The study is divided into 2 parts: part one deals with the reclassification of the genus, nomenclature, and the investigation of taxonomic characters.

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The sections, subsections and the series have been described, their distribution discussed, and a key, a synopsis of infra-generic taxa, and distributional maps have been provided.

There appears to be 2 centres of morphological diversity of the genus: 1) C. Asia and 2) S.W. Asia (Turkey, Caucasus, Iran, Iraq, etc.). The maximum morphological diversity has occurred in S.W. Asia and it is also interesting to note that about 2/3rd of the total number of species tend to be concentrated in this area.

Staminode shape and leaf vein anastomosis, which have been used in the past to delimit the sections, have been found to be unreliable. The relative length of the upper corolla lobes, which is correlated with the presence or absence of a staminode, have proved to be the most useful in the delimitation of the sections. Ventricose/cylindrical corolla together with its glabrous or glandular condition, leaf arrangement, and indumentum have been used as the principal diagnostic for separating the subsections. The series are mostly separated on the basis of a number of correlated differential characters. The morphological characters used in the classification have been illustrated, their taxonomic usefulness assessed and evolutionary trends have been discussed.
Apart from 2 types of stem cortices (with or without palisade), which has been used in the delimitation of series Leucocladae, anatomy offers little aid in classification.

Developmental studies have been carried out with regard to the following organs: stomata, indumentum, cymes, scarious margin of calyx segments, corolla lobes, staminode and stigma. Developmental studies explains at least in part the staminode variability. Due to the significant intra- and interspecific variability, the use of the staminode shape has been avoided in the classification presented here. Evolutionary trends in the corolla lobes and staminode shape are discussed.

The chromosome number has been determined for the first time in 5 species and confirmed in 3 species. Camera-lucida drawings of chromosomes and a few photographs are presented. The relationship of cytology to morphology, taxonomy, distribution, etc. is discussed.

Part 2 deals with a detailed revision of the Turkish species (including those from the Aegean islands). *S. heterophylla* has been excluded from the area, but the following 14 species have been added to the Turkish list: *S. zuwandica, S. thesioides, S. striata, S. kurdica, S. amplexicaulis, S. scaricosa; S. pumilio, S. amana, S. bitilisica, S. serratifolia, S. gypsicola, S. davisi, S. subaequiloba, S. mersinensis;* the last 3 of these are described here as new to science. The revised list (with several previously accepted species reduced to synonymy or infra-specific rank) now comprises 49 species.

The original descriptions of the species have been amplified on the basis of the material seen. A key and a synopsis of classification is also provided. The staminode is drawn for nearly all the Turkish and a few non-Turkish species. All the Turkish species are assigned to their phytogeographical regions, their distribution is given and distributional maps are also provided.

Out of 49 species, 21 are endemic in Turkey. The percentage of endemism is 43% for the species, and 46% for species, subspecies and varieties. Most of the endemics tend to be concentrated in S. & S. Anatolia; areas of rugged topography and mountain ranges seem to have been the active centres of speciation. The relationship of the endemics are discussed and their distribution is shown.

The thesis has been illustrated with 17 figures and 21 plates. An index of the species is provided.
TAXONOMIC STUDIES
IN THE
GENUS SCROPHULARIA

by
SAMUEL S. LALL

Thesis presented for the Degree of Doctor of Philosophy
of the University of Edinburgh in the Faculty of Science

November 1969
Abstract

The study is divided into 2 parts: part one deals with the reclassification of the genus, nomenclature, and the investigation of taxonomic characters.

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Part I

General: Morphology, Classification and Ecogeographical Distribution of Scrophularia.

I. INTRODUCTION
Introduction

Caspar Bauhin in 1623 used the name Scrophularia in his Pinax, Joseph Pitton de Tournefort (1700) characterized the genus. In 1737 Scrophularia was formerly described by Linnaeus in his Genera Plantarum, and in his Species Plantarum (1753) he gave binomials to 12 species, 6 of which had already been mentioned in the Pinax.

Infra-generic Classification of the Genus Scrophularia L.

The first attempt of subdividing the genus Scrophularia was made by Wydler (1828) who classified 47 species. He divided the genus into 2 groups distinguished virtually by the presence vs. absence of the staminode, although he listed a few other floral and fruit characters which were either differential or did not contrast at all. He subdivided his first ditypic group on the basis of foliate vs. aphyllous inflorescences. He divided his second group into 4 subgroups; the first three were delimited on the staminode shape as the chief diagnostic (leaf texture, incision of margin and the habit of the plant being given as the differential characters), and the last on the 'capitate inflorescence'. However, he did not name his groups and subgroups, which need not concern us further here.

Reichenbach (1830) proposed two sections for the genus, namely, Ceramanthe and Scrophularia, mainly distinguished by the absence vs. presence of a staminode.

George Don (1837-38), apparently unaware of Reichenbach's classification, divided the genus into three sections, namely, Venilia, Scorodonia and Canina; Venilia differed from the last two in lacking a staminode, whereas Scorodonia and Canina were delimited on staminode shape. He subdivided the sections Venilia and Scorodonia on the basis of foliate vs. aphyllous inflorescences, and Sect. Canina on simple (cymes few-flowered, due to the abortion of pedicels) vs. compound inflorescence (cymes many-flowered). His classification is essentially a modification of Wydler's system.
Bentham (1846) adopted G. Don's classification with a few modifications. He recognised his Sections *Venilia* and *Scorodonia* but introduced another correlated character, i.e., the relative length of the upper corolla lobes; the former was now distinguished from the latter by its subequal corolla lobes and the absence of a staminode - in *Scorodonia* the upper corolla lobes being longer than the lateral lobes. He transferred Sect. *Canina*, as well as the species with thick leaves and ± obscure vein anastomosis, from Sect. *Scorodonia* to his new Sect. *Tomiophyllum*. Sect. *Tomiophyllum* differed from Sect. *Venilia* by its unequal corolla lobes and the presence of a staminode, and from Sect. *Scorodonia* virtually by its ± obscure vein anastomosis. Sect. *Venilia* was subdivided into 2 (on the basis of exserted vs. included stamens) and Sect. *Scorodonia* into 4 unnamed groups on the basis of a combination of the following characters: exsertion of stamens, presence vs. absence of scarious margin of the calyx segments, and the foliate vs. aphyllous inflorescence. Sect. *Tomiophyllum* was divided into Subsect. *Lucidae* and Subsect. *Caninae* on staminode shape.

Boissier (1879) accepted Bentham's classification, but proposed two new monotypic Sections, namely *Pycnanthium* and *Mimulopsis*, distinguishing the first by its unequal corolla lobes apparently correlated with the absence of a staminode (this proved to be a misobservation) and 'capitate inflorescence', and the second by its peculiar staminode which is attached to the corolla along its entire length. He also introduced staminode shape and pedicel/calyx-length ratio as additional characters to separate Sect. *Scorodonia* from Sect. *Tomiophyllum*. He divided Sect. *Tomiophyllum* into two subsections, i.e., Oppositifoliae and the *Sparsifoliae*, delimiting them on the leaf arrangement, being opposite in the former and alternate in the latter. Staminode shape was used to distinguish the three unnamed series of Subsect. *Oppositifoliae*. 
Urban (1900) proposed a new monotypic section *Microscrophularia* for *S. micrantha*, and distinguished it by its annual habit, white corolla, 5 sub-equal erect, semi-ovate lobes, and filiform staminode inserted at the bottom of the corolla tube. In 1903 he described a new species, *S. eggersii*, with larger flowers (7-9 mm long corolla, vs. 3 mm in *S. micrantha*) and a yellow corolla, and placed it also in Sect. *Microscrophularia*.

Stiefelhagen (1910) proposed a new classification. He divided the genus into two sections, namely, *Anastamosantes* and *Tomiophyllum*, distinguishing them by the conspicuous leaf vein anastomosis in the former and ± obscure anastomosis in the latter. He divided Sect. *Anastamosantes* into two subsections, *Vernales* and *Scorodoniae* on the subequal vs. unequal corolla lobes, and Sect. *Tomiophyllum* into 3 subsections, namely *Orientales*, *Farinosae* and *Lucidae*. Subsect. *Farinosae* differed from Subsections *Orientales* and *Lucidae* in its cylindrical corolla, while the last two differed from each other in their subequal (*Orientales*) vs. unequal corolla lobes.

It can be seen that the classification of *Scrophularia* has remained very unstable. Overweighting of the staminode and of vein anastomosis has resulted in unnatural divisions. The sectional nomenclature has become chaotic.

The present study is divided into two parts: 1) an investigation of the characters in relation to the various systems of classification briefly described above, and to work out a more reasonable classification for the whole genus; 2) a detailed revision of the Turkish species (see p. 144).
II. MORPHOLOGY
Morphology

1. Root: The root-system is fairly simple in the genus. Both tap and adventitious root-systems are present, although the former is much more prevalent. All the seedlings to begin with have a normal tap root-system which in the course of time is replaced by an adventitious one, e.g., *S. chrysantho*, *S. cryptopilia* etc. In *S. nodosa* a normal tap root-system is at first present, but as the plant grows older short, tuberous, rhizomatous, underground branches arise in an opposite-decussate manner; each eventually terminates in an erect, aerial, green shoot and bears small scales which are again arranged in the same opposite-decussate manner, each having a small bud in its axil, some of which develop into secondary tubers. Adventitious roots arise from these tuberous suckers (Plate 1.1, p. 7). Stiefelhagen (1910) has described these short, tuberous suckers as swollen secondary roots, which is due to misobservation. I have also observed that the plants of *S. nodosa* and *S. scopoli* when grown in pots develop stilt roots from the lower nodes.

The tap root may remain short and form an intensively branched root-system near the surface, e.g., *S. scopoli*, or it may become very long, thick, woody and perennial, e.g., *S. canina* etc. A specimen of *S. przewalskii* from Eastern Tibet (Ludlow 4769) measures 8 cm in length and has a 20 cm long root which is broken at the end. The plant is reported to grow on loose gravely earthy scree and the collector's note says that the roots are several feet in length.

2. Stem: The stem ranges from 5 cm (some forms of *S. minima*) to 175 cm in the cultivated forms of *S. cryptophila* and *S. nodosa*. Stiefelhagen (1910) reports that *S. umbrosa* Dum. may attain the size of a man and its stem may become as thick as 4 cm in diameter in its native habitat. The size of the stem has been used a good deal in combination with the other characters by some workers like
Plate 1.1

*S. nodosa* L., showing tuberous suckers and the adventitious root-system.
Pennell at the specific level. It should, however, be mentioned that the plants in cultivation are usually much taller than in the wild, and some care should be taken while making the comparisons.

As a rule the stem remains herbaceous in the mesophytes (e.g. *S. chrysantha*, *S. kotschyaniana*, *S. vernalis* etc.) but somewhat woody towards the base in the xerophytes; this character has also been used as an additional diagnostic in some cases (Pennell, 1943).

The colour of the stem is green in most of the species, but sometimes it may be red especially towards the base, e.g. *S. peregrina*. In *S. lucida* the stem is usually purple with a shiny surface. The stem also acts as a photosynthetic organ and the cortical cells are richly supplied with chlorophyll; in taxa where the stem is characterised by red or purple colour, the red or purple pigment is only present in the outermost 1-2 layers of the stem. In *S. fruticosa*, *S. leucoclada*, etc., the reduction in the surface area of the leaf is compensated for by the development of palisade tissue in the cortex; the white colour of the stem, a useful taxonomic character, in these cases is probably due to the thick, white cuticle and not due to supposedly white cork-tissue, as has hitherto been thought (Stiefeilhagen, 1910). The colour of the stem is helpful in some cases at the specific level (*S. olympica*, *S. lucida* etc.).

The stem is obtusely to sharply angled in most cases, but in some cases it is almost terete (*S. fruticosa*, *S. hypericifolia* etc.). In *S. umbrosa*, *S. elatior* etc., the stem is prominently winged, especially below the leaf-bases; this character has been made the basis of the Ser. Alatae of Sect. Scrophularia.

As a rule the stem is erect in most of the species, but in some cases it is rarely prostrate, being adpressed against the rocks (some forms of *S. kotschyaniana* and *S. chrysantha*), or ascending (*S. cryptophila* etc.).
In annuals and biennials the plant usually remains single-stemmed, although it may become profusely branched higher up. In *S. xanthoglossa*, *S. striata*, *S. canina* etc., where the long, woody root becomes perennial, a number of branches arise from the base of the stem, which in turn may produce secondary branches in the same manner, with the result that the plant becomes many-stemmed at the base, which becomes considerably thickened in the course of time. In *S. scoparia*, from Afghanistan, the stem grows for a while and then branches at the base; each branch grows 0.5-2 cm in length and becomes branched again; in this way as many as 50 or more stems are produced from the base of the plant, each with a diameter of 2 mm; some of the stems also give off lateral branches. A large number of delicate stems in *S. scoparia* are closely pressed together and give the plant a broom-like appearance; this is a useful character for separating it from the closely related species like *S. nudata*, etc. - other such cases where numerous, delicate stems provide a helpful diagnostic are *S. thesioides* and some forms of *S. striata* etc.

In *S. nodosa* each stem arises from short, tuberous suckers. The short, swollen, tuberous suckers in *S. nodosa* and *S. macrobotrys* provide a useful diagnostic to distinguish them from allied species *S. scopolii*.

The lateral branches may start developing when the plant is still young or their formation may be considerably delayed. In *S. peregrina*, as observed by the author in the greenhouse, the lateral buds which can be seen at the seedling stage remain dormant for a long time. The plant grows vigorously and attains a height of about 2 feet, producing axillary cymes, some of which have produced mature capsules by this time. Then the growth almost stops in the upper region for several days, during which time the lateral branches arise in a basipetal order,
after which the normal growth is resumed in the upper region. The simple vs.
branched stem is a useful character at the specific level but needs some caution,
as the branching may be deferred for a while and some of the early collected
annuals may remain unbranched. Grazing in some cases may induce irregular
branching; the photograph of Big's new species *S. clematidifolia* from Amanus
which he related to *S. antiochus* appears to be a damaged plant of *S. scopolii*
by grazing.

Sometimes the lateral branches arise in such a way as to give the plant
the appearance of a candelabrum; this character is responsible for the specific
name of *S. candelabrum*.

3. Leaf: Usually the leaves are opposite and decussate in the vegetative
but become alternate in the floral region; occasionally a few lower floral
leaves may be opposite. Boissier (1879) used this character to divide Sect.
Tomiophyllum into Subsect. *Oppositifoliae* - at least some of the lower leaves
opposite - and Subsect. *Sparsifoliae* - all the leaves alternate or scattered.
But this character, like most of the other characters, shows intergradation.
For example, in *S. ilwensis*, all the Turkish specimens have alternate leaves,
but in Caucasian plants the lower one or two pairs may be opposite; at least
in some forms of *S. crassicaulis*, the lower leaves are opposite, and in
*S. scopolii* all the leaves may rarely be alternate. Apart from being of some
taxonomic aid at the specific level, the alternate/opposite arrangement is not
a dependable character at any level of classification. Moreover, even if
Boissier's *Oppositifoliae* and *Sparsifoliae* are maintained, they would not serve
any useful purpose, as quite unrelated species like *S. versicolor* would be placed
with *S. hypericifolia, S. leucoclada*, etc.
The leaves are whorled in two species of Sect. Ceramanthe, namely, S. orientalis and S. verticillata. In the present work this character has been used as the principal diagnostic character to distinguish subsect. Orientales from the other subsections of Ceramanthe.

As a rule, the leaves are petiolate, the size of the petiole varying from 23 (S. megalantha) to 0.5 cm, in some forms of S. rupestris var. libanotica. In S. amplexicaulis the leaves are sessile. The lamina is usually larger in size in the mesophytes, e.g. S. megalantha, S. scopolii, S. chrysanth, S. cryptophila, and smaller in the xerophytes, S. hypericifolia, S. fruticosa, etc. The size ranges from 19 x 10 cm (S. chlorantha) to 1 x 0.3 cm (S. hypericifolia), and is of limited taxonomic value in so far as it helps in separating some of the species, such as, S. scopolii and S. chlorantha.

In species with undivided leaves the lamina may be rhomboidal, ovate to broadly ovate, oblong to oblong-lanceolate, spatulate or rarely reniform in outline, and is extremely useful at the specific level - in distinguishing many closely related species, such as, S. rimarum and S. bitlisica etc. - and higher level. In the subsect. Vernales of Sect. Ceramanthe, the leaf is ovate to broadly ovate - or rarely rhomboidal or reniform - in the Ser. Chrysanthae, and oblong to oblong-lanceolate in subsect Vernales Ser. Lateriflorae; in the former the leaves are densely villous and are correlated with the foliate inflorescence and the villous non-scarious-margined calyx segments, while in the latter they are glabrous or sparingly glandular-puberulent with glabrous to sparsely glandular, scarious-margined calyx segments and aphyllous inflorescence.

Vein anastomosis has received much attention from the time of Bentham, who used this character as the principal diagnostic for separating Sect. Scorodonia from that of Torniophyllum, followed by Boissier who, although adding the staminode shape and the pedicel/calyx length ratio as additional differential characters,
retained anastomosis as the main distinguishing feature. Stiefelhagen (1910) made full use of this character and divided the genus into two sections, Anastomosantes and Tomiophyllum, exclusively on the basis of anastomosis, which was described as conspicuous (especially on the underside of the leaf) in the former, and poor to absent in the latter section. It should be mentioned that anastomosis is present even in the thickest and more leathery leaves - it becomes obscure as the leaves thicken, partly due to the filling and consequent levelling of the areas between the anastomosing veins (the veins thus come to lie at the same level or even slightly below, thereby losing their conspicuousness, as contrasted with the thin leaves where the areas surrounded by the anastomosing vein appears like shallow cavities giving the anastomosis visual distinctness) and partly due to the thickening of the cuticle. Anatomosis can be clearly seen if thick and coriaceous leaves are cleared - if the fresh leaves are kept in 1:3 acetic-alcohol for 3-4 days they are beautifully cleared. Although some taxonomic value cannot be denied to anastomosis - especially in extreme cases, where the visual difference (anatomically none) allows one to distinguish one species from another - yet a sharp division of the genus into two groups is not possible on the basis of this character alone, because of intermediate states; Stiefelhagen has himself remarked that there are many intergrading forms between the Sections Anastomosantes and Tomiophyllum. If one accepts Stiefelhagen's classification (at the sectional level), then apart from the inconvenience and overweighting of a single character, many species will remain virtually unclassifiable. The same applies to Bentham's Sections Scorodonia and Tomiophyllum, because although he lists a number of other supporting characters, they do not contrast, and do not serve as diagnostic or even differential characters. The only important diagnostic character, other than the anastomosis,
which he mentions, is the incision of the leaf margin (leaves dentate in Sect. Scorodonia and incised in Tomiophyllum), but this is again overruled by the anastomosis as he includes S. hermini, S. racemosa, S. sambucifolia, S. auriculata, etc. in the Sect. Scorodonia because of their conspicuous anastomosis (although the leaves are divided in all of these species), and several species with undivided leaves like S. marginata, S. lepidota, S. hypericifolia, S. glauca, etc. in the Sect. Tomiophyllum on account of their obscure anastomosis. The same is also true of Boissier's attempt to separate the above two sections, who also gave anastomosis an over-riding importance. He distinguished Sect. Scorodonia from Sect. Tomiophyllum on the basis of the following 4 characters: undivided vs. divided leaves, pedicels longer than calyx, transversely broader to reniform vs. oblong to reniform staminode, and conspicuous vs. obscure anastomosis. Pedicel/calyx length ratio shows a loose correlation and the staminode shape, as discussed in the following pages, is not correlated with morphological differences. Inclusion of a large number of species with undivided leaves, such as S. pulverulenta, S. rupestris, S. glauca, S. catariifolia, S. prasiifolia, S. lepidota, S. hypericifolia, etc. by Boissier in Sect. Tomiophyllum shows that the undivided vs. divided leaf character was given a secondary importance; in S. prasiifolia and some forms of S. rupestris the pedicels are also longer than the calyx and in S. catariifolia even the staminode is reniform in shape (and also in S. ramarum), and somewhat obscure anastomosis in these species was the only justification for keeping them in Sect. Tomiophyllum. There are many other species, such as, S. sambucifolia, S. calliantha, S. nabateorum etc., which if considered would hover between the two sections: they would fall in Sect. Tomiophyllum because of their divided leaves, oblong or ovate staminodes, but would be included in Sect. Scorodonia due to their distinct anastomosis and longer pedicels (longer than calyx), as
anastomosis is the main diagnostic character for distinguishing the two sections in question. Bentham, in fact, did include *S. sambucifolia* in Sect. *Scorodonia*.

In the opinion of the author anastomosis is not a distinct character for monothetic grouping at any level of classification, nor as a main diagnostic character as it has hitherto been used; it can only be useful as a differential character.

The leaf apex varies from broadly obtuse to acuminate and is helpful only at the specific level to separate some of the closely related species; for example *S. chlorantha* can be distinguished from *S. nodosa* and *S. scopolii* because of its larger and acuminate leaves.

Although predominantly the leaves are well scattered on the stem, there is a tendency, in some cases, for the leaves to be crowded towards the base to form a rosette, e.g. *S. rosulata, S. davisii, S. pumilio* etc. Rosulate leaves and the leaf colour have a limited taxonomic value at the specific level.

The leaf base may be cuneate, rounded or truncate to deeply cordate. Its taxonomic significance will be discussed in the following pages.

The cotyledonary leaves are entire-margined to begin with, but later on remain as such or develop two to three small teeth. The following serial trends can be seen in the differentiation of the leaf-margin as one moves from the base of the plant upwards:

1. an increase in the number of teeth;
2. formation of secondary teeth;
3. a gradual decrease in the depth of the teeth from base to apex of the lamina;
4. a gradual separation of the lower teeth into distinct segments;
5. the differentiation of margin of the primary, as well as that of the secondary segments essentially follows the same pattern as that of the parent leaf, the
maximum differentiation being achieved by the basal parts of the segments, as well as by the lower segments of the leaf.

Not all the above mentioned trends are fully realized in all the species of the genus. The first two trends are shown by most of the species with undivided leaves. Table 1 (p.16) shows a gradual increase in the number of teeth, in several weeks' old seedlings of *S. peregrina*, from the base of the plant upwards, and also shows the number of teeth in each pair which developed the secondary teeth (also see Fig. 1, p. 17). As the leaves enlarge in size, more and more primary teeth develop secondary teeth until the lower leaves become birostrate and the upper ones doubly dentate. This is the general pattern of development in most of the species. In a few species, e.g. some forms of *S. rupestris*, *S. pulverulenta*, the secondary teeth never develop and consequently the margin remains dentate, or crenate in the lower part of the plant and dentate in the upper (*S. davisi*). In *S. nodosa*, *S. oldhamii*, *S. kurdica* etc., the margin is serrate, that is, the teeth are sharp and directed towards the apex. Plate 1.2 (p.18) shows different types of leaf margins; the taxonomic value of the leaf margin is restricted to the specific and infra-specific levels only.

In some species, e.g. some forms of *S. rimarum*, *S. catarifolia*, *S. serratifolia* etc., the teeth especially towards the basal part of the lamina become deeper than one-third the distance from the margin to the mid-rib, with the result the leaves become pinnatifid; sometimes 1-2 basal segments may become separate (*S. bitlisica*, *S. olympica* etc.), tending towards the pinnatisect condition.

In many species incisions reach to or nearly to the mid-rib, that is, the lamina becomes pinnatisect. In *S. thesioides* the lower leaves with 2-3 pairs of long, extremely narrow and entire-margined primary segments provide a useful character for separating it from *S. canina*. More frequently, as in some forms of
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**Legend**

- **A**: Number of Primary Teeth
- **B**: Number of Secondary Teeth
- **C**: Number of Sealed Teeth
- **D**: Number of Teeth in the Oral Cavity
S. peregrina: - Leaves from a young plant, Showing a gradual increase in the number of teeth, from the base of the plant upwards. 1-2, cotyledonary leaves; 3-4, 2nd pair; 5-8, vegetative leaves; 9-10, floral leaves.

S. xanthoglossa: - 11-18, vegetative leaves from the base of the plant upwards showing a gradual division of the margin.
Plate 1.2

Leaf Margin: B, dentate to doubly dentate; A & C, crenate to bicrenate.
S. variegata and S. scabiosifolia etc., the lower half to one-third of the leaf becomes completely pinnatisect, whereas the upper part forms a pinnatifid terminal segment which shows the maximum differentiation in the basal portion.

In species where the leaf ranges from pinnate or pinnatisect to bipinnatisect (e.g. S. variegata, S. mesopotamica) or bi- to tripinnatisect (S. scarsosa, S. lucida, etc.) the variation is produced by the following features:

1. Shape and size of the terminal segments;
2. Shape and size of the lateral segments;
3. Number of the lateral segments;
4. Different degrees of margin differentiation of the terminal segment;
5. Different degrees of the margin differentiation of the lateral segments;
6. Colour of the veins and leaf;
7. Degree of visibility of anastomosis.

Although one can outline the features which bring about the minor visual variations (which are useful in separating many taxa), it is not possible to work out any taxonomically useful classificatory scheme due to the significant intra- and interspecific variability, e.g., pinnatisect to bipinnatisect forms occur in S. variegata (subsp. pinardii, variegata and depauperata); pinnate to bipinnate, in S. sambucifolia; pinnate to bipinnatisect, in S. mesopotamica; bi-tripinnatisect, in S. scarsosa, S. lucida, etc. The entire range of leaf spectrum, as outlined above, shows such a continuous intergradation, so that any attempt at making a taxonomically useful grouping would result in many species having to be classified in different taxonomic groups. In view of the above situation, the author has placed all the species in which either all the vegetative leaves are 1-3 pinnatisect or pinnate or at least some of the lower leaves are pinnatisect in Ser. Xantheglossae, and those in which either all the leaves are undivided or pinnatifid (rarely with 1-2 free or almost free basal
segments) in the Sers. Nodosae and Atropatanae; the last two series are separated on the basis of a number of correlated differential characters. In S. stewartii, S. olympica, S. pruinosa and S. polyantha the leaf ranges from almost undivided to pinnatisect or pinnate (S. polyantha); the first three are placed in the Ser. Atropatanae and the last one in the Ser. Nodosae. Within the subsect. Caninae, the series Nodosae, Atropatanae and Xanthoglossae represent assemblages of related species.

4. Indumentum: The indumentum is of two types in the genus, glandular and scaly. A typical gland consists of a head, a one-celled neck, and a stalk. The glandular type can be conveniently grouped into two categories, depending on the shape of the head which may be more or less rounded (Fig. 9) or oblong (Fig. 10).

In the rounded type the head may consist of one, two, or four to many cells. The glands with 1-2 celled head may lack a neck cell (Fig. 9; 7-8) or may have a neck cell and a 1-several-celled stalk (Fig. 9; 20). The glands with a 4-multi-cellular head usually have a neck cell, and a 1-several-celled stalk (Fig. 9; 23-26). The rounded type of glands occur in all the organs, such as leaf, stem, pedicel, calyx, corolla, stamens, staminode and ovary. These glands offer no taxonomically helpful variation, as uni-, bi-, or multicellular glands may occur on the same plant.

The oblong type of glands have not been reported before and occur only on the filaments and the dorsal side of the staminode in a large number of species. The oblong type of glands provide a good taxonomic character, although in some cases both rounded and oblong types occur on the same filament, e.g., S. oldhamii, S. polyantha, S. monibiformis, etc.

The oblong type also comprises a head, a neck cell, and a stalk. The head may be uniseriate (Fig. 10), or biseriate (Fig. 11); the stalk in both cases varies from one to several cells (Fig. 10 & 11).
The glands occurring on the filament have been referred to as 'filament glands' in the present work; those with a rounded head are round type and those with an oblong head as oblong type.

The round type of filament glands are on the whole a characteristic feature of the mesophytes, and those of oblong type of the species with xeromorphology, although a few exceptions to this general rule do occur. As already mentioned, the types of filament glands provide an additional helpful diagnostic character in separating Ser. Nodosae from Ser. Atropatanae (see p.114). The filament glands are also useful in distinguishing certain species, as S. ilvensis and S. scopulii, etc.

Glabrity vs. hairiness is a useful diagnostic for separating infra-generic taxa. All the hairs, no matter on what part they occur, are gland-tipped, and vary in size from several microns to 3 mm. In many species the whole plant may be densely covered with long hairs; such a condition is described as villous in contrast to glandular-puberulent or glandular-pubescent, in which case the plant is beset with very short-stipitate glands. At the specific level villousness vs. glabrity or glandular-puberulent condition is a helpful diagnostic in separating S. pegaea and S. luridiflora from S. scopulii, S. nodosa, S. macrophylla, etc., and at the series level as a differential character to distinguish series Chrysanthae from series Lateriflorae in Sect. Ceramanthe, etc.

The author has found the glandular/glabrous corolla to be a helpful additional diagnostic at the sub-sectional level within the sect. Scrophularia (for separating subsects. Przewalskiae and Farinosae, etc.) and at the series level within subsect. Vernales of Sect. Ceramanthe, and glandular/glabrous calyx, glandular/ovary and villous/glandular-puberulent habit at the specific (see pp.111-112) and series levels (see pp.111-112) in both sections.
Lepidote scales are present only in *S. lepidota* and occur on leaf, stem and calyx. The scale consists of a short stalk and a shield-shaped portion which is made of long, radiating cells, which gradually taper towards the apex; some of these cells become forked (Fig. 11). *S. lepidota* is a very distinct species of a doubtful affinity and is unparalleled in the genus for the development of lepidote scales. Because of its habit and distinct indumentum it has been assigned the status of a subsect. *(Lepidotae)* in sect. *Scrophularia*.

5. General Inflorescence: Cymes are the component units of the general inflorescence, and since they have been used a good deal in the present work, it seems desirable at this stage to make the application of the following terms clear. In the development of a cyme the floral axis terminates in a flower and below this flower two bracts arise each bearing a daughter axis in its axil; each daughter axis ends in a flower like the parent axis and bears two bracts in turn, and the process may be repeated several times. The portion of the cyme between the branch which subtends it and the first pair of bracts on the cyme is referred to as the peduncle, and the part between the flower and the bracts as the pedicel. All the bracts on the cyme have been referred to as bracteoles and the term bract or floral leaf is restricted to the bract or leaf in the axil of which a cyme arises. Since each daughter axis produces two bracteoles before ending in a flower, the part between the first and the second pair of bracteoles is the daughter axis of the first order, the part between the second and the third pairs of the second order, and so on.

Developmental studies suggest that it is probable that a 3-flowered cyme has apparently produced along one evolutionary line a many-flowered cyme by the production of more and more daughter axes, and along the other 2-flowered by the suppression of one or both of the daughter axes. Such a tendency can be
seen on the same plant. A few basal cymes on the main axis have the maximum number of flowers, those on the side branches have fewer, and the number gradually decreases until towards the top of both the main axis, as well as, its branches the cymes become 3-4-flowered. This is the usual pattern in most cases.

Although, theoretically each daughter axis should produce two more daughter axes before terminating in a flower, yet in most cases one of the two subsequent daughter axes is permanently suppressed after the first or the second dichotomy, with the result that a dichasium sooner or later passes into a monochasium. In Scrophularia a dichasium always ends in a scorpioid monochasium - a constant feature in the genus. Even in those species, e.g., S. capillaris, S. trichopoda etc., in which the suppressing of one of the two daughter axes occurs after the third dichotomy, only a few basal cymes show this phenomenon, the upper and those on the side branches become monochasial, as a rule after the first dichotomy.

Although the cymes are basically similar in structure, the general inflorescence may show a few differences due to the following variations: number of flowers per cyme; size of the peduncle; angle which the successive daughter axes make with the pedicels of the flowers of the preceding daughter axes respectively; size and thickness of the pedicel; relative length of the floral axis and the arrangement of cymes on it, and the floral leaves and bracts.

As already mentioned above, the number of flowers in a cyme varies even on the same plant, but when the basal cymes on the main stem are compared within the species the usual number varies from 4-15, although in some cases, S. chlorantha, S. peyronii etc., the cymes may have up to 30 flowers. The inflorescence continues to expand for several weeks, and Shaw (1962) has pointed out that "S. multiflora" represents more mature plants of S. californica. Making allowance for the environmental variations, the number of flowers per cyme is still a useful additional
characters for distinguishing certain species, such as *S. canina* and *S. peyronii*,
*S. chlorantha* and *S. nodosa*, *S. uniflora* and *S. rimarum* etc.

Whereas there has been an increase in the number of flowers in a cyme, there
has also been a decrease in number, for example in *S. pumilio* the 3-flowered cyme
is reduced to a single flower, making the general inflorescence look like a raceme
(Fig. 3) with a terminal flower; sometimes the whole axis is reduced to a
terminal 3-flowered cyme.

The peduncle varies a great deal in size. The lower peduncles on the same
plant are the longest, whereas the upper ones show a gradual reduction in length.
The peduncle ranges in size from 5 cm (*S. luridiflora*) to 0.4 cm (*S. televivensis*,
some forms of *S. michoniana*). In *S. koeiei*, endemic in Afghanistan, the 3-flowered cymes are completely sessile. In *S. calycina*, *S. pauciflora*, *S. spicata*
and *S. mandshurica*, the subsessile to sessile peduncle is correlated with glandular
to villous ovate, acute to acuminate calyx segments, shape of the upper corolla:
lobes and the general habit of the plant; these correlated characters, in the
present work, have been made the basis of the Series Calycinae of Subsect. Caninae
of Sect. Scorophularia. Size of the peduncle has a limited taxonomic value at
the specific level.

The angle which the successive daughter axes make with the pedicel of the
flowers of the preceding daughter axes respectively, together with their size,
as well as that of the pedicels, give the cymes their characteristic appearance.
In *S. atrata*, *S. obtusa*, and some forms of *S. trichopoda* etc. (Fig. 2), at least
the first two to three daughter axes spread out at or nearly at right angles to
the pedicels of the flowers of the respective preceding dichotomy; in all these
except some forms of *S. trichopoda* both the daughter axes and the pedicels are
quite long and each daughter axis lies in a straight line with the pedicel it
Fig. 2

Cymes: A, S. obtusa; B-C, S. trichopoda; D, S. nabataeorum; E, S. capillaris.
Fig. 3

Whole inflorescence: D, *S. pumilio*; E, *S. minima*.
produces. In most cases this relative angle is seldom more than 45°, and can be as narrow as 22.5° or even less. In *S. capillaris* the pedicels have been described as capillary, that is they are long and remain thin even after the fruits are mature. The long, thin, capillary pedicels provide a useful character in the separation of species like *S. kurdica, S. capillaris, S. amana* etc. from their allies. The term divaricate cyme in the literature has been applied either to denote cymes whose daughter axes spread at or nearly at right angles, or if the daughter axis makes an angle of 45°, the cymes are many-flowered, and usually show 2-3 dichotomies before becoming monochasial; the pedicels are invariably long and lie in a straight line with their respective daughter axis; consequently the cymes are large and much-spreading. The taxonomic value of this character (divaricate cymes) is limited only to the separation of a few related species, such as, *S. trichopoda* and *S. tagetifolia, S. capillaris* and *S. scopolii* etc.

The arrangement of cymes on the floral axis offers little variation. They begin either as opposite-decussate in the lower region, or alternate from the very start. In *S. orientalis* a few basal cymes are usually whorled. In *S. chrysanthha* the floral axis is shortened in the upper part and the cymes are arranged more or less in a corymbose manner; later on, however, the floral axis lengthens between the nodes and and the cymes become well separated. This character is helpful, especially during flowering, together with acute calyx segments, and short stature of the plant, to separate *S. chrysanthha* from a closely allied species *S. vernalis*. In *S. minima M.B.;* the cymes are reduced to single sub-sessile flowers which are densely crowded on a much shortened floral axis - Wydler (1828) and Boissier (1879) have referred to this specific type as 'capitate inflorescence' (Fig.3, E).

In *S. peregrina* the first 4-6 pairs of leaves are vegetative, the rest floral (i.e. bearing cymes in their axils). Depending on the shape and size of
the floral leaves, three main types of general inflorescences have been recognised
(Wydler, 1828; Bentham, 1846 and Boissier, 1879), namely: 1) aphyllous, the
vegetative leaves are sharply distinguishable from the floral ones, as the latter
are reduced to small bracts many times shorter than the former (S. amplexicaulis,
S. lepidota etc.); 2) subfoliate, the first one or two pairs of floral leaves
resemble the vegetative ones in shape and size, the upper being reduced to bracts
(S. nodosa, some forms of S. scopolii etc.), and 3) foliate, the lower several
pairs of floral leaves are similar to the vegetative ones, gradually diminishing
in size in the upper region (S. kurdica, S. chrysantha, S. cryptophila etc.).

