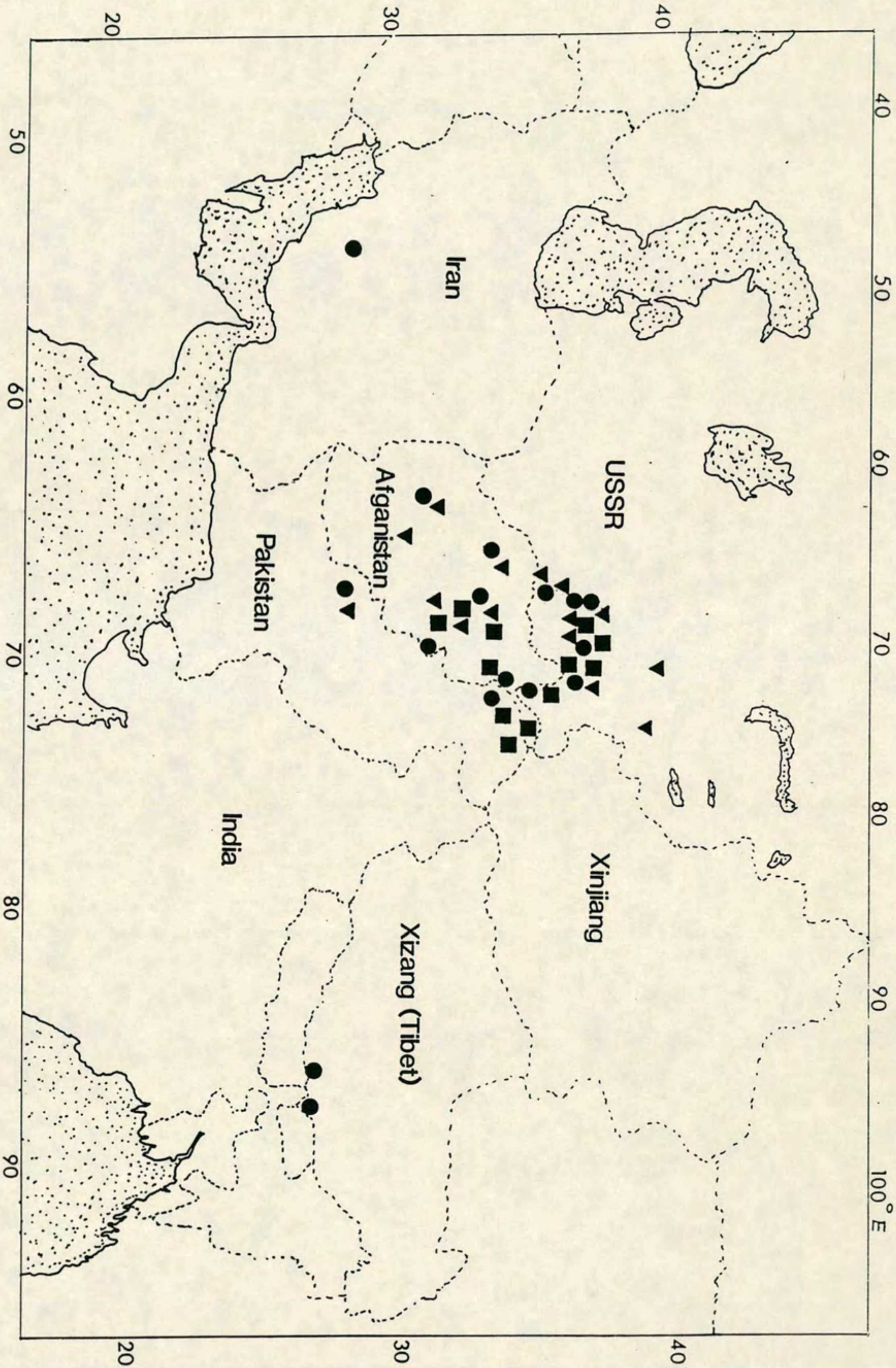


Table 8.1 Showing Sections and Species number present in Takhtajan's (1986) Floristic regions of the world. Number of endemics in brackets.

	Subgenus Scutellaria					Subgenus Lupulinaria			
Region	Section Salazaria	Section Perilomia	Section Salviifoliae	Section Anaspis	Section Scutellaria	Section Apeltanthus	Subsection Lupulinaria	Subsection Cystaspis	TOTAL
Circumboreal			3(2)		14(5)		31(30)		48(37)
East Asian					87(74)				87(74)
North American Atlantic					32(26)				32(26)
Rocky Mountain					8(2)				8(2)
Macaronesian					1(0)				1(0)
Mediterranean			3(2)		13(6)		3(0)		19(8)
E. Med.Province			3(2)		11(6)		2(0)		16(8)
Irano-Turanian			1	15(15)	11(2)	12(12)	70(65)	11(11)	120(105)
Madrian	1(1)				43(30)				44(41)
Sudano-Zambesian					4(4)				4(4)
Indian					6(2)				6(2)
Indochina					13(8)				13(8)
Malesian					3(1)				3(1)
Caribbean					25(15)				25(15)
West Indian Province					5(3)				5(3)
Central American Province					20(12)				20(12)
Andean		9(8)			22(19)				31(25)
Brazilian					5(3)				5(3)
Chile-Patagonian		3(2)			3(1)				6(3)
North-East Australian					2(2)				2(2)
Neozeylandic					1(1)				1(1)
TOTAL	1	11	5	15	242	12	119	11	

Table8.2. Showing Section and Species Number in the Irano-Turanian Region. Number of endemic species in brackets.

	Subgenus Scutellaria					Subgenus Apeltanthus			
							Section'Lupulinaria		
	Section Salazaria	Section Perilomia	Section Salviifoliae	Section Anaspis	Section Scutellaria	Section Apeltanthus	Sub-section Lupulinaria	Sub-section Cystaspis	TOTAL
1. Irano-Turanian Region			1	15(15)	11(2)	12(12)	70(65)	11(11)	120(105)
2. Mesopotamian Province									0
3. Central Anatonian Province			1(0)		4(0)			1(0)	5(0)
4. Armeno-Iranian Province				1(1)	5(1)		10(8)		16(10)
5. Hyrcanian Province					3(0)		4(2)		7(2)
6. Turanian Province					1(0)		1(1)		2(1)
7. Hindu Kush mountains of West Pakistan				4(4)	0	2(1)	10(6)	2(1)	18(12)
8. Pamir-Alay				9(9)	1(0)	10(9)	22(20)	8(8)	50(46)
9. Syr Darya					1(0)				1(0)
10. Tien Shan (including range in Sichuan)					1(0)	2(1)	32(30)		
11. Dungaria-Tarbagatai					1(0)		8(6)		9(6)
12. Mongolia					7(1)		4(1)		12(2)
13. Himalaya (Kashmir and East)				1(1)	7(4)		1(0)	1(0)	8(3)

1-6 as Takhtajan, (1986); 8-12 as delimated in Komarov et al., (1934-64).

greatest diversity, based on the number of sections and species, is in the Pamir-Alay range. The Hindu Kush and mountains of western Pakistan show similar diversity but fewer species. Both of these areas have very high degrees of species endemism, 92% and 67% respectively.

Discussion

Scutellaria is probably an ancient genus as it is isolated in the family and it is present in the Old and New Worlds. This is unlike very many isolated taxa which have localised distributions, e.g. Zhumeria Rech. f. & Wendelbo (Labiatae), is confined to S. Iran (Rechinger & Wendelbo 1967). The widespread, global distribution of Scutellaria is certainly not due to many readily dispersed species; weedy species are very rare in the genus. Only one species, S. galericulata, is present in both the Old and New Worlds and not even it has reached the geologically recent Pacific Islands.

One possibility is that Scutellaria crossed between Europe and North America before the North Atlantic opened in the Eocene, 55-40 million years ago (55-40 my) (Briggs 1987). Populus L. section Aigeros present in Europe and North America, but absent in Asia, may have migrated by this route. However it is unlikely that Scutellaria spread in this manner. If the genus was present in Europe in the Eocene it would be expected today to have a considerable amount of diversity in S.W. Europe, an area unglaciated in the Pleistocene. In fact, only 3 species are present here and only one of which, S. balearica, is endemic to the area. It could be argued that this lack of development is due to competition and lack of available habitats, but it is hard to believe that Scutellaria would now be so species-poor if it had been present here for at least 50 million years. Also if Scutellaria originated in Europe and North America in the Eocene it would still have to reach Central Asia, its area of maximum diversity today. Europe was isolated from Asia by the Turgai sea from the Jurassic to Oligocene (circa 155-40my) (Briggs 1987) and then any migration to Asia would be hampered by the Paratethys sea which covered a substantial part of Western Asia from the Mid-Miocene until the Pliocene (*circa* 15-3 my) (Adams 1981). As there is more diversity in Asia, it is more likely that *Scutellaria* migrated to Europe from Asia.

The other possibility is that *Scutellaria* crossed between the New and Old Worlds via Beringia. Beringia could serve as a migration route throughout most of the Tertiary (65-3 my) (Briggs 1987). This may have been interrupted by high sea levels between 12-10 million years ago, and intermittently during the Pleistocene (Hopkins 1967). *Scutellaria* probably did not cross Beringia in the glacial periods of the Pleistocene. Such a recent migration would make it hard to explain the areas of maximum variation at lower latitudes in both the Old and New Worlds.

Possibly it was the ancestral species of present day Section *Scutellaria* which crossed Beringia as this is the only section present in the Old and New Worlds. The species of this section are typically associated with mixed deciduous temperate forest. Such a forest linked Asia and North America via Beringia in the Mid-Miocene. These forests retreated south as the climate of Beringia became colder and drier in the late Miocene (Axelrod 1983). Examination of the migration of *Acer* by Wolfe (1984) show that these forests were probably in existence in the Eocene when this genus first crossed Beringia. Thus it is possible that *Scutellaria* crossed Beringia as a component of the herbaceous layer of these forests in the early to mid-Tertiary. (*circa* 65-40 my).

If it is assumed that a genus will be more diverse in an area that it has occupied for a longer period of time, having had opportunity to colonise a wide range of habitats; it should be possible to determine in which direction *Scutellaria* crossed Beringia in the early to mid-Tertiary. First, the diversity of this genus during this period must be analysed.

Section *Scutellaria* today is largely absent from Central Asia apart from the widespread *S. galericulata*. However, trees such as *Quercus*, *Tilia* and *Ulmus* which are often associated with species of Section *Scutellaria* are also absent here today, but fossil evidence shows that these trees to have been present in the Oligocene, (*circa* 40-30 my) (Kamelin 1967) Section *Scutellaria* may also have been present then, especially as Section *Anaspis*, which inhabits this area today, may have evolved from this section. (See later). Kamelin (1965, 1967) postulated the concept of Prashibljak* vegetation, a complex of *Quercus*, *Cedrus*, *Pinus* and *Pistacia* and herbs, such as *Eremurus* (Liliaceae), *Cousinia* (Compositae), *Ziziphora* (Labiatae) and *Eremostachys* (Labiatae), which developed in the Oligocene on the foothills of Central Asia. This vegetation is thought to have degraded with the onset of orogeny, continuing xerophilisation and cryophilisation in the late Miocene-Pliocene. The oak forests of the South Zagras mountains and the oak and cedar forests of Nuristan, in east Afghanistan, are thought to be impoverished relicts of this vegetation (Kamelin 1965). From present-day distributions (Figs. 8.3 & 8.4) it can be argued that the ancestors of Section *Anaspis* (Central Asia, Hindu Kush, South Zagros, Nuristan and possibly eastern Xizang (Tibet)), Section *Apeltanthus* (Central Asia, Hindu Kush, Nuristan) and Section *Lupulinaria* (mountains of Eurasia with the main development in Central Asia) were present in the prashibljak along with those of Section *Scutellaria*. Meanwhile, in North America only Section *Scutellaria* and possibly Section *Salazaria* were present. Thus it is possible that *Scutellaria* first migrated from Asia to North America sometime in the early mid-Tertiary. Later migrations across Beringia are also possible. Old and New World populations of *Scutellaria galericulata* are indistinguishable. Recent migrations of this species are likely as there must be sufficient geneflow to maintain this uniformity. Migration may even be occuring today by long-distance disposal. The nutlets of this waterside species float and could easily be transported by birds.

---

* from pra: a prefix, original or ancestral; and
shibljak: a Slav word for a deciduous shrub formation.

Morphological similarity between S. scordifolia from East Asia and S. angustifolia of western USA may also be attributable to more recent migration.

Due to the diversity which may well have been present in Central Asia in the early mid-Tertiary, (Sections Scutellaria, Anaspis, Apeltanthus and Lupulinaria), it is likely that this area is the centre of origin of Scutellaria. If not the place where it evolved from an ancient Labiate ancestor, then certainly it is the centre of origin of most of the different paths of evolution which have resulted in the range of variation that is seen today.

It may be that Section Scutellaria, which has the simplest form of inflorescence, is the most primitive section of the genus. It is also the only taxon present in the Old and New Worlds. This distribution may be accounted for by the ecological conditions of Beringia, which only allowed the migration of Section Scutellaria and not any other infrageneric taxon of Scutellaria. Thus the distribution does not necessarily indicate that Section Scutellaria was the most widespread taxon in the early to mid-Tertiary.

Phytogeography and Radiation of Scutellaria in the New World

After invading the New World the ancestors of Scutellaria Section Scutellaria would have spread south finding new habitats, and speciating. Today in North America the section has most species in eastern USA. The Pleistocene glaciations would have largely removed the genus from Canada and the deterioration of the climate in the north over the last 3000 years (Kozhevnikov 1979) would have driven the section south to its present northern boundary. Section Scutellaria is poorly represented in the Rocky Mountains and western USA. This may be accounted for by the uplift of the western mountains and the associated xeric climate which developed and continued in the late Miocene, (circa 15-6 my), to the present day (Briggs 1987). This change would have resulted in the extinction of many species. The eastern United States would not have been affected by such changes and so maintains its species diversity.

In the New World, Section Scutellaria shows most diversity in the mountains of Mexico and the northern Andes, where forms with red flowers, spirally arranged flowers or a combination of both, occur together with the usual forms with secund, opposite, blue, white or pink flowers. Migration between North and South America was possible in the early Tertiary, as shown by the fact that Cretaceous marsupials are found in both North and South America and caviomorph rodents reached South America from the north in the Eocene, (Briggs 1987). Nevertheless, it is unlikely that Scutellaria crossed to South America before the end of the Tertiary, (circa 3 my), because the high Andean habitats which Scutellaria occupies did not exist until then. (Simpson 1975). A permanent land connection between the two continents was formed 3-5 million years ago which would have enabled Scutellaria to enter South America. Such a recent arrival implies that the genus has undergone a vast amount of speciation and diversification and produced remarkable floral variation in the Andes in a very short time. How may this burst of evolution be explained? Simpson (1975) demonstrates that Scutellaria and other upper montane forest elements in Colombia, Venezuela, Ecuador and the eastern slopes of the Peruvian Andes may have extended their ranges during the Pleistocene glaciation when vegetation zones were lowered. In the now arid Andes of western Peru the glacial climate produced humid conditions which would also allow the expansion of the genus. Isolated populations would result when the vegetation zones were raised in the north and east Andes and when arid conditions returned to western Peru during inter glacial periods. Repeated cycles of climate change, presence of bird pollination which would provide the selection pressure for evolution of red, long tubed corollas, and migrations back and forth across Central America in the Pleistocene are probably responsible for the present diversity within Section Scutellaria present in the Andes and Sierra Madre. A similar diversity in corolla form is apparent in South and Central American members of the labiate genera Salvia L. and Satureja L. sensu lato.

From the northern Andes, where Section *Scutellaria* has its maximum development in South America, the Section appears to have migrated along the southern border of the Amazon basin to the coast of Brazil and also down the Andes to as far south as Tierra del Fuego. *S. nummulariifolia* probably reached the Falkland Is. by long distance dispersal. This is presumably also how the section reached the West Indes. It may have been transported by man. The very attractive *S. ventenatii*, native in Colombia and Venezuela, is widely naturalised on the West Indies.

Sect. *Perilomia* probably arose in Peru, where the highest number of species and endemic species are found, as shown in the table below.

Area	No. of Species	No. of Endemic Species
Colombia	2	0
Peru	7	3
Ecuador	5	1
Argentina	2	1
Chile	1	1

The taxon seems to have spread out from Peru-Ecuador, having fewer species at the edge of its area. Section *Perilomia* probably diversified from Section *Scutellaria* during the climatic changes of the Pleistocene, and is thus of comparatively recent origin.

The monotypic Section *Salazaria* may be a relict taxon like several mono- and di- typic genera in the Compositae (*e.g.* *Phalacroseris* A. Gray and *Chaetadelpha* A. Gray) found in California. These are thought to have migrated across Beringia by hopping from one xeric environmental pocket to another during the early-Tertiary (Stebbins & Major 1965). However Section *Salazaria*, which is absent in the Old World, occupies a wide geographical area from California and S. Utah to Chihuahua. This widespread colonisation of semi-desert environment does not seem typical of a genetically impoverished, early-Tertiary invader. Neither has Section *Salazaria* undergone speciation to form large, complex groups, like Erigeron L. (Compositae) and Astragalus L. (Leguminosae), which are also thought to be early-Tertiary invaders (Stebbins & Major 1965). It is more likely that Scutellaria mexicana is the produce of a later adaptive radiation from Section Scutellaria, which it strongly resembles. The chromosome number of S. mexicana is 50. This is high for Scutellaria and may indicate a high level of ploidy. This species may have evolved from some suffruticose diploid member of Section Scutellaria which was adapted to xeric environments but is now extinct. This hypothetical ancester may have resembled S. resinosa or S. suffrutescens whose ploidy levels are unknown. Generally, there are very few polyploid species of Scutellaria. The only ones identified as such are all North American members of Section Scutellaria: S. latiflora (88 chromosomes), S. churchilliana (60) (Gill & Morton 1978).

The Phytogeography and Radiation of Scutellaria in the Old World

Section Scutellaria in the northern Old World seems adapted to more mesic, lowland habitats than are Section Anaspis and Subgenus Apeltanthus. It is best developed, i.e. has the most species, in eastern Asia. This area was not glaciated in the Pleistocene, unlike northern Asia and much of Europe where the section has few species, today at least. The low number of species in Europe may also be explained by the late arrival of this taxon. From the mid-Miocene to the Pliocene (circa 15-3 my), the Paratethys Sea, and the Turgai Sea earlier, would have provided considerable barriers to migration (Briggs 1987, Adams 1981).

Of the four species present in the islands of Indonesia and New Guinea, two, S. indica and S. discolor, are widespread in continental South East Asia. This suggests a recent arrival in these areas as isolation has not produced many endemic species. The two species in South East Australia may also have arrived recently. Briggs (1987) suggests that the rodent family Muridae reached Australia by island-hopping down the East Indian chain in the Pliocene, and that the genus *Rattus* arrived even later in the Pleistocene. *S. mollis* and *S. humilis* may be isolated relicts evolved from a previously widespread *S. javanica* - like ancestor, now surviving only in the extra-tropical mountains of S.E. Australia. Such a widespread distribution could have occurred during the Pleistocene glaciation when the islands of south east Asia would have attached to the mainland and New Guinea would be linked to Australia as the sea level dropped. (Briggs 1987). *S. novae-zealandica* probably reached New Zealand from Australia. Many species and 75% of genera of New Zealand seed plants are shared with Australia (Briggs 1987). Such a migration may have occurred during the glacial period when sea level was lower.

The disjunction of Section *Scutellaria* between North East India on one hand and the Western Ghats and Sri Lanka on the other, (See map 1 & 2), probably also dates from the Pleistocene. 3 of the 4 species present in Western Ghats are also present in North East India Kurup (1974) suggests that such disjunctions are due to taxa widespread across the Deccan peninsula in glacial periods contracting into refugia. *Scutellaria* has died out on the rest of the Deccan peninsula because of dry conditions, but has survived in the Western Ghats and Sri Lanka which have a climate similar to that of North East India.

The fact that Section *Scutellaria* is represented in the temperate mountains of the Sudan and east Africa by only one species group, suggests that the taxon has also arrived here recently. If it had been present in these mountains for a long time, it would be expected that the genus would show much more diversity.

Section *Scutellaria* is now largely absent from Iran, Afghanistan and Central Asia. (See Table 8.2). Nutlet anatomy suggests that the ancestors of Section *Anaspis* were similar to members of the *S. albida* species group. (Section *Scutellaria*). Section *Anaspis* probably diverged from Section *Scutellaria* before the latter was driven from this area by the continuing xerophilisation which began in the mid-Tertiary. The testudinate calyx characteristic of Section *Anaspis* is displayed by Section *Apeltanthus* which is also chasmophytic. This character may be an adaptation to the rock crevice habitat. The S. Iran-Afghanistan disjunction shown by Section Anaspis is also demonstrated by Fritillaria imperialis L. (Liliaceae) (Hedge & Wendelbo 1978). This disjunction is probably a result of fragmentation of a much wider distribution. S. tibetica, possibly a synonym of S. kingiana Prain, may also belong to this section. Found in the eastern Himalaya (Fig. 8.4), the species may represent a relict of an earlier eastern expansion of this taxon through Tibet.

Subgenus Apeltanthus has its area of maximum diversity in the Pamir and Hindu Kush mountains. Radiating out from this area, the number of species and level of diversity decreases, only Section Lupulinaria, Subsection Lupulinaria being present at the edge of the range of Subgenus Apeltanthus. This pattern of distribution and variation is shown by several other genera, e.g. Eremostachys Bunge in Ledeb., (Labiatae). Acantholimon Boiss. (Plumbaginaceae); and Eremurus M. Bieb. (Liliaceae) (Hedge & Wendelbo 1970). These Central Asian mountains have also been considered the centre of diversity of the Labiate genera Salvia and Perovskia (Hedge & Wendelbo 1970). Both Section Lupulinaria Subsection Cystaspis and Section Apeltanthus are restricted to this area of maximum diversity of the Subgenus as a whole. Both taxa show a high degree of endemism, species being found either in Pamir-Alay, W. Tien Shan or the Hindu Kush and mountains of Western Pakistan (See Table 8.2).

Section Lupulinaria is the most widespread taxon of this subgenus ranging from the Altai in the east to mountains of Morocco in the west (See Fig. 8.3). Again Section Lupulinaria shows the greatest number of species in the Tien Shan and Pamir mountains but, unlike the genera listed above, it shows development in the Caucasus with 24 species, 22 of which are endemic. Scutellaria orientalis s.l. shows a disjunction between Spain and Morocco in the west and the Balkans in the east. This disjunction is also shown by the vicariads Lonicera nummulariifolia and L. arborea

(Caprifoliaceae). Davis & Hedge (1971) suggest that these taxa may have migrated westwards through South and Central Europe in interglacial periods; glaciation having caused extinction in Central Europe. If this is so then Section Lupulinaria may have been much more widespread than it is now.

Due to its unknown origin and intermediate nature, consideration of Section Salviifoliae has been delayed until last. It is a small section with only five species, only one of which, S. salviifolia Benth., is widespread. See Fig. 8.2 and Table below - Provinces as Takhtajan (1986).

	No. of species	No. of endemic species
Euxine Province	3	2
Central Anatolian Province	1	1
East Mediterranean Province	3	2

This distribution is consistent both with Salviifoliae being a newly evolved taxon, separated from Section Lupulinaria, or from a S. rubicunda/S. albida-like ancestor belonging to Section Scutellaria, as both these groups have morphological similarities and both are represented in the area.

Obviously the mountains of Central Asia and Afghanistan are important centres of speciation and variation in Scutellaria. The area has a wide diversity of suitable habitats; steppes, woods, forests, rock crevices and screes. It was probably not glaciated in the Pleistocene, (Kamelin 1967), so the stock of genetic diversity built up in the area since the mid-Tertiary would not have been depleted. The large number of endemic species in this area may be due to the changes which have occurred more recently in geological time, notably the uplift of the Hindu Kush. This would have provided new habitats and also deprived the Pamirs of monsoons so leading to increased aridity in the area in the late Pleistocene. These changes would have isolated populations and led to speciation.

Viewing the genus as a whole over its entire distribution, there are striking phytogeographical similarities with Salvia, the other large widespread, sub-cosmopolitan genus in the Labiatae. Both have a centre of maximum variation in Central Asia, both seem impoverished in North America and well developed in South America. (Salvia has c.50 species in North America and c.250 in South America) and both are poorly represented in Australia, Indonesia and East Africa. However unlike Scutellaria, Salvia is also present in the Cape of Africa and Madagascar. (Hedge 1986)

The distribution of Scutellaria is also similar to that of Rumex L. (Polygonaceae) except the latter is present in Hawaii and the Cape of Africa.

CHAPTER 9

Dispersal: Form and Function.

As previously indicated, calyx and nutlet characters are important in the taxonomy of Scutellaria. This chapter aims to comment on their possible role in dispersal. This is only a preliminary investigation because my observations were limited by the lack of time. Much field work remains to be done. However, the function of the various forms of the calyx and the fascinating ornamentation of the nutlets deserves some consideration.

I have tried to relate form to function. In some cases this may be inappropriate, the form having lost its function during the course of evolution, or being accidental, perhaps the result of genetic linkage to another important character. It is also possible that the form is the result of genetic drift. However, the observations and speculations presented here may encourage other workers to undertake field study of the dispersal biology of this interesting genus.

In all species of Scutellaria, the mouth of the calyx is closed in fruit by the two lips being pressed together. This presumably serves to protect the ripening nutlets. This protection of the fruit by a closed calyx is not an isolated phenomenon in the Labiatae. For example, in Origanum L. the mouth of the calyx is thickly bearded, closing off the interior. In, for instance, Ocimum L. and Lallemantia Fisch. & Mey. the lateral and lower calyx teeth converge over the mouth, thus enclosing the nutlets. The upper calyx lobe in these genera is broad and turned upwards, and reminiscent of the scutellum of Scutellaria Section Scutellaria. The problem in these plants with enclosed nutlets is how the fruit can be released from the protective, closed calyx.

Nordhagen (1936) described the dispersal process in S. altissima. My observations are in agreement with his. At maturity the nutlets fall from the gynophore and lie loose in the closed calyx. They can be heard to rattle if the plant is shaken. The pedicel is very springy at this stage of development. If the scutellum is pushed by a passing animal or the stems of neighbouring plants, the whole calyx is bent downwards. The scutellum and upper lip are completely removed from the lower lip by this force and the lower lip, now free, springs back to its original position catapulting the nutlets out up to a distance of 2½m. Nordhagen (1936) suggests that the wind and rain during stormy weather may provide the initial force on the scutellum. Experiments reveal this to be unlikely as water fired at pressure from a syringe at close range does not produce enough force to remove the upper lip of the mature calyx of *S. altissima*.