Foliate vs. aphyllous inflorescence was used by G. Don (1837) for the
further division of his sections Venilia and Scorodonia and by Boissier (1879)
for the subdivision of his informal groups of Sect. Venilia. S. tadschicorum
(Sect. Ceramanthe) has a subfoliate inflorescence, and subfoliate and aphyllous
inflorescences occur in S. scoploii. As already pointed out, the best use of
aphyllous vs. foliate inflorescence can be made as a differential character in
Subsect. Vernales, where in Series Chrysanthae and Lateriflorae, it is correlated
with leaf shape, indumentum, calyx and capsule characters. At the specific level
it is useful for separating certain allied species, such as, S. scopolii and
S. luridiflora etc.

The bracteoles may be ovate, lanceolate, narrowly oblong, or linear to
subulate, but the shape sometimes varies considerably even on the same plant,
thereby mitigating their value in taxonomy. The first pair of bracteoles is
the largest, the others show a gradual reduction in size. They may be densely
villous (S. chrysantha, S. pegaea etc.) to glabrous (S. umbrosa). There are two
types of bracteoles depending on the margin; 1) those without a scarious margin,
e.g. S. chrysantha, S. scopolii etc., and 2) those with a scarious margin, e.g.
S. scariosa, S. mesopotamica etc. - the latter type is the basis of Ser.
Scariosae of Sect. Scrophularia in the present work.

In my survey of the genus I have found that the relative length of the pedicel of the first flower of the cyme and the first pair of bracteoles is a very useful character. In species with undivided or pinnatifid leaves, the relatively longer pedicel (longer than the bracteoles) shows a high correlation with a cordate to subcordate leaf base, round type of filament glands (Fig. 9, p. 62), usually A or B-type of upper corolla lobes (Fig. 6, p. 37), tall, thick, stems and usually larger leaves. By contrast, relatively shorter pedicels (or pedicels equalling the bracteoles) are correlated with cuneate to truncate leaf bases, oblong type of filament glands, thick leaves with obscure anastomoses, C-type of upper corolla lobes (Fig. 6, p. 37), and relatively shorter, less thickened stems with smaller leaves. The pedicel in the first case is usually 5-26 mm long, whereas in the second 1-5 mm long. Although the above-mentioned characters are highly correlated, the correlation is not by any means absolute, and may break down in one or two characters. For instance, in S. luridiflora the pedicel is shorter than the bracteole, but filament glands are of round type, leaves are large and thin with deeply cordate bases, and a distinct anastomosis; stems are tall, thick, herbaceous and villous, and pedicel 7-14 mm long.

These differential characters are very useful in separating the two groups of related species, and have been made the basis of the series Nodosae and Atropatanae of Subsect. Caninae of Sect. Scrophularia.

6. Calyx: The calyx consists of 5 segments which are imbricate and persist in the fruit. The segments may be characterized by a narrow to broad scarious margin, or may lack it altogether. The terms entire-margin and immarginate have also been used in the literature to describe the absence of the scarious margin. The non-scarious-margined calyx segments may be ovate, oblong, subulate or
narrowly oblong to lanceolate in outline (Plate 1.3), and maybe glabrous to densely villous. The correlation of non-scarious-margined, villous calyx segments with the broadly ovate leaf-shape, foliate inflorescence, glandular capsules, and villous habit, and that of the scarious-margined, glabrous to sparingly glandular calyx segments with the oblong to oblong-lanceolate leaf, aphyllous inflorescence, glabrous capsules, and nearly glabrous to glabrous habit in the series Chrysanthae and Lateriflora respectively, has already been mentioned in the preceding pages. In Sect. Scrophularia non-scarious-margined calyx-segments in the subsect. Przewalskia, non-scarious-margined, ovate, acute to acuminate, glandular to villous calyx segments in subsect. Hescheri-florae and in subsect. Caninae series Calycinae provide additional useful characters for delimiting these groups.

Calyx segments are also helpful in separating certain related species. Acute calyx segments in S. chrysantha together with the "capitate inflorescence" (cymes arranged in a corymbose fashion) and long-exserted stamens are helpful in distinguishing it from a closely related species S. vernalis; villous/glabrous in S. pegaee and S. scopolii, and densely glandular/glabrous calyx segments in S. catarifolia and S. rimarum provide a useful diagnostic character in these species.

The shape of the scarious-margined calyx segments is less reliable as a taxonomic diagnostic; they may be oblong to oblong-linear, narrowly to broadly ovate, or narrowly obovate to orbicular in outline. Oblong to ovate, ovate to obovate, or obovate to orbicular segments can be seen even in the same calyx. The term orbicular in the literature is loosely used and includes broadly ovate to reniform segments. The scarious margin varies in width and colour. In some species, e.g. S. lutidiflora, S. nodosa, it may be as narrow as 0.2 mm, whereas
in other cases, e.g., *S. olympica*, *S. scariosa*, etc. (Plate 1.3), as wide as 2-3 mm. In some species, e.g. *S. olympica*, *S. scariosa*, *S. michoniaca* etc., the scarious margin grows more vigorously as compared to the inner herbaceous portion along the longitudinal plane, and is consequently thrown into folds or pleats, such a condition has been described as 'undulate margin'. In *S. scariosa* some of the otherwise ovate segments develop a large cordate base because of the faster growth of the scarious margin in this region; some of the reniform segments of *S. olympica* are also a result of such activity. The width of the scarious margin provides a useful diagnostic character in certain closely related species like *S. mersinensis* which can be distinguished from *S. myriophylla* by its leaf and pedicel characters and the calyx segments with a very wide scarious margin; other such examples are *S. nodosa*, *S. luridiflora*, *S. scopolii* etc. In *S. olympica* the wide 'undulate scarious margin' is very satisfactory in distinguishing it from the related species, like *S. rimarum*, *S. bitlisica* etc.; other species where this character can be useful are *S. michoniaca*, *S. pruinosa* etc. The colour of the scarious margin maybe white, yellowish, brown or pink, but is of limited taxonomic value, as white and brown coloured scarious margin may be present in the same species, like *S. scopolii*; pink scarious margin in *S. mesopotamica*, however, provides a good additional diagnostic for separating it from *S. scariosa*.

Sometimes, as in *S. hyssopifolia*, *S. zuvandica* etc., the scarious margin breaks up into sharp, irregular teeth; such a scarious margin has been described as dentate, and is of extremely limited taxonomic value.

7. **Corolla**: The corolla varies in size from 2.5 mm (*S. micrantha*) to 25 mm in some forms of *S. przewalskii*. It consists of 5 lobes and a tube. The corolla tube is of three types: 1) infundibular-campanulate (some forms of *S. delavayi*);
Camera lucida drawings of Corolla in Scrophularia: 
A, Corolla cylindrical (S. delavayi); B, Corolla, infundibuliform (S. delavayi); C-E, Corolla cylindrical, C, S. farinosa, D, S. przewalskii, E, S. gracilis.
A, B & D, drawn to the scale No. 1.
C & E, drawn to the scale No. 2.
2) cylindrical, usually 2–several times longer than broad (S. gracilis, S. przewalskii, Fig. 4), and 3) ventricose, the tube bulging like a belly on the lower (abaxial) side, S. nodosa, S. peregrina (Fig. 5).

Both the ventricose and cylindrical types occur in the two sections, namely, Ceramanthe and Sorophularia, whereas the infundibular-campanulate type is only present in the sect. Sorophularia. The cylindrical type, although usually straight, is sometimes somewhat curved in the posterior region. In S. farinosa and S. gracilis, the corolla is glabrous throughout, whereas in S. przewalskii, S. delavayi, S. neomaxiana etc., the corolla is glandular. In some forms of S. delavayi, where the corolla tube is infundibular-campanulate, the inner dorsal side of the corolla is densely covered with long glandular hairs (Fig. 4, B).

Likewise, the ventricose type is predominantly glabrous, but rarely in some cases, e.g., S. landroveri, S. calycina and S. megalantha etc., glandular. In S. calliantha, only the upper lip is sparingly glandular on the inner dorsal side.

Corolla lobes are usually 5 in number, the two upper dorsal lobes (posterior-lateral), which constitute the upper lip; the two lateral lobes (antero-lateral); and the median lobe (anterior) – the lateral and the median lobes make up the lower lip. The aestivation shows that the lateral lobes are overlapped by the upper lip and these in turn overlap the median lobe.

The upper and the lateral lobes may be subequal or unequal in size; when unequal the upper lobes overtop the lateral ones; the median lobe may be as long as, or slightly shorter or longer in both cases.

The survey of the genus has shown that the relative length of the corolla lobes is the most constant and reliable character for the primary division of the genus, as it is also highly correlated (though not completely) with the presence or absence of a staminode. The correlation breaks down in S. subaequiloba and
Fig. 5
Camera lucida drawings of ventricose corolla:
S. heucheriflora, but in both cases the staminode is unique: in the former it is roundly reniform with a dorsal canal, and in the latter it is ovate-spathulate, extending much beyond the corolla lobes; in the present work these two species have been placed in two separate monotypic subsections of Sect. Scrophularia.

As already mentioned above, the corolla tube is, as a rule, ventricose in the genus, but in a few cases it is cylindrical or infundibular-campanulate. In the opinion of the author this character is distinct enough to be used as a diagnostic character for the subdivision of the sections, and has been made the basis of Subsect. Graciles of Sect. Geramanthe, and those of subsections Przewalskiae and Farinosae of Sect. Scrophularia. In subsect. Graciles, the cylindrical tube is correlated with the absence of one of the two upper corolla lobes; in subsect. Przewalskiae, with the presence of glandular hairs on the corolla, and in subsect. Farinosae, with divided leaves. I observed on one herbarium sheet of S. scopolii both ventricose and somewhat tubular flowers; the latter were obviously due to the heavy pressure in the press, as I failed to confirm the presence of these two types of flowers on the living material of the species in question.

The upper corolla lobes are of three main types: A) the upper lip at least twice as long as broad, with more or less parallel sides, the lobes being joined to each other about half way up from the base of the lip (Fig. 6, A); B) the upper lip less than twice as long as broad, each lobe usually with the outer margin more or less C-shaped, and joined to the other above or below the middle, and not constricted at the base to form a short or long neck (Fig. 6, B), and C) the lobes oblong to reniform but constricted at the base to form a short or long neck (Fig. 6, C). Very rarely an intermediate type may occur where one of the two lobes develops a neck, the other being without it; such cases are of
Different types of upper corolla lobes.

Fig. 6

Camera lucida drawings.
rare occurrence and probably indicate an evolutionary tendency suggesting the
evolution of C-type from that of B. C-type of corolla lobes is a usual feature
of Ser. Atropatanae and type B of that of Nodosae; the corolla shape has been
used as a differential character to separate the two series.

Besides the shape, the corolla lobes vary in colour. All the five lobes
may be concolorous, *S. zuvandica, S. olgae, S. peregrina* (Plate 1.4,B), or the
upper lip may be different in colour from the rest (*S. variegata*). The colour
of the upper lobes may be red, *S. peregrina* (Plate 1.4,B); purple, *S. zuvandica,
S. xanthoglossa* etc.; red, on the outer white on the inner side or vice versa,
e.g., some forms of *S. variegata* (Plate 1.5,B); yellow on the outer, purple on
the inner side, *S. gypsicolia*. In *S. canina* subsp. *bicolor* (Sm.) Guert.,
*S. hyssopifolia* and some forms of *S. thesiciodes* the upper lobes are purple with
a white or yellow border, and this character is useful both at the specific and
subspecific level. In cases where the corolla lobes are not concolorous, the
laterals and the median lobes are either usually white to pale-green or have a
white or pale-green border.

Colour of corolla is a useful diagnostic character at the specific and sub-
specific levels in separating the closely allied taxa, such as *S. olgae* and
*S. gypsicolia, S. kotschyanana* and *S. chrysanthaa, S. canina* subsp. *bicolor* and the
forma etc. Corolla colour has also been used, in the present work, as an
additional character to characterize some of the series of Subsect. Vernales of
Sect. Geramanthe. In some cases the colour of the corolla (or lobes) is difficult
to tell in herbarium material; field notes are needed.

The lateral lobes show only a small variation in shape. In the Sect.
Geramanthe they may resemble the upper lobes in shape, *S. cryptophila* etc. or
Plate 1.5
A, Flower of S. scopolii Hoppe
B, Flower of S. variegata M.B.
may form a small beak on the side which is in contact with the upper lobes, e.g. *S. chrysanthà* (Plate 1,8,1-9) In the Sect. *Scrophularia*, the beak is very well developed, although rarely it may be absent, *S. gypsícola* (*S. subaequíloba*, etc.). The median lobe varies from twice as long as broad to twice as broad as long.

8. **Staminode**: In Sect. *Ceramanthe* the staminode is represented by a rudiment or may be completely lacking. In Sect. *Scrophularia*, however, it is well developed and conforms to the following main shapes, linked by intermediates:

- **linear** (Fig.16;34,40)
- **narrowly oblong** (Fig.16,22)
- **oblong** (Fig.16,41)
- **ovate** (Fig.16;37)
- **obcordate** (Fig.14;57)
- **obtriangular** (Fig.16,76 & Fig.17;130)
- **transversely oblong** with or without a notch, or the notch deepened to form two
- **divaricate** lobes (Fig.14;25-29)
- **spade-shaped** (Fig.16;16)
- **orbicular** (Fig.15;23 & Fig.17;137)
- **roundly reniform** (Fig.14;19) and **reniform** (Fig.15;15).

Staminode shape has been used from the time of C. Don to Boissier at different levels of classification and needs some space here.

G. Don (1837-38) divided the genus into three sections, *Venilia*, *Scorodonia* and *Canina* - Sect. *Venilia* differed from the other two in lacking a staminode, but the last two were distinguished by the staminode shape which was described as acute in Sect. *Canina* and dilated, spatulate or emarginate and reniform in Sect. *Scorodonia*. He also added that he named the Sect. *Canina* because the species included in it agreed in habit with *S. canina*. Out of the 12 species which he placed in this section, the following species, namely *S. calycina*, *S. hypericifolia*, *S. cretacea*, *S. dentata* and *S. minima*, do not agree in habit with *S. canina*, and the staminode is reniform in *S. caesia* and *S. heterophylla*, and ovate to almost reniform in *S. deserti* and *S. minima*. Inclusion of *S. calycina*, *S. minima*, *S. hypericifolia* etc. in the Sect. *Canina* by G. Don suggests that the *S. canina* -
like habit, although mentioned as one of the characters, was given no importance other than an explanation for the sectional name. This leaves us with only one diagnostic character, the staminode shape, as the author could hardly have used habit as a diagnostic. The present investigation has shown that an oblong to rounded staminode can occur in different forms of *S. rupestris* (Fig. 16 & 17); *S. variegata* (Fig. 17), *S. stewartii* (Fig. 17), *S. cretacea* (fig. 17); oblong to ± spade-shaped, *S. variegata* (Fig. 17); oblong to ovate, *S. canina* subsp. *bicolour* (Fig. 16) etc. Thus the two sections under discussion coalesce in the absence of a diagnostic character.

Bentham (1846) divided his Sect. *Tomiophyllum* into subsections *Caninae* and *Ludidae* on staminode shape; the former was characterized by linear-lanceolate, acute, or spatulate-tridentate, rarely (*S. rupestris* and *S. pinardi*) obovate-oblung, and the latter by orbicular or reniform staminode. Some of the examples of the species with oblong to rounded staminodes have already been mentioned above.

Boissier's three series of his subsect. *Oppositifoliæ* are essentially an elaboration of Bentham's subsections *Lucidae* and *Caninae*. His last two series 'appendix ovata oblonga vel oblongo-linearis' and 'appendix anguste linearis' (Fl. Or. 4: 389) are not very well marked, as it is very difficult to distinguish between oblong-linear and narrowly linear. Abundant material of *S. canina* has shown that the staminode varies from ovate to narrowly linear (Fig. 16). As mentioned above, oblong to rounded staminodes occur within *S. rupestris*, *S. stewartii*, *S. cretacea* etc.; spade-shaped to rounded in *S. nachitschevanica* (Fig. 15); ovate to ± rounded in *S. versicolor* (Fig. 15); cordate to reniform in *S. olympica* (Fig. 15). In *S. variegata* the staminode varies from oblong to ovate (subsp. *pinardi*, Fig. 17; 9-114), oblong to obovate (subsp. *variegata*, Fig. 17: 93-97).
and obtriangular or spade-shaped to + reniform (subsp. depauperata, Fig. 17; 101-108).

To conclude, the staminode varies from narrowly linear to + reniform in the above mentioned species, thus linking all the three series of Boissier.

The staminode shape is often not sufficiently correlated with leaf-shape, texture, incision of leaf margin, corolla colour, inflorescence characters or the general habit of the plant to be used in classification above the species level. Boissier thought orbicular or transversely wider staminodes were correlated with undivided leaves, distinct anastomosis and the longer pedicels, and used them to distinguish Sect. Scorodonia from Sect. Tomiophyllum. His decision was, however, based on the 16 species which he included in Sect. Scorodonia.

There are many species with undivided leaves, distinct anastomosis and longer pedicels (longer than the calyx) in which the staminode in neither orbicular nor transversely wider (e.g. S. megalantha, S. pauciflora, S. neomexicana, S. mandshurica, S. maximowiczii etc.). Moreover, the staminode may vary from + ovate to orbicular (S. arguta, S. kurdica), and suborbicular to reniform (S. umbrosa, S. divaricata) within the same species.

Thickness of the leaf is also not correlated with the staminode shape, for example, in S. pulverulenta and S. davisii the leaves are thick with obscure anastomosis but the staminode is reniform in the former and oblong in the latter, and as already mentioned above the shape varies from oblong to orbicular within the same species, e.g. in S. stewartii, S. rupestris and S. cretacea, etc.; all of these species are characterized by thick leaves and obscure anastomosis. The incision of the leaf margin is again not correlated with the staminode shape; for instance, in S. xanthoglossa and S. canina the leaves are 1-2-pinnatisect (these are also very similar in other characters, in fact, staminode shape is the only distinguishing character) but the former is characterized by a large, round and the latter by a linear staminode.
As regards corolla colour, *S. gypsicola* and *S. megalantha* have yellow corollas, but in the former the staminode is rounded and + ovate in the latter; *S. peregrina* and *S. mesopotamica* have rounded staminodes but the colour is red in the former and purple in the latter. Except for considerations of space, many such examples could be multiplied.

Regarding inflorescence characters, such as its general facies, number of flower per cyme, pedicel/bracteole length ratio, peduncle and pedicel length, degree of indumentum etc., cannot be correlated with the staminode shape. Nor is the meso- or the xerophytic habit correlated with the shape of the staminode.

In the opinion of the author, the staminode shape is too variable for the monothetic grouping within the genus at any level of classification above the species, and a lack of correlation with the other characters has further limited its taxonomic value; this is why C. Don's sections *Scorodonia* and *Canina*, Bentham's subsections *Lucidae* and *Caninae*, and Boissier's series, not only represent inconvenient taxonomic categories but also assemblages of partly related taxa and any positive attempt towards their maintenance would not serve any useful purpose.

Although staminode shape is a reliable diagnostic in some species, it is variable in others. I have observed, on the same plant, suborbicular to reniform (*S. umbrosa*, Fig. 14; 20-22), spade-shaped to roundly obtuseangular, or oblongish to roundly reniform (*S. variegata* subsp. *depauwera*, Fig. 17; 107-108, 105-106), oblong to lanceolate (*S. variegata* subsp. *pinardii*, Fig. 17; 87-88), ovate to subround (*S. versicolor*, Fig. 15; 29-30) staminodes. Within the same species the staminode can vary from broadly ovate, acute to + rounded (*S. kurdica*, Fig. 14), obovate to subround (*S. chlorantha*, Fig. 14), obcordate to reniform (*S. scopoli*ii, Fig. 14), round or subround to reniform (*S. umbrosa*, Fig. 14 & *S. ilwensis* Fig. 14), oblong to
rounded (S. rupestris var. libanotica, S. cretacea), oblong to almost reniform (S. stewartii), ovate to orbicular (S. arguta) etc.

The size of the staminode varies a good deal within the same or different species. Although it is true to a large extent - within the same or different species - that larger flowers usually have larger staminodes, the correlation is by no means constant, and the size of the staminode is dependant, at least to some extent, on its shape, besides other factors. For instance, the flower of S. xanthoglossa is $\frac{1}{2}$ to $\frac{2}{3}$rd the size of that of either S. przewalskii or S. neomexicana, but the staminode is much larger than in the last two. The size of the staminode is of limited taxonomic value.

The colour of the staminode also varies between the species: it may be yellow, as in S. xanthoglossa, S. peyronii; red, as in S. peregrina (Plate 1.4,3); green, as in some forms of S. scopoli, S. amplexicaulis; maroon, S. scopoli, S. umbrosa, and dark purple as in S. zuvandica. The colour of the staminode is useful at the specific level and below, but it is often difficult to tell the colour from the herbarium material; field notes can prove very useful. Variation also occurs within some species, e.g., S. scopoli etc.

The margin of the staminode is usually entire, but it may be crenate, e.g. S. xanthoglossa, or irregularly dentate, S. lepidota (Fig. 15).

The attachment of the staminode to the corolla has received some attention. In S. amplexicaulis, it is attached along its entire length; this character together with the spicate (?) inflorescence led Boissier to place S. amplexicaulis in a separate monotypic section Mimulopsis. A spicate(?) inflorescence is not in any way a diagnostic character, and this leaves us only with a single character, that is, the attachment of the staminode; Gorschkova (1956) has reduced Sect. Mimulopsis to the rank of a series and I share this view with her.
In *S. micrantha* the filiform rudimentary staminode is inserted at the bottom of the corolla tube. Urban (1900) proposed a new monotypic Sect. *Microscrophularia* for *S. micrantha*, characterizing the section by its annual habit, small (2.5-3 mm) white corolla and the staminode character. In 1908 he also included a new species *S. eggersii* (with yellow 7-8 mm corolla) in the section, using the position and attachment of the rudimentary staminode as the diagnostic characters for the section. I examined both of these species; in *S. micrantha* the rudimentary staminode is attached at the bottom of the corolla tube and is free except in the basal part, whereas in *S. eggersii* the point of attachment varies from the bottom to half way up the corolla tube. Since a rudimentary staminode is not an uncommon phenomenon in Sect. *Ceramanthe*, I have treated Sect. *Microscrophularia* as one of the series of Subsect. *Vernales* (Sect. *Ceramanthe*) and have placed *S. eggersii* in another series of the same Subsection.

I intend now to consider here briefly a few cases in which either the staminode is wrongly described, or a misobservation has led to the publication of either new species or their inclusion in the wrong sections.

Boissier (Diagn. Ser. 1(7): 40) mentioned that *S. farinosa* lacked a staminode, but later on changed his mind and described the staminode as being 'reniform-orbiculate' (Fl. Or. 4: 406). Examination of the type material on which he based his observation has shown that the staminode is more or less obtriangular in outline with a small apical notch (Fig. 17).

Farsa's *S. olympica* var. *multiflora* and *S. pinardii* var. *acutilobata* are examples where a misobservation (or lack of observation) has led to the publication of new taxa. In *S. olympica*, the staminode is large and reniform. Examination of the type material of var. *multiflora* has shown the presence of a small, oblong staminode, and the specimen also matches very well with *S. pruinosa* in habit.
The only difference being the slightly broader leaves, the first pair of cymes being opposite, and the number of flowers per cyme, which is up to 7 in this case. In *S. pruinosa* the number of flowers per cyme varies from 4-7 or more. I consider var. *multiflora* to be a form of *S. pruinosa*. Examination of the type material has revealed that *S. pinardii* var. *acutilobata* is, in fact, *S. xanthoglossa*. Also see *S. hadjariana*, p.179.

Boissier (Fl. Cr. 4: 388, 393) states that *S. minima* lacked a staminode. I have seen specimens collected by Ruprecht (1816) from Tindal and Tuschetia, and cited by Boissier in Fl. Cr. 4: 393; all of these show the presence of a big staminode. This weakens his monotypic Sect. *Pycnanthium*, in which he placed *S. minima*, which was distinguished mainly by the absence of a staminode. It should be mentioned that *S. crithmifolia* lacks a staminode and the staminode sometimes fails to develop in *S. villosa*. In my opinion the 'capitate inflorescence' alone is not a sufficiently important character for maintaining Sect. *Pycnanthium*.

Another apparent case of misobservation which needs mentioning is *S. megalantha* from N. Iran. Rechinger included it in the Subsect. *Vernales* Stiefelh., as it lacks a staminode and shows a marked resemblance to *S. chrysantha* and *S. kotschyanana* in general facies. I have not seen the type material of this species but Archibald 1143 from distr. Mazanderan shows the presence of a staminode (Fig. 17), and the upper corolla lobes are much longer than the lateral lobes.

The last example which could be mentioned in this connection is *S. pauciflora*, described from Nepal. According to Bentham this species had subequal corolla lobes and lacked a staminode, and hence he included it in section *Venilia* G. Don. I have not seen the type material of this species, but Hooker's collection from Sikkim and cited in the *Flora of British India* 4: 253, and also additional material collected later from Nepal, Sikkim and Bhutan, shows that a staminode is invariably
present (Fig. 17), and the upper corolla lobes are always longer than the lateral ones. I have placed it in Ser. Calycinae of the Subsect. Caninae of Sect. Scrophularia.

9. Stamens: There are only 4 stamens; the fifth or the dorsal is either absent or represented by a rudimentary or well developed staminode. The stamens at maturity may be long-exserted (*S. chrysantha*, plate 1.4; *S. canina* Fig. 5), or may reach only to the mouth of the corolla (*S. scopolii, S. peregrina, S. nodosa* etc., plate 1.5, and plate 1.4), or may remain included within the corolla tube (*S. delavayi, S. przewalskii*, fig. 4; Fig. 5). In colour the filaments may be yellow (*S. chrysantha*, plate 1.4); green (*S. przewalskii*) or white (*S. peregrina, S. variegata*, plate 1.5).

The anthers are dithecous and reniform in shape. They are usually yellow in colour, but may be orange-red (some forms of *S. variegata, S. peregrina* etc.). In *S. zuvandica* they are purple in colour. The pollen is tricolporate.

The degree of exsertion of stamens has been used either alone or in combination with other characters by G. Don, Bentham etc., for the informal division of the sections. This character is not useful for the monothetic grouping because of the continuous variation, but it is a helpful diagnostic at the specific level, in some cases; anther and filament colour provides useful additional characters for distinguishing certain species and should be recorded at the time of collecting (e.g., *S. zuvandica*, etc.).

The filaments have either round, or oblong, or rarely of both types of glands; their taxonomic significance is already discussed in the preceding pages.
10. Ovary, Placentation, Seed: The ovary is bicarpellary, syncarpous and bilocular. As a rule it is glabrous but in some cases, such as *S. chrysantha*, *S. kotschyanana* etc., it is densely villous; in *S. landroveri* it is densely glandular-puberulent. Glabrous vs. villous or glandular-puberulent ovary is a useful character at the specific level and has also been used either as a diagnostic (*Ser. Altaicae*) or a differential character (*Sers. Chrysanthae* and *Lateriflorae*) to distinguish the related series in the present work. The length of the style is correlated with that of the stamens. In those cases where the stamens are long exserted (*S. chrysantha*, *S. canina*, etc.), the style equals the stamens in length, whereas in *S. nodosa*, *S. scopolii*, etc., the stamens and style do not extend beyond the mouth of the corolla tube. The stigma varies from slightly notched to shortly lobed.

A pentagonal nectar-secreting disc is present below the ovary. The numerous hemianatropous ovules are borne on axile placentae (Fig. 7). The dehiscence is septicidal, the capsule opens in the upper half and the seeds are shaken out by the wind.

During the development of the seed sooner or later the endosperm gives rise to numerous processes which can be seen both in transverse, as well as, longitudinal sections (Fig. 7). The endosperm is dark brown and contrasts well with the smooth transparent testa. The testa remains transparent and smooth at maturity and if the mature seeds are taken out of an undried capsule the transparent areas of the testa in between the endosperm processes appear as cavities because of the contrast. However, as the seeds dry the epidermal cells of the testa turn brown and show somewhat thickened walls (Fig. 7), the testa collapses and sinks in the areas between the endosperm processes, and appear as hollows on the dry seeds. The embryo is axile (central) and linear according to Martin's terminology (1946).
Fig. 7
S. cryptophila: A, vertical section of the ovary; B, transverse section of the ovary. S. davisii: C, longitudinal section of the seed (semi-diagramatic); D, epidermal cells of the testa in surface view.
The pits on the seeds, though at first sight characteristic, are difficult to use in the group's taxonomy, due to their inconsistent shape and arrangement. The pit pattern is not as regular as illustrated for British species by Ross-Craig (1966). The number of pits on the seeds is inconstant even for the seeds from the same capsule. The shape of the seeds is regulated to a large extent by mutual pressure, and oblong to triangular seeds can be seen in the same capsule. The seeds vary in size from 0.4–2 mm (2 mm in S. davisii; rather large seeds for the comparatively small capsules) and in some cases provide a useful taxonomic character at the specific level (e.g., S. davisii & S. atropatana (seeds up to 1 mm), etc.).
III. ANATOMY
Anatomy

1. Root is tetrarch.

2. Stem: In some of the extremely xerophytic species (e.g., *S. fruticosa*, *S. hypericifolia* etc.), where the leaves are very small in size, there is a distinct zone of palisade tissue in the cortex (Plate 1.6 p. 54). In *S. fruticosa* the cuticle is extremely thickened and the pith cells are heavily lignified. In other cases the cortex consists of chlorenchymatous cells (Plate 1.6p. 54), and the thin-walled pith may persist or as a rule breaks down at maturity. Bands of fibres occur between the endodermis and the cambium. A little collenchyma is present below the angular ridges of the stem, but in *S. umbrosa*, where the stem is winged, the wings are made of parenchymatous tissue, except for a few collenchymatous cells at the tip.

Cork has been reported in *S. fruticosa* (Stiefeihagen 1910) but the anatomical studies do not support this view; the white colour of the stem is probably due to the enormously thickened white cuticle.

The two types of cortices, that is, with or without a distinct palisade zone, are taxonomically useful, and the presence of a palisade has been made the basis of the series *Leucocladia*. The epidermis is of two types: 1) columnar epidermis - with longer than broad cells (*S. syriaca*) - and 2) epidermis with cells which are broader than long (e.g., *S. hypericifolia*). This character is distinct enough for keeping *S. hypericifolia* and *S. syriaca* as separate species.

3. Nodal Anatomy: The nodal anatomy is of simple unilocular three-trace one-gap type and does not show any variation. Plate 1.7, 10 (1-12) shows serial transverse sections through the internodal (No. 1) and nodal regions (2-12) of *S. vernalis*, showing the outward bending of vascular cylinder (stele) into the leaf-base and the part destined to develop into an axillary branch, and its subsequent breaking up into leaf and branch traces. The branch traces break away from the main stele
Plate 1.6

A. *S. nodosa*, transverse section of stem; B. *S. cryptophila*, transverse section of capsule wall; C. *S. hypericifolia*, transverse section of stem.
Plate 1, 7  S. vernalis L.

1, T.S., through the internodal region. 2-12, T.S. through the nodal region.
13, semi-diagramatic representation of leaf and branch traces. C, cortex; P, pith; Ph, phloem X, xylem; S.St., vascular cylinder (stele of stem); B.St., vascular cylinder of branch; L.B., leaf-base; M.T., median trace; L.T., lateral trace; B.T., branch trace; L.G., leaf-gap.
and reunite higher up to form the continuous vascular cylinder of the branch. Because of its uniformity, the nodal anatomy proved of no use in the taxonomy of the genus.

2. **Leaf**: The petiole in the lower region consists of three vascular bundles, the median and the two lateral ones; a starch sheath is present around these bundles. Collenchyma is present below the ridges.

Leaves are dorsiventral. A hypodermis is absent and the epidermis is single-layered even in thickened xerophytic leaves (e.g., S. rupestris, S. pulverulenta etc.). Mesophyll consists of 2-3 layers of palisade and spongy parenchyma. Concentric leaves have been reported (Metcalf & Chalk) in S. deserti, but this is obviously a wrong observation. In their review of the literature, Metcalf and Chalk have also reported protein and carotin crystals, but all the 10 species whose fresh material was available gave a negative test for protein crystals with Millon's Reagent. Although the leaf sections turn bluish-green with concentrated sulphuric acid, no carotin crystals were visible even under oil immersion.

5. **Capsule**: Ovary wall or the pericarp at maturity can be clearly distinguished into three regions: 1) exocarp, which consists of a single epidermal layer which is heavily cutinized on the outside; 2) mesocarp, which comprises several layers of chlorenchyma, and 3) endocarp, which is made of several layers of thick-walled, lignified fibres. When seen from the innerside in surface view, bundles of fibres run more or less obliquely, forming a thick complicated net-work. In S. chrysantha, S. vernalis, etc., the capsule wall is softer and easily breakable, as compared to that of S. canina, S. xanthoglossa etc., which is harder and more resistant; anatomically there is very little difference between the two types, the former having slighter more chlorenchyma in the mesocarp and less fibres in the endocarp regions, as compared to the latter.
To conclude, except for two types of stem cortices (with or without a palisade), which provide a useful taxonomic character, anatomy offers little aid in classification.
IV. DEVELOPMENT
Development

The ontogenetic studies are carried out with regard to the following aspects:

1) Stomata, 2) indumentum, 3) cyme, 4) scarious margin of calyx segments,
5) corolla lobes and staminode and 6) stigma.

1. Stomata

Material and Method: For the developmental studies of stomata the calyx of
S. peregrina L. was selected because living material of this species was available
and the calyx is glabrous, so that examination is not encumbered by the hair-bases.
As stomata are of anomocytic type throughout the genus, it makes no difference
which species of the genus or which organ of the plant is selected for the study.

Young buds of S. peregrina L. were collected and fixed in 1: 3 acetic-alcohol
for several hours, then the epidermis of the calyx segments was peeled off and
mounted in aceto-carmine for study.

Development: The development of stomata is very simple and follows the same course
as described by Parveen Kidwai (1965) in some members of Onagraceae. One of the
ordinary cells functions as the stomatal Meristemoid (Fig. 8, s.m.). The stomatal
meristemoid cuts off a small triangular cell, the guard mother cell from one
corner (Fig. 8, g.m.c.). Each guard mother cell becomes rounded towards the base
before dividing into two guard cells; the plane of division may be parallel
(Fig. 8, 2) or at right angle to the longitudinal axis of the guard mother cell
(Fig. 8, 3). The two guard cells grow in size, form an opening in the middle,
the stomatal aperture, and develop into a mature stoma. Stomatal meristemoids,
guard mother cells, and the guard cells are shown by a double line.

2. Indumentum

Material and Method: For the study of the rounded type of glands S. chrysantha
and S. cryptophila, and for those of oblong type S. variegata and S. zuwandica,
Fig. 8

*S. peregrina*: 1-3, epidermis from a young calyx segment showing the developmental stages of stomata; 4, epidermis from the dorsal surface of a cotyledonary leaf; and, 5, epidermis from the petiole of the cotyledonary leaf. *s.m.*, stomatal meristemoide; *g.m.c.*, guard mother cell; *g.c.*, guard cell; *s.a.*, stomatal aperture.
were selected. Both fresh and herbarium material was used. In *S. chrysantha* and *S. cryptophila*, the leaf primordia, and in *S. variegata* the flower buds were collected and fixed in 1:3 acetic-alcohol. In the case of *S. suvandica* the buds were collected from the herbarium sheet, soaked in absolute alcohol for a few minutes, transferred to the boiling water for 2-3 minutes, preserved in F.A.A. for 1-2 days, washed in water for 8-9 hours and stored in 1:3 acetic-alcohol.

Leaf primordia and the filaments were mounted in aceto-carmine and the drawings were made with a camera-lucida.