A similar catapult mechanism exists in *Aeollanthus ambustus* Oliv. (Ryding 1986). In this case the distal part of the calyx is removed by the initial force and the basal part then functions as a catapult throwing out the nutlets.

Dispersal in *Lallemantia* and *Ocimum* is facilitated by a similar mechanism. The broad upper calyx lip, like the scutellum of *S. altissima*, catches on an animal, neighbouring plant stems or is hit by rain drops whereupon the whole calyx is bent upwards or downwards. When the pressure is released the calyx springs back to its original position and the nutlets are fired out between the convergent lateral and lower teeth. When viewed in this context the scutellum of *Scutellaria* is not such an odd character as it would first appear.

How typical of *Scutellaria* is the dispersal mechanism shown by *S. altissima*? During field work in Turkey I observed a similar dispersal mechanism in *S. albida* and *S. salviifolia*. Species of Section *Lupulinaria* Subsection *Lupulinaria* show a slight variation on the mechanism displayed by these species. The plants of this taxon have flattened pedicels which are adpressed to the stem, like those of *Lallemantia*, so providing a stronger catapulting force. In *S. orientalis* subspecies *pinnatifida* the cucullate bracts clasp the calyx preventing the scutellum and calyx from being pushed downwards. Not until the fruits are ripe do the bracts fall away. The nutlets are then dispersed in a similar manner to those of *S. altissima*.

However, this mechanism is not shown by *S. galericulata*. As noted by Nordhagen (1936), the pedicel of this species is less elastic and the scutellum is not as large as that of *S. altissima*. *S. galericulata* grows by watersides and the inflorescences often hang over water. Passing animals, stems of other plants, or even water at high river levels, are able to remove the upper lip of the calyx by dint of pressure on the scutellum. The fruits are not catapulted away from the plant but drop outward and downward. The fruits of *S. galericulata* float and water is probably its main dispersal vector. The nutlets can float in water for at least a month and still germinate. Kölpin-Ravn (1894) suggested that the nutlets of *S. galericulata* could float because the pericarp was composed of air-filled cells. However, the nutlets of *S. albida* and *S. altissima* do not float even though they have a pericarp composed of similarly vacuolate cells and also air-filled spaces within the larger papillae. As the nutlets of *S. albida*, *S. altissima* and *S. galericulata* have similar volumes, it may be that the buoyancy of the nutlets of *S. galericulata* is due to the chemical composition of the cell walls themselves rather than the air spaces which they surround.

The long viability in water and possible transport by water birds may explain the present widespread distribution of *S. galericulata*.

The scutellum in Section *Lupulinaria* Subsection *Cystaspis* is very large and inflated. This taxon grows where animals seldom tread and other vegetation is scarce. The membranous-inflated scutellum may be an adaptation further encouraging wind removal of the upper lip of the calyx after the cucullate bracts have fallen off. Juzepczuk (1954) suggests mountain streams may aid dispersal.

What of members of *Scutellaria* which lack a scutellum? Section *Apeltanthus* and Section *Anaspis* contain chasmophytes. In these habitats no explosive mechanisms are needed for dispersal as the nutlets will be carried by gravity far from the plant by the surrounding steep slopes. Further, there are no animals or waving branches of other plants around to 'trigger' a scutellum and remove the upper lip of the calyx. Thus it may be that the scutellum, no longer having a function in this habitat, has been lost from Section *Apeltanthus* and Section *Anaspis* during the course of evolution. However this explanation raises two questions. Why has the scutellum been lost in those members of Section *Perilomia* which have testudinate calyces and inhabit the S. American paramos, *i.e.* are surrounded by vegetation? Also, how are the testudinate calyces in Section *Anaspis*, *Apeltanthus* and *Perilomia* opened to release the nutlets? Clearly much field work is still needed.

The calyx of *S. mexicana*, (Section *Salazaria*), would appear to be an adaptation to wind dispersal. Examination of about 90 herbarium specimens showed that the calyx detaches from the plant as a whole rather than losing just its lip. The nutlets may be thrown out of the calyx at a later date. *S. utriculata* may have a similar dispersal mechanism. Field study is required to corroborate these observations and also to determine the function of the scutellum of *S. utriculata*.

The nutlets of *Scutellaria* are variously ornamented: they can be smooth, papillate or ridged, and have hairs glands or hooks. (See Chapter 4. The Taxonomic Characters).

Nordhagen (1936) suggested that the various kinds of nutlet ornamentation serve to prolong the contact of the nutlets with the lower lip of the calyx and so maximise the catapulting action. This does not explain the ornamentation of the nutlets in species which do not have the *S. altissima* mechanism of dispersal, unless of course that has been lost. There are four likely explanations for the various kinds of nutlet ornamentation.

(1) *Protection*. The pericarp functions to protect the seed, so to some extent all characters of nutlet ornamentation have this function. Conceivably nutlet ornamentation may reduce palatability, or even be a light means of increasing size, hence restricting ingestion. The various forms of papillae, ridges and hairs may serve to form a layer of

air around the fruit. The microclimate thus created may protect the seed during unfavourable conditions, so prolonging viability.

(2) Aids to dispersal.

The nutlet hairs of Section Anaspis are relatively very long. These may allow the nutlet to be carried further in air currents in the exposed chasmophytic environment. Perhaps this compensates, to some extent, for not having a catapult dispersal mechanism. The nutlets of Section Anaspis and the S. albida species-group (Section Scutellaria) may help to enlarge the surface area of the seed without adding weight. This would be an advantage if the seeds were wind dispersed. The cavities of the fruit of Prangos Lindl. (Umbelliferae) may also have this function (Pijl 1982).

The nutlet hooks of S. discolor, S. ocymoides and the S. violacea species-group may catch on to animals and so aid dispersal.

(3) Soil anchorage.

The hairs of S. albida join together when wet to form patent spikes (See Fig. 9.1). These might dig into the soil and prevent the nutlet from being dislodged. The hooks on the nutlet mentioned above may also help adhesion to the soil. Many Labiates produce nutlet mucilage which anchors the fruit to the soil. No species of Scutellaria is so far known to produce mucilage. None did so in this study.

(4) No function

Nutlets of several species, e.g. those of S. galericulata have glands on their surfaces, but these do not seem to be excretory when the nutlet is mature. Low temperature S.E.M. shows that glands on the ovary of S. galericulata excrete some substance before the calyx closes and the nutlets start to ripen. (See Fig. 9.2a). S. albida also has excretory glands at this stage but loses

Fig. 9.1. Hair of the imbibed nutlet of *S. albida* . Mag. x 110.

Fig. 9.2. *Glands of Developing Nutlets.*

(a) Excretory glands on the ovary of *S. galericulata*. Mag. x 220.

(b) Glands on the immature nutlet of *S. albida*. Mag. x 125.

(c) Four ovaries of *S. galericulata* partially covered with an excretion, presumably nectar. Mag . x 55.

Fig. 9.1 HAIRS OF THE IMBIBED NUTLET OF S.ALBIDA

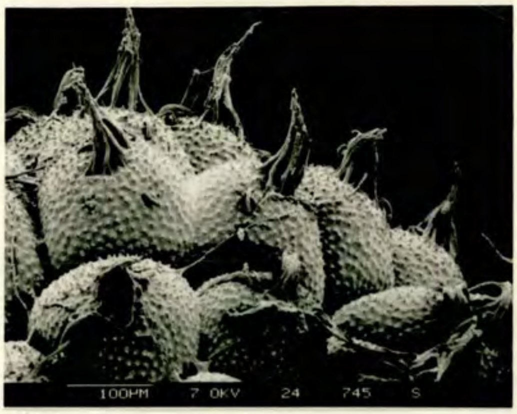
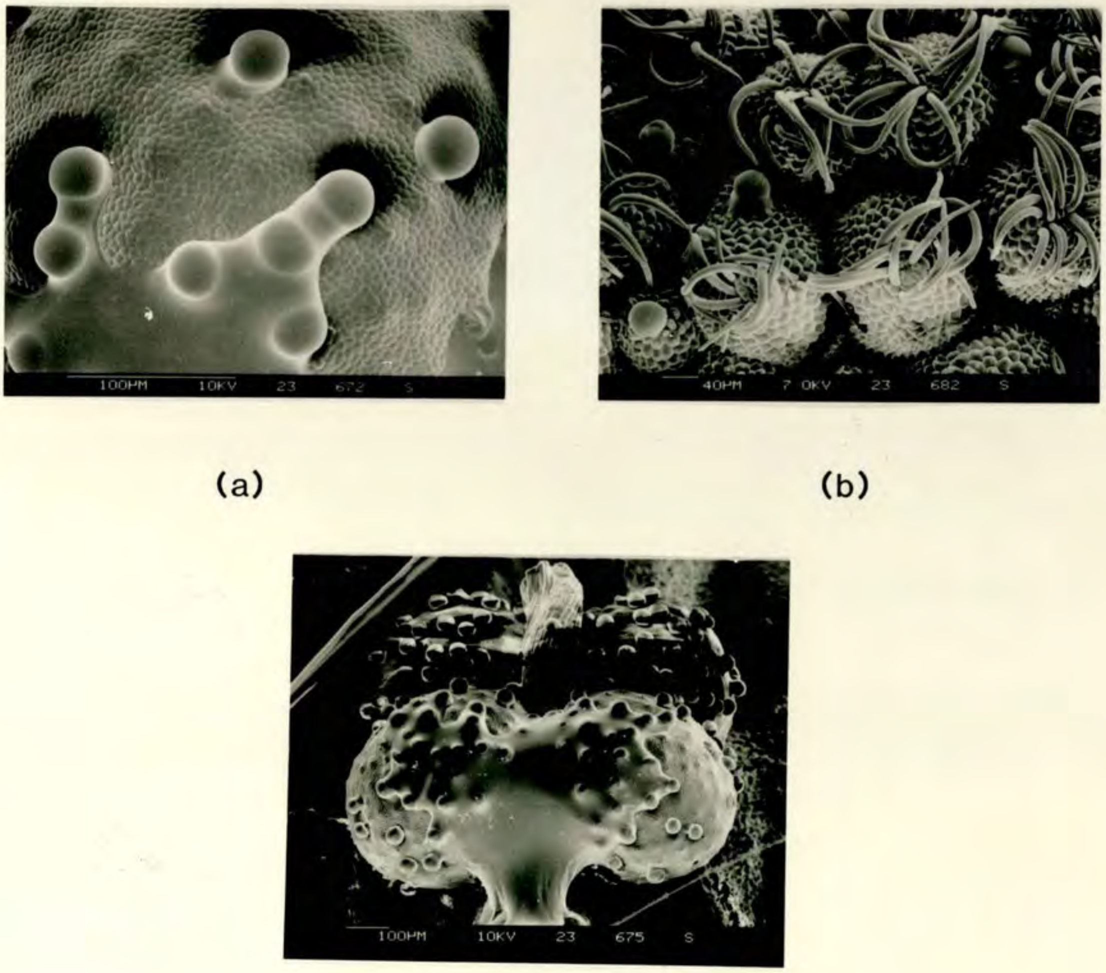


Fig. 9.2 GLANDS OF DEVELOPING NUTLETS



(a)

(b)

(c)

them as the nutlets mature. (See Fig. 9.2b). These glands may function as auxiliary nectaries. (See Fig. 9.2c). Perhaps the exterior glands of the mature pericarp of S. galericulata are non-functional relics of an earlier development stage. The internal pericarp glands, seen in most species, also do not seem to be excretory at nutlet maturity. Perhaps they also have an earlier developmental function.

REFERENCES

Titles of periodicals are abbreviated according to *Botanico-Periodicum-Huntianum* (Hunt Botanical Library Pittsburg, Pa. 1968).
Periodicals which are not abbreviated in this work are cited in full.

Adams, C.G. 1981. An outline of Tertiary paleogeography. Cocks, L.R.M., ed. *The Evolving Earth*: 221-235. Cambridge: University Press.

Ashlock, P.D. 1971. Monophyly and associated terms. *Syst. Zool*. 20: 63-69.

Axelrod, D.I. 1983. Biogeography of oaks in the Arcto-Tertiary Province. *Ann. Missouri Bot. Gard*. 70: 629-657.

Barkley, W.F.A. 1975. A note concerning two flowering plants *Phytologia* 32: 304.

Bauhin, C. 1596. Phytopinax: 4~~2~~70. Basle: Sebastianum Henripetri.

Bauhin, C. 1623. *Pinax theatri botanici*: 231. Basle: Ludovici Regis.

Bauhin, C. 1671. *Prodromus theatri botanici* ed. 2: 110-111 Basle: Johanis Regis.

Bentham, G. 1832. *Scutellaria alpina* var. *lupulina* /includes a list of all known species/ *Edward's Bot Reg*. 18: *t* 1493.

Bentham, G. 1832-1836. *Labiatarum genera et species*. London: Ridgeway.

Bentham, G. 1834. *Scutellaria* and *Perilomia* in: *Labiatarum genera et species*: 416-446 London: Ridgeway.

Bentham, G. 1848. *Scutellaria* and *Perilomia* in: Candolle, A.P. de, *Prodromus systematis naturalis* 12: 412-432. Paris.

Bentham, G. 1876. *Scutellaria*, *Salazaria* and *Perilomia* in: Bentham, G. & Hooker, J.D. *Genera Plantarum* 2: 1201-1203. London: Lovell Reeve & Co.

Boissier, P.E. 1879. *Scutellaria* in: *Flora Orientalis* 4: 681-691. Basle, Geneva: H. Georg.