**Development:** As already mentioned, the rounded type of glands occur on all the organs of the plant, such as stem, leaf, calyces, corolla, ovary, stamens etc. Their development takes place as follows: One of the protodermal cells, destined to form a gland, enlarges in size and divides into a lower cell, the basal or foot - which remains embedded in the tissue and may remain single or divides into a few cells - and the upper gland initial cell (Fig. 9; B.c. & g.i.c.; 1,10, & 15).

The gland initial cell (g.i.c.) enlarges in size and divides again into a lower, stalk cell (st.c.), and an upper gland cell (g.c.) - Fig. 9; 4, 11 & 16. The stalk cell may remain single, e.g., *S. chrysantha* (Fig. 9; 5-9), or cut off a small upper cell, the neck cell (n.c.), after which it may divide into 2 or more cells (Fig. 9; 13 & Fig. 11; K), or remain single (Fig. 9; 14,20,21-22). The gland cell enlarges in size and may remain unicellular (Fig. 9; 7, 20) or may become bi-multicellular (Fig. 9; 8,9,14,21-26).

The oblong type of glands occur only on the filaments and staminode. The initial stages of development are similar to those of the rounded type. The protodermal cell cuts off a small basal cell and an upper gland initial cell which gives rise to the stalk and the gland cell. The stalk cell may remain single (Fig. 10, M-R), or become 2-several-celled after cutting off a small neck cell.
S. chrysanth: 1-14, stages in the development of a glandular-hair, from a leaf primordium; S. cryptochila; 15-20, stages in the development of a glandular-hair; 21-26, the same species showing bi-multicellular gland head.

b.c., basal cell; g.i.c., gland initial cell; st.c., stalk cell; n.c., neck cell; g.c., gland head cell.
S. variegata: Stages in the development of a uniseriate filament gland;
b.c., basal cell; st.c., stalk cell; n.c., neck cell; g.i.c., gland initial cell; g.c., gland head cell.
Fig. 11

S. zuvandica; A-F, stages in the development of a biseriate filament gland.
S. lepidota, G-J, lepidote scales. S. chrysantha, K-O, small and large glands, from a leaf.
b.c., basal cells; g.i.c., gland initial cell; st.c., stalk cell;
g.c. gland head cell; n.c., neck cell.
The gland cell elongates and becomes uniseriate by transverse divisions (Fig. 10; C-J; M-R), or biseriate as the first transverse wall is followed by a vertical one, and the two apical cells thus formed cut off daughter cells in the posterior region (Fig. 11; B-F).

3. Cyme

Young cymes of *S. peregrina* were examined with a particular reference to the relative length of the first pair of bracteoles to the pedicel of the first flower of the cyme. In the early stages of development the rate of bracteole growth is much faster than that of the pedicel. In the later stages, however, the pedicel elongates and gradually becomes longer than the bracteole. Table No. 2, gives the length of the first pair of bracteoles and the corresponding pedicel of the first flower of cyme in case of a young plant.

Examination of a number of young plants showed that only one member of the first pair of bracteoles bore a flower rudiment; the formation of the second rudiment was deferred until long after the full anthesis of the first flower. If a number of young plants are left in a pot, so that there is not enough nutrition available, the second bracteole never develops a flower rudiment, with the result that the lower cymes are 2-flowered, whereas the upper ones are 1-flowered, as the second flower fails to grow beyond the bud stage.

Discussion: A glance at the table (No. 2; p. 66) and the graph (p. 66) shows that in *S. peregrina* in the early stages of development the bracteole is not only longer than the pedicel, but also shows a greater rate of growth. In species such as *S. canina*, *S. xanthoglossa*, etc., where the first pair of bracteoles is 2–several times longer than the pedicel of the first flower of the cyme, the bracteoles are not only longer to begin with but also grow at a much faster rate in the early stages as compared to the pedicels, whose further prolongation is arrested at the time when the bracteoles are probably still growing.
Table 2

Relative growth rate of pedicel and bracteoles in the young plants of *S. peregrina*

<table>
<thead>
<tr>
<th>Serial no. of cymes from the top to the base</th>
<th>First pair of cyme bracteoles</th>
<th>Pedicel of the first flowers of cyme</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length in mm</td>
<td>Length in mm</td>
</tr>
<tr>
<td>1</td>
<td>0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>2</td>
<td>0.4</td>
<td>0.2</td>
</tr>
<tr>
<td>3</td>
<td>0.8</td>
<td>0.3</td>
</tr>
<tr>
<td>4</td>
<td>0.9</td>
<td>0.4</td>
</tr>
<tr>
<td>5</td>
<td>1.0</td>
<td>0.6</td>
</tr>
<tr>
<td>6</td>
<td>1.3</td>
<td>1.1</td>
</tr>
<tr>
<td>7</td>
<td>1.3</td>
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<tr>
<td>8</td>
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<td>4.2</td>
</tr>
<tr>
<td>9</td>
<td>2.0</td>
<td>7.0</td>
</tr>
</tbody>
</table>

Graph showing the relative growth rate of the pedicel and the bracteoles in *S. peregrina*.
4. Scarious margin

Material and Method: The development of the scarious margin of the calyx segments was carried out only in one species, *S. variegata* M.B. The young buds were collected and stored in 1:3 acetic-alcohol. The calyx segments of very young buds were mounted in aceto-carmine.

Development: The calyx segments develop a scarious margin at an early stage of ontogeny. To begin with, the cells in the marginal zone of the calyx segment of a very young bud have large nuclei and dense protoplasm, and cannot be distinguished from the cells of the inner zone destined to give rise to the barbaceous or green portion of the segment. Later stages, however, show the failure of the cells of the marginal zone to develop chlorophyll, which is followed by a gradual loss of the protoplasmic contents in the course of time.

Discussion: It seems probable that the scarious margin evolved in response to xeric conditions, the failure of the cells of the marginal zone to develop chlorophyll, which is followed by the gradual death of the protoplasm. Presence of stomata in the scarious region of some species, e.g., *S. orientalis*, also suggests its derivation from the herbaceous portion. The function of the scarious margin is apparently to protect the corolla before, and the corolla tube after anthesis, and the ovary after fertilization when the corolla sooner or later falls off, against the xeric conditions. As the bracteoles enclose the rudiments of a daughter axis and the flower in their axils, the development of the scarious margin by them in such cases, e.g. *S. scariosa*, *S. mesopotamica* etc., is a further specialization in this direction.

5. Corolla lobes and Staminode

The division of the genus *Scrophularia* into two main sections, *Ceramanthe* and *Scrophularia*, by Reichenbach (1830), is supported by the present author.
The relative size of the corolla lobes together with the presence or absence of the staminode provide the basic diagnostics for the above two sections. Since shape of the staminode has been so widely used both at and above specific level, it has become of over-riding importance in the taxonomy of this genus. Present investigation, however, with a particular reference to its shape, has revealed that this character is more variable than has been thought; in some cases its reliability can be questioned even at the specific level or below.

Considerations like these led the author to a study of the development of the corolla lobes and staminode in the hope that ontogeny might give some clue to the understanding of the intra- and inter-specific variability of staminode.

Material and Methods: For the developmental study both fresh and herbarium material was used. The herbarium material of *S. xanthoglossa* and *S. subaequiloba* - flower buds of all stages - was soaked in absolute alcohol for a few minutes and then transferred to hot water. A previous soaking in absolute alcohol makes the tissues imbibe hot water very quickly - the buds swell up in a few minutes - and there is no danger of the tissues becoming soft and unfit for dissection, as is inevitable if they are boiled in water. The material was kept in water for an hour and then preserved in FAA. Both fresh and treated material (herbarium material) was dissected in a drop of water and glycerine and the drawings were made with a camera-lucida.

a. Corolla lobes

Development: For the developmental studies of the corolla lobes, six species were selected: two from Sect. *Ceramanthe*, namely, *S. cryptophila* and *S. chrysantha* - as the upper and the lateral corolla lobes are subequal in size; one from Sect. *Scrophularia* Subsect. *Subaequiloba*, *S. subaequiloba* - upper and lateral corolla lobes are subequal, and a staminode is present; and three from Sect. *Scrophularia*
Subsect. Caninae, namely, S. scopoli var. adenocalyx, S. peregrina and S. xanthoglossa — in all these three species the upper corolla lobes are longer than the lateral ones and staminode is always present. In S. scopoli var. adenocalyx the upper corolla lobes are of B-type (Fig. 6; B4), whereas, in the last two of C-type (Fig. 6; C).

In all the above mentioned six species the lateral and the upper lobes are equal in size during the very early stages of development (Plate 1.8; 1,10,17 & Plate 1.9; 1,19,26). In S. subaequiloba the upper and the lateral lobes remain equal during all the later stages of development, being, however, overtopped by the median lobe (Plate 1.8; 18-27). In S. chrysantha, S. cryptophila, S. scopoli var. adenocalyx, and S. xanthoglossa, the lateral lobes in the later stages grow faster and overtop the upper ones (Plate 1.8; 2-3, 11-12 & Plate 1.9; 4-5, 28). In S. cryptophila and S. chrysantha, the upper lobes fail to catch up completely with the lateral ones and remain slightly shorter in size (Plate 1.8; 2-9, 11-16, 27-28). In S. scopoli var. adenocalyx, S. peregrina and S. xanthoglossa, the upper corolla lobes grow at a much faster rate, in the last stages, and become longer than the lateral ones (Plate 1.9; 6-13, 20-25, 30-36). In S. scopoli var. adenocalyx the upper corolla lobes do not develop a neck at maturity and become B-type in shape. Plate 1.9, shows that the stages 13 and 28 are comparable suggesting that B-type is simply an arrested stage of growth in the development of the C-type of corolla lobes.

The early developmental stages show that the lateral corolla lobes are similar in shape in all the species included in this study — the shape being more or less oblongish (Plate 1.8; 3-4, 12,21 & Plate 1.9; 2-3, 27). Except in S. cryptophila (Plate 1.8; 16), these develop a lateral beak on their inner side which is in contact with and overlapped by the upper corolla lobes (Plate 1.8; 9, 26 & Plate 1.9; 13, 25, 36).
b. Staminoda

Development: Ontogeny of staminode was studied in the following five species; namely, *S. cryptophila*, *S. peregrina*, *S. subaequiloba*, *S. scopulii* var. *adencalyx* and *S. xanthoglossa*.

In all the above five species the staminode is oblong in the early stages of development (Plate 1.8; 10, 11, 17-19 & Plate 1.9; 19, 1-3). In *S. cryptophila* the free part of the staminode does not grow beyond this stage and remains a rudimentary structure (Plate 1.8; R. STD., 16). In others it becomes somewhat broader in the upper region and obtusely pointed at the apex and assumes more or less an ovate shape (Plate 1.9; STD., 22, 7, 26-27), or the apex may remain somewhat truncate and the staminode may be somewhat spade-shaped (Plate 1.8; STD., 20-21), after which it directly becomes rounded (Plate 1.8; 22-27). The base of the staminode in all these cases is, however, cuneate up to this stage. After this stage the staminode becomes at first broadly ovate (Plate 1.9; STD., 8, 23), and then acquires an obovate to triangular shape (Plate 1.9; STD., 9-10, 24, 30) which becomes rounded as in *S. peregrina* (Plate 1.9; 25) where the further growth stops, or transversely broader in which the base changes from cuneate to subcordate (Plate 1.9; STD., 11-13). In *S. xanthoglossa*, this is carried a step further; the transversely broader staminode becomes very large and rounded and the base becomes deeply cordate (Plate 1.9; 31-36).

In *S. subaequiloba* the staminode shows an interesting structure (Plate 1.8; 28-30). When seen from the dorsal side it consists of an upper large, rounded portion and a lower tubular part (t), which opens into a canal (c) a little further down. There are two flaps (F), in the lower region of the upper rounded part which are reflexed like the collar of a shirt. The canal extends right down to the corolla base and also to the nectar-secreting hypogynous disc - and probably stores nectar. The staminode of *S. subaequiloba* represents the
Plate No. 18

Dissections of the flowers showing the developmental stages of the staminode and the corolla lobes. U.C.L., upper corolla lobes; L.C.L., lateral corolla lobes; M.L., median lobe; ST.R., stamen rudiment; STD.R., staminode rudiment; ST., stamen; STD., staminode; R.STD., rudimentary staminode; STD.T., staminode trace; ST.T., stamen trace; T., staminodal tube; C., staminodal canal; F, staminodal flap. 1-9, S. chrysantha; 10-16, S. cryptophila; 17-30, S. subequiloba. 1-6, 10-12, 17-21, drawn to the scale 1st, from the bottom; 7, 13-14, 22-25, 2nd from the bottom; 8, 15, 26, 3rd from the bottom, and 9, 16, 27, 4th from the bottom.
Dissections of the flowers showing the developmental stages of the staminode and the corolla lobes. U.C.L., upper corolla lobes; L.C.L., lateral corolla lobes; M.L., median lobe; STD., staminode; STD.R., staminode rudiment; ST., stamen; Fl. Pr., flower Primordium; C.R., carpel rudiment; C.S., calyx segment; ST.R., stamen rudiment. 1-13, S. scopulii; 14-25, S. peregrina; 26-36, S. xanthoglossa. 1-7, 14-23, 26-30, drawn to the scale; 1st. from the bottom; 8-10, 31-32, 2nd from the bottom, and 11-13, 24-25, 33-36, 3rd from the bottom.
most specialized structure in the whole genus.

c. Discussion: Referring back to the development of the staminode of *S. peregrina*, *S. scopolii* var. adenocalyx and *S. xanthoglossa*, the ontogenetic stages can be broadly divided into the following intergrading categories in terms of shape:

1) oblong, 2) ovate, 3) obovate to obtriangular, 4) rounded, 5) transversely broader and 6) roundly reniform. All of these types occur in the genus and are characteristic of certain species, e.g., the oblong occurs in *S. amana*, *S. canina*, *S. davisii*; ovate, in some forms of *S. rupestris* and *S. variegata*; obovate to obtriangular in *S. chiorantha*, *S. kurdica*, some forms of *S. rupestris* etc.; rounded in *S. scariosa*, *S. mesopotamica* etc.; transversely broader in *S. pogaea*, *S. scopophii*, *S. umbrosa* etc.; and roundly reniform in *S. striata*, *S. xanthoglossa* etc. A roundly reniform staminode recapitulates all the above 6 types in its ontogeny and it is not unreasonable to assume that different staminode shapes which characterize certain species represent any one of the 6 ontogenetic stages whose further development is arrested for some reason — presumably genetically controlled. On the basis of the present evidence the author is inclined to think that oblong and roundly reniform staminodes occupy the two ends of the evolutionary series.

Ontogenetic studies also throw some light on the variability of staminode shape. As already mentioned above, the 6 types of staminode characteristic of different species are probably arrested ontogenetic stages towards the development of a roundly reniform staminode. Strict mathematical precision of shapes, however, cannot be usefully applied to the staminode because of its developmental plasticity — as the staminodes may not be exactly alike even on the same plant. Frequently in the development of a particular type the final ontogenetic stage may pass into the next before its growth is arrested, or the differentiation may cease before all the ontogenetic phases are completed; for example, a species characterized by an ovate
staminode may sometimes develop an obovate or oblongish staminode, depending on whether the growth ceases after or before the required developmental stage. This explains why the earlier attempts at the monothetic grouping in the genus at different levels of classification (sectional, G. Don, 1837; subsectional, Bentham, 1846 and series Boissier, 1879), have ended in confusion. It has already been pointed out that staminode shape is not sufficiently correlated with other morphological differences, which further limits its taxonomic value.

The question whether the Ceramanthe or Scrophularia type of corolla is more primitive has been considered without any satisfactory conclusion being reached.

Rarely S. rupestris var. libanotica, a member of Sect. Scrophularia, produces a peloriate flower with 5 stamens and subequal corolla lobes, thus resembling the Ceramanthe type of corolla. But this pattern of abnormality, well known in so many zygomorphic flowers, cannot be taken as evidence that the primitive flower within the genus was more or less actinomorphic.

All the cytologically investigated species of Sect. Ceramanthe are polyploids, while those of Sect. Scrophularia are both diploids and polyploids. Again there is no evidence to prove that Sect. Ceramanthe polyploids were derived from Sect. Scrophularia diploids, or to negate that Ceramanthe polyploids were not derived from Ceramanthe diploids. Out of the 17 species of Sect. Ceramanthe, cytological work has been carried out only on 5 species (see p. 92), and future investigation may reveal the presence of diploids in this Section as well.

Developmental studies show that the Ceramanthe type of corolla is a stage in the development of the Scrophularia type, but again we have no means of saying whether it is a Scrophularia type of corolla arrested at an incomplete stage, or whether Scrophularia corolla is a further ontogenetic development of Ceramanthe corolla. S. heucheriflora and S. subaequiloba (both placed in Sect. Scrophularia) represent an intermediate state of flower between the two sections, resembling
Sect. Ceramanthe in their subequal corolla lobes and Sect. Scrophularia in the presence of a staminode, but there is no way of finding out the direction of the evolutionary trend in corolla shape.

Vegetative morphology and distribution also do not give any clue about the relative age of the two sections. Xerophytism and mesophytism, divided and undivided leaf condition, annual, biennial or perennial habit, non-scarious and scarious-margined calyx segments, etc., occur in both the sections. Evidence from distribution is also inconclusive. Although Sect. Scrophularia is the largest and the most widespread of the two sections, Sect. Ceramanthe is highly disjunct (see map 6, p. 141) and cannot be considered of recent origin.

To conclude, in our present state of knowledge it is difficult to say which of the two sections is more primitive. As stated above, Ceramanthe and Scrophularia type of flowers occupy the two ends of an evolutionary series, with subsections Houcheriflorae and Subaequilobae showing the intermediate state, but whether the direction of evolution has been from Ceramanthe to Scrophularia or vice versa remains a dilemma.

6. Stigma

Material and Method: Developmental studies of the stigma were carried out in the following five species, namely S. peregrina, S. nodosa, S. cryptophila, S. chrysantha and S. californica subsp. californica. In the first four species fresh material was available, whereas, in the last one herbarium material was used. In the case of the first four species, buds of all stages and the mature flowers were collected and stored in 1:3 acetic-alcohol. In the case of the last species, i.e., S. californica subsp. californica, the buds and flowers were collected from herbarium sheet, soaked in absolute alcohol for a few minutes, transferred to hot water for an hour and then preserved in FAA. They were then washed with water
for about 8 hours and stored in 1:3 acetic-alcohol for at least one hour before dissecting in aceto-carmine.

**Development:** The stages in the development of stigma are similar in all the above mentioned 5 species. In all these the very young bud has a small protuberance like, hollow, style which is slightly notched at the apex (Plate 1.10; 1). A slightly older bud shows the lengthening of the style, a slightly deepening of the notch, and the appearance of the stigmatic papillae (Plate 1.10;2-3). In still older buds the style becomes considerably longer, the stigmatic portion broader than the style and the papillae increase in length and number (Plate 1.10;4-5). In a mature flower the stigma is much broader than the style and the papillae and the style attain their maximum size. The mature papillae in *S. chrysantha* have a very broad bulbous base. In *S. nodosa* the stigmatic notch becomes deep enough to form two distinct short lobes with papillae both on the inner and outer sides.

**Discussion:** The stigma in the genus was described as lobed (Wydler, 1828) or notched (Hooker, 1833). Recently Shaw (1962) has described two distinct types of stigmas, the capitate (e.g., *S. californica* subsp. *californica*) and bilobed (e.g. *S. peregrina*). The developmental stages of the stigma of *S. californica* subsp. *californica*, however, are in no way different from that of *S. chrysantha* except that the notch is deeper in the former.

As already mentioned, Shaw has also reported a bilobed stigma with long divaricating arms with interlocking stigmatic papillae (Aliso 5, fig. 5b., 1962). I have not seen Shaw's voucher specimen of *S. peregrina*, but the form of *S. peregrina*, in cultivation in the Royal Botanic Garden, Edinburgh (raised from the wild seeds; Kayacik & Yaltirk 3444), does not show the presence of two long divaricating arms with interlocking papillae as shown by him. In *S. cryptophila* which is included in the present study, the stigma and the upper part of the style may split into
two parts on some of the mature capsules which appear like two arms, although a
close examination shows the lack of stigmatic papillae on both sides of the arms
in the region where the splitting takes place. Plate 1.10 shows two photographs
of the stigmas of *S. peregrina*, the first (No. 7) was taken at full anthesis of
the flower, and the second (No. 8) long after the seeds had been shed from the
capsule. To conclude, my findings do not agree with those of Shaw.
S. chrysantha, 1–6, stages in the development of stigma.
S. peregrina, 7, a mature stigma at full anthesis of the flower; 8, an old stigma from the capsule from which the seeds had fallen off.
V. CYTOLOGY
Cytology

1. Introduction: The cytological information about the genus Scrophularia is still fragmentary. Recently Vaarama and Hiirsalmi (1967) have published chromosome numbers of 24 Old World species, 13 of which were previously unknown cytologically. The most thorough biosystematic work which has so far been carried out is on the 10 North American species by Shaw (1962) and Carlbom (1969). In the present investigation the chromosome number has been determined for the first time in S. cryptophila, S. chrysantha, S. scopolii var. adenocalyx, S. rupestris var. libanotica and S. variegata subsp. depauperata, and confirmed in S. nodosa, S. umbrosa and S. peregrina. The chromosome counts of these species are tabulated on page 81.

2. Material: With the exception of S. nodosa, plants were raised in the Royal Botanic Garden, Edinburgh, from seed of wild origin. The seeds were collected from 2-15 year old herbarium sheets, but the seeds more than 2-3 years old failed to germinate. The chromosome counts were taken in one case (S. umbrosa) from root-tips, in the remainder from the pollen mother cells.

3. Method: The seeds were floated on blotting papers in petri dishes and kept in the dark. Floating of seeds quickens germination. Except for S. umbrosa, the root tips did not yield countable chromosomes.

Floral buds were collected between 10 a.m. to 1 p.m., but some buds collected at 4 p.m. gave equally good results. They were fixed in 1:3 acetic-alcohol and left under refrigeration at least for 2-3 hours before use.
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<th>Longitude, Longitude Format</th>
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Fig. 12. Camera lucida drawings of meiotic and mitotic chromosome compliments, X 1850.

A, B, C, D & F, meiotic chromosomes; E, mitotic chromosomes.

A, S. cryptophila, Ist. meiotic telophase, 2n = 44; B, S. nodosa, Ist. meiotic telophase, 2n = 36; C, S. chrysanth, n = 18, one pole of a Ist. meiotic telophase; D, S. scopoli var. adenocalyx, Ist. meiotic telophase, 2n = 26; E, S. umbrosa, somatic metaphase, 2n = 26; F, S. peregrina, Ist. meiotic telophase, 2n = 36.
Fig. 13. Camera lucida drawings of meiotic chromosome compliments, X 1850.
A. S. variegata subsp. depauperata, Ist. meiotic metaphase, 2n = 32.
S. rupestris var. libanotica: B, Ist. meiotic telophase, the bivalent like bodies uppermost in the figure are precociously separating chromatids, 2n = 48; C-D, n = 11, each only represents one pole of a Ist. meiotic telophase. The strand connection to chromosomes in D is probably caused by "stickiness".
Plate 1.11
A, *S. cryptophila*, 1st. meiotic telophase.
B, *S. chrysantha*, one pole of a 1st. meiotic telophase.
Plate 1.12

A-B, S. nodosa, one pole of a 1st. meiotic telophase.
C, S. peregrina, one pole of a 1st. meiotic telophase.
Plate 1.13
*S. ruprechtii* var. *libanotica*: 
A, 1st meiotic telophase; 
B, one pole of a 1st meiotic telophase.
Root-tips were pretreated with para-dichlorobenzene for 2-3 hours, fixed in 1:3 aceto-alcohol and stored under refrigeration for at least 48 hours. Both pollen and root-tips were stained with iron aceto-carmine and drawings were made with a camera-lucida at a magnification of x 1850.

4. Basic Chromosome Number: Basic numbers of 7, 9, 10, 12 and 13 have been proposed for the genus (Darlington & Wylie, 1955; Larsen, 1960; Vaarama & Hiirsalami, 1967). The present investigation shows that 11 (S. cryptophila and S. rupestris var. libanotica) and possibly 8 (S. variegata subsp. depauperata 2n = 32 represents a tetraploid of this number) can be added to these base numbers. The 2n = 48 of S. rupestris var. libanotica might also represent hexaploidy on a base number of x = 8 but on the other hand it might be a doubling of 2n = 24, the number reported from the related S. variegata by Vaarama and Hiirsalami (1967); if the latter explanation were true it is interesting, since the count for 2 other stocks of S. rupestris var. libanotica is 2n = 22 and this would indicate that they have probably been derived by dysploid reduction from an ancestral 2n = 24. Clearly as in so many large herbaceous genera alteration of basic numbers at the diploid level (dysploidy) has been important in evolution (cf. Crepis, Babcock 1947; Haplopapus, Smith 1966; Carex, Davis 1956). Polyploidy has also been important (see tab. 5, p.92) and some of the higher basic numbers, e.g. x = 13, may themselves have been derived by polyploidy (e.g. 7 + 7 = 14 or 7 + 6 = 13).

There is little direct evidence as to the type of polyploidy occurring amongst the species. Most of the meiotic figures show bivalent pairing and this cytologically diploid behaviour suggests that allopolyploidy has been frequent. On the other hand this cytological behaviour might be a result of the diploidization of autopolyploids, and it is interesting in this connection to note that S. variegata subsp. depauperata shows an irregular meiosis with multivalents present.
Cytology and Morphology: Comparison of chromosome number and morphology fails to reveal any significant correlations. The following characters were examined with this end in view, but no relationship with either polyploidy or basic number were found: glandular calyx, scarious margin, length of corolla lobes, presence of staminode together with its shape, flower colour, stamen exertion, filament glands, foliate inflorescence, leaf incision, anastomosis, villousness and perennial habit.

Hybridization has not been reported in nature but may well have been overlooked. The most thorough work on artificial hybridization has been done on the N.W. American Scrophularia (Shaw, 1962; Carlbom 1964 & 1969). The crossing polygon of the N.W. American species (Carlbom, 1969, p. 296) shows that gene exchange can be easily effected in these 9 species. In the Old World, Vaarama and Hiirusalmi (1967) have reported successful crosses between S. alata (2n = 26) and S. auriculata (2n = 78), S. scopolii (2n = 26) and S. alata (2n = 26) and S. scopolii and S. herminii (2n = 52).

S. scopolii, S. alata and S. herminii are well separated species and successful crosses between these suggest that genetic barriers in the genus are probably poorly developed (N.W. American species lack genetic barriers), although such a conclusion must wait until sufficient information on hybridization of Old World Scrophularia becomes available. From a cross between S. lanceolata and S. oregana, Carlbom (1964) recovered two F2 recombinants, one having the characteristic leaves of S. lanceolata and the flowers of S. oregana, and the other the flowers of S. lanceolata and the leaves of S. oregana; both of these recombinants have been reported to be vigorous. Evidence of this sort of situation occurring in nature should be sought: it would provide an explanation for the blending of specific distinctions of many taxa due to the
production of various, vigorous recombinants. *S. scopolii* is a variable species and its successful hybridisation with *S. umbrosa (S. alata)* and *S. herminii* has already been mentioned above. Vaarama and Hiirsalmi (1967) regard tetraploid *S. umbrosa (S. alata)* to be a suspect hybrid between *S. umbrosa (S. alata)* and *S. auriculata*, and its similarity with *S. czernjakowskiana* is so marked that they have expressed doubts about the specific status of the latter.
Cytology and Taxonomy: Vaarama and Hiirsalmi (1967) have suggested a correlation between basic chromosome numbers and Stiefehagen's classification (1910) based on comparative morphology. They have, however, attributed the discrepancies in the correlation to the leaf vein anastomosing character, which is Stiefehagen's diagnostic for the two sections and they think is of limited phylogenetic value (also Shaw, 1962). As already mentioned, there is no correlation between morphological differences and chromosome numbers, although in some cases interesting clusters of related species, e.g., S. lucida, S. olympica, S. tanacetifolia, C. canina etc., do occur which have the same basic chromosome number (13), but at the same time one should not overlook the fact that some quite unrelated species, e.g., S. rupestris and S. cryptophila (11), S. scopoli in and S. lucida (13), and S. chrysantha and S. nodosa (9), have the same basic number.

A comparison of the basic chromosome numbers with Stiefehagen's grouping of the genus is adapted from Vaarama and Hiirsalmi (1967) and 3 more species have been added to the diagram; namely, S. cryptophila, S. chrysantha and S. rupestris (Table 4, p. 91). Their investigation showed that subsections Vernales and Orientales were correlated with the basic number 10. S. chrysantha and S. cryptophila, which belong to the subsect. Vernales, have 9 and 11 as the basic number respectively. Subsect. Lucidae was characterised by base numbers 12 and 13, but now 11 (S. rupestris) can also be added to the list. Table 4 p. 91 shows that the basic chromosome numbers cut across Stiefehagen's classification.

A comparison has also been drawn between the known basic chromosome numbers and the classification presented in this work: the comparison is of course incomplete, because cytological information is wanting in most of the species (Table 5, p. 92). As is evident from Table 5, the basic numbers discovered so far cut across the sections, subsections (in Sect. Scrophularia, the
Basic Chromosome Numbers

Table 5

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<th>Sp. Centrales</th>
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Note: The chromosome numbers are determined by the author.
chromosome numbers are only known in Subsect. Caninae), and series; within
the series the basic chromosome numbers may be helpful in separating clusters
of related species, but much more work is required before the taxonomic assess-
ments of basic numbers could be made at the subseries level.

At the specific level the taxonomic value of chromosomes is also limited,
partially because detailed karyotypic studies are not feasible due to extremely
small size, large number and relatively uniform morphology of the chromosomes.
Vaarama and Hiirsalmi (1967) have proposed specific status for *S. hoppii*, which
was regarded as a form of *S. canina*, on cytological grounds. It differs in
having one pair of chromosomes less than *S. canina* and has 4 satellite and 4
isobrachial chromosomes which seem to be absent in *S. canina*. In the absence
of any morphological difference, *S. hoppii* is best maintained as a cytological
race of *S. canina*. *S. nodosa* and *S. scopolii* are difficult to distinguish on
staminode shape because of its variability; leaf margin, although serrate in
the former and doubly crenate to dentate in the latter, may not hold good in
some forms of *S. nodosa*. Presence of swollen suckers, perennial habit
(*S. scopolii* var. *alenoacalyx* is also perennial but can be distinguished by the
glandular calyx and short-peduncled cymes) and the chromosome number (36 in
*S. nodosa, 26 in *S. scopolii*) are the only reliable diagnostic characters;
here the chromosome number has proved a useful taxonomic character for keeping
the two species apart. *S. chrysantha* differs from *S. vernalis* in its longer
exserted stamens, acute calyx segments and corymbosely arranged cymes (at least
in the flowering stage); glabrous ovary in the latter is not a reliable
diagnostic. The chromosome number (2n = 36 in *S. chrysantha, 2n = 40 in *S.
vernalis*) provides a helpful additional character. However, many species have
still to be studied karyotypically before taxonomic assessment can be made.
Carlbom (1964) proposed the following species concept adopted from his experimental results: 'If gene exchange can be occasioned between two plants, either naturally or artificially, and the first filial generation is highly fertile, the two plants are deemed conspecific'. In 1969 he expressed the view that the above mentioned biological concept was 'basically conservative' and if applied to the N.W. American Scrophularia would lead to the lumping of all the taxa (although reflecting their true evolutionary status) into a single species or into a polytypic species complex. Earlier Shaw (1962) expressed a similar view about the specific concept: 'A criterion of strict genetic isolation cannot be used in treating the Neartic species of Scrophularia. If such an approach were used, it would result in the lumping of most or all the species into one. Geographical barriers seem more important in isolating the Western North American species. If genetic barriers do exist in the genus within this area, they are probably not strongly expressed in the first hybrid generation'.

Probably a strict biological concept could not be usefully applied (even if information on hybridization were available) to the Old World Scrophularia as well, as it would result in the lumping of some well separated species like S. scopolii, S. alata and S. herminii into a single species, although more information on hybridization of Old World Scrophularia would reveal many interesting relationships of many taxa and throw light on their evolutionary status.

For a general purpose classification, we must classify the situation as we find it in nature, not in the experimental plot.
7. Polyploidy, Evolution and Distribution: Recently Carlom (1969), while dis-
cussing the higher frequency of polyploidy in the Sect. Anastomosantes Stiefelh.
(1910), has proposed that Sect. Anastomosantes has evolved from Sect. Tomic-
phyllum. He bases his argument on the fact that all the species of Sect.
Anastomosantes whose cytology is known are polyploids (tetraploids and higher),
with the exception of S. alata which has diploid and tetraploid forms of 2n = 26,
and 54. On the other hand, out of the 8 species of Sect. Tomiophyllum whose
chromosome numbers have been published, 7 are diploid with a base number of 12
and 13. He has suggested that the cytologically aberrant species S. orientalis
should be transferred to Subsect. Vernales Stiefelh., on the basis of its corolla
characters, intermediate morphology between the two sections, polyploidy and the
basic number (x = 10) which conforms to that predominantly found in this group;
I have placed it in the Subsect. Orientales of Sect. Cramantho.

He has argued that polyploids are more youthful than the diploids, and
since all the cytologically known Anastomosantes are polyploids with the base
numbers x = 7, 9, 10, 12 and 13, whilst those of the Tomiophyllum are diploids
with the base numbers x = 12 and 13, the former must therefore have had their
ancestry among the latter. He has further pointed out that some of the mesophytes
have developed xeromorphy secondarily. It should be pointed out that the species
of Sect. Anastomosantes are predominantly mesophytic, while those of Sect. Tomic-
phyllum are xerophytic.

Although the fact that polyploids are ultimately derived from diploids is
indisputable, this does not necessarily mean that polyploids are more youthful as
species or groups than diploids. In general, new species are being produced
at both levels during plant evolution. We can therefore postulate the case where
we have young actively evolving diploid species and ancient polyploids in the
same group.
Any attempt at the derivation of Anastomosantes (mesophytes) from Tomio-
phyllum (Xerophytes) would presuppose: 1, that these two sections are natural
(groups; 2, absence of diploids with especially higher base numbers among the
Anastomosantes; 3, a change from xero-, to mesomorphy accompanying polyploidy;
4, the absence of polyploidy in the Sect. Tomio phyllum.

On the basis of overall resemblance, the two sections are not natural
(phenetic) groups. Their phylogenetic significance is also questioned by Shaw
(1962); Vaarama and Hiirasalmi (1967) have also expressed doubts about the phylo-
genetic value of the anastomosing character which is the basis for the two sections.

Among the Anastomosantes, S. umbrosa (S. alata) and S. scopolii are diploids
with a base number of 13, and further investigation may reveal more diploid high
base numbers, as there are many species in this section which are cytologically
unknown. Both diploid and polyploid forms occur in S. rupestris, and the poly-
ploid forms do not show any change from xero- to mesomorphy; not that this
would be expected, since polyploidy can only operate on the genotype already
present at the diploid level and confers no 'magical' new properties. As has
already been pointed out, both floral and vegetative morphology are genically
controlled, and polyploidy can only have a relatively crude influence on them;
radically new adaptations involving a change from xero- to mesomorphy could
hardly arise simply by doubling of the chromosomes.

Maps 1-4 (p.98-101) show the distribution of a number of species in which
cytological information is available. Study of these maps reveals the following
facts: 1) some of the polyploids, e.g., S. nodosa, S. vernalis have attained
the furthest northern distribution; 2) some of the diploids, e.g., S. scopolii,
S. canina, show a greater northern distribution than some of the polyploids;
3) some of the diploids and polyploids have an equally wide northern distribution,
and 4) some of the most widely distributed species (e.g., S. umbrosa) have
both diploid and polyploid races.
Table 3 (p. 81) shows a comparison between cytology, habitat, altitude and distribution of a few Turkish species. It is not, however, possible to cover the whole range of distribution of the species regarding complete information about their cytology, altitude and habitat. The evidence gathered from this table, however fragmentary, does suggest that some of the diploids may grow at as high an altitude, or even higher than the polyploids, and may show an equally wide northern distribution.