Bothmer, R. von, 1985. Differentiation patterns in the *Scutellaria albida* group (Lamiaceae) in the Aegean area. *Nordic Journal of Botany*, 5: 421-439.

Bothmer, R. von, 1987. Differentiation patterns in the E. Mediterranean *Scutellaria rubicunda* group. (Lamiaceae) *Plant Systematics and Evolution* 155: 219-249.

Briggs, J.C. 1987. *Biogeography and plate tectonics* (Developments in Paleontology and Stratigraphy, 10). Amsterdam: Elsevier.

Britton, N.L. & Brown, A. 1913. *An Illustrated Flora of the northern United States*. 2nd. ed. New York.

Briquet, J. 1895-97. Labiatae in: Engler, A. and Prantl, K.A.E. *Die natürlichen Pflanzenfamilien* ed. 1 4.3a: 183-184.

Briquet, J. 1896. *Scutellaria*, *Salazaria* and *Perilomia* in: Engler, A. and Prantl, K.A.E. *Die natürlichen Pflanzenfamilien*. ed. 1. 4.3a. [*Scutellaria* and *Salazaria*: 224-227; *Perilomia* : 232-233; Position of seed: 199].

Cantino, P.D. & Sanders, R.W. 1986. Subfamilial Classification of Labiatae. *Syst. bot*. 11: 163-185.

Caruel, M.T. 1886. Sur la nouvelle famille des Scutellariacées. *Bull. Soc. Bot. France* 33: 226-268.

Clapham, A.R., Tutin, T.G. & Moore, D.M. eds. 1987. *Scutellaria* in: *The Flora of the British Isles*. 3rd ed.: 417-418 Cambridge: University Press.

Clifford, H.T. & Stephenson, W. 1975. *An introduction to numerical classification*. New York: Academic Press.

Clos, D. 1849. Theresa in: Gay, C. ed., *Historia fisica y politica de Chile*..... *botanica* 4: 497-498. Paris. E Thunot y ca.

Collins, J.L. 1976. *A revision of the annulate Scutellaria* Ph.D. thesis. Vanderbilt University, Nashville, Tennessee.

Colonna, F. 1606. *Εκφρασις* ed. 1 Rome: Guilelmum Faciottum.

Colonna, F. 1616. *Cassida* in: *Εκφρασις* ed. 2: 187. Rome: Jacobum Mascardum.

Cortuso, J. A. 1591. *Scutellaria* in: *L'horto dei simplici di Padova*. Venice: Girolamo Porro.

Crisci, J.V. & Stuessy, T.F. 1980. Determining primitive character states for phylogenetic reconstruction. *Syst. Bot*. 5: 112-135.

Davis, P.H. & Hedge, I.C. 1971. Floristic links between North-West Africa and South West Asia. *Ann. Naturhist Mus. Wien*. 75: 43-57.

Day, W.H.E. 1983. Computationally difficult parsimony problems in phylogenetic systematics. *Journal of Theoretical Biology* 103: 429-438.

Donoghue, M.J. & Cantino, P.D. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. *Syst. Bot.* 9: 192-202.

Edmondson, J.R. 1982 *Scutellaria* in: Davis, P.H., ed. *Flora of Turkey* 7: 78-100 Edinburgh: University Press.

El-Gazzar, A. & Watson, L. 1970. Some economic implications of the taxonomy of Labiatae. Essential oils and rusts. *New Phytol*. 69: 487-492.

Epling, C. 1942. American species of *Scutellaria*. *Univ. Cal. Publ. Bot*. 20: 1-146.

Epling, C. 1955. *Harlanlewisia* a recently discovered genus of Labiatae. *Amer. J. Bot*. 42: 436.

Epling, C. & Jativa, C. 1968. *Harlanlewisia* in: Supplementary notes on American Labiatae x. *Brittonia*: 20: 295-313

Erdtman, G. 1945. Pollen morphology and plant taxonomy iv. Labiatae, Verberaceae and Avicenniaceae. *Svensk. Bot. Tidskr*. 39: 279-285.

Felsenstein, J. 1982. Numerical methods of inferring evolutionary trees. *Quart. Rev. Biol*. 57: 379-404.

Funk, V.A. & Stuessy, T.F. 1978. Cladistics for the practising plant taxonomist. *Syst. Bot*. 3: 159-178.

Gams, H. 1927. *Scutellaria* in: Hegi, G., ed. *Illustrierte Flora von Mittel-Europa* 5.4: 2508-2518.

Gill, L.S. & Morton, J.K. 1978. *Scutellaria churchilliana* - hybrid or species? *Syst. Bot*. 3: 342-348.

Gower, J.C. 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27: 857-871.

Graham, R.L. & Foulds, L.R. 1982. Unlikelihood that minimal phylogenies for a realistic biological study can be constructed in reasonable computer time. *Mathematical Biosciences*. 60: 133-142.

Gray, A. 1872. *Scutellaria* in: Notes on Labiatae *Proc. Amer. Acad. Arts*. 8: 367-372.

Grossheim, A.A. 1945. Caucasian representatives of Section *Lupulinaria* Ham. of genus *Scutellaria* L. *Izv. Azerbajdžansk Fil*. 3: 79-90. /In Russian; Section *Heteranthesia*: 89/

Hagemann, J.M., Earle, F.R. & Wolff, I.A. 1967. Search for new industrial oils. xiv. Seed oils of Labiatae. *Lipids* 2: 371-380.

Hamilton, A. 1832. *Esquisse d'une monographie du genre Scutellaria ou toque*. Lyon: Louis Perrin.

Hedge, I.C. 1968. Studies in the flora of Afghanistan: viii Labiatae: conclusions and key to genera *Notes Roy. Bot. Gard. Edinburgh*. 28: 163-172.

Hedge, I.C. 1982. *Salvia* in: Rechinger, K.H., ed. *Flora Iranica* 150: 403-476. Graz: Akademische Druck-u. Verlagsanstalt.

Hedge, I.C. 1986. Labiatae of South-West Asia: diversity, distribution and endemism. *Proc. Roy. Soc. Edinburgh*. 89B: 23-35.

Hedge I.C. & Wendelbo, P. 1970. Some remarks on the endemism in Afghanistan. *Israel Journal of Botany* 19: 401-417.

Hedge, I.C. & Wendelbo, P. 1978. Patterns of distribution and endemism in Iran. *Notes. Roy. Bot. Gard. Edinburgh* 36: 441-464.

Hitchcock, A.S. & Green, M.L. 1929. *International Botanical Congress Cambridge (England), 1930 Nomenclature Proposals by British Botanists*: 166.

Holmgren, P.K., Keuken, W. & Schofield, E.K. 1981. *Index Herbariorum Part 1. The herbaria of the world*. ed. 7. Hague/Boston: Junk.

Hopkins, D.M. 1967. Cenozoic history of Beringia - a synthesis. in Hopkins, D.M., ed. *The Bering Land Bridge*: 451-484. Stanford: University Press.

Jeffree, C.E., Read, N.D. Smith, J.A.C. & Dale, J.E. 1987. Water droplets and ice deposits in leaf intercellular spaces: redistribution of water during cryofixation for S.E.M. *Planta* 172: 20-37.

Johansen, D.A. 1940. *Plant microtechnique* London/New York: McGraw-Hill.

Juzepczuk, S.V. 1951. *Scutellarum* novarum decades i-vi. *Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk. SSSR* 14: 356-435. [In Russian].

Juzepczuk, S.V. 1954. *Scutellaria* in: Shishkin, B.K. & Juzepczuk, S.V. eds. *Flora URSS* 20: 71-225. Moscow: Academiae Scientarum URSS [In Russian].

Kamelin, R.V. 1965. Generic endemism of the flora of Central Asia *Bot. Zhurn.* (*Moscow* and *Leningrad*) 50: 1702-1710 [National Lending Library for Science and Technology, Russian Translating Programme RTS 4383].

Kamelin, R.V. 1967. Some remarkable anomalies in the flora of the Central Asiatic mountain province. *Bot. Zhurn.* (*Moscow* and *Leningrad*) 52:447-460.[National Lending Library for Science and Technology, Russian Translating Programme RTS 4381].

Kølpin-Ravn, F. 1894. Sur la faculté de flottez chez les grains de nos plantes aquatiques *Bot.Tidsskr.* 19:178

Komarov, V.L. & Shishkin, B.L. et al. (eds) 1934-1964. *Flora URSS*. 30 vols. Moscow: Academie Scientarum URSS.

Kooiman, P. 1972. The occurrence of iridoid glycosides in the Labiatae. *Acta Bot. Neerl.* 21:417-427

Kozhevnikov, J.P. 1979. The historical interpretation of the modern peculiarities of the Chukotsk and Arctic Floras. (of vascular plants) *14th Pacific Science Congress Abstract Committee*:217-218.

Kudo, Y. 1929. *Scutellaria* in :Sino Japonicarum Prodromus. *Mem. Fac. Sci. Taihoku Imp. Univ.* 2:250-272.

Kunth, C.S. 1818. *Perilomia* in:Humboldt, A., Bonpland, A.,& Kunth, C.S. *Nova Genera et Species Plantarum* 2:326-329. Paris.

Kurup, G.U. 1974. Mammals of Assam and the mammal geography of India, in Mani, M.S. ed.,Ecology and Biogeography in India: 585-613.Hague: Junk

Linnaeus, C. 1735. *Scutellaria* in:*Systemma Naturae* ed.1.,Lieden:Theodore Haak. [listed under Order *Didynamia*]

Linnaeus, C. 1753. *Scutellaria* in:*Species Plantarum* ed.1.,2:598-600. Stockholm.

Lundberg, J.G. 1972. Wagner networks and ancestors. *Syst*. *Zool*. 18:1-32.

Maddison, W.P., Dondhue, M.J., & Maddison, D.R. 1984. Outgroup analysis and parsimony *Syst*. *Zool*. 33:83-103.

Martin, A.C. 1946. The comparative internal morphology of seeds. *Amer*. *Midl*. *Naturalist* 36:513-660.

Meacham, C.A. & Duncan,T. 1987. The necessity of convex groups in biological classification. *Syst*. *Bot*. 12:78-90.

Melchior, H. 1964. *Scutellaria*,*Salazaria* and *Perilomia* in: Engler,A.,ed. *Syllabus der Pflanzenfamilien* Berlin:Nikolasee

Morison, R. 1669. *Scutellaria* in *Praeludia Botanica*: 384. London:Roycroft.

Nevski, S.A. 1935. In Pavlov, N.V. Plantes tintorales des Monts Karatacu. *Trudy Sredne-Aziatsk*. *Gosud*. *Univ*. *Ser*. *8b*, *Bot*. 19. [In Russian, French summary; *Apeltanthus*:35]

Nordhagen, R. 1936. Uber dorsiventral und transversal Tangentballisten: Eine Verbreitungbiologische Studie. *Svensk*. *Bot*. *Tidskr*. 30:443-473.

O'Brien, T.P. & McCully, M.E. 1981. *The study of plant structure, principles and selected methods*. Melbourne: Termarcarphi: PTY. Ltd. [Acrolein: 6.51. OsO_4: 6.53]

Penland, W.C. 1924. Notes on North American *Scutellarias*. *Rhodora* 26: 61-79.

Phillipi, R.A. 1895. Cruzia Ph. novum genus Melittearum. *Anales Univ. Chile*. 90: 558.

Pijl, L. van der, 1982. *Principles of dispersal in higher plants* Berlin: Springer-verlag.

Rechinger, K-H. 1941. *Anaspis* eine neue Labiatengattung aus Zentralasien, Notizbl. *Bot.* Gart. Berlin-Dahlem 15: 630-632.

Rechinger, K-H. 1982 *Scutellaria* in: Rechinger, K-H. ed. *Flora Iranica* 150: 48-84. Graz: Alademische Drück-u. Verlagsanstalt.

Rechinger, K-H. & Wendelbo, P. 1967. *Zhumeria*, eine neue Labiaten-Gattung aus Süd-Iran. *Nytt. Mag. Bot*. 14: 39-43.

Richardson, K.C., Jarret, C. & Finke, E.H. 1960. Embedding in epoxy resins for ultra thin sectioning in electron microscopy. *Stain Technol*. 35: 313-323.

Rothamstead Experimental Station 1983. *A general statistical program. Genstat Manual*. Oxford: Numerical Algorithms Group Ltd.

Ryding, O. 1986. The genus *Aeollanthus* *s*. *lat*. (Labiatae) *Acta Universitatis Upsaliensis Symbolae Botanicae* Upsaliensis xxxi:i.

Seguier, J.F. 1754. *Plantae Veronenses* 3: 130-131 Verona.

Simpson, B.B. 1975. Pleistocene changes in the flora of the high tropical Andes. *Paleobiology* 1: 273-294.

Sneath, P.H.A. & Sokal, R.R. 1973. *Numerical Taxonomy* San Francisco: Freeman & Co.

Spurr, A.R. 1969. A low viscosity epoxy resin embedding medium for electron microscopy. *Journal of Ultrastructural Research* 26: 31-43.

Stearn, W.T. 1968. *Humboldt, Bonpland, Kunth and Tropical American Botany*. Lehre: Cramer.

Stebbins, G.L. & Major, J. 1965. Endemism and speciation in the Californian flora. *Ecol.Monogr.* 35: 1-35.

Swofford, D.L. 1985. *PAUP. Phylogenetic Analysis Using Parsimony*. *Version 2.4*. Users manual. Champaign: Illinois Natural History Survey.

Takhtajan, A.L. 1986. *Floristic Regions of the world*: University of California Press.

Torrey, J. 1858. *Salazaria* in: Emory, W.H. *Rep. U.S. Mes. bound 2(1), Botany of the Boundary*: 133-135.

Tournefort, J.P. 1700. *Cassida* in: *Institutiones rei herbariae*. ed. 1, 1: 181. Paris.

Visiani, R. de 1847. Tribe *Scutellarineae*: in *Flora Dalmatica* 2: 219. Leipzig: Hofmeister.

Wolfe, J.A. 1981. Vicariance biogeography of angiosperms in relation to paleobotanical data in Nelson, G. & Rosen, D.E., eds. *Vicariance Biogeography*: a critique: 413-435. New York: Colombia University Press.

Wu, C.Y. & Li, H.W. 1977. *Scutellaria* in: *Flora Reipublieae Popularis Sinicae* 65(2): 124-248. Beijung: Scientific Press.

Wunderlich, R. 1967. Ein Vorschlag zu einer natürlichen Gliederung der Labiaten auf Grund der Pollenkörner, der Samenentwicklung und des reifen Samens. *Oesterr. Bot. Z.* 114: 383-483.

Zoz, I.G. & Litvinenko, V.I. 1979. On the division of the family Lamiaceae Juss. into natural groups. *Bot. Zhurn.* (*Moscow* and *Leningrad*) 64: 989-997. /In Russian/.

Appendix 1. List of species and specimens studied.

A representative sample of all specimens studied is listed here. Details of the study are given on the individual herbarium sheet. If no details are supplied, the specimen was examined for macromorphological characters only. All specimens are housed at Edinburgh (E), unless otherwise stated. The abbreviations given follow Holmgren *et al*. (1981).

The specimens are listed alphabetically with their authorities and date of publication. The code used to represent the species in the cladistic and numerical phenetic computer programmes, (See Appendices 2 & 3), is given in parenthesis.

S. albida L. 1753 (27 ALBI)

USSR, Crimea: *Davis* 33620.
Turkey: *Davis* 22705, (subsp. *condensata*); *Woronow*, Flora Caucasia Exsiccatae 274, (Isotype subsp. *colchica*); *Balls* 1622, (subsp. *colchica*); *Ekim* 657, (subsp. *albida*).
Iraq: *Harris R.W.* 20/6/1961 *s.n.*, (subsp. *pycnotricha.*

S. alpina L. 1753 (42 ALPI)

Albania: *Lempberg* 843; *Dörfler* 451.
Hungary: *Richter* 5154.
Spain: *Reverchon* 620.

S. altissima L. 1753 (57 ALTI)

Jugoslavia: *Uotila* 10167.
Spain: *Blacki* *s.n.* (Dörfler).
Hungary: *Kummerele & Javorka* 873.
USSR, Armenia: *Mulkidjanian* 28/5/1962 *s.n.*

S. angustifolia Pursh 1814 (111 ANGU)

USA, Idaho: *Macbride* 482; *Nelson & Macbride* 1208; *Macbride* 104; *Heller* 3150.
USA, Oregon: *Jeffrey* 1852-53 *s.n*; *Cusick* 2145.
USA, Washington: *Suksdorf* 30/5/1909, *s.n.*

S. antirrhinoides Benth. 1832 (16 ANTI)
USA, California: *Hansen* 1808; *Tracy* 3670; *Hall* 9477;
Hansen 110; *Hall & Babcock* 4423; *Heller* 5894;
Butler 1633.
Idaho: *Macbride & Payson* 3005.

S. arabica Jaub. & Spach 1842 (55 ARAB)
Yemen Arab Rep.: *Wood* 75/225; *Miller & Long* 3540.
Saudi Arabia: *Podzorski* 1202; *Collenette* 2177.

S. araxensis Grossh. 1928 (91 ARAX)
Iran: *Lamond* 4032; *Lamond* 3890.

S. ariana Hedge 1968 (41 ARIA)
Afghanistan: *Hedge & Wendelbo* W.3718; Hewer 1165;
Hedge & Wendelbo W.3407, TYPE; *Hedge & Wendelbo*
W.4108; *Grey-Wilson & Hewer* 1306A.

S. atriplicifolia Benth. 1832 (53 ATR)
Ecuador: *Jameson* 537; *Lugo* 387 (K); *Hartweg* 244 TYPE (K).

S. austinae Eastw. 1903
USA, California: *Howell* 29030; *Gray* May 1885
(Ball Herb.) *s.n.*; Thorne 39995; *Abrams & McGregor*
344; *Heller* 7889; *Abrams* 2778; *Hall & Essig* 10178.

S. baicalensis Georgi 1775 (59 BAIC, 71 BAIC)
China, Yunnan: *Forrest* 10533.
Japan: *Togasi* 1509.
USSR, Chitinskaya Oblast: *Karo* 173.

S. balearica Barcelo 1877 (17 BALE)
Majorca: *White* 4/5/1903 *s.n.*; *Boissier*, May and June
1881 *s.n.*; *Bianor* 1098; *Bianor* 1080; *Marcos* 67, (K).

S. barbata D. Don 1825 (18 BARB)
China, Yunnan: *Forrest* 9975; *Forrest* 13719.
China, Zhejiang: *Ching* 1567.
China, Sichuan: *Forrest* 16499.
Nepal: Wall. Cat. 2140, (Roxburgh *s.n.*), (TYPE
S. rivularis).
India: *Koelz* 22763.

S. bolanderi A. Gray 1868 (112 BOLA)
USA, California: *Hall & Chandler* 39a; *Congdon* June 14 1896 *s.n.*; *Hansen* 448.

S. brittonii Porter 1894 (19 BRIT)
USA, Colorado: *Clements*, F.E. & E.S. 15 June: 15 Aug. 1901 *s.n.*; *Osterhout*, June 15 1905 *s.n.*; *Henry & Henry* 1894 *s.n.*
Wyoming: *Nelson* 3218; *Nelson* 1918.

S. bushii Britton 1901 (45 BUSH)
USA, Missouri: Bush 49, (MO); *Redfearn* 32960, (MO); Anderson, Nov. 1928 *s.n.* (MO); *Redfearn* 32964 (MO); *Bush* 378, (MO); *Steyermark* 12128, (MO); *Steyermark* 19407, (MO); *Bush* 48 (MO); *Steyermark* 12758, (MO); *Bush* 189, (MO).

S. caerulea Mocino & Sesse 1832 (107 CAER)
Mexico: *Balls* B.4804; *Pringle* 4154; *Hartweg* 378; *Purpus* 3968; *Balls* 4400; *Arsene*, 17/6/1902 *s.n.*; *Mexia* 2717, (K); *Pringle* 11102 (K).

S. californica A. Gray 1878 (113 CALI)
USA, California: *Balls* 10840; *Heller* 7020; *Hall & Babcock* 4548; *Heller* 11551a; *Heller* 5743; *Ferlatte* 841.

S. cardiophylla Engelm. & Gray 1845 (36 CARD)
USA, Taxas: *Lindheimer* 144.

S. cavaleriei A. Lévl. & Vaniot 1910 (106 CAVA)
China, Jiangsu: *d'Argy* 2105, Syntype.

S. churchilliana Fern. 1902 (33 CHUR)
USA, Maine: *Long* 260; *Knight*, 6/8/1905 *s.n.*
Canada: *Victorin & Rolland-Germain* 56003.

S. colpodea Nevski 1937 (22 COLP)
USSR, Pamir-Alay: *Britkov* 75; *Nevski* 378 (LE); *Bochantzer* 161 (LE).

S. costaricana H. Wendl. 1863 (82 COST)
Costa Rica: *Almeda* 3841, (K); Herb. Surrer, 1895 *s.n.*, TYPE, (K).

S. dependens Maxim. 1859 (5 DEPE)

Japan: Yokohama nursery Co. Ltd., Aug. 1907, s.n.; Mwata & Tagema 495; Ohwi & Okamoto 1796; Mizushima 617.

USSR: Melvil., 2/8/1926 s.n.; Karo 198.

S. discolor Wall. ex Benth. 1830 (63 DISC)

China. Yunnan: Maire 2178; Forrest 25144; Forrest 8812.

Thailand: Hansen & Smitinand 11961.

Nepal: Wall. Cat. 2134a, (H. Bruce s.n.), SYNTYPE.

S. drummondii Benth. 1834. (6 DRUM)

USA, Taxas: Ruth 1295; Tracy 7994; Tracy & Earle 118; Earle & Earle 269.

USA, New Mexico: Heller 1503 (TYPE S. helleri); Lindheimer 143.

Mexico: Pringle 166; Pringle 2712.

S. flocculosa Epling & Mathias 1957 (118 FLOC)

Peru: Sandeman 4151, TYPE, (K).

S. forrestii Diels 1912 (24 FORR)

China, Yunnan: Forrest 5705; Forrest 2281, TYPE; 1984 Sino American Botanical Expedition 269; Forrest 10266.

S. franchetiana A. Lévl. 1911 (80 FRAN)

China, Hubei: Henry 3559A.

China, Shanxi: Purdom 942.

China, Sichuan: Fang 1304.

China, Fujian: Carles 612.

S. galericulata L. 1753 (10 GALE)

Great Britain: Anthony 4142; Beattie 469/1; Ord 61.

Turkey: Davis 37172; Polunin 15077; Davis 30633.

USSR, Yakutski: McNeil 651.

Altai: Exherbario horti Petropolitani Pulidon s.n.

Kashmir: Drummond 1/7/1902 s.n.; Polunin 56/813.

Yugoslavia: Halliday 398/77.

Denmark: Svendsen 165.

USA, Colorado: Baker 815.
USA, Montana: Jones 18/8/1901 s.n.
USA, New Jersey: Mackenzie 828.
USA, Philadelphia: Shaw 762.
Canada, Nova Scotia: De Wolf July 18 1868 s.n.

S. gardoquioides Benth. 1848
Peru: Matthews 1835 s.n., TYPE, (K); Weberbauer 7592 (K).

S. ghorana Hedge 1968 (95 GHOR)
Afghanistan: Rechinger 19022, TYPE, (W).

S. glabrata Vved. 1954 (99 GLAB)
USSR, Pamir-Alay: Vvedensky 55.

S. glechomoides Boiss. 1848. (94 GLEC)
Iran: Th. Kotschy Pl. Pers. Bor. Ed. R.F. Hohenacker, 1846, 568 Scutellaria glechomoides Boiss. sp. nov. 23 July 1843, s.n. TYPE.

S. guilielmi A. Gray 1872 (46 GUIL)
China, Shanxi: Hao 3968, (PE).
Zhejiang: Chen 367, (PE).
Japan: Mayebara June 7, 1920 s.n., (TI); Hatusima & Sako 21605, (TI); Toyama 100, (TI); Magofuku 4, (TI); Sako 5493, (TI).

S. hastifolia L. 1753 (7 HAST)
USSR: Tichomirov 5291.
Italy: Mor. 1889 (Dörfler) s.n.
Czechoslovakia: Dvorakova et al. 1552.
Austria: Janchen 244.

S. havanensis Jacq. 1762 (8 HAVA)
Haiti: Leonard & Leonard 13193; Ekman 2380, (K); Leonard & Leonard 12357, (K).
Santo Domingo: von Türckheim 2928 (K).

S. heydei Hook. f. 1885 (39 HEYD)
Chitral & Kashmir: Broadhead 73; Bowes Lyon 1091; Burt 57; Stainton 2822.
Afghanistan: Hedge & Wendelbo W.5482.

S. hintoniana Epling 1939 (120 HINT)
Mexico: *Hinton* 1136, TYPE, (K); *Hinton* 8275, (K).

S. humilis R. Br. 1810 (9 HUMI)
Australia: Tasmanian plants coll. Bufton, *s.n.*;
R. Brown, Iter Australiense, 1802-5, *s.n.*;
received in 1875 from Wm. R. Guilfoyle, *s.n.*;
R. Brown 23574; *Rodway* 1775, (K); *Hemsley* 6455, (K).

S.x hybrida Strail (108 XHYB)
Great Britain: *Nicholson* 974; *Nicholson*, 7/83;
Sinclair 1140; *Stewart*, 15/9/1983 *s.n.*;
Dod 26/8/1893, *s.n.*

S. incana Spreng. 1807 (97 INCA)
USA, Washington DC: *Steele*, Aug. 17 1896, *s.n.*
USA, Pennsylvania: *Heller* July 24 1901 *s.n.*;
Pierron July 30 1878 *s.n.*; *Hook* v.ii p114, *s.n.*

S. indica L. 1753 (64 INDI)
China, Yunnan: *Ducloux* 354; *La Touche* 85.
Japan: Yokohama Nursery Co. Ltd., 29/5/1912 *s.n.*;
Mochizuki Aug. 1910 *s.n.*

S. inflata Epling 1939 (116 INFL)
Guatemala: *von Türckheim* 112029, TYPE.

S. integrifolia L. 1753 (98 INTE)
USA, New Jersey: *Mackenzie* 1456.
USA, Tenessee: *Ruth* 589.
USA, North Carolina: *Leonard* 2484.
USA, Louisiana: *Drummond* 248.

S. intermedia M. Pop. 1926 (38 INTE)
USSR: *Popov & Vvedensky* 201.

S. javanica Junghuhn 1853 (26 JAVA)
Papua: Croft LAE 65179; *Stevens & Veldkamp* 54035.
Philippines: *Borden* 2110; *Elmer* 6984.