It might be true that in Scrophularia polyploidy has provided 'evolutionary flexibility' in the 'northward migration and establishment' of the polyploids, but the claim (Carlson, 1969) that the polyploids have outstripped the diploids in the northern distribution (also altitudinally) is not entirely justifiable. The evidence gathered from the distributional maps and the table mentioned above suggest that although some of the polyploids have outstripped the diploids in the more northern migration, others seem to have lagged behind. Although 'evolutionary flexibility' may have played a significant part in the successful northward migration and establishment of the polyploids, some of the diploids seem to be equally successful without it. Are these 'diploids' with a high base number (e.g. S. scopolii, 2n = 26; S. canina, 2n = 26) really diploidised polyploids? The information on this aspect is still wanting and only future research can settle this problem.

Vaarama and Hiirsalu (1967) have shown that in Scrophularia a correlation exists between high basic chromosome numbers and extreme conditions (mountain ranges, deserts, cultivated lands in the arid and semi-arid regions). It also seems likely that polyploidy in Scrophularia is correlated in a general way with moist habitats, although some exceptions do occur (e.g. S. scopolii which is a diploid is mesophytic. S. umbrosa and S. rupestris have both diploid and polyploid races; S. umbrosa is mesophytic while S. rupestris is a saxatile xerophytic species).
VI. CLASSIFICATION
Classification

It has already been stated in connection with the stamínode morphology that G. Don’s Sections Canina and Scorodonia which were separated on stamínode shape are indistinguishable and therefore cannot be maintained as separate sections. Again Urban’s Sect. Miorosphularia (see p. 46) which was founded on the rudimentary stamínode being inserted at the bottom of the corolla tube has also been criticized by Stiefelhagen, and has been reduced to the rank of a series by the present author. It has also been shown (see p. 12) that if Bentham’s Section Scorodonia and Tomiophyllum, and Stiefelhagen’s Section Anastomosantes and Tomiophyllum which are distinguished virtually or exclusively on the degree of anastomosis visibility are maintained many species will remain unclassifiable. Boissier’s monotypic sections Pycnanthium and Mimulopsis have been reduced to the rank of series by Gorschova (1955). If G. Don’s Sect. Canina and Bentham’s sect. Tomiophyllum are recombined with the Sect. Scorodonia (as they are inseparable from it), one is left with only two sections, that is, Venilia and Scorodonia, which are well separated on the relative length of the corolla lobes and the presence or absence of the stamínode. The author has accepted Reichenbach’s Sections Ceramanthe and Scrophularia, as these are the earlier names. I have followed Boissier in applying Ceramanthe and Scrophularia as sectional names, although Reichenbach does not mention their taxonomic rank.

Within the section Ceramanthe the author has recognised three subsections, namely, Vernales, Orientales and Graciles, which are delimited on leaf-arrangement (Whorled/opposite) and the corolla shape (cylindrical/ventricose). Sect. Scrophularia is divided into 6 subsections, namely, Haecheriflorae, Subaequilobae, Przewalskiae, Farinosae, Caninae and Lepidotae; the first two subsections are distinguished by their subequal corolla lobes and the peculiar staminodes; the
last four by the corolla shape (cylindrical/ventricose), and the indumentum, as the main distinguishing characters. The author has recognised 5 series within the Subsect. Vernales, and 11 series in subsect. Caninae. The series are delimited either on the basis of a single distinct character, or, more frequently, a number of correlated differential characters, and an attempt has been made, as far as possible to place the related species in each series. A key, descriptions and a synopsis of classifications have also been provided for the infra-generic taxa.

All the species in the genus have been classified at least to the subsectional level. Wherever the actual material of a species is not seen and the information is based on descriptions, photographs, or illustrations, 'n.v.' is inserted in front of the species. Except for the Turkish species the author has relied mainly on the following works for synonymy:


- 1943, The Scrophulariaceae of Western Himalayas.

Shaw, R.J., 1962. The biosystematics of Scrophularia in Western North America.


In Fl. URSS Vol. 22 (1956) Gorschkova's series do not appear to have been provided with Latin descriptions, so that their names remain invalid.

In the synopsis of species (p.115), the species are arranged alphabetically within their subsections and series.
1. Synopsis of Infra-generic Groups


Type: *S. vernalis* L.


Lectotype: *S. vernalis* L.


2. Ser. *Microsorophulariae* (Urb.) Lall

Type: *S. micrantha* Desv.


Type: *S. eggersii* Urb.

Lectotype: S. lateriflora Trautv.

5. Ser. Landroveriana G. Lall

Type: S. landroverii Wendelbo


Lectotype: S. orientale L.

III. Subsect. Graciles Lall

Type: S. gracilis Blakelock


Type: S. nodosa L.

Syn: Sect. Scorodonia G. Don, Gen. Syst. 4: 507 (1837-38); Benth.
in D.C. Prodr. 10: 304 (1846); Boiss., Fl. Or. 4: 388 (1879).

Lectotype: S. scorodonia L.


Lectotype: S. canina L.


Sect. Fycnamthium Boiss., Fl. Or. 4: 388 (1879).
Type: S. minima M.B.
Sect. Mimulopsis Boiss., Fl. Or. 4: 388 (1879).
Type: S. amplexicaulis Benth.

I. Subsect. Heucheriflorae Lall
Type: S. heucheriflora Schrank.

II. Subsect. Subaequilobae Lall
Type: S. subaequiloba Lall

III. Subsect. Przewalskiae Lall
Type: S. przewalskii Batal

Type: S. farinosa Boiss.

Lectotype: S. canina L.

Sect. Scorodonia C. Don, Gen. Syst. 4: 507 (1837-38); Benth. in D.C. Prodr. 10: 304 (1846); Boiss., Fl. Or. 4: 388 (1879).
Lectotype: S. scorodonia L.
Type: *S. minima* M.B.

Type: *S. amplexicaulis* Benth.


Lectotype: *S. altaica* Murr.

2. Ser. *Duplicato-Serratae* Lall
Type: *S. duplicato-serrata* Makino

Type: *S. calycina* Benth.

Lectotype: *S. umbrosa* Dum. (Syn: *S. alata* Gilib.).

Type: *S. amplexicaulis* Benth.

Type: *S. amplexicaulis* Benth.

Lectotype: *S. nodosa* L.

Syn: Ser. *Ilvenses* Gorschk. (lectotype: *S. ilwensis* C. Koch.);

Lectotype: *S. atropatana* Gorschk.

Syn: 
- *Ser. Fymanthium* (Boiss.) Gorschk. (lectotype: *S. minima* M.B.);
- *Ser. Rupestres* Gorschk. (lectotype: *S. rupestris* M.B.);
- *Ser. Frigidae* Gorschk. (lectotype: *S. frigida* Boiss.);
- *Ser. Olympicae* Gorschk. (lectotype: *S. olympica* Boiss.);
- *Ser. Cretaceae* Gorschk. (lectotype: *S. cretacea* Fisch.);
- *Ser. Pruinosae* Gorschk. (lectotype: *S. pruinosa* Boiss.);


Type: *S. leucoclada* Bge.


Type: *S. scariosa* Boiss.

10. *Ser. Callianthae* Lall

Type: *S. calliantha* Webb. & Berth.


Lectotype: *S. xanthoglossa* Boiss.

Syn: 
- *Ser. Rostratae* Gorschk. (type: *S. rostrata* Boiss. et Buhse.);
- *Ser. Rutifoliae* Gorschk. (lectotype: *S. rutifolia* Boiss.);
- *Ser. Schugnanicae* Gorschk. (lectotype: *S. fedtschenkoi* Gorschk.);
- Syn: *S. schugnanica* B. Fedtsch. nomen in herb.);
- *Ser. Multicaules* Gorschk. (type: *S. multicaulis* Turcz.);
- *Ser. Haemantantheae* Gorschk. (type: *S. haemantanthe* Boiss. et Holár.);
- *Ser. Caninae* Gorschk. (lectotype: *S. canina* L.)


VI. Subsect. Lepidotae Lall

Type: *S. lepidota* Boiss.
2. Key to the Sections, Subsections and Series

1. Corolla lobes subequal, staminode either rudimentary or absent .................................................. A. Sect. CERAMANTHE

1. Corolla lobes unequal, the two upper lobes longer than the laterals; staminode present, very rarely rudimentary or absent (S. villosa). Rarely corolla lobes subequal with a large staminode (S. subaequiloba & S. heucheriflora). B. Sect. SCROPHULARIA

A. Sect. CERAMANTHE

1. Corolla cylindrical, lobes 4 .................................. III. Subsect. Gracilis

1. Corolla ventricose, lobes 5

2. Leaves whorled, oblong-lanceolate, deeply lobed at the base, or with a free pair of basal lobes, or 1-2-pinnate, margin sharply dentate to serrate, apex acute (leaves undivided and entire-margined in S. verticillata). Calyx segments scarious-margined, glabrous ............................................. II. Subsect. Orientalis

2. Leaves opposite, undivided, shape and margin various. Calyx segments glabrous to densely glandular, with or without a scarious margin ............................................. I. Subsect. Vernalis

I. Subsect. Vernalis

1. Corolla glandular, lobes with or without a pale border .................................................. 5. Ser. Landroveriagae

1. Corolla not glandular, lobes without a border

2. Corolla white, 3 mm long; cymes subsessile (peduncle 1-4 mm long); calyx segments narrowly oblong, acute, without a scarious margin ............................................. 3. Ser. Microscrophulariae

2. Corolla never white, longer than 3 mm; cymes long-peduncled (peduncle always longer than 10 mm); calyx segments various in shape, with or without a scarious margin
3. Corolla yellow, rudimentary staminode inserted in the lower middle half of the corolla tube; stamens included; ovary not glandular ........................................ 3. Ser. Eggersianae

3. Corolla either not yellow, or if yellow, then rudimentary staminode lacking, stamens exserted and ovary glandular

4. Plants villous; leaves ± broadly ovate, base cordate (rarely leaves rhomboidal, e.g. some forms of S. kotschyanus), apex acute to round. Calyx segments villous (rarely glabrous, S. cryptophila), without a scarious margin; ovary glandular (rarely glabrous, e.g. S. cryptophila and S. tadschicorum). Inflorescence foliate (rarely subfoliate, e.g. S. tadschicorum) ................................ 1. Ser. Chrysanthae

4. Plants ± glabrous to puberulent. Leaves oblong to oblong-lanceolate, apex acute to acuminate, base cordate to cuneate. Calyx segments scarious margined, rarely sub-marginate (S. lateriflora), glabrous or glandular. Ovary glabrous. Inflorescence usually aphyllous, only rarely foliate (S. lateriflora) ................. 4. Ser. Lateriflorae

B. Sect. SCROEGLHLARIA

1. Corolla either cylindrical, or infundibular-campanulate

2. Corolla cylindrical or infundibular-campanulate, glandular on the outer or inner or both surfaces, longer than 10 mm, upper lobes of E-type; stamens included, filament glands of round type; leaves undivided; calyx segments without a scarious margin

III. Subsect. Przewalskiae
2. Corolla cylindrical, glabrous on both sides, smaller than 10 mm, upper lobes of C-type; stamens shortly exserted; filament glands of oblong type; lower leaves pinnatisect, calyx segments scarious-marginated ..................... IV. Subsect. Farinosae

1. Corolla ventricose

3. Corolla lobes subequal, staminode either ovate-spathulate extending much beyond the upper corolla lobes or reniform with a dorsal canal

4. Leaves undivided; calyx segments without a scarious margin; staminode ovate-spathulate without a dorsal canal

........................ ........................ I. Subsect. Heucheriflorae

4. Leaves bipinnatisect; calyx segments with a scarious margin; staminode reniform with a dorsal canal

........................ ........................ II. Subsect. Subaequilobae

3. Corolla lobes unequal; staminode various, without a dorsal canal, and never extending beyond the upper corolla lobes

5. Plants with lepidote scales ........................ VI. Subsect. Lepidotae

5. Plants without lepidote scales ..................... V. Subsect. Caninae

V. Subsect. Caninae

Relative length of the pedicel and bracteole in this Key always refers to that of the first flower of the cyme and the first pair of bracteoles.

1. Ovary glandular .................................................. 1. Ser. Altaicae

1. Ovary not glandular


2. Bracteoles not scarious-marginated


3. Stem not winged, at the most angled
4. Staminode spathulate, green, attached to the corolla along its entire length; upper corolla lobes oblong (of B-type); leaves ovate, sessile; inflorescence aphyllous ............... 5. Ser. Mimulopsis

4. Staminode not attached along its entire length, leaves not sessile (rarely sessile, e.g. S. kurdica but then inflorescence not aphyllous); other characters various

5. Cymes sub- to sessile; calyx segments submarginate to non-scarious-margined, sparingly glandular to villous, acuminate to acute; leaves ovate with a cordate base ........... 3. Ser. Calycinae

5. Cymes not sessile (if sessile, e.g. S. koeiei then the calyx segments with a scarious margin and leaves either oblong with cuneate base or divided); calyx segments if as above (S. villosa), then the cymes long-peduncled; leaves various

6. Corolla more than 11 mm long; filament glands of round type

7. Leaves large, pinnate to bipinnate ............... 10. Ser. Callianthae

7. Leaves undivided, margin duplicate-serrate

........................... 2. Ser. Duplicato-Serratae

6. Corolla always less than 11 mm; filament glands of either type

8. Stem with palisade tissue in the cortex; stem usually white in colour; leaves small, thick, undivided

............................... 8. Ser. Leucocladae

8. Stem cortex with chlorenchyma only, palisade tissue absent (chlorenchyma not differentiated into palisade tissue); stem not white; leaves various

9. Either all leaves undivided, or at the most the lamina of a few lower leaves pinnatifid, usually with 1-2 small, free basal segments
10. Pedicel longer than the bracteole (if shorter, *S. luridiflora*, then plants villous, filament glands of round type, leaf base cordate and anastomosis conspicuous), 5–26 mm long (only rarely 3–4 mm); median vegetative leaves with subcordate to cordate bases; leaf vein anastomosis conspicuous; filament glands predominantly of round type; upper corolla lobes usually of B-type; plants mesomorphic ......................... 6. Ser. Nodosae

10. Pedicel as long as or shorter than the bracteole (if rarely longer, then filament glands of oblong type; leaves thick, anastomosis inconspicuous, and bases not cordate), 1–5 mm long (rarely, 7.5–9 mm, some forms of *S. rimarum* and *S. davisii*); median vegetative leaves with a truncate to cuneate bases; leaf vein anastomosis inconspicuous; filament glands of oblong type (rarely of round type, e.g. *S. dentata*, *S. cretacea*); upper corolla lobes nearly always of C-type; plants xeromorphic .................................................. 8. Ser. Atropatanae

9. Either all the vegetative leaves divided (pinnate or 1–3-pinnatisect) or at least some of the lower leaves pinnatisect - lamina incised to or nearly to the mid-rib .......... 11. Ser. Xanthoglossae
3. Descriptions of Sections, Subsections and Series and Synopsis of Species.

A. Sect. **CERAMANTHE** Reichenb., Fl. Germ. Exc. 1: 376 (1830); Boiss., Fl. Or. 4: 388 (1879). - Annual, biennial or perennial. Plant 5-120 cm, glabrous to villous; stem erect or ascending. Leaves oblong-lanceolate to reniform, rarely rhomboidal, sometimes lobed at the base or bipinnate, opposite-decussate, rarely whorled. Inflorescence foliato to aphyllous; cymes subsessile to long peduncled, few- to many-flowered; pedicel longer or shorter than the bracteoles. Calyx segments ovate to lanceolate, ovate, acute to subround, glabrous to villous with or without a scarious margin. Corolla ventricose, rarely cylindrical, 3-3.5 mm, white, yellow, red, purple, reddish-; or paleish green, glabrous rarely glandular, lobes 5, rarely 4, subequal; stamens included to long exserted; filament glands with a round or oblong head; staminode absent, rarely rudimentary. Ovary glabrous or villous; capsules broadly to narrowly ovate, mucronate to beaked.

I. Subsect. **Vernales** Stiefelh., in Engler's Bot. Jahrb. 44: 428 (1910). - Annual, biennial or perennial, plant 20-120 cm or more in cultivation, glabrous to villous. Leaves opposite-decussate, oblong-lanceolate to reniform. Calyx segments oblanceolate to ovate, acute to obtuse, glabrous to villous, with or without a scarious margin. Corolla ventricose, glabrous, rarely glandular; stamens included to long exserted; filament glands of both type; staminode absent or rudimentary; ovary glabrous or glandular. Plants meso-, or xeromorphic.


*S. chrysantha* Jaub. et Sp.

*S. clausii* Boiss. et Buhse
S. cryptocphila Boiss. et Heldr.
S. hyrcana Grossh. (n.v.)
S. kotschyanana Benth.
S. tadschicorum Gontsch. (n.v.)
S. vernalis L.

2. Ser. Microscrophulariae (Urb.) Lall


S. micrantha Desv.

3. Ser. Eggersianae Lall


S. eggersii Urb.


Perennial, plants glabrous to sparingly glandular. Leaves oblong to oblong-lanceolate, apex acute to acuminate, base cordate to cuneate. Inflorescence aphyllous, rarely foliate (S. lateriflora), cymes long-peduncled. Calyx segments scarious-margined, rarely submarginate (S. lateriflora), glabrous or glandular. Corolla variously coloured (not yellow), glabrous; filament glands of round type. Ovary glabrous.

S. boissieriana Jaub. et Sp.
S. lateriflora Trautv.
S. nervosa Benth.
5. *Ser. Landroverianae* Lall

Perennial, densely glandular-puberulent. Leaves oblong-lanceolate. Calyx segments ovate to oblongish, glandular, scarious-margined. Inflorescence sphyllous. Calyx segments ovate, glabrous to glandular, scarious-margined. Corolla greenish-brown to pale-yellow, glandular; filament glands of round type (not known in *S. nikitinii*).

*S. landrovérii* Wendelbo

*S. nikitinii* Guschk. (n.v.)


Biennial or perennial, plants 57-120 cm, glabrous to glandular. Leaves whorled, undivided, entire-margined to bipinnate with serrate margin. Calyx segments glabrous, ovate, scarious-margined. Corolla ventricose, glabrous, stamens slightly exserted; filament glands of round type (not known in *S. verticillata*); staminode absent. Ovary glabrous. Plants xeromorphic.

*S. orientalis* L.

*S. verticillata* Gontsch. et Grig. (n.v.)

III. Subsect. *Gracilés* Lall

Perennial, plants 5-15 cm, many-stemmed, glandular-puberulent. Leaves small, opposite-decussate, dentate to slightly lobed, Calyx segments ovate, glandular, scarious-margined. Corolla cylindrical, lobes 4, glabrous; stamens slightly exserted, filament glands of oblong type; staminode absent. Plants xeromorphic.

*S. gracilis* Blakelock


Annual, biennial or perennial, plants 10-175 cm, 1-many-stemmed, glabrous to villous, winged to almost terete, erect, rarely ascending. Leaves sessile to long petiolate, lamina of various shape, undivided to 3-pinnatisect, opposite-
decussate, rarely alternate. Inflorescence thyrsiform, rarely sub-subcapitate
(S. minima M.B.); cyms long-peduncled to sessile, 30-4-flowered; pedicel longer
to shorter than the bracteoles, glandular, rarely glabrous. Calyx segments
subulate to orbicular, glabrous to villose, with or without a scarious margin.
Corolla cylindrical, or ventricose, rarely infundibular-campanulate, glabrous
rarely glandular; stamens included to long exserted; filament glands of round
or oblong type; staminode of various shape and colour. Ovary glabrous, rarely
glandular; capsules globular to narrowly ovate, mucronate to beaked.

I. Subsect. Heucheriflorae Lall

Leaves large, undivided, villous, anastomosis conspicuous. Calyx segments
oblong, glandular. Corolla ventricose, glabrous, lobes subequal; staminode
spathulate, extending much beyond the upper lobes; stamens long exserted.
Lepidote scales absent.

S. heucheriflora Schrank. (n.v.)

II. Subsect. Subaequilobae Lall

Leaves bipinnatisect. Calyx segments obovate to orbicular, scarious-
margined, glabrous. Corolla ventricose, glabrous, lobes subequal; staminode
large, roundly reniform with a dorsal canal; stamens shortly exserted; filament
glands of oblong type. Lepidote scales absent.

S. subaequiloba Lall

III. Subsect. Przewalskiae Lall

Leaves large, undivided, vein anastomosis conspicuous. Calyx segments
without a scarious margin. Corolla cylindrical or infundibular-campanulate,
lobes unequal, glandular on the outer or both surfaces, longer than 10 mm, upper
lobes of B-type; stamens included, filament glands of round type. Inflorescence
conferted or lax. Capsules ovate, beaked. Lepidote scales absent.
S. chasmophila W.W. Smith
S. delavayi Franch.
S. neomexicana Shaw
S. przewalskii Batal

IV. Subsect. Farinosae Stiefelh. in Engler’s Bot. Jahrb. 44: 429 (1910). -

Lower leaves pinnatisect, densely white glandular-puberulent, vein anastomosis inconspicuous. Inflorescence lax. Calyx segments scarious-margined, glandular. Corolla cylindrical, lobes unequal, glabrous on both sides, less than 10mm long, upper lobes of C-type; stamens slightly exerted, filament glands of oblong type. Capsules globular, apiculate. Lepidote scales absent.

S. farinosa Poiss.

V. Subsect. Caninae Benth. in D.C. Prodr. 10: 315 (1846). -

Leaves undivided to 3-pinnatisect, glabrous to villous, vein anastomosis distinct to obscure. Calyx segments subulate to orbicular, glabrous to villous, with or without a scarious margin. Corolla ventricose, glabrous, rarely glandular (S. calycina Benth.), lobes unequal, upper lobes of A-, B-, or C-type; stamens included to long-exserted; filament glands of both types; staminode not exceeding the upper corolla lobes, without a dorsal canal. Capsules narrowly ovate, beaked to globular, mucronate. Lepidote scales absent.


Plants villous, leaves undivided, anastomosis conspicuous. Stem angular, Cymes not sessile; bracteoles without a scarious margin. Corolla 8-12 mm long, yellow to yellowish white. Calyx segments lanceolate, villous, without a scarious margin, rarely submarginate. Ovary glandular.

S. altaica Murr. (n.v.)
S. megalantha Rech. f.
2. Ser. Duplicato-serratae Lall

Plants glandular, leaves undivided, anastomosis conspicuous. Stem not winged. Cymes not sessile, bracteoles not scarious-margined. Corolla more than 11 mm long, not yellow; staminode not attached along its entire length; filament glands of round type. Ovary not glandular.

S. duplicato-serrata Makino

3. Ser. Calycinae Lall

Plants glandular to villous; stem angular. Leaves undivided, anastomosis conspicuous. Cymes sub- to sessile, bracteoles not scarious-margined. Calyx segments narrowly ovate, acute to acuminate, sparingly glandular to villous, not scarious-margined, rarely submarginate. Corolla less than 10 mm long, not yellow; staminode free in the upper part; filament glands of round type. Ovary not glandular.

S. calycina Benth.

S. mandschurica Maxim. (n.v.)

S. pauciflora Benth.

S. spicata Franch.


Plants glandular-puberulent. Stem winged, especially below the leaf-bases. Cymes not sessile, bracteoles not scarious-margined. Calyx segments ovate, scarious-margined, glabrous. Corolla less than 11 mm long, not yellow. Ovary not glandular.

S. elatioir Benth.

S. umbrosa Dum.


Plants sparingly glandular-puberulent. Stem angular. Leaves sessile, undivided, anastomosis obscure. Cymes not sessile, bracteoles not scarious-
margined. Calyx segments oblong to orbicular, scarious-margined, glabrous to sparingly glandular. Corolla 6.5-8.5 mm long; staminode oblong-spathulate, attached along its entire length; filament glands of round type. Ovary not glandular.

*S. amplexicaulis* Benth.

6. Ser. Nodosae Gorschk, in Fl. U.R.S.S. 22: 266 (1955). - Plants glabrous to densely villous. Leaves usually large, thin, undivided, rarely divided (some forms of *S. polyantha*), glabrous to villous, anastomosis conspicuous; median leaves with cordate to subcordate bases. Cymes not sessile, bracteoles not scarious-margined; pedicel 5-26 mm long, rarely 4-3 mm (some forms of *S. ilwensis*) longer than the bracteoles (rarely shorter, *e.g.* *S. luridiflora*). Calyx segments various in shape, with or without a scarious-margin, glabrous to villous. Corolla less than 11 mm long, upper lobes usually of B-type; staminode not attached along its entire length; filament glands usually of round type, rarely of oblong type (*S. ilwensis*). Ovary not glandular. Capsules ovate to narrowly ovate, mucronate to beaked. Plants mesomorphic.

*S. aestivalis* Grisb. (n.v.)

*S. alpestris* Gay

*S. angunensis* F. Schmidt (n.v.)

*S. arguta* Sol.

*S. atrata* Pennell (n.v.)

*S. bourgaeana* Lge.

*S. bosniaca* Beck (n.v.)

*S. californica* Chem. & Schlecht.

*S. capillaris* Boiss. et Bal.

*S. chlorantha* Ky. et Boiss.

*S. desertorum* (Munz) Shaw (n.v.)
S. divaricata Ledeb.
S. glabrata Sol. (n.v.)
S. grayana Maxim.
S. henryi Hemsl. (n.v.)
S. himalayensis Royle
S. hirta Lowe (n.v.)
S. ilwensis C. Koch
S. kansuensis Batal
S. kurdica Eig
S. lanceolata Pursh.
S. longifolia Benth. (n.v.)
S. luridiflora Fisch. et Mey.
S. macrobotrys Ledeb. (n.v.)
S. macrophylla Boiss.
S. mandarinorum Franch. (n.v.)
S. marilandica L.
S. maximowiczii Gorschk. (n.v.)
S. mollis Somm. et Lev. (n.v.)
S. montana Wooton & Standley
S. nodosa L.
S. obtusa Edgeworthii
S. oldhamii Oliv.
S. oregana Pennell (n.v.)
S. oxysepala Boiss. (n.v.)
S. parviflora Wooton & Standley (n.v.)
S. pegaea Hand-Mazzt.
S. peregrina L.
$S.$ *polyantha* Royle

*S. pyrenaica* Benth. (n.v.)

*S. scopolii* Hoppe

*S. scorodonia* L.

*S. smithii* Hornem.

*S. sprengeriana* Somm. et Lev. (n.v.)

*S. tenuipe* Coss.

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*S. urticifolia* Wallich

*S. villosa* Pennell

7. Ser. *Atropatanae* Gorschk. in Fl. U.R.S.S. 22: 279 (1955). - Plants sparingly to densely glandular-puberulent. Stem angular to almost teret. Leaves coriaceous, undivided to pinnatifid, usually with 1-2 free or almost free basal segments; anastomosis inconspicuous; median leaves with truncate to cuneate bases (only rarely subcordate or cordate, but then the filament glands of oblong type, leaves thick, and anastomosis inconspicuous). Cymes long peduncled to sessile; bracteoles not scarious-margined; pedicel 1-5 mm long (rarely 7-9 mm), as long as or shorter (very rarely longer) than the bracteoles. Calyx segments scarious-margined, glabrous to glandular-puberulent. Corolla less than 11 mm, colour various, upper lobes nearly always of O-type, staminode not attached along it entire length; filament glands nearly always of oblong type. Ovary not glandular. Capsules ovate to globular. Plants xeromorphic.

*S. amana* Lall

*S. atropatana* Grossh.

*S. benthamiana* Boiss. (n.v.)

*S. bitlisica* Lall
S. canescens Bong.
S. charadzei Kem-Nath. (n.v.)
S. crassicaulis Boiss.
S. catarifolia Boiss. et Heldr.
S. cretacea Misch.
S. davsiii Hall
S. dentata Royle
S. donetzica Kotov.
S. diffusa Somm. et Lev.
S. edelbergii Rech. f.
S. elegantissima Rech. f. et Wendelbo (n.v.)
S. frigida Boiss.
S. glauca Decaisne
S. horizontalis Rech. f. (n.v.)
S. hyssopifolia Boiss. et Hausskn.
S. imerethica Kem-Nath. (n.v.)
S. incisa Weinn.
S. integrifolia Pavl.
S. koeiei Rech. f.
S. litvinovii B. Fedisch. (n.v.)
S. marginata Boiss.
S. minima M.B.
S. nachitschevanica Grossh.
S. nana Stiefelh. (n.v.)
S. olympica Boiss.
S. petraea Aitchinson & Hemsley (n.v.)
S. pruinosa Boiss.
S. pulverulenta Boiss. et Nöe
S. Pumilio Lall
S. rimarum Bornm.

S. rupestris M.B.

S. serratifolia Hub.-Mor.

S. suffruticosa Pennell (n.v.)

S. stewartii Pennell
S. uniflora Richter ex Stapf (n.v.)
S. volkii Rech. f. (n.v.)


Plants glabrous to sparingly glandular. Stem almost terete, usually white; cortex with palisade tissue. Leaves coriaceous, small, undivided, anastomosis inconspicuous. Cymes not sessile; bracteoles not scarious-margined. Calyx segments ovate, glabrous, scarious-margined. Corolla less than 10 mm long, not yellow; filament glands of oblong type; staminode not attached along its entire length. Ovary not glandular.

S. fruticosa Bornm.

S. hyperclfolia Wydl.

S. leucocladia Bge.

S. syriaca Benth.

9 Ser. Scariosae Lall

Plant glandular-puberulent. Stem angular, rarely winged. Leaves undivided to pinnatisect, anastomosis conspicuous to obscure. Cymes not sessile; bracteoles with a scarious margin. Calyx segments ovate, scarious-margined, glabrous to sparingly glandular. Corolla 6-9 mm long, not yellow; filament glands of both types; staminode not attached along its entire length. Ovary not glandular.

S. aquatica L.

S. auriculata L.

S. mesopotamica Boiss.

S. scariosa Boiss.
10. **Ser. Callianthae Lall**

Plants glandular. Stem not winged. Leaves pinnate to bipinnate, anatomosis conspicuous. Cymes not sessile; bracteoles not scarious-margined. Calyx segments ovate, scarious-margined. Corolla less than 11 mm long, not yellow; filament glands of round type; staminode not attached along its entire length. Ovary not glandular.

*S. calliantha* Webb. et Berth.

*S. sambucifolia* L.

*S. trifoliata* L.


Plants densely to sparingly glandular-puberulent. Stem angular to almost terete. Leaves 1-3-pinnatisect, anatomosis conspicuous to obscure. Cymes short-, to long-peduncled; bracteoles not scarious-margined; pedicel shorter or longer than the bracteoles. Calyx segments oblong to orbicular, scarious-margined, glabrous to glandular. Corolla less than 11 mm long, colour various, upper corolla lobes nearly always of C-type; filament glands predominantly of oblong type. Ovary not glandular. Capsules ovate, mucronate to beaked, or globular, mucronate.

*S. candelabrum* Heywood (n.v.)

*S. canina* L.

*S. caucasica* Somm. et Lev. (n.v.)

*S. crithmifolia* Boiss.

*S. czapandaghii* B. Fedtsch. (n.v.)

*S. decomposita* Royle

*S. deserti* Del.

*S. dissecta* B. Fedtsch. (n.v.)

*S. exserta* Pennell (n.v.)

*S. farakulumensis* Rech. f.
S. frutescens L.
S. gypsicola Hub.-Mor.
S. haematentha Boiss. et Heldr. (n.v.)
S. herminii Hoffm. et Link (n.v.)
S. heterophylla Willd.
S. hispida Deaf.
S. kabadianensis B. Fedtsch. (n.v.)
S. koezii Pennell
S. laevigata Vahl.
S. lucida L.
S. mersinensis Lall
S. michoniana Coll. et Kral.
S. moniliformis Pennell
S. multicaulis Turcz.
S. myriophylla Boiss.
S. nabataecorum Eig
S. nudata Pennell
S. olgae Grossh.
S. pamiro-alaica Gorschk. (n.v.)
S. peyronii Post
S. racemosa Lowe (n.v.)
S. rosulata Stiefelh.
S. rostrata Boiss. et Buhse
S. ruprechtii Boiss.
S. scabiosifolia Benth.
S. scoparia Pennell
S. schousboeij Lge.
S. stenothyrsa Pennell
S. striata Boiss.
S. tagetifolia Boiss. et Hausskn.
S. tanacetifolia Willd.
S. tagetea Boiss.
S. televivensis Eig.
S. thesioides Boiss. et Buhse
S. trichopoda Boiss.
S. turcomanica Bornm. et Sint.
S. variegata M.B.
S. versicolor Boiss.
S. xanthoglossa Boiss.
S. zavartiana Gabr.
S. zuvandica Grossh.

VI. Subsect. Lepidotae Lall

Plants thickly covered with lepidote scales. Leaves thick, coriaceous, undivided. Calyx segments ovate, widely scarious-margined. Corolla ventricose, lobes unequal, upper lobes of C-type; filament glands of oblong type; staminode neither exceeding the upper corolla lobes, nor with a dorsal canal.
S. lepidota Boiss.

The following species which belong to Subsect. Caninae have not been considered due to the inadequate information:
S. armeniaca Bordz. (n.v.)
S. alaschanica Batal (n.v.)
S. autumnalis Forman. (n.v.)
S. czernjakowskiana B. Fedtsch. (n.v.)
S. diplodonta Franch (n.v.)
S. ebulifolia Hoffm. et Link (n.v.)
S. elbursensis Bornm. (n.v.)
S. erecta Stiebel. (n.v.)
S. exilis Ppl. (n.v.)
S. fargesii Franch. (n.v.)
S. fedtschenkoi Gorschk. (n.v.)
S. gaubae Bornm. (n.v.)
S. goldeana Juz. (n.v.)
S. kiriloviana Schischk. (n.v.)
S. laxiflora Lge. (n.v.)
S. macrantha Greene (n.v.)
S. microdonta Franch. (n.v.)
S. moellendorfii Maxim. (n.v.)
S. pallecens Lowe (n.v.)
S. puberula Boiss. (n.v.)
S. sanctodensis B. Fedtsch. (n.v.)
S. sareptana Kleop. (n.v.)
S. zaravchanica Gorschk. et Zakir. (n.v.)
VII. GENERAL ECOLOGY

AND DISTRIBUTION
General Ecology and Distribution

1. **Ecology**: With a few exceptions, Sect. Ceramanthe consists of mesophytes, whereas in Sect. Scrophularia both mesophytes and xerophytes are abundantly represented. In Subsect. Caninae the bulk of the species falls into 3 series, namely Nodosaes, Atropatanae and Xanthoglossae. Ser. Nodosaes comprises mesophytic species, while Ser. Atropatanae and Xanthoglossae consist of xerophytic species which differ in their degree of tolerance to xeric conditions.

Subsect. Vernalis (except Ser. Lateriflorae) among Ceramanthe and Ser. Nodosaes in subsect. Caninae can be considered as representative of the mesophytes. These grow in wet forests or wet and shady places near water courses, and are usually characterized by tall, stout stems with large leaves predominantly well scattered along the stem; large leaves are connected with low light intensity, as these plants grow more or less in shady places. Perennation occurs either by the formation of suckers or rhizomes. In S. nodosa (Plate 1.1, p. 7) the suckers are short and swollen. In biennials the plant probably remains short and stumpy and produces abundant leaves in the first year. (According to Salisbury, 1961, in S. vernalis the seeds germinate in the late summer or early autumn, and the winter is passed as a rosette of woolly, heart-shaped and serrated leaves).

Plants of S. umbrosa and S. acopolii were planted outside in the Royal Botanic Garden, Edinb. They did not grow more than 6 or 7 inches in height in the first year but produced large abundant leaves with the result that the stem became very thick and the internodes were too short to be visible. These plants were periodically under snow for a few days from November to February but most of the leaves did not die. In the second year the plants grew vigorously and attained a height of about 4 feet and showed the production of rich foliage and many stems. Some of the biennials are probably better adapted to cold than...
some of the xerophytes. *S. rupestris* and *S. variegata* (both perennial in nature) were also planted with *S. umbrosa* and *S. scopolii* in the same place in the same year. They flowered in the first year but did not manage to revive the following year; it is not clear whether their failure to survive was due to wet or cold, or both.

The tap-root in mesophytes is short but gives rise to an intensively branched horizontal root-system from below soil level; in perennials abundant adventitious roots are given off from the rhizomes, suckers, etc. (Plate 1.1, p. 7).

Among annuals *S. arguta* is the most specialized and is characterized by amphicarpic fruits. The species always grows in shady places in arid areas. According to P.H. Davis (in verbis) it often forms pure stands beneath dense-caponied Argania trees. Here its subterranean fruits may serve as an adaptation against grazing (goats climb the Argania trees), or as a means of keeping the population in the shade of the tree.