S. komarovii Lévl. & Vaniot 1910 (105 KOMA)
Korea: *Faurie* 819, TYPE.

S. kotkaiensis Rech. f. 1982 (44 KOTK)
Afghanistan: Lamond 2483; Rechinger 35847; Koelz 11558; Hedge & Wendelbo W.8931; Rechinger 32265, TYPE.

S. lateriflora L. 1753 (32 LATE)
Canada, Ontario: Chalmers, 1875 s.n.; Radeau 484.
USA, Pensylvania: Ag, 5 Aug. 1886, s.n.
New York: Lawrence & Dress 409.

S. leonardi Epling 1939 (11 LEON)
USA, Illinois: A. Gray, 11/1873 s.n. (K).
USA, Wisconsin: McFarland 81.
USA, Washington DC: E.S. Steele, 1896 s.n.
USA, Iowa: Anderson June 16 1945 s.n., (K).

S. leptosiphon Nevski 1937 (101 LEPT)
Afghanistan: Hedge & Wendelbo W.3930; Hedge & Wendelbo W.3858; Hedge & Wendelbo W.3679; Grey-Wilson & Hewer 837; Hedge, Wendelbo & Ekberg W.8482.

S. lindeniana Benth. 1848 (122 LIND)
Venezuela: Linden, April 1842, S.A. (K) TYPE.

S. linearis Benth. 1830 (58 LINE)
Pakistan: Lace 3487; Watt 9714; Lamond 1876.
Afghanistan: Rechinger 35513.

S. litwinowii Bornm. & Sint, 1914 (31 LITW)
Iran: Edmondson 1191; Rechinger 4500; Rechinger 51098; Rechinger 4948.

S. lutea J.D. Smith 1888 (47 LUT)
Guatamala: von Türckheim 1309, TYPE, (US); Seler 3406 (K).

S. macrochlamys Rech. f. & Fitz 1954 (100 MACR)
Afghanistan: Koeie 2640, TYPE; Furse 8779.

S. mexicana (Torrey) Paton 1858 (50 SALA)
Syn. Salazaria mexicana Torrey 1858
USA, California: Munz & Young 15189, (RSA); Pringle, May 24 1882, s.n., (K); Elmer 3671, (K); Stauffer & Thorne 5930 (K).

New Mexico: Fremont 433, TYPE (K).
Utah: Hitchcock 3079, (RSA).
Arizona: McKelvey 2180, (RSA); Cotton 8502.
Nevada: Clokey 7687 (RSA).
Mexico, Baja California: Henrickson 32642, (RSA).

S. minor L. 1753 (12 MINO)
Spain: Deverall & Flannigan 0665; Jordan, Pyrenees, Bagneres s.n.
Germany: Wingen, 5/8 1881, s.n.
France: Noffray, 8 July 1895, s.n.
Portugal: Sinclair 4653.
Great Britain: Hedge, 23/8/1963 s.n.
Ireland: Long 11595.

S. mollis R. Br. 1810 (13 MOLL)
Australia: Brown 2353; Drummond s.n.; Cunningham 1835 s.n.; Grose & Hawkeberg, R. Brown, Inter Australiense 1802-5 s.n.; Melville 2856 (K).

S. moniliorrhiza V. Komarov 1907 (86 MONI)
Manchuria: Komarov 1331, (K), TYPE.

S. multicaulis Boiss. 1846 (62 MULT)
Afghanistan: Hedge & Wendelbo W.4360; Rechinger 47583; Koelz 11947, (TYPE, S. koelzii).
Pakistan: Sinclair 2755; Lace 4073.

S. nana A. Gray 1876 (109 NANA)
USA, California: Heller 8086.
USA, Oregon: Cusick 1980.

S. nervosa Pursh. 1814 (104 NERV, 102 NERV)
USA, Kentucky: C.W. Short, Kentucky 1835, s.n.
USA, New Jersey: Long 11889.
USA, Washington DC: E.S. Steele, 1896, s.n.

S. novae-zealandiae Hook. f. 1855 (49 NZ)
New Zealand: Nelson 1878 s.n.; Monro 87 SYNTYPE (K); Bodmill 16 SYNTYPE (K).

S. nummulariifolia Hook. f. 1847 (1 NUMM)
Argentina: *Shattsberg* 148; Ayerdam, *Beetle & Grondona* 24250 (K); *Moore* 1306 (K); *Tweedie* 278 (K).

S. ocymoides (Kunth) Epling 1936 (20 OCYM)
Syn. *Perilomia ocymoides* Kunth 1818.
Peru: *Hutchison & Saravia* 7105 (K).

S. orbicularis Bunge 1854 (89 ORBI)
USSR, Pamir-Alay: *Bunge* 7234 TYPE (LE); *Pederenko* 20 May 1869 *s.n.* (LE); *Michaelson* 2456 (LE).

S. orientalis subsp. *alpina* (Boiss.) O. Schwarz 1934 (93 OREI)
Turkey: *Bisby* 9; *Davis* 272; *Haradjian* 2340; *Lambert & Thorp* 569.

S. ovata Hill 1768 (35 OVAT)
USA, Kentucky: *Griswold* 1855 *s.n.*
USA, Missouri: *Tracy* 715.
USA, Louisiana: *Drummond* 250.
USA, Texas: *Drummond* 279.

S. pallidiflora Epling 1939 (83 PALL)
Mexico: *Rose* 2487, TYPE, (GH).

S. parvula Michaux f. 1803 (2 PARV)
USA, Ankansas: *D'Arcy & Ponter* 4354.
USA, Delaware: *Meaconu*, June 1884, *s.n.*
USA, Illinois: *McDonald* 521.
Canada, Ontario: *Cody* 6337.

S. paucifolia Baker 1895 (28 PAUC)
Malawi: *Buchanan* 144; *J. Buchanan*, 15 Sept. 1877, *s.n.*; *Hilliard & Burtt* 4451.
Zambia: *Adamson* 36.

S. pinnatifida A. Ham. 1832 (92 PINA)
Iran: *Wendelbo & Foroughi* 11539; *Wendelbo, Assadi & Shirdelpur* 12180; *Rechinger* 53145.

S. platensis Speg. 1902 (103 PLAT)
Argentina: *Sparre* 431 (K).

S. platystegia Juz. 1939 (90 PSTE)
Iran: Lamond 3721

S. polyadena Briq. 1898 (124 POLY)
Congo: De Beers 96, TYPE, (BG).

S. pontica C. Koch 1848 (60 PONT)
Turkey: Stainton & Henderson 6004; Davis 20952;
Balls 570; Davis & Hedge D.32317.

S. purpurascens Sw. 1788 (30 PURP)
Trinidad: D'Arcy & D'Arcy 6236.

S. racemosa Pers. 1807 (3 RACE)
Argentina: Gillier Buenos Aires s.n., s.d.
Colombia: Hartweg 1341.
Brazil: Reineck & Czermak 7.
Mexico: Pringle 3067; Stundal, s.n., s.d.
Paraguay: Fiebrig 167; Morong 826.

S. regeliana Nakai 1921 (85 REG)
Korea: Furnsin 423, (TI); Nakai 9369, (TI);
Mosi 107, (TI); Nakai 3382, (TI).

S. repens Buch.-Ham. 1825 (42 REPE)
Pakistan: Inayet 2009; Lace 10097; Lace 684.
Nepal: Stainton, Sykes & Williams 4250.

S. resinosa Torrey 1828 (4 RESI)
USA, Colorado: Beattie Mts Gordon s.n. s.d. (K).
USA, Taxas: Lindheimer 674, (K); Heller 1606 (K).

S. sarmentosa Epling 1936 (123 SARM)
Syn. HarlanleWisia sarmentosa (Epling) Epling &
Jativa 1968.
Ecuador: Løjtnant & Molau 13930 (GB); Harling, Storm
& Ström 9002 (GB); Spruce, June 1860 s.n., TYPE (K).

S. saxatilis Riddell 1836 (37 SAX)
USA, Tenessee: Rugel 1842.
USA, West Virginia: Steele & Steele 31.
USA, Virginia: Gray & Carey, July 1841, s.n.

S. schugnanica B. Fedtsch 1913 (88 SHUG)
USSR, Pamir-Alay: Grubov 207 (K); Kamelin 13140, (LE);
Korinshinsky 1297. SYNTYPE, (LE).

S. schweinfurthii Briq. 1894 (SCHW)
Sudan: Jackson 2202 (K).

S. sciaphila S. Moore 1875 (81 SCIA)
China: Carles 215.

S. scordifolia Fischer 1822 (14 SCOR)
China, Beijing: Hemeling 355; Hemeling 356.
China: Bodinier 271.

S. scutellarioides (Kunth) R. Harley 1983 (21 SCUT)
Syn. Perilomia scutellarioides Kunth 1818.
Ecuador: Harling, Storm & Ström 9640, (GB);
Hart 1355 (K).
Peru: Sagastegui, Fukushima & Vasquez 6490, (K);
Sagastegui & Mastacero 9198, (K).

S. shweliensis W.W. Smith 1917 (SHWE)
Yunnan: Forrest 9871 (TYPE)

S. sieberi Benth. 1848 (115 SIEB)
Crete: Reverchon 144; Bourgeau 129; Leonis, May 1900,
s.n.

S. si~~n~~phocampyloides Vatke 1972
USA, California: Hall & Chandler 242; Purpus 5005;
Elmer 4434

S. speciosa Epling 1930 (52 SPEC, 72 SPEC)
Peru: Spruce 4050, (K); Ule 6580, TYPE, (K);
Schunke 6084, (K).

S. splendens Link ex Klotysch & Otto 1814 (117 SPLE)
Mexico: Purpus 5910; Purpus 1930.

S. stocksii Boiss. 1859 (40 STOC)
Afghanistan: Hedge & Wendelbo W.4262; Lamond 23 98.
Pakistan: Lace 3881; Sinclair 2736.

S. strigillosa Hemsley 1890 (15 STRI)

China, Ganshu: Rock 12900.

Korea: Taquet 3089, (Type S. taquetti Levl.).

Japan: Faurie 707; Faurie 706; Nambu, 6/8/1913, s.n.; Iwatsuki 6331.

S. suffrutescens Wats. 1890 (51 SUFF, 73 SUFF)

Mexico: Pringle 2 535, TYPE, (K); Reveal & Atwood 3390, (K); Lyonnet 3934, (MEXU); C.H. & M.T. Mueller 149, (MEXU).

S. tenax W.W. Smith 1920 (65 TENA)

China, Yunnan: Forrest 13050, TYPE; Maire 365 (Type S. veronicifolia Levl.); Maire 936; Duclaux 856.

S. tibetica C.Y. Wu & H.W. Li 1977 (87 TIBE)

Syn. S. kingiana Prain (1890).

Xizang (Tibet): White 1617/1906 s.n.

S. tournefortii Benth. 1832 (56 TOUR, 70 TOUR)

Iran: Hewer H3967; Wendelbo 523; Sabeti 7437.

Turkey: Davis 24277.

S. tuberosa Benth. 1834 (110 TUBE, 114 TUBE)

USA, California: Heller 1834; Heller 6649; Thorne 34373; Heller 7288; Elmer 2351; Baker 4756; Bolander 6818; Heller 11231.

S. tubifera C.Y. Wu & H.W. Li 1977 (84 TUBI)

China, Yunnan: Wang 88108, (KUN).

S. valdiviana (Clos) Epling 1936 (96 VALD)

Syn. Theresa valdiviana Clos. 1849.

Chile: Gray 1066 Syntype, (P).

S. violacea Heyne 1830 (25 VIOL)

China, Yunnan: Ducloux 363; Ten 291; Maire, s.n., s.d., (Type S. coleifolia Levl.)

India: Cave 13/8/1913.

S. violascens Gürke 1901 (29 VIOL)
Malawi: *Buchanan* 12, *Gürke* 999, TYPE.

S. ventenatii Hook. f. 1846 (121 VENT)
Jamaica: *Harris* 12387, (K).
St. Vincent Is.: *Smith & Smith* 1274,(K).
Venezuela: *Steyermark & Manara* 125293, (K).

S. volubilis Kunth 1818 (48 VOLU)
Syn. *Perilomia volubilis* (Kunth) Briq. 1896
Ecuador: *Lehmann* 716, (K); *Lehmann* 4952, (K);
Harling & Anderson 13366, (GB); Harling 11282,
(GB); *Harling & Anderson* 14529, (GB); *Hart* 1366.

S. zaprjagaevii Koczk. & Zhogoleva 1986 (23 ZAPR)
USSR, Pamir-Alay: *Elias* 10063.

Appendix 2

This appendix lists the input file used in PAUP to generate the fifty equally parsimonious trees of length 585. The character states of the hypothetical ancestor used to root the trees in Lundberg rooting are given by the outstates command near the end of the programme. See Swofford (1985) and Chapter 5: Taxonomic Philosophy.

The three lines of character codes given at the top of each section of data matrix were omitted when the programme was run. They have been added to enable the reader to determine the nature of the character states of any particular species. The character codes are given in Chapter 3: The Taxonomic Characters, and the species codes are given in Appendix 1.

When using this input file, PAUP will prompt the user at the end of the run with: Do you want maxtree extended? By giving the answer 'No', PAUP will then prompt: Do you want to swap remaining trees? answer 'Yes' is given in order to find a shorter tree length.

When 50 trees of length 585 had been produced, they were stored in a tree file using the command: write tree all/file = Alltrees.

The file Alltrees was then entered into the programme Contree distributed with PAUP. The following commands were used:

```
Assign Alltree. dat for 005
Assign  Strict. out for 006
   R  Contree.
```

A strict consensus tree, based on the 50 trees of length 585, is thus created in the file Strict. out.

INPUT FILE

```
PARAM NOTU=114 NCHAR=58 MISSING=9 ECHO MAXTREE=50 NORELEASE
ROOT=LUNDBERG;
DATA (A7,A1,58I1);

*CHAR-  AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEEFFFFFFFFFFFFF
*ACTERS 1234567891111123456781234123451234567891111111234567891111
*                0123                          012345         0123
  1NUMM 0000032000030000000002000000000000003020003003000003200030000
  2PARV 3000332000000000320223000000000033000003000000003130030000
  3RACE 3030032000300020299400000000000000020003000000353200000399
  4RESI 0000334000030000002002005000000003300003000000003200000099
  5DEPE 3100000990300020299400000000000030000003000001303200033000
  6DRUM 0000332000030303003030000000000303313003000000005900030000
  7HAST 3030002330300020202200000000000003303000000000033200030000
  8HAVA 0300002000000040004000000003000000003003000003003000000099
  9HUMI 0400002000000020202200000000000030000000000000003100030099
 10GALE 3100002000000020202200000000000003000000000000003200000300
 11LEON 3000300000300020202200000000000033000000000000053230030099
 12MINO 3200300330300020202200000000000030020000000000303200010000
 13MOLL 0300002330000303230230000000000303300003000000303200030099
 14SCOR 3300000900300020202200000000000003303000000000003320030099
 15STRI 3300002330000320032000000000000303303000000000003320030099
 16ANTI 3000032000000020002000000000000000300000300000305331003 0099
 17BALE 0400002330000030003100000000000303300000000000003300000099
 18BARB 9300000900330020202200000009000033000003000002003090000099
 19BRIT 0000332000000040000000000000000003300000000000003320030099
 20OCYM 0400000900300020002005009000003000043330000340003200330000
 21SCUT 0300302330030020000005009003002000040330000040033200330000
 22COLP 3000334000030040030002005045030003033000003004003005030099
 23ZAPR 0003032300030003000033005045033303333000003004003203000099
 24FORR 0300030900300300030000005000030303003000000000003200030099
 25VIOL 0300002300300003030030003000300030003303000300000003200330000
 26JAVA 0300002300303020002000003000300030003000000000000003200000099
 27ALBI 0300004000000023030030003000000000303303000000004003203000033
 28PAUC 3300002000300043000030003000000000003323000003000003200000399
 29VIOL 3300902330300020230030003000000000303303000900000003200000099
 30PURP 3300000900000040000000003300000000010000000304003200030000
 31LITW 0000032000000040030002005005030003033000000004003005030000
 32LATE 3300000900300020202000000000030000000000000000003200000000
 33CHUR 0300000900300020202200000000030000000000000000003200000099
 34SESS 0300000990500999400030003003300003303000000300303000000000
 35OVAT 0300902000000020002030003003000000300000000000003230030099
 36CARD 0300300900000040004000300000000000000000000000003200030099
 37 SAX 0300000300300999499401000003000003000000000000003200030099
 38INTE 3200330900000020030032005045030003333000909904003005030099
 39HEYD 0400034300000000030003005045031503033000000004003005030000
 40STOC 0003334300000303030033005045033503023000003004303203030099
 41ARIA 0000334000003020002002005000002000000000003004003203030033
 42REPE 0300002000300020000031003003300000333000000004003005030099
 43ALPI 3300032000030340030003005045000030303000000004003005030000
 44KOTK 0400032300030300030003005045030303033000000004003005030099
 45BUSH 3000032000030020002000003000000000000300030000003200030099
 46GUIL 0400002330000020200031300000000000003300000000000003330030003
 47 LUT 0400032300030300030005009003000303030300900000003200030099
 48VOLU 0400302330030300030005009000302003040330530040000990000000
 49  NZ 0200002000000020230001000000000000030010003900900003200000099
 50SALA 3000032000000040004005009000004000000000000300003200030000
 51SUFF 0000032000000040004002005000000000000304030040000003200030099
 52SPEC 3300002000003020000030003303000000334030000300003200030300
```

```
*CHAR-   AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEEFFFFFFFFFFFFF
*ACTERS 1234567891111123456781234123451234567891111111234567891111
*                 0123                                012345       0123
 53 ATR 3300300900030020002000003303000000004000010000300320003039 9
 54GARD 0000000900300090002005009003000000030330533040003203030099
 55ARAB 0300002000000020030030003003000300303000000000300320300009 9
 56TOUR 0300000900000020002000003003030303303000000000400320303009 9
 57ALTI 0300000900000020230230003003030003303000000000000320003003 3
 58LINE 3000034000000020030032005045030303320000000004003005030099
 59BAIC 3000000900300990404000003000000000303000300003003200030000
 60PONT 0400032300330040030003005000000333323000000000430300503009 9
 61SHWE 0300032000030003030030003000000000330300000000040032030000 99
 62MULT 3300032000003043030032005045030003333000000000400300503009 9
 63DISC 0400002330330000000030300303000000300300040000000320030000 0
 64INDI 0400002330303330303003000300303000330300000000033032003300 99
 65TENA 0400002000530020000030003003000003303000300000003200300099
 70TOUR 0300000900000999402000003003030303300000000000400320303009 9
 71BAIC 3000000900300040204030003000000000303000300003003200030000
 72SPEC 0300002000003003000030003303000003340300000300003200030300
 73SUFF 0000032000000040030002005000030003340300400000003200030099
 80FRAN 0300302000030020002000003003300000032300000003099999999999999
 81SCIA 3300032300300020230030003003030003303000000000999999999999 9
 82COST 0300900900330020002000003323000000004030010030999999999999 9
 83PALL 0300002000030003000030003003030003310000400009999999999999
 84TUBI 0400002330000300030002033000030303000000099990999999999999 9
 85 REG 3100002000300020202200000000000000000300000000999999999999 9
 86MONI 3300900900300990499400000000000000000300099990999999999999 9
 87TIBE 0400333000030000030003005000002000093003000000999999999999 9
 88SHUG 0300330000000000030003005000002303020000000309999999999999 99
 89ORBI 0003333300030300030003005045033503033000000030999999999999 9
 90PSTE 3500033000000040000003005045030003333000000000999999999999 9
 91ARAX 3500032000000020000002005045030003333000000000999999999999 9
 92PINA 0500033300000300000003005045030003033000000030999999999999 9
 93ORIE 0500033300000040000003005045030003033000000030999999999999 9
 94GLEC 0400032300030300000000100004503000330300000000999999999999 9
 95GHOR 0300032000000990400032005003002003300000000000999999999999 9
 96VALD 0300000900030000000005009003000000040330999929999999999999 9
 97INCA 0300002000030020002000003003000000000000300009999999999999 9
 98INTE 3000002330030020002000003003000003300000300009999999999999 9
 99GLAB 3200332000000020030032005045030003333000000000999999999999 9
100MACR 0500032300000300030003005045031503023000000000999999999999 9
101LEPT 0003332300030300030003005045033503023000000000999999999999 9
102NERV 0300002330300020200230000000000033300003000009999999999999 9
103PLAT 0300902000300999499400000000000000030000000000009999999999999 9
104NERV 0300002330300023200230000000000033300003000009999999999999 9
105KOMA 9300002000330020202200000000900003300000300009999999999999 9
106CAVA 9300002000030020202200000000900003300000300009999999999999 9
107CAER 0400002330300040234200003003000333000300000000999999999999 9
108XHYB 3300002000300020202200000000000003300000000000999999999999 9
109NANA 0000334000000040004001000000000000000100003000099999999999 99
110TUBE 0300032000000300220201030000000303000000000000999999999999 9
111ANGU 0000032000000020002000000000000000300300000000999999999999 9
112BOLA 0300932000000303230230000000000030331000300000999999999999 9
113CALI 3000032000000023002030000000000000301000300000999999999999 9
114TUBE 0000032330000300220201030000000303000000000000999999999999 9
115SIEB 0300004000000020030000003003030303310000000000999999999999 9
116INFL 0300000330300300030030009303000000004030000000999999999999 9
117SPLE 0300000330000303000030003303030003340300100009999999999999 9
```

```
*CHAR-   AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEEFFFFFFFFFFFFF
*ACTERS 1234567891111123456781234123451234567891111111234567891111
*                 0123                          012345         0123
118FLOC 0400002093000000000000000900000000302933000999999999999999
119SCHW 3000002000300020002000003003000003003000000000999999999999
120HINT 3300002330330300030000003003000303040300000000999999999999
121VENT 0300002000000040000030009303000000304030000030999999999999
122LIND 3300000900030040002000009003000000334030000000999999999999
123SARM 0400002093300300002005009000000900304033050302999999999999
124POLY 0300902330300000030030003003000000330300090000999999999999
UNORDER ALL;
DELETE TAX 66 67 68 69;
OUTSTATES 6*0 2 41*0 3 2 8*0;
GO/SWAP=GLOBAL MULPARS;
```

Appendix 3

This appendix lists the control and data files used in Genstat, (Rothamstead experimental station 1983), to produce the dendrograms on which the numerical phenetic classifications are based. Control and data file A were employed to generate Fig. 6.2: the dendrogram based on the similarity of all taxonomic characters. Control and data file B were used to generate Fig. 6.3: the dendrogram produced if nutlet characters were ignored.

Once again the 3 lines of character codes at the top of each section of the data matrix were omitted when the programme was run. They have been added to allow the reader to determine the character states of any particular species. Character codes are given in Chapter 3: The Taxonomic Characters. Species codes are given in Appendix 1.

An asterisk in the data file means the state of that character was unknown or the character was not applicable in that circumstance.

The Genstat programme was run using the following command:

```
Genstat Control = control file, data = data file,
Listing = output file.
```

The dendrogram produced appears in the output file.

CONTROL FILE A

```
'REFE'
'VARI'A(1...58) $114
'SYMMAT' SYM $114
'INTEGER' RES $114
'INTEGER' TYPE=58(2)
'INPUT'2
'READ'A(1...58)$F,7X,58(1),/
'INPUT'1
'SMATRIX' SYM;A(1...58);TYPE
'HIERARCHY/CM=4,CT=2.5'SYM;RES
'RUN'
'STOP'
'CLOSE'
```