The members of Ser. Atropatanae grow on dry rocky slopes and waste places and are representatives of mainly saxatil species. The plants have long woody roots which penetrate deep into the rock crevices. The basal part of the plant becomes extremely thickened, woody and many-stemmed as more and more branches are produced every year from the base; the branches die out at the end of each growing season, or are frequently grazed and the remains of their woody bases add to the thickening of the basal part of the plant.

The leaves in the saxatil xerophytic species are smaller than those of the mesophytes and become thick and leathery. The mesophyll tissue is more compact although there is no appreciable increase in the number of palisade layers; the thickness being accompanied by an increase in the length of palisade cells; these thick, somewhat fleshy leaves with a thicker cuticle are better adapted to reduce the loss of water by excessive transpiration. Some of the desert species,
S. hypericifolia and S. fruticosa, provide interesting examples in which a decrease in the surface area of the leaf (leaves are very small in these species) has been compensated for by the development of palisade tissue in the cortical region of the stem; the stem cuticle of these species is white and extremely thickened. The stem in most of these species is either glabrous and shiny or is densely glandular-puberulent; the leaves in a few species tend to be crowded near the base. S. lepidota in this group provides an extreme example of xerophytism, the whole plant (except for corolla and capsules) being thickly covered with lepidote scales; it grows on dry gypsum and perennates by rhizomes. In this species the vegetative shoots are produced from the basal part of the plants towards the end of the growing season and produce aphyllous inflorescences the following year.

The members of Ser. Xanthoglossae are predominantly xerophytic and usually grow on rocks or dry places. Some of the species, like S. xanthoglossa, S. canina etc. have invaded secondary habitats and grow along the edges of the cultivated fields, etc. Most of the members of this Series are similar in their xeromorphy to those of the Atropatanae but show a further trend in this direction by the further division of their leaves. S. gypsicola, a biennial, which grows on gypsum, can be regarded as the extreme xerophytic example in this Series.

2. Pollination and Dispersal: Pollination in Scrophularia has been studied by Sprengel (1739), Wilson (1878), Müller (1883), Knuth (1909) and Schremmer (1959) in Europe, and by Trelease (1881), Robertson (1891), and Shaw (1962) in the United States. According to these investigators, in addition to the wasps which are the chief pollinators, the flowers are also visited by humble-bees and syrphid flies. In Turkey, Davis has observed many Scrophularia species being visited by wasps in the field. In Britain S. vernalis is visited by humble-bees. Shaw (1962) records the visiting of the flowers of S. lanceolata by ants of the genus
Formica at 2 localities in Grant County and Oregon.

The flowers are protogynous and the stigma becomes receptive when the unripe anthers, still bent over their filaments, lie at the base of the corolla tube; this stage of anthesis has been referred to as the first or "female" stage of anthesis (Knuth, 1909), followed by the "male" anthesis, when the anthers are ready to shed their pollen. The nectar is produced in large drops from a pentagonal hypogynous disc, and in Sect. Scrophularia the staminode most probably serves as a nectar-guide. Knuth (1909) thinks that yellow anthers and brown upper lip present a noteworthy agreement with the colour of the wasps which visit the flowers. Protogyny favours a certain degree of outcrossing, although some species, such as S. arguta and S. peregrina (as observed in the greenhouse by the author), are capable of setting full capsules by self-pollination. Knuth (1909) has shown in S. nodosa, if outcrossing fails, seed production is ensured by self-pollination. Warnstorf (1896) reports the following interesting observation on S. vernalis (Sect. Ceramanthe): 'In the second stage (male anthesis) which succeeds the first (female) one, the two long stamens extend to the stigma or somewhat beyond it, and as their anthers come to lie below it and dehisce on the under-surfaces autogamy is rendered very difficult. In the third stage the style bends up and the short stamens stretch forward, their anthers in front of the stigma. The plant exhales an agreeable balm-like odour, and is eagerly visited by humble-bees.' It is not known to what extent the species of Scrophularia are isolated in nature by these pollinators. S. neomexicana is probably isolated from the other N. American Scrophularias, as it is thought to be pollinated by humming birds (Shaw, 1962).

In S. arguta, besides the normal open flowers, cleistogamous flowers are also present. These cleistogamous flowers are produced on short underground branches.
arising from the lowest nodes. The cleistogamous flowers differ from the aerial ones by their much smaller size, lack of pigmentation (except for purplish anthers), much reduced staminode (which may be absent in some flowers), extremely low production of pollen, and cleistogamy. The style is short and twisted and the sticky stigma becomes firmly attached to the mature anther on the side along which the dehiscence occurs. Nectar is apparently absent. The ovary develops a strong beak at an early stage which seems well adapted for drilling its way through the soil.

The seeds in Scrophularia are small (usually 0.4-1 mm) and light. Salisbury (1961) has given 0.00017 gm as the average seed weight in S. vernalis. The number of seeds per capsule may vary from 30-140 and probably depends on the amount of fertilization. Salisbury (1961) has estimated that a single plant of S. vernalis can produce on the average about 4,700 seeds. The dehiscence is septicidal; at maturity the capsules split open in the upper part, and the seeds are shaken out and carried away by the wind. Ridley (1930) records a plant of S. nodosa from the top of a 10-12 feet high wall which in his opinion grew from the seeds carried up to the top of the wall by convective currents. In S. vernalis the dispersal of seeds is partly affected by birds (Salisbury, 1961). In S. arguta, the dispersal of the aerial seeds is by wind, while the geocarpic capsules at maturity dehise under the soil and deposit the seeds in it. According to Ridley (1930), in S. aquatica dispersal takes place by the floating seedlings. The species grows along river banks. The tiny seeds which are blown into the water sink immediately and remain under water for several days where germination takes place. In a few days' time the seedlings float to the surface and are disseminated by water.
3. Distribution: The genus Scrophularia is confined to the N. hemisphere and occurs in Asia, Europe, N. Africa and N. America.

Sect. Ceramanthe is represented only in Europe, C. Asia and a few Caribbean islands (Haiti, Porto Rico and Cuba). As already stated in the preceding pages the author has divided Sect. Ceramanthe into 3 subsections and 5 series. The monotypic Subsect. Graciles, which is characterized by cylindrical corolla with 4 instead of 5 lobes, is endemic to N. Iraq (map 5). The ditypic Subsect. Orientales extends from E. Anatolia to C. Asia (map 5, p.140) and is unique in having whorled leaves which vary from entire-margined to rarely bipinnate (S. orientalis is the only example in Sect. Ceramanthe where the leaves are divided). The third subsection, Verna, which consists of 5 series, shows a wider distribution. Series Landoverianae extends from Afghanistan to C. Asia (Turkestan) and differs from the others in having a glandular corolla (map 6, p.141). Series Microscrophulariae and Eggersianae are exclusively confined to Haiti, Porto Rico and Cuba (map 6, p.141). Series Microscrophulariae stands out on 3 features, namely, the smallest corolla (2.5-3 mm long) which is white in colour, and the rudimentary staminode which is inserted at the bottom of the corolla tube. Since the insertion of the staminode at the bottom of the corolla tube is due to the faster growth first of the corolla lobes and then of the corolla tube, this could be one way of getting rid of the rudimentary staminode. The evolution of all the above three characters is apparently confined to this region only. The related series Chrysanthae and Lateriflorae differ in a number of correlated differential characters. The series Chrysanthae is distributed in Turkey, Iran, Caucasia, Europe and C. Asia (Turkestan, Pamir-Alai), while Ser. Lateriflorae is confined to Caucasia and Iran only.
Sect. Ceramanthe is poorly developed in Europe and is represented by a single species, *S. vernalis*, which is a member of Subsect. Vernales. The distribution of the series of Subsect. Vernales (map 6, p. 141) shows that there appears to be 3 centres of morphological differentiation of this subsection: 1) Turkey, Caucasus and Iran; 2) C. Asia (Afghanistan, Turkestan and Pamir-Alai), and 3) West Indies. Turkey, N. Iraq, Caucasus and Iran are floristically an interesting area. All the 3 subsections of Ceramanthe as well as two-third of its species occur in this area. In contrast Europe is represented by one subsect. and C. Asia by 2 subsections. (map 5, p. 140) containing about one third of the total number of species in Sect. Ceramanthe.

Unlike Sect. Ceramanthe, Sect. Scorophularia is also represented in N. Africa and N. America. The author has recognised the following 6 subsections in this section: 1. Przewalskiae, 2. Farinosae, 3. Heucheriflorae, 4. Subaequilobae, 5. Caninae and 6. Lepidrotae. The subsections Przewalskiae and Farinosae are characterized by a cylindrical corolla which in the former is much longer and in addition densely glandular. Przewalskiae occurs in China and N. America (where it is represented by a single species, *S. neomexicana*), while Farinosae is endemic to S. Iran (map 5, p. 140). The occurrence of a cylindrical corolla is rather sporadic; it occurs in N. Iraq, Iran, China and N. America. The glandular cylindrical corollas of *S. neomexicana* and the Old World members of subsect. Przewalskiae are probably a case of convergent evolution. The ventricose-glandular corolla also shows a sporadic distribution and is known to occur only in *S. landroveri* (Afghanistan), *S. nikitinii* (Turkmenistan), *S. calycina* (W. Himalaya; Hazara to Kumaun), and *S. calliantha* (endemic in the Canary Islands), and is absent from Europe, Africa and N. America.
The monotypic Subsections Subaequilobae and Heucheriflorae provide a morphological link between the two Sections. They have subequal corolla lobes and the presence of a staminode. Heucheriflorae is restricted to C. Asia (map 5) and is characterized by a spatulate staminode which extends much beyond the upper corolla lobes. Subaequilobae, on the other hand, is endemic to E. Anatolia (map 5).

The monotypic Subsection Lepidotae is unparalleled in the development of lepidote scales and is endemic to the eastern part of C. Anatolia (map 5).

The Subsection Caninae is the largest in this section and consists of 11 series. It is the most widely distributed and extends from the British Isles to N. America in the east and from N. Africa to Scandinavia and Sikkim to Siberia in the North (map 5). Maps 7-8 (pp.142-143) show the distribution of the 11 series of Subsect. Caninae. Series Nodosae is the most widely spread and corresponds to Subsect Caninae in its distribution. Series Atropatanae, Xanthoglossae and Alatae are widely distributed in Europe and Asia and the first 2 also extend into N. Africa. Series Scariosae is fairly widespread in Europe and N. Africa, but in Asia only occurs in Syria and Turkey. Series Altaicae extends from N. Iran to E. Siberia and series Leucocladae from Russian Tien-Shan to Morocco. The other series are more restricted in their distribution.

Of the 6 subsections of Sect. Sorophularia, two (subsects. Lepidotae and Subaequilobae) are endemic in Turkey, one (subsect. Parinosae) endemic in Iran. Subsects. Heucheriflorae and Przewalskiae are restricted to C. Asia, although the last also occurs in N. America. Europe and N. Africa are represented only by one subsection Caninae.

Out of the 11 series of Subsect. Caninae, 1 occurs in N. America, 6 in Europe, 7 in N. Africa and 10 in Asia. If Turkey, Caucasus and Iran are compared
with C. & E. Asia, both are represented by 3 series each. The comparison of
the number of Subsections in these two areas is also interesting; the former
is represented by 4 and the latter by 3 subsections. If the number of the sections,
subsections and series in an area is indicative of the degree of morphological
diversity in the genus, then the following are the collective figures of infra-
generic taxa (sections, subsections & series) for each continent: a) N. America,
4; b) N. Africa, 9; c) Europe, 10, and Asia, 24. The above figures show that
the maximum morphological diversity of this genus has occurred in Asia and the
minimum in N. America. Within Asia there are two major centres of morphological
diversity: a) C. & E. Asia (including Afghanistan and W. Pakistan), and b)
S.W. Asia; the figures for infra-generic taxa in these two areas are 16 and 19
respectively. It is also interesting to note that maximum concentration of
species occurs in this area (S.W. Asia, more than two-third of the species),
and the number of species gradually decreases towards the east (Afghanistan to
Far East), South (Syria to Egypt and N. Africa) and west (Europe).

It is concluded that maximum morphological diversity and concentration is
present in Turkey, Caucasus, Iran and N. Iraq. When Turkey is compared with
each of these neighbouring countries, it shows not only a greater degree of
morphological diversity but also stands higher in the number of species. This
can be partly explained by the fact that Turkey is the meeting place of 3
floristic regions, Euro-Siberian, Irano-Turanian and Mediterranean. A number
of species which are centred in Caucasus, Iran, N. Iraq or Syria have evidently
migrated into N. and E. Anatolia (thereby adding to the number of Anatolian
species). Rugged topography and diversity of habitats in E. (including Sivas)
and S. Anatolia (Taurus) have presumably provided favourable niches for endemics.
PART 2

REVISION OF THE TURKISH SPECIES OF SCROPHULARIA

VIII. INTRODUCTION
Introduction

Boissier (1879) recognised 35 species from Turkey. Since Boissier's time until 1910 the following new species had been added to the Turkish list: S. uniflora (Richter, 1882), S. antiochla (Post, 1892), S. bornmülleri, S. glandulosissima, S. sintenisii (Freyn & Sint., 1892-96) and S. micradenia (Freyn, 1910). Stiefelhagen (1910) listed 39 species from Turkey. Eig (1944) described a new species, S. clematidifolia, from the Amanus and reported S. macrophylla and S. peyroneii from the same area. Heywood (1952) reported S. rimarum from W. Anatolia and described the following 7 species and 3 varieties: S. praeterita, S. ballsii, S. lyrata, S. candelabrum, S. ciliicica, S. epicalycina, S. umbrosa, S. libanotica var. oligantha, S. scopolii var. longirostrata and S. rupestris var. pinnatisecta.

The classical collections worked on by Boissier, in his fairly well balanced pioneer account in Flora Orientalis, have provided the foundation for the present revision. However, my work relies heavily on the prolific post-Boissier collections of Sintenis, Siehe, Bormmüller, Aznavour etc., and especially the recent collections of Huber-Morath and of Davis and his colleagues, much of which often provides ecological data and notes on flower colour. This mass of new material has extended the range of known variability, which has necessitated some reassessment of specific limits; at the same time, recent exploration has led to the discovery of new species and records presented here for the first time.

I have in the present revision excluded S. heterophylla from Turkey, but have added the following 14 species to the Turkish list, the last 8 of which are here described as new to science. S. zuvandica, S. thesioides, S. striata, S. kurdica, S. amplexicaulis, S. scariosa; S. pumilio, S. amana, S. bitlisica, S. serratifolia, S. gypsicola, S. davisii, S. subaequiloba and S. mersinensis.
The revised list (with several previously accepted species reduced to synonymy or infra-specific rank) now comprises 49 species.

1. **Species Concept:** Morphological criteria have been relied on for separating the taxa, although information on cytology (where available), geography and ecology have, in some cases, been used as additional supporting characters. Discontinuous variation in two apparently correlated taxonomic characters has been accepted as a minimum requirement for specific rank (although rarely in critical species the criterion has been a little less rigid); a single diagnostic character either with a few differential characters or distinct geographical distribution (or both), has been adopted for subspecific rank, and a minor diagnostic and one or two differential characters for varietal rank. I can recognise three distinct groups of species in Turkey: a) taxonomically isolated species (whose close relatives are apparently extinct) which differ from other species in several striking diagnostic characters (e.g., *S. lepidota*, *S. amplexicaulis*, etc.), b) species whose immediate relatives are outside Turkey and which are distinct from the other Turkish species (e.g., *S. chrysanthae*, *S. orientalis*, etc.), and c) species with their nearest relatives inside Turkey (e.g., *S. pegaea*, *S. scopoli*, etc.). It is the last group in which most of the taxonomic problems occur. Wherever the author found that the additional material broke down distinctions between two or more taxa so that it was now impossible to distinguish the one from the other, the taxa in question have been treated as synonymous (e.g., *S. variegata*, *S. scopoli*, etc.). *S. xanthoglossa* is more widely distributed (Balkhash, mount. Turkmenia, Syr Darya foothills, Pamir-Alai, Tien Shan, Iran, Caucasus, Turkey, Iraq, Syria, Palestine and Egypt) than *S. striata* (mount. Turkmenia, Pamir-Alai, W. Pakistan, Afghanistan, Iran and Turkey). In Turkey (and presumably in other countries as well) wherever they grow sympatrically
intermediates occur, but the extreme forms of the two species are strikingly different. In such cases, the species have been maintained in spite of the occurrence of some intermediate specimens. Whenever the taxonomic status of a taxon is uncertain, due to scanty material or insufficient information, this has been clearly stated in observations under each species.

2. Presentation of Data

a) Keys: The main key has been broken down into 6 artificial groups which are based on vegetative and calyx characters that are available whether the specimens are in flower or fruit. In species where the staminode shape is found not to be reliable it has not been used in the key, but has been freely used wherever dependable; the same is true of other such characters. If necessary a species has been keyed out several times; no attempt has been made to force species to key out only once.

b) Descriptions: Except in S. uniflora, the original descriptions have been amplified and are based on the material seen. In order to avoid confusion about the staminode shape, as it is often difficult to describe the exact shape or to demonstrate the range of variability in words, the staminode has been drawn for nearly all the Turkish species. It has also been drawn for some of the non-Turkish species, either to demonstrate the striking range of variability within a particular species, or for clarification in certain species where the staminode was either wrongly described (e.g. S. farinosa), or there has been much dispute about its shape (S. subxylocephala, Fig. 17, p. ), or misobservation has led to the publication of new taxa or their placing in the wrong sections (e.g. S. hadjariana, Fig. 17, p. ); S. pauciflora, Fig. 17, p. ). All the drawings have been made with a camera-lucida to the same scale. For the sake of future reference, the staminode in each case is labelled with the collector's number; in addition the staminode of the type specimen has been marked with an
Asterisk. Information about habitat and altitude is given for nearly all species. Wherever type material of a synonym has been examined, this has been indicated by the insertion of an exclamation mark (!) at the end of a synonym's reference. A new synopsis of the classification of the Turkish species is provided, and the species in each series have been arranged as far as possible according to their overall relationships.

c) Citation of Specimens: The distribution of each species in Turkey is based mainly on specimens seen. The author has followed the grid system as adopted in the Flora of Turkey, and when giving the distribution only one specimen per province per square has been cited. If the specimen cited has been examined by the author, this has been indicated by an exclamation mark. A summary of the distribution within Turkey is also given for each species. In addition, distribution maps are also provided for all the species, including additional records not cited in the text; distribution records from the literature have been accepted with considerable caution.

d) Typification: With the exception of Linnaean species, type localities and material of the species and taxa of lower rank have been cited as an aid to further research. Type localities are given as originally published, allowing for some contraction when necessary, and translation of feet (altitude) into metres. The whereabouts of holotypes and isotypes have only been cited when the precise nature and location of the type is certain. Wherever type material has been examined, it has been indicated by an exclamation mark.
IX. SYNOPSIS OF THE
IX. TURKISH SPECIES
Synopsis of the Turkish Species

A. Sect. CERAMANTHE Reichb.

I. Subsect. Vernalis Stiefelh.

   S. chrysantha, kotschyanra, cryptophila

II. Subsect. Orientalis Stiefelh.
   S. orientalis

B. Sect. SCROPHULARIA

II. Subsect. Subaequilobae Lall
   S. subaequiloba

V. Subsect. Caninae Benth.

   S. umbrosa

5. Ser. Mimulopsis (Boiss.) Gorschk.
   S. amplexicaulis

   S. kurdica, peregrina, pegaea, luridiflora, capillaris, secoloba, macrophylla, ilwensis, nodosa, chlorantha

   S. davisii, pulverulenta, oatarifolia, uniflora, rimarum, bitlisica, serratifolia, rupestris, marginata, pumilio, nachitschevanica, hyssopifolia, olympica, amana
9. Ser. Scariosae Lall
   S. mesopotamica, scariosa

   S. variegata, trichopoda, tagetifolia,
   candelabrum, lucida, mersinensis, myriophylla,
   versicolor, canina, thesioides, striata, xanthoglossa,
   peyronii, zuvandica, gypsicola

VI. Subsect. Lepidotae Lall
   S. lepidota
X. KEY TO THE TURKISH SPECIES
Key to the Turkish Species

The following key is broken down into six artificial groups; these are based on vegetative and calyx character that are available whether specimens are in flower or fruit.

The relative length of the pedicel and bracteoles refers to that of the first flower of the cyme and its first pair of the bracteoles. For the types of filament glands and corolla lobes, see pp. 37&63.

1. Calyx segments without a scarious margin ........................................ Group 1
1. Calyx segments with a scarious margin

2. Plants with lepidote scales ...................................................... Group 2
2. Plants without lepidote scales

3. Bracteoles with a scarious margin ............................................ Group 3
3. Bracteoles without a scarious margin

4. Either all leaves alternate or leaves whorled ................................ Group 4
4. At least a few lower leaves opposite

5. Either all or the median leaves undivided; margin simply
   or doubly crenate to dentate .................................................. Group 5
5. Either all vegetative leaves 1-3-pinnatisect, or the lamina of
   some of the leaves pinnatifid, or with 1-3 small, free or
   ± free basal segments ......................................................... Group 6

Group 1

1. Ovary glandular; calyx segments glandular either on the outer, or
   inner, or both sides

2. Corolla yellow; calyx segments acute to acuminate; pedicel shorter
   than the bracteole; cymes subcapitate ............................... 1. chrysantha
2. Corolla red or white flushed with pink; calyx segments obtuse; pedicel longer than the bracteole; cymes not subcapitate ............ 2. kotschyana

1. Ovary not glandular; calyx segments glabrous on both sides

3. Corolla lobes unequal; staminode large, round ............... 9. peregrina

3. Corolla lobes subequal; staminode either absent or rudimentary .................................................. 3. cryptophila

Group 2

Plants with lepidote scales; leaves whitish-grey, spathulate, margin entire, at the most tridentate at the tip, stems numerous, perennial ................................................................. 49. lepidota

Group 3

1. Calyx segments glandular, scarious margin white, very broad; leaves tripinnatisect; capsules 8.5-11 mm long .............. 33. scariosa

1. Calyx segments eglandular, scarious margin pinkish; leaves pinnate to bipinnate, capsules 6.5 mm long ............... 32. mesopotamica

Group 4

1. Leaves whorled; staminode absent; corolla lobes subequal; filament glands of round type ........................................ 4. orientalis

1. Leaves alternate; staminode present; corolla lobes unequal, filament glands of oblong type (rarely of round type: S. scopolii var. longirostrata)

2. Leaves undivided to pinnatifid

3. Filament glands of round type; pedicel 11-15 mm, 2-4 times longer than bracteole ........................ 13. scopolii

3. Filament glands of oblong type; pedicel 1-9.5 mm, longer or shorter than the bracteole ................. 15. ilwensis

2. Leaves bipinnatisect .................................................. 44. versicolor
Group 5

1. Corolla lobes subequal, staminode absent or rudimentary, plants villous .................................................. 3. cryptophila

1a. Corolla lobes unequal, staminode present, plants villous to glabrous

2. Pedicel longer than the bracteole

3. At least some of the leaves with cordate bases; leaf vein anastomosis conspicuous (rarely conspicuous to poor, as in S. kurdica and S. amplexicaulis); filament glands of round type; upper corolla lobes usually of B-type, rarely of C-type; pedicel 6.5-20 mm (rarely 3.5-5 mm, S. amplexicaulis)

4. Stem winged, especially below the leaf bases; bracteoles glabrous; staminode transversely oblong with cuneate to subcordate base, usually slightly retuse with two divaricate lobes, rarely roundish ............................................. 6. umbrosa

4a. Stem not winged, at the most angled, bracteoles sparingly to densely glandular; other characters various

5. Median leaves large, 5-9 long; apex acuminate; margin crenate or serrate; floral leaves long-acuminate ...... 17. chlorantha

5a. Median leaves smaller than 5, acute to obtuse, margin various

6. Calyx segments glandular to densely villous

7. Inflorescence foliate; calyx segments densely villous with a narrow white scarious margin; capsules broadly ovate, slightly longer than the calyx; plants villous .................................................. 10. pegaea
7. Inflorescence subfoliate to aphyllous; calyx segments glandular but not villous, scarious margin broad, brown; capsules ovate, twice as long as calyx; plants not villous ................................ 13. scopolii

6. Calyx segments neither glandular nor villous

8. 1-2 lower pairs of leaves subsessile, all upper sessile, margin crenate to serrate

9. Inflorescence aphyllous, bracts 0.4-0.6 cm long; cymes alternate; pedicel 3-5 mm long ................................................................. 7. amplexicaulis

9. Inflorescence foliate, floral leaves 5-9 cm; cymes axillary, opposite; pedicel 7-24 mm ......................... 8. kurdica

8. Leaves not sessile, lower long-, upper short-petiolate

10. Pedicel long, 18-20 mm, slender, capillary even after fruiting; cymes divaricate; inflorescence foliate .............. 12. capillaris

10. Pedicel thick, woody, usually less than 17 mm; cymes not divaricate; inflorescence subfoliate to aphyllous

11. Cymes subsessile, pseudoverticillate; leaves often lobed at the base; corolla red in colour ...................... 14. macrophylla

11. Cymes long peduncled, opposite to alternate; leaves undivided; corolla either not red or only reddish-purple

12. Median leaves serrate; corolla tube or at least the lower lip yellow; calyx segments very narrowly scarious-margined; leaves glabrous on both sides; plants perennating by short swollen suckers .................................................. 16. nodosa

12. Median leaves doubly crenate to dentate; neither corolla tube nor the upper lip yellow; calyx segments broadly scarious-margined; leaves villous to glandular especially on the lower side; plant without swollen suckers .............. 13. scopolii
3. Leaf bases cuneate to truncate (rarely cordate, in S. catarifolia & S. davisii, but then the leaves usually very thick); leaf vein anastomosis inconspicuous; filament glands of oblong type; upper corolla lobes of C-type; pedicel 1-5 mm, rarely 7-9 mm
(S. davisii & S. rimarum)

13. Staminode narrowly oblong; plants with a basal rosette of leaves

14. Plants 5-11 cm long; basal leaves spathulate to oblong, not red; cymes 1-flowered by reduction, 1 cm long; calyx segments glandular, scarious margin 0.1 mm wide .......... 27. pumilio

14. Plants 18-68 cm, basal leaves ovate to rhomboidal, red; cymes 10-4-flowered, 4-14 cm long; calyx segments glabrous, scarious margin 1-1.5 mm wide ......................... 18. davisii

13. Staminode ovate, obovate to reniform; plants without a basal rosette of leaves

15. Staminode reniform; calyx segments glandular

16. The whole plant (including the calyx segments) densely glandular ............................................... 20. catarifolia

16. Plants glabrous to nearly glabrous; calyx segments with a few glands or none ............... 22. rimarum

15. Staminode ovate, acute to suborbicular; calyx segments glabrous ............................................... 25. rupestris

2. Pedicels as long as, or shorter than the bracteole

17. At least some of the leaves with deeply cordate bases, leaf vein anastomosis conspicuous; filament glands of round type; plants villous ............................................... 11. luridiflora
17. Leaf bases cuneate to truncate (rarely cordate in S. catarifolia, but then the plants not villous); leaf vein anastomosis inconspicuous; filament glands of oblong type; plants not villous, densely glandular-puberulent to glabrous

18. Calyx segments glandular

19. Staminode reniform

20. The whole plant (including the calyx segments) densely glandular ........................................ 20. catarifolia

20. Plants glabrous to nearly glabrous; calyx segments with a few glands ........................................ 22. rimarum

19. Staminode linear, suborbicular or spade-shaped

21. Staminode linear, leaves oblong-lanceolate, entire-margined ........................................ 29. hyssopifolia

21. Staminode suborbicular or spade-shaped, leaves oblong-lanceolate to narrowly oblong; margin dentate ........................................ 28. nachitschevanica

19. Calyx segments glabrous

22. Staminode reniform

23. Lower leaves rosulate, small, roundly ovate; margin roundly incised to crenate; lower and median leaves with a white border ........................................ 26. marginata

23. Lower leaves not rosulate; leaf margin without a white border

24. Leaves oblong, margin obtusely to sharply dentate ........................................ 19. pulverulenta

24. Leaves ovate, margin simply to doubly dentate, rarely serrate ........................................ 22. rimarum
22. Staminode not reniform
   25. Leaves oblong-lanceolate to narrowly oblong, dentate; base
cuneate; staminode suborbicular or spade-shaped; plants
biennial or perennial ........................................ 28. nachitschevanica
   25. Leaves ovate, rarely lanceolate, simply to doubly dentate;
base truncate to cuneate; staminode ovate, acute, rarely
obovate, plants perennial ..................................... 25. rupestris

Group 6

1. Corolla lobes subequal; staminode large, reniform with a dorsal
   canal; (leaves bipinnatisect, segments narrow; calyx segments
   obovate to round) ............................................... 5. subaequiloba

1. Corolla lobes unequal; staminode without a dorsal canal

2. Lower leaves pinnatifid; lamina with or without 1-2 small,
   free, or nearly free basal segments
   3. Calyx segments narrowly oblong, scarious margin 0.2 mm wide;
pedicel slender, capillary, purplish-green; petiole and leaf
   veins of the median leaves purple; staminode narrowly
   oblong .......................................................... 31. amana
   3. Calyx segments not narrowly oblong, scarious margin wider than 0.2
   mm; other characters various

4. Calyx segments glandular
   5. Staminode oblong; median leaves oblong-lanceolate
      6. Upper corolla lobes with a white or yellow border;
         median leaves entire-margined, at the most with 2-5 teeth;
pedicel 2-3 mm long .............................................. 29. hyasopifolia
      6. Upper corolla lobes without a white or yellow border; median
         leaves with a deep serrate margin; pedicel 4-5 mm long

................................................................. 24. serratifolia
5. Characters not as above

7. Plants (including calyx segments) densely glandular

.............................................................. 20. *catariifolia*

7. Plants glabrous to nearly glabrous; calyx segments
   sparsely glandular ...................................... 22. *rimarum*

4. Calyx segments glabrous

8. Scarious margin of calyx segments + plicate (thrown into folds);
   nearly as wide as the herbaceous portion; epalish-brown pinkish,
   very rarely white, calyx segments orbicular to reniform, petiole
   and veins usually purple ................................. 30. *olympica*

8. Scarious margin of calyx segments not plicate, less than
   2/3rd as wide as the herbaceous portion

9. Lamina oblong-lanceolate, deeply pinnatifid with 1-2 free or
   nearly free basal segments ...................................... 23. *bitlisica*

9. Lamina ovate, pinnatifid, without any free or nearly free
   basal segments

10. Staminode ovate, acute to obovate .......................... 25. *rupestris*

10. Staminode reniform

11. Cymes 1-flowered; inflorescence subfoli ate, at the
    most 8-flowered .............................................. 21. *uniflora*

11. Cymes 7-2-flowered, inflorescence aphyllous, many
    flowered ..................................................... 22. *rimarum*

2. Leaves 1-3-pinnatisect

12. Pedicel always longer than the bracteole

13. Pedicel 14-20 mm, twice as long as the bracteole

14. Leaves pinnatisect to pinnate, cymes widely divaricate;
   scarious margin of the calyx segments 0.9 mm
   wide .............................................................. 35. *trichopoda*
14. Leaves bipinnate; cymes not divaricate; scarious margin of
the calyx segments 1.5-2 mm wide .......................... 39. mersinensis
13. Pedicel less than 12 mm, less than twice as long as the bracteoles
15. Calyx segments glandular; cymes divaricate .......... 35. trichopoda
15. Calyx segments glabrous; cymes not divaricate
16. Staminode oblong to ovate ................................. 34. variegata
16. Staminode spade-shaped, obovate, obtriangular to reniform
17. Plants densely glandular-puberulent throughout ... 34. variegata
17. Plants glabrous, sparsely glandular in the floral region
18. Leaves pinnatisect, lateral branches arranged in a
candelabrum manner ........................................ 37. candelabrum
18. Leaves bi- to tripinnatisect, lateral branches not
arranged in a candelabrum manner
19. Staminode roundly obovate ............................. 36. tagetifolia
19. Staminode reniform
20. Scarious margin of the calyx segments 0.3-0.5 mm
wide; leaves tripinnatifid to tripinnatisect; peduncles
and pedicels purplish-black ...................... 40. myriophylla
20. Scarious margin 1.5-2 mm wide; leaves bipinnatifid
to bipinnate; ultimate segments crenate-mucronate;
peduncles and pedicels green .................. 39. mersinensis
12. Pedicels as long as, or shorter than the bracteoles
21. Pedicels as long as, or less than twice as short as the bracteole
22. Corolla bright yellow, upper lip purple on the inner side;
stamens long exserted ...................................... 48. gypsecola
22. Corolla not bright yellow; stamens included, very rarely
slightly exserted
23. Leaves tripinnatisect; staminode reniform, transversely as wide as the base of the upper lip ................. 38. lucida

23. Leaves 1-2 pinnatisect; staminode spade-shape, roundly obovate to ± reniform, not as wide as the base of the upper lip .................. 34. variegata

21. Pedicel 2 - several times shorter than the bracteole

24. Staminode orbicular, nearly as large as the upper corolla lip, yellow, margin + crenate

25. Leaf pinnatisect (rarely bipinnatisect then the segments extremely narrow, 4.5-12 x 0.8-1.2 mm), segments narrow to broad; stems slender and more numerous; inflorescence usually more delicate; perennial .................. 44. striata

25. Leaf bipinnatifid to bipinnatisect, primary segments median to broad; stem thick, stout usually hollow; biennial or perennial .................. 45. xanthoglossa

24. Staminode not as above

26. Staminode oblong to linear

27. Staminode oblong, base cordate; monochasial branches of cyme very long (up to 12 cm), usually each bearing 10-many flowers .................. 46. peyronii

27. Staminode not as above; monochasial branches shorter, usually with 3-10 flowers

28. Upper corolla lobes without a yellow or white border; anthers purple; calyx segments sparingly glandular; leaves pale-green .................. 47. zuvandica
28. Upper corolla lobes with a yellow or white border (if without a yellow or white border, then calyx segments not glandular); anthers not purple; calyx segments glabrous; leaves green

29. Stems slender; lower leaves pinnatisect with 1-3 pairs of primary segments, the terminal segments longest (3-20 x 0.6-1.5 mm), entire-margined; upper median leaves narrowly oblong, 60 x 2 mm, entire-margined .................. 43. thesioides

29. Stems stout; lower leaves bipinnatifid to bipinnatisect, primary segments much broader; upper median leaves pinnatisect .................................................. 42. canina

26. Staminode reniform .................................................. 38. lucida
XI. DESCRIPTION OF THE

TURKISH SPECIES

   **Syn:** *S. vernalis* M. Bieb., *Fl. Taur-Cauc.* 2: 76 (1808), non Linn. (1753);

   *S. minim*a Benth. in D.C. *Prodr.* 10: 303 (1846), non M. Bieb. (1808);

   *S. congesta* Stev. in *Bull. Soc. Nat. Mosc.* 30 (1): 348 (1857);

   *S. chrysanth* Jaub. et Spach var. *calycina* Boiss., *Fl. Cr.* 4: 390 (1879);

   *S. lunariaefolia* Boiss. et Bal. in *Boiss.* *Fl. Cr.* 4: 390 (1879);


   *ross.* (1887);


Perennial (or biennial?), 10-61 cm, nearly glabrous to densely villous, branched at the base. Stem ± reddish, subangular, ascending or adpressed. Lower leaves long-petiolate (petiole 1.5-12 cm), the upper shortly petiolate. Lamina broadly ovate to reniform, 6.8 x 5.8 cm or 2-6 x 3-7.5 cm; apex obtuse to round with apical tooth crenate to acuminate; base slightly to deeply cordate; margin crenate-mucronate, bicrenate, crenate-dentate, or simply to doubly dentate. Floral leaves subsessile to sessile, broadly ovate, base cordate to cuneate, apex acute to acuminate; rarely reniform apiculate. Lower cymes long-peduncled (peduncle 1.6-2.4 cm), distant, 10-5-flowered; the upper subsessile, shortly distant to condensed, corymbose; pedicel 4-6 mm, glandular; bracteoles 6.5-12 mm, narrowly oblong, lanceolate to linear-lanceolate, margin toothed to entire, apex acute to acuminate, densely villous. Calyx segments oblong-linear to lanceolate, 4.5-8 x 1.2-2 mm, glandular on both sides, without a scarious margin. Corolla yellow, urceolate, 5-6.8 mm; stamens long-exserted, filament glands of both type; staminode absent. Capsules narrowly to broadly ovate, 5-10 x 5-6 mm, apiculate to beaked, glandular. *Fl. 4-8.*
Habitat: Sheltered cliffs, shady banks, crevices, mixed forests on metamorphic lime- and non-limestone rocks, 1800-3300 m, rarely 10 m.