DATA FILE A

```
CHAR-  AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEEFFFFFFFFFFFFF
ACTERS 1234567891111123456781234123451234567891111112345678911111
                0123                          012345         0123
  1NUMM00000320000300000000020000000000003020003003000003200030000
  2PARV30003320000000003202230000000000003300000300000000313003000 0
  3RACE30300320003000202**40000000000000000200030000000353200000 3**
  4RESI0000334000030000002002005000000000033000030000000003200000 0**
  5DEPE3100000**03000202**400000000000003000000300000130320003300 0
  6DRUM00003320000303030300303000000000303313003000000005*0003000 0
  7HAST30300023303000202022000000000000003303000000000033200030000
  8HAVA030000200000004000400000000030000000003003000003003000000 0**
  9HUMI0400002000000020202200000000000000300000000000000031000300**
 10GALE3100002000000020202200000000000000300000000000000320000030 0
 11LEON3000300000300020202200000000000000330000000000000532300300**
 12MINO32003003303000202022000000000000003002000000000003032000100 00
 13MOLL030000233000030323023000000000003033000030000000303200030 0**
 14SCOR3300000*0030002020220000000000000033030000000000003320030 0**
 15STRI3300002330000320032000000000000030333030000000000003320030 0**
 16ANTI3000032000000002000200000000000000300000300000030533100300**
 17BALE04000023300000003000031000000000030330000000000000330000000**
 18BARB*300000*0033002020220000000*00003300000300000200030*00000**
 19BRIT000033200000004000000000000000000033000000000000033200300**
 20OCYM0400000*0030002000200500*000003000043330000340003200330000
 21SCUT03003023300300200000050 0*0030020000403300000400332003300 00
 22COLP300033400003004003000200504503000303300000030040030050300**
 23ZAPR000303230003000300003300504503330333300000300400320300 00**
 24FORR0300030*0030030003000000500003030300300000000000032000300**
 25VIOL030000230030000303003000300003000330300030000000320033000 0
 26JAVA0300002300303020002000003000030003000000000000000320000 00**
 27ALBI030000400000002303003000300000030333030000000004003203000033
 28PAUC330000200030004300003000300000000033230000003000003200000 3**
 29VIOL3300*0233030002023003000300000030330300 0*000000032000000**
 30PURP3300000*0000004000000000330000000001000000030400320003000 0
 31LITW00000320000000400300020050050300030330000000004003005030000
 32LATE3300000*0030002020200000000003000000000000000000003200000000
 33CHUR0300000*0030002020220000000000300000000000000000003200000 0**
 34SESS0300000**0500***40003000300330000330300000030030300000000 0
 35OVAT0300*020000000200020300030030000000300000000000000032300300**
 36CARD0300300*00000040004000300000000000000000000000000032000300**
 37 SAX0300000300300***4**401000000300000300000000000000032000300**
 38INTE3200330*00000020030032005045030003333000*0**040030050300**
 39HEYD04000343000000000030003005045031503033000000000400300503000 0
 40STOC00033343000003030300330050450335030230000030043032030300**
 41ARIA0000334000003020002002005000000200000000000030040032030300 33
 42REPE030000200003002000003100300330000333000000000400300503 00**
 43ALPI33000320000303400300030050450000303030000000000400300503000 0
 44KOTK0400032300030300030003005045030303033000000000400300503 00**
 45BUSH300003200003002000200000300000000000030003000000003200030 0**
 46GUIL04000023300000202000313000000000003300000000000000333003000 3
 47 LUT0400032300030300030005 00*0030003030303030 0*000003200030 0**
 48VOLU040030233003030003000500*0003020030403305300400 00**000000 0
 49  NZ02000020000000202300010000000000030010003*00*0000320000 00**
 50SALA30000320000000040004005 00*000004000000000000030000320003000 0
 51SUFF000003200000000400040020050000000030403004000000003200030 0**
 52SPEC330000200000302000003000330300000033403000000300003200030300
```

```
CHAR-  AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEEFFFFFFFFFFFFF
ACTERS 1234567891111123456781234123451234567891111111234567891111
                0123                          012345         0123
 53 ATR3300300*00030020002000003303000000004000010000300320003O3**
 54GARD0000000*003000*000200500*003000000003033053304000320303OO**
 55ARAB0300002000000020030030003003000300303000000000300320300OO**
 56TOUR0300000*0000002000200000300303030330300000000400320300300**
 57ALTI0300000*0000002023023000300303000330300000000000032000300 33
 58LINE3000034000000020030032005045030303320000000004003005030O**
 59BAIC3000000*00300**040400000300000000030300030000300320003OOOO
 60PONT040003230033004003000300500000033332300000000430300503OO**
 61SHWE030003200003000303003000300000000330300000000400320300OO**
 62MULT330003200000304303003200504503000333000000000400300503OO**
 63DISC04000023303300000000030300303000003003000400000003200300000
 64INDI040000233030330303003000300303000330300000000330320033OO**
 65TENA040000200053002000003000300300000330300030000000320030OO**
 70TOUR0300000*00000***40200000300303030330000000000040032030300**
 71BAIC3000000*00300040204030003000000000303000300003003200030000O
 72SPEC030000200000300300003000330300000334030000030000320003030O
 73SUFF000003200000004003000200500003000334030040000000320003OO**
 80FRAN03003020000300200020000030033000003230000003O*************
 81SCIA33000323003000202300300030030300033030000000O*************
 82COST0300*00*0033002000200000332300000000403001003O*************
 83PALL03000020000300030000300030030300033100004000O*************
 84TUBI040000233000030003000203300003030300000O****0*************
 85 REG31000020003000202022000000000000000003000000O0*************
 86MONI3300*00*00300**04**400000000000000000003000****0*************
 87TIBE0400333000030000030003005000002000O*30030000O0*************
 88SHUG03003300000000000300030050000023030200000003O*************
 89ORBI00033333000303000300030050450335030330000003O*************
 90PSTE35000330000000400000030050450300033330000000O*************
 91ARAX35000320000000200000020050450300033330000000O*************
 92PINA05000333000000300000003005045030003033000003O*************
 93ORIE05000333000000400000003005045030003033000003O*************
 94GLEC04000323000303000000001000045030003303000000O*************
 95GHOR0300032000000**0400032005003002003300000000OO*************
 96VALD0300000*000030000000000500*00300000000040330****2*************
 97INCA030000200003002000200000300300000000000003000O*************
 98INTE300000233003002000200000300300000033000003000O*************
 99GLAB32003320000000200300320050450300033330000000O*************
100MACR05000323000003000300030050450315030230000000O*************
101LEPT00033323000303000300030050450335030230000000O*************
102NERV03000023303000202002300000000000033300003OOOOO*************
103PLAT0300*02000300***4**40000000000000300000000000O*************
104NERV03000023303000232002300000000000033300003OOOOO*************
105KOMA*3000020003300202022000000O*00003300000300000O*************
106CAVA*3000020000300202022000000O*00003300000300000O*************
107CAER04000023303000402342000030030003330003OOOOOOO*************
108XHYB330000200030002020220000000000000033000000000O*************
109NANA000033400000000400040010000000000000010000300OO*************
110TUBE030003200000030022020103000000003030000000000O*************
111ANGU000003200000000200020000000000000000300300000O*************
112BOLA0300*3200000030323023000000000000303310003000OO*************
113CALI300003200000000230020300000000000000301000300OOO*************
114TUBE00000323300003002202010300000000303000000000O0*************
115SIEB030000400000000200300000003003030303310000000O0*************
```

224

```
CHAR-  AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEEFFFFFFFFFFFFF
ACTERS 1234567891111123456781234123451234567891111111234567891111
                0123                         012345         0123
116INFL030000033030030003003000*30300000004030000000*************
117SPLE030000033000030300003000330303000334030010000*************
118FLOC04000020*300000000000000*00000000302*33000****************
119SCHW300000200030002000200000300300000300300000000*************
120HINT330000233033030003000000300300030304030000000*************
121VENT030000200000004000003000*30300000304030000030*************
122LIND3300000*0003004000200000*00300000334030000000*************
123SARM04000020*330030000200500*00000*00304033050302*************
124POLY0300*0233030000000300300030030000033030 00*0000*************
'EOD'
```

CONTROL FILE B

```
'REFE'
'VARI'A(1...45) $114
'SYMMAT' SYM $114
'INTEGER' RES $114
'INTEGER' TYPE=45(2)
'INPUT'2
'READ'A(1...45)$F,7X,45(1),/
'INPUT'1
'SMATRIX' SYM;A(1...45);TYPE
'HIERARCHY/CM=4,CT=2.5'SYM;RES
'RUN'
'STOP'
'CLOSE'
```

DATA FILE B

```
CHAR-  AAAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEE
ACTERS 1234567891111123456781234123451234567891111111
                0123                           012345
  1NUMM0000032000030000000000200000000000302000300300
  2PARV3000332000000000320223000000000003300000300000
  3RACE3030032000300020 2**4000000000000000002000300000
  4RESI0000334000030000002002005000000000330000300000
  5DEPE3100000**03000202**40000000000000300000030000
  6DRUM0000332000030303030030300000000030331300300000
  7HAST3030002330300020202200000000000000330300000000
  8HAVA0300002000000040004000000000300000000300300000
  9HUMI0400002000000020202200000000000003000000000000
 10GALE3100002000000020202200000000000000300000000000
 11LEON3000300000300020202200000000000000330000000000
 12MINO3200300330300020202200000000000000300200000000
 13MOLL0300002330000303230230000000000003033000030000
 14SCOR3300000*0030002020220000000000000033030000000
 15STRI3300002330000320032000000000000030330300000000
 16ANTI3000032000000002000200000000000000300000300000
 17BALE0400002330000003000031000000000030330000000000
 18BARB*300000*003300202022000000000*00003300000300000
 19BRIT0000332000000040000000000000000000330000000000
 20OCYM0400000*00300020002005 00*00000300004333000034
 21SCUT0300302330030020000005 00*003002000040330000 04
 22COLP3000334000030040030002005045030003033000000300
 23ZAPR0003032300030003000033005045033303333000000300
 24FORR0300030*003003000300000050000303030030000000 0
 25VIOL0300002300300003030030003000030003303000030000
 26JAVA0300002300303020002000003000030003000000000000
 27ALBI0300004000000023030030003000000303303000000000
 28PAUC3300002000300043000030003000000000332300000300
 29VIOL3300*02330300020230030003000000303303000*0000
 30PURP3300000*0000004000000000033000000000100000030
 31LITW0000032000000040030002005005030003033000000000
 32LATE3300000*0030002020200000000003000000000000000 0
 33CHUR0300000*003000202022000000000030000000000000000
 34SESS0300000**0500***4000300030033000003303000000 30
 35OVAT0300*0200000000200020300030030000000300000000 00
 36CARD0300300*000000400040003000000000000000000000 00
 37 SAX0300000300300***4**40100000300000300000000000
 38INTE3200330*000000200300320050450300033330 00*0**0
 39HEYD0400034300000000030003005045031503033000000 00
 40STOC0003334300000303030033005045033503023000000300
 41ARIA0000334000003020002002005000000200000000000300
 42REPE0300002000030020000031003003300000333000000000
 43ALPI3300032000030340030003005045000030303000000000
 44KOTK0400032300030300030003005045030303033000000000
 45BUSH3000032000030020002000003000000000000300030000
 46GUIL0400002330000002020003130000000000003300000000 00
 47 LUT0400032300030300030005 00*003000303030300*00
 48VOLU0400302330030300030005 00*000302003040330530 04
 49  NZ0200000200000002023000100000000000030010003*00*0
 50SALA3000032000000040004005 00*000004000000000000030
 51SUFF0000032000000040004002005000000000304030040000
 52SPEC3300002000003020000030003303000003340300000 30
 53 ATR3300300*0003002000200000330300000000400001000 0
```

```
CHAR-  AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEE
ACTERS 1234567891111123456781234123451234567891111111
                0123                          012345
 54GARD0000000*003000*000200500*003000000003033053304
 55ARAB0300002000000020030030003003000300303000000000
 56TOUR0300000*000000200020000030030303033030000000
 57ALTI0300000*000000202302300030030300033030000000
 58LINE30000340000000200300320050450303033200000000
 59BAIC3000000*00300**04040000030000000003030003000
 60PONT04000323003300400300030050000000333230000000
 61SHWE03000320000300030300300030000000033030000000
 62MULT33000320000030430300320050450300033330000000
 63DISC04000023303300000000303003030000003003000400
 64INDI04000023303033030300300030030300033030000000
 65TENA04000020005300200000300030030000003303000300
 70TOUR0300000*00000***4020000030030303033000000000
 71BAIC3000000*0030004020403000300000000030300030000
 72SPEC03000020000030030000300033030000033403000003
 73SUFF00000320000000400300020050000300033403004000
 80FRAN03003020000300200020000030033000000323000000030
 81SCIA33000323003000202300300030030300033030000000
 82COST0300*00*0033002000200000332300000000403001003
 83PALL03000020000300030000300030030300033100004000
 84TUBI04000023300003000300020330000303030000000****0
 85 REG3100002000300020202200000000000000000030000000
 86MONI3300*00*00300**04**40000000000000000003000****0
 87TIBE0400333000030000030003005000000200000*30030000
 88SHUG030033000000000000300030050000002303020000000030
 89ORBI0003333300030300030003005045033503033000000030
 90PSTE3500033000000004000000300504503000333300000000
 91ARAX3500032000000020000000200504503000333300000000
 92PINA0500033300000030000000300504503000303300000030
 93ORIE0500033300000040000000300504503000303300000030
 94GLEC0400032300030300000000100004503000330300000000
 95GHOR0300032000000**04000320050030020033000000000
 96VALD0300000*000030000000000500*0030000000040330****2
 97INCA0300002000030020002000003003000000000000030000
 98INTE3000002330030020002000003003000000330000030000
 99GLAB3200332000000002003003200504503000333300000000
100MACR0500032300000300030003005045031503023000000000
101LEPT0003332300030300030003005045033503023000000000
102NERV030000233030002020023000000000000333000030000
103PLAT0300*02000300***4**400000000000000300000000000
104NERV030000233030002320023000000000000333000030000
105KOMA*3000020003300202022000000*0000330000030000
106CAVA*3000020000300202022000000*0000330000030000
107CAER04000023303000402342000030030003330003000000
108XHYB33000020003000202022000000000000330000000000
109NANA00003340000000400040010000000000000100003000
110TUBE030003200000030022020103000000030300000000000
111ANGU00000320000000200020000000000000000300300000000
112BOLA0300*32000000303230230000000000303310003000000
113CALI3000032000000023002030000000000000301000300000
114TUBE00000323300003002202010300000000303000000000000
115SIEB0300004000000020030000000300303030331000000000
116INFL03000003303003000300300*30300000000403000000
117SPLE03000003300003030000300033030300033403001000
118FLOC04000020*300000000000000*00000000302*33000***
119SCHW30000020003000200020000030030000003003000000000
```

```
CHAR-  AAAAAAAAAAAAABBBBBBBBCCCCDDDDDEEEEEEEEEEEEEEE
ACTERS 123456789111112345678123412345123456789111111
                0123                          012345
120HINT330000233033030003000000300300030304030000000
121VENT030000200000004000003000*30300000304030000030
122LIND3300000*0003004000200000*00300000334030000000
123SARM04000020*330030000200500*00000*00304033050302
124POLY0300*02330300000030030003003000003303000*0000
'EOD'
```

Appendix 4.

Few biographical notes concerning Arthur Hamilton have been published. The following material has come to light during the course of this work.

Arthur Hamilton, born 2nd Feb. 1806 in **Bhaugulpin, Bengal.** 2nd son of Frederick, 5th Baronet of Silverton Hill, Lanarkshire, (now a suburb of Hamilton), and Eliza Ducarel, daughter of John Collie from Calcutta.
School: Eton.
University: Cambridge, Trinity, Feb. 27, 1823; Civil Law Classes, 1st Class, 1825-26. LL.B. 1829.
Geneva University: Externe en Sciences et Lettres.
The monograph of Scutellaria was written in order to become acquainted with taxonomic work and to demonstrate that French is an appropriate language in the taxonomic field. Hamilton worked on the Candolle herbarium and does not cite any other source of herbarium specimens.

1833-58, Chaplain in the service of the East India Company, stationed at Moulmein, diocese of Calcutta.

Died late July 1858 on board the Prince of Wales on passage home from India.

Sources: Alumni Cantabrigiensis 1947. 2.3: 212.
Cambridge: University Press.
Eton School Lists from 1791-1850, 1854.
2nd ed.: 113A. London.
Burke's Peerage 1970. 150th ed.: 1220. London.
The Gentlemans Magazine 1858. 11: 200
The Clergy List 1855: 340 London: Cox & Co.