Type: in Armeniae rupibus, Aucher-Eloy 5103 (P).

Distribution in Turkey: N. & E. Anatolia.

A8 Rize: Rize, 10 m, Stainton 8153!

A9 Coruh (Artvin): Tiryak Da. above Murgul, 1800 m, Davis 29923!

A9 Kars: Ziyaret Da. (Yalnizcan-Dagli) above Yalnizcan, 2500 m, Davis 30331!

B9 Agri: d. Sulucem (Musun), S. end of Balik G., 2300 m, Davis 47005!

B9 Van: Erek Da., 2338 m, Davis 22902!

B9 Bitlis/Van: Mt. 10 km SE of Pelli, 2896 m, Davis 22569!

External Distribution: Caucasus (rare in the West).

Related to S. vernalis from which it differs in its longer exserted stamens, acute calyx segments, corymbose cymes and chromosome number (2n = 36, in S. chrysantha; 2n = 40, in S. vernalis). Not all the specimens of S. vernalis have glabrous capsules, although they are less hairy as compared with those of S. chrysantha, so on the present evidence I am unable to agree with Heywood in maintaining glabrousity of capsules as a reliable diagnostic character between the two taxa. I have not seen Boissier's S. chrysantha ver. calycina, but all the three diagnostic characters suggested by him in Fl. Or. 4: 390 (namely, lower longer pedunculate, distant cymes, enlarged calyx lobes, and the longer tubular unceolate corolla) are indistinct both on the Turkish and Caucasian specimens. S. lunariifolia was distinguished by Boissier from S. chrysantha only in being nearly glabrous. Additional material breaks down this distinction, so there seems no justification for maintaining S. lunariifolia as a separate species.
2. S. kotschyana Benth. in D.C. Prodr. 10: 303 (1846).

Syn: S. byzantina Benth. in D.C. Prodr. 10: 303 (1846);
S. viscosa Boiss., Fl. Or. 4: 391 (1879);
S. bornmülleri Freyn. et Sint. in Freyn Öst. Bot. Zeitschr. 13: 348 (1892);

Biennial (Perennial?), 9-52 cm, sparingly to densely villous, branched at the base. Stem greenish-red to black, tortuous, fistular, prostrate, ascending to erect. Lower leaves long (petiole 4.5-14 cm), the upper short-petiolate; lamina 2.3-6.5 x 1.4-7 cm, + round, reniform, broadly ovate, or triangular to rhomboidal; base deeply cordate to cuneate; apex round, broadly obtuse to ± acute; margin crenate, bicrenate or simply to doubly dentate. Floral leaves broadly ovate, triangular to rhomboidal; apex obtuse to acute. Inflorescence foliate, lax. Cymes 5-3-flowered; peduncle 1-6 cm, slender to woody, greenish-red to black; pedicel 5-20 mm, straight to tortuous, black reddish to green, slender to woody; lower bracteoles triangular to rhomboidal, toothed, upper lanceolate to linear, entire-margined, densely glandular, 2.5-11 mm. Calyx segments oblong, 2.7-5 x 1.5-2 mm; apex acute, rarely broadly ovate, outer surface glabrous, inner densely beset with sessile glands, or the outer surface hairy with the inner surface glabrous to hairy, without a scarious margin. Corolla 5-9 mm, red, laterals and the median lobes concolorous or white to yellow; stamens exerted. Filament glands of round type; staminode absent. Capsule glandular, globular, 4-4.5 x 3-3.4 mm.

Fl. 4-8.

Habitat: Sheltered cliffs, crevices, rock ledges in forest, lime-, and non-limestone rocks, also in ruins and waste places, 690-2400 m.

Type: Turkey 057: in monte Tauro (Kotschy 376, K!).
Distribution in Turkey: N.C. and S. Anatolia.

A5 Amaaya: Logman, 800-900 m, 14. iv. 1889, Bornmüller 594.
A6 Sivas: Yeildisdagh, 1300 m, 9. vi. 1890, Bornmüller 1653.
A7 Trabzon: distr. Macka, 1000 m, Stainton 8150.
A8 Rize: Ikizdere, 600 m, Davis 20834A.
A9 Gümlüane: Mounte Almuska, Bayburt, 1862, E. Bourgeau.

B6 Sivas/Ak Da., 2200 m, Siehe 132.
B6 Kayseri: 15 miles south of Pinarbasi, 1800-1900 m, Coode & Jones 1434.
C5 Nigde/Kayseri/Adana: viii. 1962, Harald Urdl.
C5 Icel: Guaguta Thal, 1895, Siehe 227.
C5 Adana: Bürücek, 1219 m, E.K. Balls 260.
C5 Konya/Icel/Nigde: at foot of Karli Boghas Valley, 400-600 m, 3 July 1853.

Kotschy 43.

External Distribution: Georgia.

Allied to S. vernalis L. but differing from it in its red-coloured flowers, calyx segments which are glabrous on the outer surface, densely glandular capsules (capsules-glandular to nearly glabrous capsules in S. vernalis) and smaller stature.

J. Freyn distinguished S. bornmüllerii from S. kotschyana by its prostrate or ascending habit, smaller leaves, and flowers, pedicels being twisted only at the base, concolorous corolla lobes etc. The additional material has shown that all the above diagnostic characters given by Freyn are no longer reliable. Heywood distinguished S. ballsii from S. kotschyana on the basis of the following characters: smaller stature, much larger flowers with soft flushed apricot colour, smaller round or cuneate leaves, frequently glandular-pubescent calyx segments and occasionally glabrescent capsules; all these characters overlap. S. ballsii and S. bornmüllerii must therefore be treated as synonyms of S. kotschyana.


Perennial, 50-175 cm, sparingly to densely villous, branched at the base. Stem ascending or erect, green to pinkish-green, subangular to terete, branched. Lower leaves long-petiolate (petiole 5-7 cm); lamina 4.5-15 x 2.5-5 cm, broadly ovate with deep cordate to truncate base; tip obtuse to roundish; margin crenate-mucronate, or bicrenate to doubly dentate; upper shortly petiolate, broadly ovate. Floral leaves ovate to triangular, the uppermost + rhomboidal; base subcordate to cuneate; apex acute to acuminate; margin bicrenate to sharply dentate. Inflorescence foliaceous; cymes distant, 9-5-flowered; peduncle 2.5-5 cm; pedicel 5-12 mm, glandular. Bracteoles, 2.5-8 mm, lanceolate, rarely linear, glandular; tip acute, margin entire. Calyx segments triangular to broadly ovate with acute tip, or longish-acute, 2-3.5 x 1.5-2 mm, glabrous, very rarely slightly pubescent. Corolla pale-green-red, 5-8 mm long, stamens long-exserted; staminode absent. Capsules broadly ovate to roundish, mucronate, 5-6 x 5 mm, glabrous. Fl. 6-8.

Habitat: Ledges of shady limestone rocks, cliffs, summits and ruins and waste places, 600-1850 m.

Syntypes: *Turkey Chl* Anatolia: in Speluncis obscuris montis Gheidagh (Geyik Da.) Isauriae, 1676 m, Heldreich; Chl Konya, in ruinis veteris ecclesiae ad cacumine montis Karadagh Lycaoniae, 1845 Heldreich! Chl Nigde in Monte Bereket Lycaiae, Pestalozza.

Distribution in Turkey: NW., W., C., & S. Anatolia.

A2 Istanbul: sine loco, Lady Lister!

B3 Ankara: Mihalićkik to Sariyaz baraji, 1250 m, Davis 37222!

B3 Konya: Sultandagh, 1850 m, 28.6.1899, Bornmüller 5365!

B4 Ankara: (Galatia): Kibris gorge near Kayas, Davis 13134!
C1: Izmir, distr. Odemis: Boz Da., 2000 m, Davis 18196!

C2: Antalya: distr. Elmali (Lycia), mount Elmulu, 26.5.1860, Bourgeau 176!

C3: Antalya (Pisidia): Bozburun Da. above Tuslu Çukur Y., foot of north cliff, Davis 15630!

C4: Içel: Kirobaşi-Silifke, 17 km to Kirobaşi, 15 6 1950, 1350 m, Huber-Morath 10312!

C5: Içel (Cilicia Trachea): River Lamas, 600 m, June 1909, Siehe 119!

Endemic. The closest relative is *S. kotschyana* Benth. from which it can be easily distinguished by its glabrous capsules and calyx segments. Heywood related *S. praeterita* to *S. vernalis* from which he distinguished it by its ovate-lanceolate acute and glabrous calyx segments, stipitate-glandular filaments and smaller capsules. I have seen the type material of *S. praeterita* and consider it to be a synonym of *S. cryptophila*.

A specimen from C2 Muğla; Gıdev Göl, 1760 m, Davis 13754, differs in having the calyx segments with a very narrow scarious margin, otherwise it resembles *S. cryptophila*. Heywood recognised this as a distinct "forma" of *S. cryptophila* (fide Notes R.B.G. 21: 77(1952)).
4. **S. orientalis** L., Sp. Pl. 620 (1753)


Perennial, 57-120 cm, stem erect, solid, 8-angled, glabrous in the lower part, minutely glandular in upper floral region, simple or branched. Leaves whorled, sparingly glandular, petiole 1.5-2.5 cm, lamina 3-10 cm, the upper simple, the lower pinnatifid to imparipinnate with a large terminal lobe; margin sharply serrate, base cuneate and tip acuminate. Floral leaves narrowly linear, acuminate, entire-margined, + whorled. Inflorescence aphyllous, cymes usually whorled, distant, ascending 9-5-flowered. Peduncle 2-3 cm, delicate to woody. Bracteoles 2.5-6.5, linear, acuminate, nearly glabrous, upper lanceolate, acute, gradually diminishing in size. Pedicel 8-12.5 mm, glandular. Calyx segments ovate-orbicular, 1.5-2.5 x 1.5-2.5 mm, glabrous, scarious margin white, 0.3-0.5 mm wide. Corolla green with the lower portion tinged with brown, 5-6 mm long, lobes subequal; stamens exserted, filament glands of round type; staminode absent. Capsules ovate, 6-8 x 4-4 mm; apiculate, glabrous, 3 times longer than the calyx. Fil. 6-8.

Habitat: Rocky volcanic, igneous and meadow slopes and water meadows, 1180-2400 m.

Described from "Orient", Tournefort, Linn. 773/11!

Distribution in Turkey: N.E. & E. Anatolia

A7 Gümüşane: Gümüşane, 13. 6. 1894, Sintenis, 5842!

A8 Erzurum: distr. Tortum, Bachufer 7 km South west of Tortum, 1800 m, 16.6.1953, Huber-Morath 15549!

A9 Kars: Yalnızçan Da. between Yalnızçan & Ardanuç, 2250 m, Davis 29682!

B7 Elazığ: Tigris ruins 5-7 km below Gölcük-See, 1180-1210 m, 2.6.1951, Huber-Morath 11583!

B8 Erzurum: 29 km from Hinis to Pasinler, Davis 46420!

B9 Ağrı: E. side of Tahir Da. pass, 19 km from Elegirt to Horasan, 2400 m, Davis 47166!

A very distinct species. The closest relative is S. verticillata from C. Asia (Pamir-Alai) which differs from it in its undivided and entire-margin leaves.
5. *S. subaequiloba* Lall, sp. nov.

Perennial, plant 30 cm, several stemmed, glabrous. Stem erect to ascending, simple or slightly branched, subangular, purplish at the base, green in the upper region. Leaves small 3.5 cm, lower shortly petiolate, upper subsessile, gradually becoming sessile; bipinnatisect, primary segments or pinnae 1.4 cm long. Inflorescence aphyllous, bracts narrowly oblong 4.5-0.5 mm, glabrous; cymes alternate, 3-2-flowered; peduncle 8-9 mm, sparingly glandular; pedicel 4-5.5 mm, glandular; bracteoles oblong-linear, 2 mm long, glabrous. Calyx segments obovate to round, 2.5 x 3 mm, glabrous, scarious margin white, narrow, 0.5 mm. Corolla 5 x 5 mm, tube maroon, lobes pale-greenish, subequal; stamens shortly exserted, filament glands of oblong type; staminode reniform, with a dorsal canal. Capsules unknown.

Fl. 7-9.

**Habitat:** Rocky limestone slopes, 2800 m.

**Type:** *Turkey B7 Tunca*: Munzur dag above Ovacik, 2800 m. Rocky limestone slopes. Perennial; flowers pale greenish-maroon; stamens strongly reflexed. 17.7.1957, Davis 31231 (Holo: E. iso. K).

**Distribution in Turkey:** C. Anatolia.

Endemic. Approaching the S. Anatolian *S. myriophylla* Boiss. et Heldr. in general facies, but distinguished from it by the subequal corolla lobes, and the staminode with a dorsal canal.

The new species is unique in providing a connecting link between the two sections, approaching Sect. *Geramanthe* in its equal corolla lobes and Sect. *Scrophularia* in having a large reniform staminode, but standing on its own because of its unique staminode which is provided with a dorsal canal - which probably stores nectar. The species, although intermediate between the two sections in the floral morphology, is placed in Sect. *Scrophularia* on account of its general facies, where it is given the status of a new subsection.
Davis a Hedge  (D. 31239).
Scrophularia schlepicha Lett et sp. nov.

Turkey. Prov. Zonguldak, Munzur valley above
Oradik, 1200m. Rocky limestone slopes.
Perennial. Flowers pale greenish maroon.

Plate 10.14

  Syn: S. alata Gilib., Fl. Lithuan. 2: 127 (1781), nomen illegit. (vide
    Hylander in Uppsala Univ. Årskr. 7: 280, 1945);
    S. auriculata Ass. Syn. Stirp. Arag. 81 (1779), non Linn. (1753);
    S. aquatica Koch., Syn. Fl. Germ. ed 1: 515 (1837), non Linn. (1753);
    S. betonicfolia Viv., Fl. Cors. 10 (1824), non Linn. (1767);
    S. rivularis Moris, Stirp. Sard. Elench. App. 8 (1827-29);
    S. cinerea Dum., Not. Scroph. 11 (1834);
    S. balbisii Koch., Syn. Fl. Germ. ed 1: 515 (1837);
    S. ehrhartii Stevens in Ann. Nat. Hist. ser. 15: 3 (1840);
    S. neesii Wirtg. in Verh. Nat. Rheinl. 1: 29 (1844);
    S. samaritana Boiss. et Heldr. ex Boiss., Fl. Or. 4: 400 (1879);
    S. pisidica Boiss. et Heldr. in Boiss., Fl. Or. 4: 400 (1879);
    S. robusta Pennell., Scroph. W. Himal. 46 (1943);
    S. epicalycina Heywood in Notes R.E.G. Edinb. 21: 78 (1952);

  Perennial, 54-135 cm, glabrous. Stem erect, simple, or branched, narrowly or
  broadly winged. Petiole 3.5-11 cm; lamina 3.7-14 x 2-8 cm, ovate, oblong or
  elliptical, base cordate to round, margin dentate, serrate to serrulate, crenate
  to crenulate, rarely bicrenate; apex obtuse to acute. Floral leaves with
  round to cuneate base, and dentate to serrate or serrulate margin, gradually
  becoming linear, acuminate, and entire-margined in the upper region. Peduncle
  0.3-3.5 mm, cymes 3-25-flowered, lower glabrous upper sparingly glandular; pedicel
  4-25 mm, sparingly glandular, rarely eglandular; bracteoles triangular to linear,
  acuminate, glabrous 3-8 mm. Calyx segments 2.5-3 x 1.8-2.5 mm, ovate to broadly
  ovate, or almost orbicular, scarious margin broad, white to brown. Corolla
pale greenish-brown or greenish purple, 3-6.7 mm; stamens included to slightly exserted, filament glands of round type; staminode transversely oblong, reniform, non-lobed to bilobed, rarely transversely obcordate to roundish. Capsules broadly ovate to globular, 3-6 x 3 mm, twice as long as calyx. Fl. 4-7.

Habitat: Wet granite slopes and stream banks in forests, 30-1950 m.

Type: in Umbrosis Luxemburgii.

Distribution in Turkey: Widespread.

A3 Bolu: Düz to Akoakoca, 320 m, Davis 37491!

A3 Adapazari: Arifiye, 30 m, Davis 36270!

A5 Sinop: distr. Ayancık, Çangal Da., 1050-1100 m, 1.7.1955, Huber-Morath 155544!

A6 Tokat: Niksar-Karakus, 1100 m, Davis 24933!

A7 Giresun: distr. Sebinkarahisar, 1300-1330 m, 1.7.1955, Huber-Morath 13991!

A8 Gümüşane: Gümüşane, 9.8.1894, Sintenis 7232!

A9 Gümüşane: Gümüşane, 27.7.1862, E. Bourgeau 186!

A8 Čoruh (Artvin): Savval Tepe above Murgul, 1700 m, Davis 32333!

B1 İzmir: Yamanlar Da., 9.6.1966, Reino Alava 5100!

B2 Denizli-(Caria); Boz Da., 1372, Davis 13356!

B7 Tunceli: Munsur Da., in Aksu Da., above Ovacik, 1500 m, Davis 31380!

B9 Van: near Şatak, Davis 23190!

C2 Muğla: distr. Kemer, 1100 m, 9.6.1933, Huber-Morath 5587!


C6 Hatay: Iskenderum-Antakya, 150 m, Davis 27273!

C8 Mardin: Mardin, 15.6.1888, Sintenis 1079!

C10 Hakkari: Gevar Ovasi between Yusksekova and Varegöz, 1950 m, Davis 45529!

External Distribution: Throughout Europe, Crimea, S. & C. Russia, Caucasus, Syria, Lebanon, N. Iran, Afghanistan, W. Pakistan and Siberia.
Related to *S. elatior* from which it differs in its non-scarious-margined calyx segments and longer exserted stamens. Also allied to *S. macrophylla* from which it can be distinguished by its winged stem and the corolla colour (red in *S. macrophylla*).

Heywood distinguished *S. epicalycina* from *S. umbrosa* by its transversely elongate, entire-margined staminode, slightly crenate-serrate leaves, glabrous pedicels, subexserted stamens and the epicalycine structure. About the doubtful nature of epicalycine structure Heywood remarks as follows: 'The exact nature of the epicalycine structure is not known: they can be seen with the naked eye and are not present in all flowers; they are a quarter to a third as long as the calyx and appear to be adnate - at least they are not detachable'.

I have failed to detect any epicalycine structure on the type material, and as it is not "present in all flowers" it appears to be some sort of artifact. Of all the above distinguished characters the glabrous pedicels is the only reliable diagnostic, and because of its overall similarity with *S. umbrosa* I have treated it as a synonym of the latter.

Heywood separated *S. umbrosoides* from *S. umbrosa* by its longer pedicels, subsagittate leaf base and the broadly ovate-orbicular staminode. The 'subsagittate base' - 'The development of the base of the lamina is a distinctive feature: the proximal teeth are markedly reflexed, giving a winged appearance almost suggesting a subsagittate base' - is a common feature, especially of gatherings from Mardin and Amanus; the pedicel length shows integration within the species, and the staminode varies from round to reniform-emarginate in the type material (Fig. 14; 20422). I therefore see little justification for keeping *S. umbrosoides* as a separate species.

The species is variable regarding leaf and staminode shape. Pennell's *S. robusta* (from Afghanistan & W. Pakistan) shows a good match with specimens of
S. umbrosa from Lebanon, Syria, Turkey, Iran, Europe and the Caucasus, and is therefore treated as a synonym of the latter.

**Syn:** *S. hadjariana* Parsa in *Kew Bull.* 217 (1948)

Perennial, 26-43 cm, glandular-puberulent throughout, several-stemmed. Stem simple, subquadrangular, erect, purplish-green. Leaves sessile, 3.5-6 x 2.8-3 cm, ovate; apex acute; margin sharply dentate to serrate, rarely serrulate; base cordate to round. Inflorescence aphyllous, bracts 4-6 mm long, narrowly triangular. Cymes alternate, solitary, 5-1-flowered; peduncle 5.5-8 mm; pedicel 3-5 mm, glandular; bracteoles 2.5-4.5 mm, glandular. Calyx segments oblong to orbicular, 2.3-3.5 x 1.5-2.5 mm, glabrous to sparingly glandular, scarious-margin white, 0.3-0.6 mm wide. Corolla green to pale-green, 6.5-8.5 mm long; stamens included, filament glands of round type; staminode oblong-spathulate, attached dorsally to the upper lip along its entire length. Capsules narrowly ovate, acute to beaked, 9-11 x 4-6 mm, 4 times longer than calyx. Fl. 5-8.

**Habitat:** Scree slopes, stream sides, moist sheltered crevices, 3040-3305 m.

**Type:** *F. Iran*: Ad Savalan in Ghilan (*Aucher*, n. 5060, K!)

**Distribution in Turkey:** E. Anatolia.

B9 Hakkari: Kara Da. 3305 m, Davis 24502!

C9 Bitlis: Pelli Da. above Pelli, 3048 m, Davis 22510!

**External Distribution:** N. Iraq, N. Iran & Caucasus.

Distinguished from all other species of the genus by having the staminode adnate to the corolla throughout its length.

Parsa related *S. hadjariana* to *S. pulverulenta*, but examination of the type material has shown the presence of an obovate staminode which is attached to the corolla along its entire length. As the specimen perfectly matches the specimens of *S. amplexicaulis*, I have treated *S. hadjariana* as a synonym of the latter.
Biennial or perennial, plant 35-50 cm, completely glabrous to densely glandular-puberulent; stem erect or ascending, terete to subangular, simple, rarely branched. Petiole of lower leaves 0.6-1.4 cm, median and upper leaves usually subsessile to sessile; lamina 4.3-9.2 x 2.2-6.3 cm, ovate to narrowly ovate; base cordate to cuneate; apex acute to acuminate; margin crenate-mucronate to serrulate. Inflorescence foliate; cymes 20-4-flowered; peduncle 1.4-3.5 cm, glabrous to glandular-pubescent; pedicel 7-24 mm, 4-6 times longer than the bracteoles, glabrous to glandular; bracteoles, 1.5-5 mm, narrowly linear, glabrous to glandular, upper subulate, gradually diminishing in size. Calyx segments, 2-2.5 x 1.5 mm, ovate to oblong, glabrous; scarious margin, narrow, white. Corolla greenish-red to brown, 6-7 cm long; upper lobes B- and C-type; stamens included, filament glands round-headed; staminode ovate to subround. Capsule 4.2-5 x 3-4 mm, globular, shortly apiculate, glabrous 2-3 times longer than calyx. Fl. 6-8.

**Habitat:** Wet, shady rocks and crevices, 1200-3749 m

**Syntypes:** [Iraqian Kurdistan]: Sulaimani District; Pir-i-Mukurun Dagh, rocks, near the snow, 19.9.1933, Big. Duvedani (HUJI); there Mergapan, rocks, 1200-1300 m, 19.9.1933, Zohary, Amurad (HUJI).

**Distribution in Turkey:** S.E. Anatolia.

G9 Hakkari: Cilo Da. in Diz deresi, 1764 m, Davis 24008!

C10 Hakkari: Cilo Da., 3749 m, Davis 24191!

**External Distribution:** Iraqi Kurdistan.

Related to *S. divaricata* Ledeb. from which it differs in its subsessile leaves, which are not "acute lobatis", and the globular capsules. Also distantly allied to *S. ampllexicaulis* Benth. from which it is distinguished by its inflorescence, axillary cymes, longer pedicels and the staminode being free in the upper part.

Syn: *S. geminiflora* Lam., Fl. Fr. 2: 336 (1776);
*S. sexangularis* Moench, Meth. 445 (1794);
*S. minor* Savi, Fl. Pis. 2: 31 (1798);
*S. paniculata* Seenus, Reise Istrien: 67 (1805);
*S. meridionalis* Presl., Fl. Sic. 1: 35 (1826);

Annual, Plant 20-100 cm, glabrous to sparingly glandular, simple to profusely branched, erect, angular, purplish in the lower part. Petiole 1.5-5 cm, lamina 3.1-8.2 x 2.4-5.5 cm, ovate to broadly ovate, base cordate to round; apex acute to slightly obtuse; margin crenate to sharply dentate, rarely biorenate.

Inflorescence foliate; lower floral leaves shortly petiolate, opposite to alternate, broadly ovate to ovate, base cordate to subround; upper usually triangular-ovate, apex acute, margin dentate. Peduncle 0.6-4 cm; cymes 8-2-flowered; pedicel 6.5-18 mm, sparingly glandular; bracteoles 2-3 mm, sparingly glandular, shorter than the pedicel. Calyx segments triangular, acute, 2.3-3 x 0.6-1.8 cm, glabrous, without a scarious margin. Corolla red, 5-6.5 mm; stamens included; filament glands of round type; staminode roundly ovate to suborbicular, red. Capsules broadly ovate, 5 x 4 mm, mucronate, twice as long as calyx. Fl. 3-6.

Habitat: Rocky limestone slopes, roadsides, waste places and stream banks, 0-250 m.

Described from Italy, Pisa (Herb. Cliff., Herb. Linn. 773/19).

Distribution in Turkey: NW, W & S. Anatolia.

AJ-4, Bolu (Bithynia): anon.

E1 Smyrne, 26 4 1854, Balansa 341.

C1 Izmir: North foot of Samsun Da., west of Guzel-Gamli, 0-50 m, Davis 41713.

C2 Mugla: Marmaris to Gökova, 50-100 m, Davis 41091.

C3 Antalya: Antalya, 23.5.1950, Huber-Morath 10314.

Cl. Iğel: Anamur, 1872, Peronin.

Islands: Lesvos, Tal Andria, M. Malathra beside monastery Limonos (Cand.); Ikaria, Hag. Kirykos, K.H. Rechinger fil. 4376; Samon, between Vathy and Cape Kotsikas, K.H. Rechinger fil. 34,32; Kalimnos, Forsyth Major 23, 743; Simi, K.H. Rechinger fil. (obs.); Rodhos, Salakos, 250 m, Davis 40330.


Related to S. arguta Sol. (N.W. Africa) in general facies which differs from it in its sub-marginate, glandular calyx segments, narrowly ovate, beaked capsules and amphicarpic fruits.

Perennial with a thick, fleshy, densely fibrous, simple or branched rhizome. Stem 50-150 cm, villous, erect, simple, branched only in the floral region, thick, fistular, quadrangular. Petiole 4 cm; lamina 3.5-10 x 2.5-6 cm, ovate, obtuse, base cordate; margin crenate to slightly bicrenate. Floral leaves ovate; base cordate to truncate; apex obtuse to acute; margin crenate to dentate; uppermost sessile, linear, entire-margined. Inflorescence foliate, cymes on the main stem up to 20-flowered, those on the branches 5-1-flowered; peduncle 3 cm long; pedicel 9-13 mm long, glandular; bracteoles 8-11 mm long, linear-lanceolate glandular, shorter than the pedicel. Calyx segments ovate, obtuse, 2.5-4.5 x 2-2.3 cm, densely glandular-pubescent, narrowly white scarious margined. Corolla brown to purple-brown, lower lip green, 6.5-7.5 mm; stamens included; filament glands of oblong type (glands also present on the anthers); staminode transversely oblong, retuse. Capsules broadly ovate, 4.5 x 3 mm, slightly longer than calyx. Fl. 5-7.

Habitat: Limestone rocks, 1900-2200 m.

Syntypes: Turkey B7 Elazig: an einer Quelle auf der Hasarbabab Dagh an Goldschik (Quellsee des westlichen Tigris) auf der langgestreckten Terrasse am Aufstieg vom Dorf Goldschik aus, auf serpentine 1900 m, 29 vii 1910, Hand.-Mazz. 2613 (W!).

B8 Bitlis 8: auf Kalk Zweischen Hasoka und dem Fuss des Gipfelmassivs des Meleto Dagh im Sassum, Vilajet Bitlis, 2200 m, 10 8 1910, Hand.-Mazz. 2730 (W!).

Distribution in Turkey: E. Anatolia.

Endemic. Known only from the type. Handel-Mazzetti related *S. pegaea* to *S. chlorantha*, *S. luridiflora* and *S. urticifolia*. It is, however, closest to *S. luridiflora* from which it differs in its perennial habit, transversely oblong retuse staminode, ovate calyx segments, smaller capsules, glandular anthers, and the pedicels longer than the bracteoles.

Biennial, plant more than 80 cm, densely villous, glandular hairs 2-4 mm long. Stem simple, erect, purplish in the lower region, quadrangular. Petiole 3.5-4 cm; lamina ovate to broadly ovate, 7-10 x 4 x 7 cm; base truncate to roundly cordate; tip broadly obtuse to slightly acute; margin crenate to slightly bicrenate, mucronate. Inflorescence foliate; cymes 9-5-flowered; peduncle 3-5 cm, pedicel 7-14 cm, glandular; bracteoles of the lower cymes peticolate, narrowly oblong to lanceolate-linear, acuminate, glandular, longer than the pedicel; upper bracteoles linear to subulate. Calyx segments ovate-oblong to oblong, 3.5-5 x 0.8-2.5 mm, obtuse, rarely slightly acute, densely villous (hairs 1-2 mm long), narrowly scarious-margined. Corolla reddish-green, 7 mm long, stamens included; filament glands of round type; staminode obcordate to transversely broader, with or without an apical notch. Capsules ovate, 6 x 3.5 mm, apiculate, longer than calyx. Fl. 6-8.

Habitat: Wet and shady places, 2000 m.

Syntypes: Turkey A5 Amasya, Mersiwan (Mersifon), Wiedemann (LE!); A5 Kastamonu, Tosya, Wiedemann, (LE!).

Distribution in Turkey: N. & adjacent C. Anatolia.

B7 Tunceli: Ovacik-Hozat, 2000 m, Davis 31536!

Endemic. Allied to *S. pegaea* from which it can be separated by its pedicels which are shorter than the bracteoles, and larger capsules.

Biennial, somewhat glabrous; stem 92 cm, erect, thick, internodes long, 10-15 cm in the lower region, reddish, angular. Leaves on the main stem petiolate, petiole 5 cm; lamina ovate to broadly ovate, 9 x 7-5 x 5.5 cm, base cordate to subcordate, margin bicrenate-lobate, mucronate, apex acute to round; those on the branches petiolate, ovate, base cordate to cuneate, apex obtuse to acute, margin bicrenate to dentate. Floral leaves ovate to lanceolate, base truncate to cuneate, margin dentate. Inflorescence foliate; cymes distant, 15-5-flowered; peduncle 3.5 cm; pedicels capillary, 18-20 mm, divaricate. Bracteoles linear to narrowly linear, acute, glandular, gradually diminishing in size. Calyx segments oblongish to broadly ovate, 2.5-1.7 x 1.4-2.3 mm, broadly obtuse, with a wide, reddish-brown scarious margin. Corolla reddish-green, 6 x 5.2 mm, upper lobes B-type; stamens included, filament glands of round type; staminode transversely obtriangular, emarginate. Capsules globular, 7 x 6.5 mm, apiculate, 3 times longer than calyx. 

*Fl.* 4-7.

**Habitat:** Meadows, among rocks, c. 457 m.

**Type:** Turkey A8; *Hab, in regione inferiori Ponti Lazici prope Rhize, Balarea* (Hol. G!).

**Distribution in Turkey:** N.E. Anatolia.


Endemic. Related to *S. divaricata* Ledeb., from which it differs in its acutely angular stems, glabrous and long, capillary pedicels; also distantly allied to *S. scopolii* but differing in its foliate inflorescence, short-peduncled divaricate cymes, and long capillary pedicels. *Purse & Synge* 1431 differs from the type specimen in its more deeply toothed leaves, only once dichotomous cymes, more acute upper floral leaves, and narrower calyx segments.

Biennial or perennial, 20-100 cm, glabrous to sparingly woolly, erect or ascending, quadrangular, purplish. Leaves opposite-decussate, rarely alternate; petiole 1-6.5 cm, lamina 2.5-12.5 x 2.2-8.5 cm, broadly ovate to oblong; base deeply cordate to cuneate; apex round to acutish, margin biirenate-mucronate to deeply dentate. Inflorescence subfoliate to aphyllous; lower 1-2 pairs of floral leaves ovate, narrowly ovate to oblong; base truncate to cuneate, apex ± acutish, margin dentate to serrate; upper entire-margined, narrowly ovate to subulate. Peduncle 0.4-6.5 cm; cymes 13-2-flowered; pedicel 4-17 mm (rarely 22 mm), glandular; bracteoles narrowly lanceolate to subulate, 2-13 mm, glandular. Calyx segments ovate to broadly ovate, rarely oblongish, 2-4 mm long, scarious margin white to dark brown, 0.3-1.1 mm wide. Corolla 5-8 mm, green-brown, or purplish-red; stamens, rarely exserted; filament glands of round type; staminode transversely oblong, reniform, suborbicular, non-retuse to + lobed, rarely obcordate. Capsule ovate to broadly ovate, 4.5-7.5 x 3.5-4.5 mm, beaked to apiculate, glabrous. Fl. 4-9.

**Habitat:** Moist rocky slopes, stream sides, river beds, scrubs and forests, 15-2300 m.

1. Calyx segments glabrous

2. Leaves alternate; capsules with long-drawn beaks
   (more than 3 mm long) ........................................... d. var. *longirostrata*

2. Leaves opposite; capsules with short beaks (2-2.5 mm long)

3. Median and lower leaves with + deeply acutely doubly dentate lobes

4. Plants + glabrous, much branched in upper region with slender inflorescence, and 8-6-flowered cymes with + divaricate pedicels ...................................................... b. var. *nusairiensis*
4. Plants villous, not or only poorly branched, inflorescence not slender, cymes 5-2-flowered, without divaricate pedicels .............................................. c. var. amyrnaea

3. Median and lower leaves simply or doubly crenate to dentate (teeth not deepened into lobes) ....................... a. var. scopolii

1. Calyx segments glandular .............................................. c. var. adenocalyx

a. var. scopolii.

Syn: S. glandulosa Waldst. et Kit., Pl. Rar. Hung. 3: 238: tab. 214 (1807);
S. rugosa Willd., Enum. Hort. Berol. Suppl. 42 (1813);
S. glandulifera Clark, Travels 1(2): 21 (1813);
S. grandidentata Tenore, Fl. Neap. Suppl. 2: 69 (1819);
S. hirsuta Hornem. in Hort. Hafn. Suppl. 68 (1819);
S. melissaefolia Urv. in Mem. Soc. Linn. 1: 331 (1822);
S. betonicæfolia Wydł. in Mem. Soc. Phys. Genev. 4: 151 (1823);
S. scorodonia Host, Fl. Austr. 2: 214 (1831);
S. decumbens Fisch., Mey. et Ave-Lall. in Ind. Sem. Horti Petrop. 10: 58 (1842);
S. taeolea Boiss., Diagn. Ser. 1(4): 66 (1844);
S. orenophila Boiss., Diagn. Ser. 1(7): 44 (1844);
S. grandifolia C. Koch in Linnaea 22: 707 (1849);
S. oligantha Boiss. et Heldr. in Boiss., Diagn. Ser. 1(2): 33 (1853);
S. taurica Hort. ex Schur. in Enum. Fl. Transsilv. 485 (1866);
S. pantos окол Griseb. ex Pantoc. in Öst. Bot. Zeitschr. 23: 267 (1873);
S. puberula Boiss. et Hausskn. ex Boiss., Fl. Or. 4: 396 (1879); S. scopolii Hoppe var. grandidentata (Ten.) Boiss., Fl. Or. 4: 396 (1879); var. oligantha (Boiss.) Boiss., loc. cit!
var. tinea (Boiss.) Boiss., loc. cit!
S. guestii Eig. in Pal. Journ. Bot. J. Ser. 3: 80 (1944)!

Type: Hab. in Carinthia, Austria.

Distribution in Turkey: All over Anatolia.
A2(E) Istanbul: Therapia, Aznavour 21.3.1890!
A2(A) Istanbul: Maltepe, between Kartal & Kadıköy, Aznavour!
A2 Bursa: Ulu Da., near Bursa, 1700 m, 9.6.1964, De Wilde 4024!
A3 Çankiri: Çankiri-Ilgaz, 1524 m, Davis 21465!
A4 Çankiri: distr. Ilgaz, S. of Ilgaz Da., pine forest 24, km N. of Ilgaz, 1630 m, Huber-Morath 13990!
A4 Ankara: Hacikadin valley near Keçiören, Davis 18754!
A4 Kastamonu: 41 km S. of Kastamonu, 1320-1350 m, Huber-Morath 15543!
A5 Çorum: Iskilip, 1300 m, Coode & Jones 1760!
A5-6 Amasya: Akdağ, 8.5.1893, Manissadjian 981!
A6 Samsun: Orman Isletme, 15 m, Tobey 156!
A8 Çoruh (Artvin): above Artvin, 1800 m, Davis 29752!
B1 Balikesir: Karukas, 1883, Sintenis 670!
B1 Izmir: Ciplak Da. above Armutlu, 600 m, 22.5.1935, Erik Wall 2463!
B2 Kütahya: Murat Da., 1900 m, Davis 36770!
B3 Bilecik: Söğut-Eskişehir, 1020 m, 12.6.1954, Huber-Morath 13989!
B4 Ankara Cascade de Baglum, 15.8.1907, Aznavour 415!
B5 Niğde: Hasan Da. below Taşpınar Y., 1900 m, Davis 19016!
B5 Yozgat: Sakarya valley, Yarimca Çayır, June 1960, E.W. Curtis 199!
B6 Maras: distr. Göksun: Binbogă Da., 1900 m, Davis 20098!
B6 Sivas: Bey Da., 2000 m, Stainton & Henderson 5291!
B7 Tunceli: Hozat-Ovacık, 2000 m, Davis 31086!
B9 Ağrı: distr. Suluçem, 2300 m, Davis 47172!
C3 Antalya: Antalya, Ak Da., 2200 m, Davis 4366!
C4 Konya: distr. Ermenek, Yelbel Dag-Ermenek, 35 km N. of Ermenek, 1870 m, 9.6.1948, Huber-Morath 3624!
C6 Adana: distr. Bahçe (N. Amanus) Dumanlı Da., near Haruniye, 1300 m, Davis 26892!
C6 Hatay: Körtilli Kıyı Ormani, Amanus Da., 1400 m, 15.6.1967, Akman 192!

Islands: Lesbos; Watusa, K.H. Rechinger fil. 5845a; Samos; M. Ambelos, 800 m, K.H. Rechinger fil. 3914; S. Rhodos, Cadet de Font.
External Distribution: C. & S. Europe, S. Russia, Caucasus, N. Iran, N. Iraq, Syria.

b. var. nusairiensis (Post) Lall, comb. et stat. nov. S. nusairiensis Post, Fl. Post, 5: 13 (1893)!
Syn.: S. antiochiae Post, Fl. Post, 5: 13 (1893)!

Type: Syria borealis: Habitat prope Banias montium Nusairiensis, Post 111!
Distribution in Turkey: S. Anatolia.
C6 Hatay: Antiochiae (Antakya); Husayniyyah near Antakya, Post 112!
External Distribution: Syria.

c. var. smyrnæa (Boiss.) Boiss., Fl. Or. 4: 396 (1879).

Type: Turkey B1 Izmir): Hab. in pratis ad rivulos montium Lydiae, montes supra Bournabat prope Smyrnan, 1842, Boissier!

Distribution in Turkey: Western Anatolia, Islands.
B1 Izmir: Yamanlar Da. above Izmir, 800 m, Huber-Morath 2432! Reino Alava 5101!
Islands: Lesbos: Watusa, 18.5.1969, K.H. Rechinger fil. 5845b!

Endemic. Davis 3738b from Ala Da. (A3 Bolu) is an intermediate between var. smyrnaea and var. scopoli. Rechinger 5845 from Lesbos is intermediate between var. smyrnaea and var. musairiensis.

The leaf shape is characteristic of var. smyrnaea, but the plant approaches var. musairiensis in glabrous and the greater number of flowers per cyme.

Rechinger 585 from Lesbos is intermediate between var. smyrnaea and var. nusairiensis.

Davis 3738b from Ala Da. (A3 Bolu) is an intermediate between var. smyrnaea and var. scopoli.

The leaf shape is characteristic of var. smyrnaea, but the plant approaches var. musairiensis in glabrous and the greater number of flowers per cyme.


Type: Turkey C4 Antalya; distr. Alanya (Isauria): Han Boğaz forest near Geyik Da. in Abietum, 1580 m, 30 Sept. 1947, Davis 14710 (holotypos in Herb. Kew!; isotypus in Herb. Edin.?).

Endemic. Known only from the type.

var. adenocalyx Somm. et Lev. in Acta Horti Petrop. 16: 361-62 (1900).

Syn: S. scopoli var. grandicrenata Somm. et Lev. in Acta Horti Petrop. 16: 362 (1900).

Type: Georgia in herbosis alpinis jugi Latperi merid., 2100 m, 4.viii.1890, Sommier & Levier.

Distribution in Turkey: N. E. & (rarely) S. Anatolia.

A6 Ordu: below Çambası, 1600 m, 14.7.1965, Tóby 1291!

A7 Giresun: below Tamdere, 1600 m, Davis 20620A!

A7 Trabzon: Meryman, 30 miles south of Trabzon, 1219 m, 21.6.1962, Hutchison 62!

A7 Gümüşane: Gümüşane, 22.7.1894, Sintensis 7232!

A8 Trabzon: N. slope of Soğanlı Da. above Çaykara, 1700 m, Davis 32062!

C5 Niğde: Ala Da. Arpalik Gorge, 2190 m, 26.6.1963, Elizabeth Parry 155!

External Distribution: Georgia.
S. scopolii is a variable species regarding its leaf, staminode, glabrous etc. The leaf ranges from broadly ovate to oblong in outline, and the margin varies from acutely lobate-dentate to doubly crenate. The staminode was described by Boissier as transversely broader with truncate base and subretuse apex, but it varies from obcordate to reniform.

Boissier distinguished S. crenophila from S. scopolii by its dense crisped hairs, long-pedicelled paniculate inflorescence, and narrowly scarious margined calyx. I find it impossible to separate Kotschy 632 (the type of S. crenophila) from S. scopolii on the basis of the above mentioned diagnostic features, therefore treat S. crenophila as a synonym of S. scopolii. Rechinger fil. 5698 from Luristan (determined as S. crenophila by him) differs from S. scopolii in its divericate pedicels, extremely narrow scarious-marginated calyx segments and simple crenate leaves. It presumably represents an undescribed species related to S. divaricata which can be distinguished from Rechinger 5698 by its acute calyx segments, acuminate leaves with acutely lobate-dentate margin.

Post distinguished S. nusairiensis from S. scopolii by its glabrous, corolla colour (brown-purple) and size (nearly twice as long). Corolla colour and size do not hold good, and glabrous to villous forms occur within S. scopolii. S. antiochia is also inseparable from S. scopolii. In my opinion both S. nusairiensis and S. antiochia should be treated as synonyms of S. scopolii. Stiefelhagen reduced S. antiochia to a synonym of S. nusairiensis and I share this view with him, although Eig (1942) treated them as specifically distinct. Within S. scopolii, S. nusairiensis is closer to the Western Anatolia var. smyrnaca (which also extends into the Aegean Islands) in its more deeply acutely doubly dentate lobes, but departs from it in glabrous, luxuriant inflorescence and greater number of flowers per cyme. Rechinger fil. 584,5b from Lesbos has leaves characteristic of var. smyrnaca, but approaches S. nusairiensis in glabrous,
tallness and greater number of flowers per cyme. I have treated *S. musairiensis* as a var. of *S. scopoli*.  

**Eig** related *S. guestii* (from Iraqi Kurdistan) to *S. crenophila*, from which he distinguished it by its acute and acutely dentate leaves, larger and less numerous flowers, and the staminode without a subretuse apex. A comparison of *S. guestii* with *S. scopoli* shows that it is not possible to separate the two.  

Boissier separates vars. *grandidentata*, *oligantha*, and *tmoela* on the basis of such characters as non-retuse staminode, large oblongish leaves, narrowly scarious-margined segments, etc. Abundant Turkish material breaks down these distinctions.

**Syn:** *S. balbisii* var. *macrophylla* (Boiss.) Boiss., *Diagn.* 2(3): 154 (1859).

Perennial, 100-200 cm, glabrous. Stem sharply 4-angled, erect, simple or slightly branched. Leaves petiolate, lamina of the median leaves ovate-oblong, 8-10 x 4-5 cm; margin crenate-mucronate to dentate, or crenate-dentate near the base of lamina; apex acute, base cordate to truncate. Inflorescence aphyllous; cymes 13-7-flowered; peduncle 0.8-20 mm, delicate, glabrous; pedicel sparingly glandular, 8-10 mm, capillary; bracteoles 2-3 mm, linear, acute, glabrous. Calyx segments 2-2.5 x 1.5-2 mm, ovate to obovate, glabrous, scarious margin white, 0.4-0.6 mm wide. Corolla red, 6-7 mm long, upper lobes of B-type; stamens included, filament glands of round type; staminode transversely broader, base nearly subcordate. Capsules ovate, 6 x 4 mm, shortly beaked, twice as long as calyx. Fl. 4-7.

**Habitat:** Wet places, 488 m.

**Syntypes:** Hab. ad aquas in valle Jordani; ad fontem Ain Sultan prope Jerico, Boissier; ad lacum Samochonitidem, Pinard.

**External Distribution:** Lebanon, Syria, Iraq, Palestine.

Approaching some forms of *S. umbrosa* in the general facies but distinguished by its non-winged stem and red corolla.

Eig (1943) reported *S. macrophylla* from the Amanus and Gaziantep, but I have not seen any material of this species from Turkey, and its inclusion in the Turkish record is tentative.

**Syn:** *S. calverti* Boiss., *Diagn. Ser.* 2(3): 152 (1853).

Annual, 20-75 cm. Stem erect, simple, green to purplish, glandular. Leaves petiolate (petiole 1.5-6 cm), forming a rosette at the base, alternate; lamina thick, anastomosis poor to inconspicuous, oblong to broadly ovate, or rhomboidal to narrowly ovate, 1.9 x 1.5 - 9 x 8 cm, base round to cuneate, rarely truncate to subcordate, apex round to acute, margin of basal leaves crenate to bi-crenate, mucronate, that of the upper ones sharply doubly dentate; rarely deeply lobed, lobes crenate to dentate. Inflorescence subfoliate to aphyllous, floral leaves rhomboidal, acute to subulate, margin dentate to entire. Cymes 1-4-flowered, peduncle 0.7-4 cm, pedicel 3-11 mm, glandular. Bracteoles lanceolate to triangular, glandular, 2.5-10 mm long. Calyx segments ovate, obtuse to somewhat orbicular, glabrous, very rarely glandular; scarious margin usually broad, rarely narrow, white or yellow to brown, 3-4 x 2-4 mm. Corolla maroon or red, 5-8 mm long, upper lobes of B-type; stamens included, rarely shortly exserted, filament glands of oblong type; staminode reniform to transversely oblong, rarely oblongish. Capsules ovate 6-8.5 x 4-6.5 mm, beaked, 2-3 times longer than the calyx. Fl. 4-7.

**Habitat:** Wet and shady places, forests and woodlands. 1100-2743 m.

**Type:** [Soviet Azerbaidjan]: in montibus ilwensis tractus somchetici, Abotz.

**Distribution in Turkey:** N.E. & C. Anatolia.

A7-8 Gümüşane: Stadvalopi, 1894, Sintenis 5585!;

A8 Çoruh: Artvin, 1100 m, 23/4 1960, Stainton 8297!;

A9 Çoruh: Korçevan Da., 2000 m, Davis 3023!;

A9 Kars: S.W. side of Kisir Da., 2450 m, Davis 29640!;

A8-88 Erzurum: on E., 100, 75 km, N. from Erzurum, D. Walton 21!;

B5 Yozgat: Akdağmadeni to Büyük Nalbant Da., at Rasih Ihsan lead mine, 1800 m, Coode & Jones 2028!
B8 Sivas: Divriği, 3.VI. 1968, Baytop 13040!
B9 Van: distr. Başkale, Çuh gediği between Hoşap and Başkale, 2690 m.
Ruber-Morath 11584!

External Distribution: Caucasus.

Related to *S. scopolii* Hoppe from which it differs in its alternate leaves and oblong type of filament glands. In the Caucasian specimens of *S. ilwensis* the lower 1-2 pairs of leaves may be opposite, whereas in the Turkish specimens all the leaves are alternate; however, in both cases the filament glands are of oblong type, and this is a constant and dependable diagnostic.

Davis 23066 (B9 Van: distr. Şatak; Kavuşşahap Da., 2743 m) differs from the typical *S. ilwensis* in its smaller stature (20-30 cm), small rhomboidal leaves, short-peduncled, (4-)2-flowered cymes, aphyllous inflorescence, and glandular, narrowly scarious-margined calyx segments. Coode & Jones 1904 (A5 Çorum: Kösse Da., 1500 m) has thick, pinnatifid leaves and oblongish staminode.

Although these two gatherings apparently belong to *S. ilwensis*, their status is somewhat uncertain.

**Syn:** *S. italicà* Mill., *Gard. Dict.* ed. 8: 6 (1768);  
*S. reckelli* Spreng., *Syst.* 2: 733 (1825);  
*S. halleri* Glädenst. ex Ledeb., *Fl. Ross.* 3: 219 (1847);  
*S. hemschinica* C. Koch, in *Linnæa* 22: 708 (1849);  
*S. wirtgenii* Koch, ex Opiz *Seznárn* 90: (1852);  
*S. ternata* Schur. in *Verh. Siebenb. Ver. Naturw.* 5: 53 (1853);  
*S. kakudensia* Franch. in *Bull. Soc. Bot. Fr.* 26: 67 (1879);  

Perennial, 40-125 cm, glabrous except for the sparingly glandular inflorescence;  
perennation by short, swollen, suckers. Stem erect, sharply 4-angled, purplish.  
Petiole 1.5-3 cm; lamina 6-13 x 3-7 cm, ovate; base truncate to cordate, usually  
the corners well developed; apex acute; margin ± serrate; petiole and veins  
purplish, anastomosis conspicuous. Inflorescence subfoliately, lower floral leaves  
large, acute to acuminate, upper narrowly lanceolate to linear, acuminate,  
diminishing in size. Cymes distant, axillary, lower opposite, upper alternate,  
peduncle 1.5-4.5 cm long, 10-5-flowered; pedicel 9-16 mm; glandular; bracteoles  
3.5-5 mm, linear, acuminate, sparingly glandular. Calyx segments 2-2.5 mm, ovate,  
obtuse to subacute, very narrowly scarious-margined, glabrous. Corolla 6-8.5 mm,  
upper lobes purple, rest of the corolla lobes and the tube palish-green-purple to  
yellowish; stamens included, filament glands of round type; staminode obtriangular,  
retuse, rarely ± reniform. Capsules 6-8 mm, ovate, acute, 3 times longer than  

**Habitat:** Stream-sides.

Described from Europe: (Herb. Cliff! Herb. Linn. 773/21).

**Distribution in Turkey:** N.E. Anatolia.

A8 Rize; distr. Rize, 400 m, 12.7.1958, Huber-Morath 15547!
External Distribution: Almost all over Europe except in S. Spain, S. Portugal and S. Italy. W. Iran, Altai, Urals, China, Korea and Japan. N. America.
17. *S. chlorentha* Ky. et Boiss. in Boiss., Fl. Or. 4: 399 (1879).

Perennial, 1.5-2 m, erect, many-stemmed at the base. Stem densely and minutely glandular to glabrous in the lower part, thick, fistular, terete to angular. Lower leaves long-petiolate, petiole 6-7 cm; lamina thick, sparingly glandular to glabrous, ovate to broadly ovate, 13-19 x 3.5-10 cm, base cordate to truncate, apex acuminate; margin crenate-serrate; the upper shortly petiolate. Floral leaves long-lanceolate with a cuneate base to narrowly linear, serrate to entire-margined, apex long, acuminate. Inflorescence subfoliate, densely glandular; cymes 30-8-flowered, ascending, distant; peduncle 1-3 cm, pedicel 8-15 mm, glandular. Bracteoles narrowly linear, acuminate, glandular, 6-12 mm. Calyx segments ovate, 2-2.5 x 1.5-1.8 mm, obtuse, densely glandular, narrowly scarious-margined. Corolla red to yellowish, 6-8 mm, upper lobes of B-type; stamens included, filament glands of round type; staminode obtriangular, rarely spadiciform. Capsule ovate, 5.8 x 3.2 cm, beaked, 2-3 times longer than the calyx. *Fl.* 5-8.

**Habitat:** Stream-sides, 1372-2896 m.

**Type:** Turkey B8 Mus/ in arenosis ad fontes Pagi Goschkar, Alt. 1500 m, 19.8.1859, Kotschy 346 (iso. K!).

**Distribution in Turkey:** E. Anatolia.

B8 Bitlis: Hurmuz, 1372 m, Davis 23426!

B8 Mus/ : Goschkar, 1500 m, 19.8.1859, Kotschy 346!

C9 Hakkari: Kara Da., 2896 m, Davis 24356!

**External Distribution:** Caucasus.

Related to *S. nodosa* from which it differs in its obtusely angular stem, glandular calyx segments, and distinctly acuminate leaves.
18. *S. davisi*Lall, sp. nov.

Biennial, plant 18-68 cm, sparingly glandular-puberulent (glands white), many-stemmed; stem simple or branched. Basal leaves 2-4 cm, rosulate, large, thick, petiolate reddish; lamina 2.5-3 x 1.8-7 cm, thick, coriaceous, base round, rarely truncate to cuneate, margin crenate; upper leaves petiolate gradually becoming sessile, ovate, base cordate to cuneate, margin bicrenate to twice dentate. Inflorescence aphyllous; peduncle 3-4 cm; cymes distant ascending, divaricate, 10-4-flowered; pedicel (4-)5-9 mm long, sparingly glandular. Bracteoles linear, 2-3.5 mm long, shorter than the pedicel, sparingly glandular. Calyx segments ovate to orbicular 2.8-4 x 3.5-4 mm, glabrous, scarious margin white to pale, 0.6-1.2 mm wide. Corolla 6.5-7 mm, upper lobes of C-type reddish-brown, the lower and the laterals green-white; stamens included to shortly exserted, filament glands of oblong type; staminode oblong. Capsules 4.7 x 5-6 mm, globular, apiculate. FI. 5-7.

Habitat: Gravel terraces, limestone screes and eroded steep calcareous slope, 700-1800 m.

Type: Turkey C9 Hakkari: Zap gorge beneath (8 km from) Hakkari, 1250 m, Limestone screes. Annual? or biennial. Stems several from base. 21 June 1966, Davis 54367 (Holo: E.).

Distribution in Turkey: E. Anatolia.

C9 Hakkari: near Hakkari, + 1800 m, 21 v 1966, Eiselt; Zap gorge beneath Çukurova, 700-750 m, Davis 47846; Cilo Da., in Dizeresi, 1644 m, Davis 23903; Morinos De., opposite Marunis, 1550 m, Davis 45324.

Endemic. The nearest relative is the Caucasian *S. atropatana* Grossh., from which it differs in its widely divaricate ascending cymes, longer pedicels (1-2 mm in *S. atropatana*), oblong type of filament glands, staminode extending beyond the
point of junction of the two upper corolla lobes (situated below this point in *S. atropatana*), calyx segments with a broader scarious margin and larger flowers and seeds (2 mm long; twice as long as in *S. atropatana*). Davis 23903 differs from the other material in its relatively shorter pedicels and lamina with a cordate base.
Scrophularia davieana \textit{L}ee et \textit{v}an \textit{H}outte.

TURKEY.09 Hakkari: Morinos Dere, opposite Karumis, 1950 m. Eroded steep calcareous slope. Biennial or Annual? Stems few from base. Upper lip reddish-brown, erect, other lobes greenish-white, the lowest deflexed! 21 June 1936.

Plate 1.15

Perennial, erect, densely glandular-puberulent. Stem quadrangular, simple or branched. Leaves petiolate, 6-9 × 2-3 cm, oblong-lanceolate; base cuneate, rarely sub-truncate; apex acute, margin obtusely to sharply dentate. Inflorescence aphyllous, cymes 9-5-flowered; peduncle 1-2.5 cm; pedicel 1.5-3 mm, glandular; bracteoles 2-7 mm, linear, glandular. Calyx segments ovate, obtuse, 4 × 5 mm, glabrous, scarious margin white, 1-2 mm wide. Corolla 7-8 mm, pale brownish-pink, upper lip maroon, of C-type; stamens subexserted, filament glands of oblong type; staminode reniform. Capsule 5.5 × 6 mm, apiculate, twice as long as calyx. Fl. 5-7.

Habitat: Igneous slopes, shale, 1180-1210 m.

Type: E. Turkey: Hab. in subalpinus et ruderatis Armenia meridionalis circa Ardana ubi legit Maio 1852 cl. Nöe.

Distribution in Turkey: E. Anatolia.

B7 Elazığ: Tigris ravine 5-7 km beyond Gölçük-lake, 1180-1210 m, Huber-Morath 11585!

B7 Diyarbakır: Maden 1300 m, Davis 29084

Endemic. Allied to *S. catariifolia* Boiss. et Heldr. (q.v.) from which it differs in its glabrous calyx segments, shorter pedicels which are nearly twice as short as the bracteoles, larger oblong-lanceolate leaves with cuneate to truncate bases, and larger capsules.

Syn: *S. nepetaefolia* Boiss. et Heldr. ex Boiss., Fl. Cr. 4: 407 (1879);

*S. glandulosissima* Freyn. et Sint. in Bull. Herb. Boiss., 4: 49 (1896);


Perennial, 30-50 cm, densely glandular-puberulent, many-stemmed. Stem reddish especially towards the base, quadrangular, erect. Leaves thick, densely glandular-puberulent; petiole 0.5-2.3 cm, lamina 3.3-6 x 2-3 cm, ovate to oblong ovate, apex obtuse to acute, base round to sub-cordate; margin singly to doubly crenate or dentate rarely pinnatifid. Inflorescence rarely subfoliate, lower floral leaves ovate to lanceolate, sessile, rarely subsessile, margin singly to doubly dentate, rarely ± entire; upper linear, gradually diminishing in size. Cymes alternate to rarely a few opposite, distant, 5-3-flowered, the upper 2-1-flowered, peduncle 8-16 mm, pedicel 1.5-6 mm; bracteoles 2-7 mm, usually longer than the pedicel (rarely slightly shorter), densely glandular. Calyx segments ovate, broadly obtuse, or obovate to orbicular, densely glandular, 2.2-3.5 mm, scarious margin white, pale or brown, 0.5-1.5 mm wide. Corolla 6-7 mm, light brown-green or brown, upper lobes of C-type; stamens included to slightly exserted, filament glands of oblong type; staminode reniform. Capsules globular, apiculate, 5-3 mm long, 2-2.5 times longer than calyx. Fl. 5-7.

Habitat: Gravel of ravine beds, limestone rocks, 880-1900 m.

Type: Turkey Ch. Konya: in cacumine montis Karadagh Lycaonias in ruinis ecclesiae Graecae veteris cum *S. cryptophila* mixta, 1524 m, Fl. Junio, Heldreich.

Distribution in Turkey: Mainly inner Anatolia.

A7 Gümüşane, 22.8.1894, *Sintenis* 5662B!

B6 Maras: distr. Gökştn, Binboga da., 1900 m, Davis 20104!

B6 Malatya: Akçadağ, 1450 m, Huber-Morath 9327!

B7 Sivas: distr. Sivas, 7 km, W. of Sivas, 13.6.1939, Huber-Morath.

C4 Iğel: 4.3 km N. of Mut (Str. Karaman), 1600 m, 9.6.1966, Sorger 66-34-3.

Endemic. Related to S. pulverulenta.

Stiefeihagen (1910) reduced S. glandulosissima Freyn. et Sint. and S. sintonisii Freyn. et Sint. to simple synonyms of S. pulverulenta, but they differ from it in their densely glandular calyx segments, longer pedicels (4-6 mm), which are slightly longer than the bracteoles, and smaller leaves which are pinnatifid in S. sintonisii. However, it is difficult to separate them from S. catariifolia and I therefore treat them as synonyms.

Perennial, glabrous, many-stemmed. Stem ascending, partly branched. Leaves petiolate, lower opposite, upper alternate; lamina narrowly ovate, incised-dentate or pinnatifid, lobes acute, dentate. Thyrses foliaceous, lax, elongate, glandular-pilose, few-flowered, racemose by reduction of cymes to a single flower. Calyx segments ovate, obtuse, scarious-margined. Staminode reniform. Capsules globular.

**Type:** [Turkey C2 MUGLA], Lycia; in monte Ak Da. (d. Fethiye), 17 VII 1882 Luschan.

Endemic. Known only from the type. Richter related it to *S. canina* from which he distinguished it by its few-flowered thyrses, and reniform staminode, etc. I have not seen the type of *S. uniflora* (which could not be traced), but from the description it appears that it is probably a depauperate form of *S. rimarum*. The matter needs further investigation.
22. **S. xromarum** Bornm. in Feddes Repert. 7: 202 (1909).

_Syn_: **S. cilicica** Heywood / Notes R.B.G. Edinb. 21: 75 (1952)!

Perennial, 14-62 cm, many-stemmed, densely glandular-puberulent to glabrous. Stem erect to ascending, quadrangular, simple or rarely slightly branched in the floral region. Leaves thick, glabrous to densely glandular-puberulent, lower shortly petiolate (petiole 0.5-2.5 cm), upper usually sessile, lamina 0.2-4.3 cm, ovate, base truncate to cuneate, apex obtuse to sharply acute, margin singly to doubly dentate, occasionally serrate; rarely the lamina of the median leaves pinnatifid especially towards the base. Inflorescence aphyllous; cymes 7-2-flowered; peduncle 0.6-2.5 cm; pedicel 1-6 mm, glandular; bracteoles linear to narrowly linear, acute to acuminate, rarely subulate, longer or rarely shorter than the pedicel, sparingly to densely glandular. Calyx segments obovate to orbicular 2-4 x 1.5-4 mm, glabrous to sparingly glandular, scarious margin white 0.5-1.3 mm wide. Corolla greenish brown to pink or brownish red with lower green lobes, 6 mm long, upper lobes of C-type; stamens included or slightly exserted, filament glands of oblong type; staminode reniform. Capsules globular, apiculate, twice as long as calyx. F1. 5-7.

**Habitat**: Stony ground, rocky slopes and ledges, 800-3050 m.

**Type**: N. Iraq; Kurdistania Turcica Persiae finitima, in fissuris rupium regionis alpinae alpis Helgurd Algird DaF; 3000 m. s.m. (16. vi. 1957 det. exsiccat. Bornmüller 1624).

**Distribution in Turkey**: E., C. & S. Anatolia.

B2-3 Kütahya: Eskişehir to Kütahya, 800-900 m, Davis 36104!
B6 Maras: dist. Gökşun, Binboga Da., 1900 m, Davis 20103!
B9 Van: dist. Gevaç, Artos Da., 3048 m, Davis 22821!
C2 Denizli: distr. Denizli, 1000 m, Huber-Morath 5588!
C2 Burdur: distr. Tefenni, 1980 m, Huber-Morath 86261!
C3 Antalya: Bozburun Da. above Tozlu Çukur Yayla, 1900-2100 m, Davis 15605!
C4 İçel: distr. Anamur: between Çamurlu Y. and Oluçak, (Ermenek-Anamur), 2000 m, 
Davis 16298!
C5 Nigde: Ala Da., 2100 m, E. Parry 70!
C9 Hakkari: Pass between Hakkari and Kaval, 2500 m, Davis 45398!
C10 Hakkari: Sat Dağı, N.W. of Sat Gölü, 2900-3000 m, Davis 45685!

External Distribution: N.W. Iran, N. Iraq.
23. *S. bitlisica* Lall, sp. nov.

Perennial, plant 59-68 cm, many-stemmed, densely glandular-puberulent. Stems erect, simple, subangular. Leaves thick, pale green, glandular; median 5.5 x 2.5 cm, narrowly ovate to lanceolate, shortly petiolate; upper subsessile; base cuneate, margin deeply pinnatifid, terminal lobe acuminate, serrate, lateral lobes pointed, sharply dentate; some of the leaves with a pair of free basal segments. Inflorescence is aphyllous, bracts 5-7 x 0.5-1 mm, linear, acute, sessile, glandular. Cymes alternate, distant, 10-3-flowered; peduncle 1.4-2.4 cm; pedicel 1.5-2.5 mm; bracteoles 2-2.5 mm, glandular. Calyx segments ovate to obovate, 3-4 x 3-4 mm, glabrous, scarious margin white, 0.5-1.2 mm wide. Corolla 6 mm long, yellowish-green to greenish-brown, upper lobes purplish-brown, of C-type; stamens included, filament glands of oblong type; staminode reniform. Capsules globular 4 x 5 mm, apical, twice as long as calyx. **Fl. 4-6.**

Habitat: Waste places, slopes in steppe, mixed forests, 1550-1829 m.


Distribution in Turkey: S. & SE. Anatolia.

B9 Bitlis: Tatvan-Ahlat, nr. Sogurt, *Davis 24613*; W. flank of Nemrut Da., 1829 m, *Davis 23595*; 3 km south of Tatvan, 1700-1720 m, *Huber-Morath 11581*; distr. Bitlis, 3 km N. above Bitlis, *Huber-Morath 11586*;

C5 Seyhan: distr. Karaisali, 1750 m, *Huber-Morath 15542*!

Endemic. Allied to *S. rimiarum* Bornm. from which it can be distinguished by its narrowly ovate to lanceolate, deeply pinnatifid lamina with 1-2 free basal segments.
24. S. serratifolia Hub.-Mor., sp. nov.

Perennial, 36 cm, ascending, densely glandular-puberulent, many-stemmed. Stem reddish, quadrangular, branched. Leaves simple, ± thick, coriaceous, lower and median petiolate (petiole 1.4-1.2 cm); lamina ovate, 1.9 x 1.1 cm, base cuneate, apex acute, margin deeply serrate, lamina of some of the lower leaves pinnatifid especially towards the base; upper leaves subsessile, oblong, with a serrate margin, cuneate base and acute apex. Inflorescence aphyllous; cymes distant, 3-1-flowered; peduncle 1.2 cm. Pedicel 4-5 mm long, glandular, longer than the bracteoles. Bracteoles linear, glandular, 2.8 mm long. Calyx segments obovate to orbicular, 2.5 x 2.2 mm, glandular, white scarious-margined. Corolla 4.5 mm, upper lobes of C-type, purple, lower and the laterals palish; stamens included, filament glands of oblong type; staminode oblong. Capsules sub-globular, apiculate, 5 x 6.5 mm, 2-3 times longer than calyx. Fl. 5-6.

Type: Turkey A6 Sivas; distr. Suşehri, Serefiye Yayla-Suşehri, Eruptionsstein 11 km NE. Serefife, 1900 m, 30 June 1955, Huber-Morath 13994!

Distribution in Turkey: C. Anatolia.

Endemic. Known from the type only, approaching some forms of S. rupestris var. libanotica, from which it can be distinguished by its densely glandular calyx segments and deeply serrate leaves.

Perennial, 16-75 cm, many-stemmed, densely glandular-puberulent to glabrous. Stem subangular to terete, simple or branched. Lower leaves petiolate (petiole 0.5-3.8 cm), upper subsessile to sessile; lamina thick, glabrous to densely glandular-puberulent, base truncate to attenuate, apex ± obtuse to sharply acute, margin dentate (rarely lower leaves pinnatifid), or bicrenate to doubly dentate. Inflorescence aphyllous, rarely subfoliate; cyme 7-2-flowered, rarely up to 10-flowered; peduncle 1-2.4 cm; pedicel 1.7-6 mm (very rarely 7.5 mm), densely glandular to nearly glabrous; bracteoles 1-4.5 mm (rarely 6 mm), lanceolate to narrowly linear, densely glandular to nearly glabrous. Calyx segments ovate to suborbicular, 2-3 x 2-1.5 mm, glabrous, scarious margin white, 0.3-0.6 mm wide. Corolla 4-5.5 mm, greenish to brownish pink or red, upper lobes of C-type; stamens included to short exserted, filament glands of oblong type (rarely of both type); staminode oblongish to ovate to nearly reniform. Capsules globular, apiculate, 3-5 x 3.5-5 mm, twice as long as calyx. Fl. 5-7.

Habitat: Rocky slopes and crevices, 300-3048 m.

1. Plants glabrous to sparingly glandular .................. b. var. *libanotica*

1. Plants densely glandular

2. Staminode spade-shaped or obovate to reniform

3. Pedicel shorter than the bracteole; if longer then the leaves oblong-lanceolate .................................................. b. var. *libanotica*

3. Pedicel longer than the bracteole, leaves broadly ovate ................................................................. c. var. *mesogitana*

2. Staminode oblong to ovate

4. Lamina of the median leaves at the most 2 cm long, if more than 2 cm then either the lamina irregularly lobate-dentate or the pedicels capillary ........................................... b. var. *libanotica*
4. Lamina of the median leaves more than 2.5 cm long, not lobate—
   dentate, pedicels stout ...................... a. var. rupestris
   a. var. rupestris

Syn: S. ani C. Koch in Linnaea 17: 285 (1843); 
S. saxatilis Boeb. ex Ledeb., Fl. Ross. 3: 221 (1847); 
S. chamaedrifolia Boiss. et Hausskn. in Boiss., Fl. Or. 4: 418 (1879); 
S. variegata var. rupestris (M.B.) Boiss., Fl. Or. 4: 418 (1879); 
Type: Crimea; in Tauriae meridionalis rupestribus, Bieberstein.
Distribution: Crimea; Caucasus?

It is doubtful whether var. rupestris grows in the Caucasus. The plants
reported as S. rupestris from this area may well be referable to our var.
libanotica, although it has not been recorded from this area. 3, viii. 1963
Gabrielian from the Soviet Armenia is certainly var. libanotica.

b. var. libanotica (Boiss.) Lall, comb. nov.

   non. Wyd. (1828); 
S. libanotica Boiss., Diagn. 1(12): 36 (1853); 
S. urvillei Walp. in Ann. 5: 624 (1860); 
S. variegata var. libanotica (Boiss.) Boiss., Fl. Or. 4: 418 (1879); 
S. incisa C. Koch ex Boiss., Fl. Or. 4: 418 (1879); 
S. nitida Richter ex Stapf. in Denkschr. Akad. Wien 50(2): 24 (1885); 
368 (1890); 
22(2): 109 (1907).

Lectotype: [Turkey C5-6 Hatay/Syria?; Mount Cassio (Akra Da.), 1846, Boissier! 
[see Heywood in Notes R.B.C. Edinb. 21: 80 (1952)].
Distribution in Turkey: Wide spread in Anatolia and Islands.

A4 Ankara: Kalecik, Baykus Bogasi, 3.6.1967, Daytop 11279!
A4 Kastamonu: 5 km west of Kastamonu, 900 m, Davis 38773!
A5 Samsun: Kizilirmak, after Asar, 300 m, 20.5.1967, Tobey 1799!
A6 Tokat: distr. Tokat, 600-700 m, 1893, Bommüller 3465!
A7 Gümüşane: Gümüşane, 1400 m, 3.5.1960, Stainton 8327!
A8 Erzincan: Tercan-Agkale, 1850 m, Davis 29313!
B5 Kayseri: Develi, Davis 19174!
B Nevşehir: 3 m north of Derinkuyu, 1600 m, 21.5.1965, Coode & Jones 1268!
B5 Yozgat: Sorgun to Çekerek, 20 miles from Sorgun, 1200 m, 27.5.1965, Coode & Jones 1590!
B6 Sivas: distr. Zara, Şerefiye Yayla, 1550 m, 4.7.1953, Huber-Morath 14001!
B6 Maras: 3 km west of Elbistan, 1100 m, Davis 27628!
B6 Adana, distr. Saimbeyli: Bozoğlan Da, above Obruk Yayla, 2100 m, Davis 19730!
B7 Malatya: distr. Malatya, 1330 m, 13.6.1949, Huber-Morath 9235!
B7 Tunceli: Munzur Da, above Ovacik, 2500 m, Davis 31407!
B7 Diyarbekir: Ergani to Diyarbekir, 28.7.1906, Post 303!
B8 Erzurum: Pasinler-Horasan, 1650 m, Davis 29414!
B9 Bitlis: Pelli Da, above Pelli, 3048 m, Davis 22446!
B10 Hakkari: Cilo Da, below Cilo Yayla, 2743 m, Davis 23968!
B10 Ağrı: 3 km east of Doğubayazit, 1750 m, Davis 43936!
C1 İzmir: İzmir-Kuşadası, 8.5.1965, Kayacık & Yaltırık 3387!
C3 İsparta: Egridir Gölü, 19.v.1965, J. Eiselt!
C2 Konya: Ermenek, 10.6.1948, Reese!
C5 Iğdır: Boulgarmaden, 22.7.1855, Balansa 679!
C5 Niğde: Ala Da., 2190 m, 26.6.1963, Elizabeth Parry 156!
C6 Maras: Ahir Da., above Maras, 1100 m, Davis 27488!

C7 Urfa: distr. Siverek, east of Siverek, 800 m, Davis 28293!

C9 Hakkari: Elkiyayla Da., above Pass between Marunis and Beytüşsebap, 2550 m, Davis 45344!

Islands: Khios, monte Flaka, 600 m, K.H. Rechinger fil. 5410! Samos, Karlowasi, K.H. Rechinger fil. 4033!

External Distribution: Caucasus, Iran, Iraq, Lebanon, Syria, Palestine.

Variable regarding leaf and staminode shape and in its stature. The staminode varies from narrowly oblong to rounded. The leaves are thick, coriaceous, and vary from petiolate to subsessile, and oblong-lanceolate to broadly ovate-cordate in outline. The lamina ranges from 1-5.5 x 0.6-3.5 cm, and the margin may be crenate to deeply crenate or vary from lobate-dentate to sharply (regularly or irregularly) dentate, and the apex from subacute to acuminate. In staminode shape and pedicel/bracteole length ratio some forms of var. libanotica approach var. rupestris on the one hand and var. mesogitana on the other.

c. var. mesogitana (Boiss.) Lall, comb. et stat. nov.

Syn: S. mesogitana Boiss., Fl. Or. 4: 407 (1879).

Type: [Turkey C1 Aydin]: in rupestribus calcareis regionis medias-montis Mesogis Lydiae, Boissier (G!).

Distribution in Turkey: W. Anatolia.

B2 Manisa: distr. Demirci, Akçakertik-Pass between Demirci and Simav, 1300 m, 24.6.1954, Huber-Morath 13995!

C1 Aydin: Mesogis Lydiae (Aydin Da) Boissier!

C2 Denizli: distr. Denizli, Honaz Da., north slope, 900-1100 m, 30.5.1935, Reese 2734!
Endemic. The closest relative is *S. rimarum* from which it can be distinguished by its densely glandular habit and spade-shaped to orbicular staminode. Some densely glandular forms of *S. rimarum* occur in E. Anatolia, and very rarely the staminode approaches reniform in some forms of *S. rupestris* var. *mesogitana*; the former taxon can be separated from the latter by its smaller ovate, ± serrate leaves, shorter pedicels which are also shorter than the bracteoles, and the distinct geography. The leaves in var. *mesogitana* are broadly ovate with a deep irregularly dentate margin.

Perennial, 20-30 cm, glabrous, many-stemmed, woody at the base. Stem erect or ascending, quadrangular, slightly branched. Leaves thick, fleshy, roundly ovate, with a white margin; margin roundly incised to crenate; base cuneate; basal leaves rosetulate, petiolate, median shortly petiolate. Cymes 5-1-flowered; peduncle 4-6 mm, thick, woody; pedicel 1-2 mm, thick, woody, sparingly glandular; bracteoles 1.5-2 mm, narrowly oblong, glabrous. Calyx segments 2-2.5 x 1.5 mm, ovate to obovate, glabrous, narrowly white scarious-margined. Corolla reddish, 5-5.5 mm, upper lobes of C-type; filament glands of oblong type; staminode almost reniform. Capsule 4-4.5 x 4-4.5 mm, globular, apiculate, nearly as long as calyx. Fl. ?

Habitat: Sandy soil, alluvial knoll on sandstone bluff, 300 m.

Type: *Iran*: monte Elwend, Aucher 2898.

External Distribution: Iran, Iraq.

Related to *S. hypericifolia* from which it can be distinguished by its opposite leaves which have a white border, and the staminode.

Stiefelhagen reported this species from Turkish Mesopotamia (between Urfa and Siverek) and Diarbekir. I have not seen any material of this species from Turkey, and its inclusion in the Turkish list is tentative.
27. S. pumilio Lall, sp. nov.

Perennial, 5-11 cm, densely glandular-puberulent, with prostrate rhizomes with persistent leaf-bases and sending off 5-11 cm long, simple or branched flowering shoots. Stem + black, subquadrangular. Leaves small, petiolate, subopposite, mostly crowded near the base of the shoots, thick, coriaceous, 2-3.2 cm long, spatulate to oblong, margin crenate to obtusely dentate. Inflorescence aphyllous, subracemose forming a conflated few-flowered raceme ending in a 3-flowered cyme (sometimes reduced to a 3-flowered cyme); pedicel 3-7 mm, glandular; bracteoles 1.5-2.5 mm; linear, glandular. Calyx segments oblong, 2.3- x 1.5 mm, very narrowly scarious-margined, glandular. Corolla maroon, 5 mm, upper lobes of C-type; stamens included, filament glands of oblong type; staminode oblong. Capsules ovate 5-6 x 5-5.5 mm, thin-walled, mucronate, 2-3 times longer than calyx. Fl. 6-8.

Habitat: - Loose scree and limestone crevices, 3000-3353 m.

Type: [Turkey C10 Hakkari]: Cilo Tepe, 3353 m, 8 Aug. 1954. Loose scree, Davis 24064, O. Polunin, (Holo: K; iso, E.). C10 Hakkari: Cilo Da., Regko Tepe, 3000 m, S. facing limestone crevices, 5 Sept. 1967, Duncan & Tait 242.

Distribution in Turkey - S.E. Anatolia

Endemic. A very distinct alpine species of doubtful affinities. Perhaps distantly related to S. nachitschevanica Grossh. from which it is distinguished by its small stature, narrowly oblong staminode, aphyllous subracemose inflorescence and rosulate leaves. The limited material makes it difficult to be sure of the exact structure and development of its conflated, subracemose inflorescence.
Scrophularia pumilio Lall sp. nov.


Holotypus

Davis 24,064, O. Polunin

Biennial or perennial, plant 20-30 cm, glabrous to sparingly glandular-puberulent. Stem subquadrangular, green erect to ascending, branched. Lower leaves petiolate (petiole 2-2.5 cm); lamina 5.5 x 1.7 cm, oblong-lanceolate to narrowly oblong, deeply crenate to dentate; base cuneate, apex ± obtuse; the upper subsessile, gradually becoming sessile. Inflorescence aphyllous; cymes distant, shortly pedunculate (peduncle 0.8-1.4 cm), 7-5-flowered, pedicel 0.5-1 mm, glandular. Bracteoles small, 1-2 mm. Calyx segments ovate to semi- orbicular, glabrous or with a few glands, scarious margin, narrow, white. Corolla 6 mm long, maroon, lobes concolorous, upper lobes of C-type; stamens shortly exerted, filament glands of oblong type; staminode spade-shaped to roundish. Capsules 3.5 x 4.5 mm, globular, apiculate, twice as long as calyx. Fl. 5-8.

Habitat: Sandy Calligonum steppe, 850 m.

Described from Nachitsohovan (type: LE, original description not seen).

Distribution in Turkey: E. Anatolia.

B9 Kars: 3-5 km. E. Aralik (Aras Valley), 850 m, Davis 43669!

External Distribution: S. Caucasus: Nachitschevan.

Related to *S. frigida* Boiss. from which it differs in smaller pedicels (which measure 0.5-1 mm in *S. nachitschevanica* and 3.5-6 mm in *S. frigida*), and dentate leaves; the basal leaves in *S. frigida* are pinnatifid.

In *S. nachitschevanica* the staminode was described as reniform and the habit as biennial, but in our specimens the staminode varies from spade-shaped to roundish, and the habit biennial to perennial, otherwise the specimens match very well with the photographs of the type of *S. nachitschevanica*.

Davis 43824 Kars; Iğdir D.U.C. (Aras Valley), rocky volcanic hillocks (sandy) differs from *S. nachitschevanica* in its alternate, oblong + pinnatifid leaves with obtusely crenate lobes, and reniform subretuse staminode. It's status however, remains uncertain until more material is gathered from this area.
29. *S. hyssopifolia* Boiss. et Hausskn. in Boiss., Fl. Or. 4: 413 (1879).

Perennial, 30 cm or more, branched, especially towards the base, subangular, ascending, totally glandular-puberulent. Leaves oblong-lanceolate, 3 x 0.3-0.7 cm (petiole included), thick, subsessile; base attenuate; apex acute; margin entire to irregularly dentate, some of the lower leaves pinnatifid. Floral leaves oblong-lanceolate to subtriangular, acute, entire-margined, sessile. Peduncle 14-18 mm; cyme, 3-2-flowered, becoming 1-flowered in the upper region; pedicel 2-3 mm, as long as or shorter than the bracteoles, glandular. Bracteoles 3-4 mm, subtriangular to oblong-lanceolate, glandular-puberulent. Calyx segments, 2.5-3 x 2-2.5 mm, obovate, sparingly glandular; scarious margin white, lacerate, 0.5-0.8 mm. Corolla red in the dry state 4.5-5 mm long, 2½ times longer than the calyx, upper as well as, the lower corolla lobes narrowly white-bordered; stamens slightly exserted, filament glands of oblong type; staminode linear. Capsules broadly ovate, 5 x 5 mm; apiculate 2.5-3 times longer than the calyx. Fl. ?

Lectotype: Turkey 'B6 Maras': Hab. ad rupes mont. Berytdagh Cataoniae, 2134 m, Haussknecht 1244 (G!, BM!).

Endemic. Known only from the type. Resembling *S. canina* L. subsp. bicolor (S.&S) Greuter, in staminode shape and in having the upper corolla lobes with a yellow or white border, but differing in the leaf-shape.

Boissier described the staminode as oblong-linear, canaliculate. He probably saw an abnormal flower. The staminode is oblong-linear or oblong-lanceolate, but there is no canal. Kotschy Suppl. 714, which was cited as a syntype of *S. hyssopifolia*, has a large reniform staminode, white corolla with red stripe, globose capsules, ovate, glabrous calyx segments and the bracteoles smaller than the pedicel. The specimen is leafless; it is probably a form of *S. ramarum*. 

**Syn:**
- S. oliveriana C. Koch. in Linnaea 22: 709 (1849);
- S. lasica Boiss. et Bal. ex Boiss., Fl. Or. 4: 409 (1879);
- S. pyrrolepha Boiss., Fl. Or. 4: 409 (1879);
- S. olympica Boiss. var. lasica Boiss., Fl. Or. 4: 409 (1879);
- S. olympica Boiss., var. integrifolia Freyn. & Sint. in Bull. Herb. Boiss. 4: 51 (1896);

**Perennial,** 25-65 cm, erect to ascending, ± glabrous in the lower, while glandular-puberulent in the upper region, many-stemmed. Stem purple throughout, rarely purplish in the basal part green in the upper, simple angular. Leaves petiolate, petiole and veins purplish, some of the leaves with 1-3 small basal lobes and a very large doubly dentate to deeply incised terminal lobe with dentate secondary lobes; others simple; ovate to oblong, margin lobed especially towards base, lobes dentate. Inflorescence aphyllous, peduncle 1.8-2.8 cm, 5-2-flowered, usually becoming 1-flowered in the upper region. Pedicel 1-3.5 mm, glandular; bracteoles 1.7-5 mm, linear to narrowly oblong, glabrous, longer than the pedicel. Calyx segments orbicular to reniform, glabrous, scarious-margin palish to brown, 1-3.5 mm wide. Corolla 6 mm, upper lobes dark purple, of C-type, tube pale-brownish to pink; stamens shortly exerted, filament glands of oblong type; staminode reniform. Capsules subglobose, apiculate, 1.5-2 times longer than calyx. Fl. 5-8.

**Habitat:** Scrrees and rocky slopes, 2600-3658 m.

**Type:** Turkey A2 Bursa7: Hab. in cavis rupium regionis alpinae Olympi Bithyni (Ulu Da.) ad originem vallis Kirkbounar, viii.1842, Boissier!

**Distribution in Turkey:** N. & E. Anatolia.
A7 Giresun: Karagöl, 2600 m, 5.8.1965, Tobey 1883!

A8 Rize: distr. Ikizdere: Germanin Tepe, 3200 m, Davis 21098!

B9 Bitlis: Sıphan Da., 3353-3685 m, Davis 24646!

B10 Ağrı: Grand Ararat / Büyük Ağrı Da., 2850 m, Aznavour 2148!

C9 Hakkari: Kara Da., 3505 m, Davis 24421!

External Distribution: Caucasia, Transcausia, Crimea.

Closely allied to the Persian *S. pruinosa* from which it can be easily distinguished by its reniform staminode. Parsa (1948) described *S. olympica* var. *multiflora* from Iran. Examination of the type material of var. *multiflora* has shown the presence of a + oblong staminode and matches the specimens of *S. pruinosa* from Iran well. I therefore consider var. *multiflora* to be *S. pruinosa* and hence exclude *S. olympica* s.s. from Iran on the basis of the material seen.
31. S. amana Lall, sp. nov.

Perennial, 34 cm; several-stemmed, glabrous. Stems pinkish-red, shiny, erect to ascending, quadrangular, simple. Lower leaves 5.5 cm (petiole 3 cm, purple), ovate to lanceolate, base truncate to cuneate, margin deeply pinnatifid in the lower leaves with 1-2 free basal segments, lobes and segments serrate, veins purple, anastomosis inconspicuous. Lower floral leaves 2.8 x 1.1 cm, shortly petiolate, lanceolate with cuneate base and dentate margin; upper sessile, narrowly linear, diminishing in size higher up. Cymes alternate, 10-6-flowered; peduncle 13 mm, purplish-black; pedicel 6 mm, purple, capillary, glandular; bracteoles 3.5 mm, narrowly linear, purplish-green, sparingly glandular. Calyx segments narrowly oblong, obtuse, 2.3 x 1 mm, glabrous, scarious margin white, 0.2 mm wide. Corolla purplish-brown, 6.5 mm, upper lobes (C-type) purple, laterals and the median lobe palish-brown; stamens exerted, filament glands of oblong type; staminode oblong. Capsule? Fl. 4-6.

Type: Turkey C6 Hatay; distr. Antakya (Amanus); Antakya-Yayladağ, near Şenköy, 1000 m. Crevices of limestone rocks. Perennial. Collar woody, flowers purplish brown. 29.4.1957. Davis 27175 (Holotype).

Endemic. Related to S. variegata M.B. from which it can be distinguished by its linear-oblong, narrowly scarious margined calyx segments, capillary pedicels, and pinnatifid leaves with, at the most, 1-2 free basal segments.
Soraphelaria amana LALL sp. nov.

Turkey, Prov. Sivas dist., Kizilca (Nominal); alt. 500 m., July 1953, Permin (1823).

Habitat: Collar woody; flowers purplish brown.

Biennial, 40-110 cm, glabrous, erect, simple or branched, purplish, sub-angular. Leaves pinnate, pinnae lanceolate to linear-lanceolate, a few basal pinnae with deeply divided basal lobes, both the pinnae as well as the lobes dentate. Lower leaves petiolate upper subsessile. The first few floral leaves pinnate, upper + spathulate with a palish scarious margin, tip subacute to broadly obtuse, margin entire. Peduncle 8-12 mm; cymes distant, 9-7-flowered; pedicel 3-5 mm, shorter than the bracteoles. Bracteoles oblong-spathulate with a pale-brown scarious margin, glabrous 6-8 mm. Calyx segments ovate to obovate 4-4.5 x 2-3 mm, glabrous, scarious margin wide, undulate, purplish to purplish brown. Corolla purple, 3-9 mm long upper lobes of C-type; stamens included, filament glands of oblong type; staminode orbicular. Capsule ovate, apiculate, 6.5 x 5 mm, twice as long as calyx. Fl. 5-7.

Habitat: By streams, wet fields on basaltic and volcanic clay, 823-1450 m.

Type: [Turkey C7 Urfa & Siverek] in Mesopotamia inter Orfa et Suerek, Kotschy 57 (K!).

Distribution in Turkey: E. S. Anatolia.

B7 Diyarbakir: Skinciköy, Ergani, 823 m, 26.5.1958, E.S. Brown No. 570!

C7 Urfa: distr. Siverek, W. foot of Karacadag, between Siverek & Diyarbakir, 1050 m, Davis 23282!

C9 Siirt: above Sirnak, 1450 m, Davis 42611!

Endemic. Related to *S. scariosa* in habit and leaf form, but differing in its glabrous calyx segments with a pinkish scarious margin, and smaller capsules.

Biennial, 53 cm or more. Stem erect, glabrous, branched at the base and above, subangular. Leaves tripinnatisect; lower petiolate (petiole 4-5 cm); upper sub-sessile, becoming sessile. Inflorescence aphyllous, lower one or two floral leaves small, pinnate, upper oblong, broadly obtuse, gradually becoming linear, acute, with a wide scarious margin. Bracteoles oblong, ovate-oblong to somewhat elliptic, widely white scarious-margined, glandular, longer than the pedicel. Cymes distant, 7-5-flowered; peduncle 10-25 mm, pedicel 3-12 mm long. Calyx segments ovate, oblongish to somewhat orbicular, obtuse to broadly obtuse, sparingly glandular, scarious margin white, 2-3 mm wide. Corolla maroon, 8.5 mm, upper lobes of C-type; stamens included; filament glands of oblong type; staminode orbicular. Capsule ovate, 8.5-11 x 5-6 mm, drawn out into a long beak, twice as long as calyx. Fl. 4-6.

Habitat: Grainfields, 610-762 m.

Type: [Turkey/Syria]: prope Alep et Antab [Gaziantep], Aucher 1765.

Distribution in Turkey: East Anatolia (Mesopotamia).

C6 Gaziantep: Kilis, 610-762 m, 25.5.1911, Rechinger 4458.

External Distribution: Syria.

Perennial, plant 20-50 cm or more, with a thick well-developed woody stock, many-stemmed, densely glandular-puberulent to glabrous, especially in the vegetative region. Stem quadrangular, red to green in colour, erect, or ascending, simple to branched. Lower leaves petiolate (petiole 1-4 cm), 1-2-pinnatisect, median shortly petiolate to subsessile, usually becoming sessile in the upper region; lamina 1.5-6 cm long, irregularly to regularly pinnatifid to pinnatisect with 2 or more free basal segments, or pinnate, especially in the lower 1/2-2/3 part of the leaf with distinct petiolate pinnae, the upper part variously dentate to pinnatisect; the free basal segments or pinnae oblong to ± rhomboidal with a dentate to pinnatifid margin. Peduncle 5.5-19 mm; cymes 3-5-flowered; bracteoles 1.3-4 mm, narrowly linear to ± triangular, larger or shorter than the pedicel. Calyx segments oblong or oblong-ovate to obovate, glabrous, scarious margin narrow, white, rarely brown. Corolla maroon, rarely white flushed with red, lower lip concolorous with the upper or white to pale, upper lobes of C-type; stamens short to long exserted, filament glands of oblong type; staminode oblong to nearly reniform. Capsules glabrous, rarely subglobular, mucronate to apiculate, 2-3 times longer than calyx. Fl. 3-7.

**Habitat:** Cliffs, limestone rocks, crevices of metamorphic rocks, 200-2438 m.

1. Lower corolla lip white to white pale; pedicel of the first flower of cyme longer or shorter than the first pair of bracteoles; lamina of the median leaves pinnatifid to pinnatisect, segments ± narrow, sharply dentate to entire-margined; plants sparingly to densely glandular-puberulent; staminode variable.

2. Staminode ovate, obovate to oblong; plants sparsely glandular-puberulent ........................................ i. subsp. variegata

...
2. Staminode obtriangular to reniform, rarely spade-shaped; plants densely glandular-puberulent .......... ii. subsp. depasperata

1. Lower corolla lip concolorpue; pedicel of the first flower of cyme always longer than the first pair of bracteoles; lamina of the median leaves distinctly pinnate in the lower half with shortly petiolate pinnae; pinnae obtusely dentate to obtusely pinnatifid; plants glabrous; staminode ovate or oblong .......... iii. subsp. pinardii

i. Subsp. variegata

Syn. S. laciniata C. Koch in Linnaea 23: 710 (1850);
S. laciniata C. Koch var. adenophora C. Koch. in Linnaea 23: 710 (1850).
S. xylorrhiza Boiss. et Hausskn. in Boiss., Fl. Or. 4: 406 (1879)!

Type: in Saxosis Caucasi, circa thermas Constantinomontanas frequens, Bieberstein.

Distribution in Turkey: E. & S. Anatolia, Islands.
B10 Van: 6 km from Üsälp to Saray, 2250 m, Davis 44286!
C6 Urfa: Urfa, 600 m, Davis 28039!
C6 Hatay: Dört yol, 10 miles from Toprakkale, near sea level, 8-5-1965, Goode & Jones 673!

Islands: Ikaria, K.H. Rechinger fil. 4434! Kalimnos, K.H. Rechinger fil. 7862!

External Distribution: Balkans (Rumania), S. Russia, Crimea, Caucasia, N. & W. Iran, Syria and Palestine.

ii. Subsp. depasperata (Boiss.) Lall, comb. et stat. nov.

Syn: S. depasperata Boiss., Diagn. ser. 1(4): 68 (1844);
Syntypes: Lydia \( \sqrt{2} \) Manisa; mt. Tmolus (Boz Dağ) above Philadelphia (Alaşehir) and Sardes (Sart), June 1842, Boissier; Lydia \( \sqrt{1} \) Aydin; mt. Mesogis (Aydın Da.) above Tralles (Aydın); Caria \( \sqrt{2} \) Denizli; Cadmus (Honaz Da.), Boissier.

Distribution in Turkey: E., S.W. & W. Anatolia.

A8 Gümüşane: S. foot of Soganli Da. N. of Bayburt, 1650 m, Davis 32006!

A9 Kars: Ziyaret Da. (Yalnizcan-Dagları) above Yalnizcan, 2500 m, Davis 30329!

B2 Manisa: mount. Tmolus (Boz Da.), June 1842, Boissier!

B3 Izmir: distr. Odemis, 1900-2000 m, Davis 18204!

B3 Isparta: Sultan Da., on the way Gelendost to Alaşehir, 1500 m, 3.6.1935, Boissier!

B7 Erzincan: Keği Da. above Cimin, 1900-2100 m, Davis 31770!

B8 Erzurum: about 14 km from Erzurum to Pasinler, 2000 m, Davis 47432!

B9 Erzurum: about 20 km from Horasan to Tahir, 1700 m, Davis 47296!

B9 Van: Varek Da., 2438 m, Ch. Kronenburgh 25a!

External Distribution: Caucasus, N. & W. Iran.

iii. Subsp. S. pinardii (Boiss.) Lall, comb. et stat. nov.

Syn: S. pinardii Boiss., Diagn. ser. 1(4): 70 (1844);

S. lyrata Heywood in Notes R.G.B. Edinb. 21: 81 (1952);

S. rupestris M.B. var. pinnatisecta Heywood in Notes R.B.G. Edinb. 21: 84 (1952);

Type: Hab. in rupestribus Cariae (Pinard!)

Distribution in Turkey: S.W. Anatolia, Aegean Islands.

C2 Afyon: Dinar-Denizli, on fields north of Aci Gölda, 800 m, 12.6.1938, Huber-Morath 5649!

C2 Mağla: distr. Marmaris: Inijdibi, sea level, Davis 41030!

C3 Antalya: (Adalia): 19.4.1860, Bourgeau 176!
Islands: Kalimnos, Forsyth Major 742! Samos, K.H. Rechinger fil. 3592! Kos, K.H. Rechinger fil. 3012! Davis 40475!

Parsa (1946) described a new taxon, S. pinardi var. acutilobata, from N. Iran. On examination of the type material, I considered it to be a form of S. xantho-glossa, and exclude subsp. pinardi from Iran.

Boissier characterized S. xylorrhiza by its undivided to pinnatisect leaves, and a roundly ovate staminode, basing this description of the species on the following syntypes:

- Turkey C5 Icel: Cilician Gates, Balansa 680 (Sub. S. heterophylla)
- Turkey C5 Icel: Gilek Boghas, Kotschy 100 (Sub. S. pinardi)
- Turkey C6 Gaziantep: Tullup distr. Aintab, 23.6.1865, Haussknecht
- Turkey C6 Urfa: Nimrud Da., March 1867, Haussknecht
- Turkey C7 Urfa: Gebel Taktak, Mesopotamia, Haussknecht 737 (lectotype)
- Kotschy 121 (Sub. S. caesia var. pumila)
- Palestine: Turfileh, Roth 396

Kotschy 100 and Balansa 680 are in fruit (as Boissier mentions, Fl. Or. 4: 46). The lamina in these two syntypes is undivided to pinnatifid at the base, and as the specimens are in fruit nothing can be said about the staminode shape; Boissier presumed the staminode to be roundly ovate. The above two gatherings in no way differs from S. rupestris var. libanotica in general facies and I consider them to belong to that variety.

In the rest of the 5 syntypes the lower leaves are pinnatisect and the segments vary in shape, size, dentation etc. Haussknecht 23.6.1865 is in fruit, so again nothing is known about the staminode shape. In the rest of the 4 syntypes the staminode is as described below: Nimrud Da., 1867, Haussknecht (ovate, acute, Fig. 17; 98); Haussknecht 737 (oblong, Fig. 17; 97); Kotschy 121
Eig (1943, P. 85) mentioned the following two specimens from Palestine: E. Wadi Musa and Petra (17.iv.1929, Eig & Zohary!), and Wadi Musa village (29.iii.1936 Eig, Feinbrun & Zohary!). He described the staminode in these as well as in Haussknecht's specimens as oblong-linear. The staminode in both of these specimens is ± obovate (Fig. 17; 83, 100). The first of the above two specimens is S. variegata and the second S. rupestris var. libanotica.

S. xylorrhiza, as understood by the author, is a mixture of S. rupestris var. libanotica and S. variegata. Kotschy 100 and Balansa 680, as already mentioned, represent misidentified material of S. rupestris var. libanotica and the rest of the syntypes are S. variegata. If Haussknecht 737 is chosen as a lectotype, then S. xylorrhiza becomes a synonym of S. variegata.

Freyn based his description of S. micradenia on Kronenburgh 25 from Van; there are two distinct gatherings under this number in Geneva, which I have designated as 25a and 25b. I have chosen 25a as the lectotype of S. micradenia as it agrees with the type description; 25b represents misidentified material of S. rupestris var. libanotica. For staminodes of these see Figs. 16-17; 76-77, 103-104.

S. grossheimii intergrades in staminode and leaf characters, on the one hand, with S. micradenia and S. depauperata, and on the other with S. variegata; all the three taxa belong to S. variegata sensu lato. For staminodes of these see Fig. 17; 101-110.

S. lyrata and S. rupestris var. pinnatisecta are indistinguishable from S. variegata subsp. pinardii and should be treated as synonyms of the latter. For the staminodes of these, see Fig. 17; 90 (D.15366A, D.15366B).
Perennial, 90-120 cm. Stem erect, red, glabrous, subquadrangular, simple, or slightly branched in the region of inflorescence. Leaves lyrately pinnatisect to pinnate, terminal lobe much larger, lateral lobes lanceolate, sharply dentate, acute. Inflorescence aphyllous, lower floral leaves shortly petiolate, elliptic, entire-margined, glabrous; the upper subsessile to sessile, narrowly oblong to linear, acute. Cymes 9-5-flowered; peduncle 2-2.5 cm, sparingly glandular, pedicel 7-20 mm, extremely divaricate; bracteoles 3-5 mm, sessile, linear, densely glandular to nearly glabrous. Calyx segments densely glandular to glabrous, ovate-oblong to obovate, 3-4 x 2-3 mm, scarious margin white, 0.8-1 mm wide. Corolla purple, 6 mm long, twice as long as calyx, upper lobe of O-type; stamens included, filament glands of oblong type; staminode transversely longer, twice as long as calyx.

Habitat: Limestone rocks, 1350 m.

Type: Turkey C 5 Içel: in fauce Guzel Dere, Cilicia littoralis supra Sedichig, Balansa: Mai:jam fructifera.

The following specimen may be conspecific: Ch. Içel; Kirobaçi, Kirobaçi-Silifke, 17 km S. of Kirobaçi, 1350 m, Huber-Morath 10315, but differs from the type in its shorter pedicels (7-8 mm) and glandular calyx segments; it is otherwise a good match.

Endemic. Related to S. tagetifolia from which it differs in its larger pedicels (20 mm), divaricate cymes, and perennial habit. Huber-Morath 10315 can be distinguished from S. tagetifolia by its glandular calyx segments, divaricate cymes and perennial habit.

Biennial, 60-100 cm. Stems erect, simple or branched, glabrous in the lower, sparingly glandular in the upper region, subangular. Leaves shortly petiolate, bipinnatisect or bipinnatifid with elliptic to narrowly elliptic deeply toothed segments. Inflorescence aphyllous; peduncle 3.3 cm, woody, cymes 15-7-flowered; pedicels 8 mm, woody, glandular; bracteoles 6 mm, narrowly oblong to narrowly triangular, almost glabrous. Calyx segments broadly ovate to orbicular 4 x 3.5-4 x 5 mm, glabrous, scarious margin white, 1-1.5 mm wide. Corolla 6 mm long, lobes concolorous, upper of C-type; stamens included, filament glands of oblong type; staminode obtiangular or roundish slightly longer than broad. Capsule broadly ovate 5 x 5 mm, apiculate, slightly longer than calyx. *Fl. Or.* 4: 5.

Habitat: Grainfields.

Type [Turkey C5 Hatay/Syria]: Hab. ad Segetes Syriæ borealis ad Samandara inter Aleppo et Aintab, 21.4.1865, Haussknecht!

Eig recognised for Turkey *S. tagetifolia* Boiss. et Hausskn. subsp. *diversifolia* Eig in Pal. Journ. Bot. J. ser. 3: 83 (1941). The syntypes (which have not been seen) are as follows:

Syntypes: [Turkey C5 Icel]: Gökne NW of Mersin, 1000-1100 m, in a maquis (16.8.1931, Eig, Zohary); there, shady rocks (17.8.1931, Eig, Zohary); there, in a Pinetum Brutiae (16.8.1931, Eig, Zohary); there, fields (7.8.1931, Eig, Zohary).

He distinguished subsp. *diversifolia* from subsp. *tagetifolia* (by comparison with the original description of the latter; he did not see the type specimens of subsp. *tagetifolia*) by its few flowered cymes. A comparison of the original description of subsp. *diversifolia* with the type specimens of subsp. *tagetifolia* shows that the former differs from the latter by its few flowered cymes (5-2 vs.
15-7-flowered), reniform staminode (obtriangular to roundish in subsp. tagetifolia) and slightly longer calyx segments. Type material of both taxa needs to be compared before the status of Eig’s subspecies can be settled.

Perennial, 68 cm, nearly glabrous, several-stemmed. Stem erect, purplish especially near the base, quadrangular, branched, branches arranged in a candelabrum fashion. Lower leaves pinnatisect (segments narrow, dentate, 2.5–6 x 1–2 mm), petiolate (petiole 2 cm) gradually becoming sessile in the floral region; floral leaves lanceolate, apex acute, margin dentate. Cymes distant, 5–1-flowered; peduncle 2–3 cm; pedicel 6–11 mm, glandular; bracteoles narrowly oblong, acute, glandular, 3–4.5 mm, shorter than the pedicel. Calyx segments ovate to obovate, 2–2.5 x 1.5–2 mm, glabrous, scarious margin white, 0.6 mm wide. Corolla dark reddish brown, 6.5 mm, upper lobes of C-type; stamens slightly exserted; filament glands of oblong type; staminode broadly cordate. Capsules globular, 3.5–4 x 4.5–5.5 mm, apiculate, 1.5–2 times longer than calyx.

Fl. 5–7.

Habitat: Rocks, 2000–2100 m.

Type: [*Turkey C3 Antalya*]: Çalbali Da., 14.7. 1949, Davis 15293 (Holo. K!, iso! E).

Endemic. Known only from the type. Allied to *S. variegata* subsp. *depanzerata* from which it differs in its narrower leaf segments, broadly obovate staminode and the peculiar candelabrum branching habit.

Syn: *S. livida* Sibth. et Sm., Fl. Graec. Prodr. 1: 437 (1806);
*S. glauca* Sibth. et Sm., Fl. Graec. 5: 78, tab. 599 (1827);
*S. filicifolia* Mill. var. minor Boiss., Diagn. 1 (4): 70 (1844);
*S. lucida* var. boissieri Benth. in D.C., Prodr. 10: 312 (1846);
*S. sphaerocarpa* Boiss. et Reut. in Boiss., Diagn. 2(3): 158 (1856);
*S. rutaefolia* Boiss., Fl. Or. 4: 404 (1879);
*S. lucida* var. genuina Boiss., Fl. Or. 4: 405 (1879);
*S. lucida* var. filicifolia Boiss., Fl. Or. 4: 403 (1879);
*S. livida* Heldr. in herb, norm. 738 ex Nym., Conspr. 534 (1881);

Perennial or biennial, 40-130 cm, one to few-stemmed, glabrous, rarely sparingly glandular-puberulent. Stem simple, or branched, erect or ascending, greenish to purplish-black, shiny, acutely quadrangular. Basal leaves petiolate, thick, oblong, spatulate to round; apex obtuse; margin deeply bicrenate to lobate. Lower median leaves 7-20 cm long (petiole 3-8 cm), deeply lyrate pinnatifid to tripinnatisect; primary segments 1-4 x 0.5-2 cm, oblong, ovate, lanceolate, or round in outline; margin crenate or dentate to variously pinnatisect. Inflorescence aphyllous, bracts lanceolate to narrowly triangular; lower 6-20 x 1-10 mm, pinnatifid to entire margined, gradually diminishing in size in the upper region. Cymes alternate, distant, 15-3-flowered, usually once, rarely twice dichotomous; peduncle 0.8-3 cm; pedicel 0.5-1 mm, bracteole 2-8 mm, glandular. Calyx segments ovate to orbicular, 1.5-4.5 x 1.2-3.5 mm, glabrous, scarious margin 0.5-1.5 mm wide. Corolla 4-8 mm, tube pale brownish pink to dirty white red, upper lobes (of *C*-type) brownish pink to maroon; stamens included, very rarely slightly exserted, filament glands of oblong type; staminode reniform. Capsules glabrous, rarely subglobose, 5-4 x 5.5-3.5 mm, twice as long as calyx. Fl. 3-6.
Habitat: Limestone cliffs, rocks, slopes, scree, dry river beds, 10-2200 m.

Described from "Orient", Tournefort, Linn. 773/18!

Distribution in Turkey: W.S. & N.E. Anatolia, Islands.

A8 Çeruh (Artvin): Ziyaret Da., (Yalnızçan-Dağlari) between Ardahan & Artvin, 2200 m, Davis 30292!

B1 İzmir: Yamanlar Da., Karagöl, in Macchia on the slope east of the lake, 9.6.1966, Reino Alava 5082!

B6 Mersin: distr. Gıksun, Binboğa Da., in ravine above Yalak, 2000 m, Davis 20126!

C2 Muğla: distr. Fethiye, Xanthus, 10 m, Davis 25456!

C3 Burdur: Burdur-Antalya, 720 m, Davis 35687!

C4 Antalya: distr. Alanya, 7 km, S.W. of Alanya, 20 m, 15.5.1956, Huber-Morath 14005!

C6 Hatay: Belen, Soğuk-Derebağçe, 25.v.1933, Reese!


External Distribution: France, Italy, Cyprus, Greece, Aegean, Syria.
39. *S. mersinensis* Lall, sp. nov.

Perennial, 40 cm, many-stemmed, except for the inflorescence nearly glabrous. Stem simple, erect or ascending, subangular, dark-purple especially in the lower region. Leaves 9.5 cm long, long-petiolate in the lower, gradually becoming sub-sessile in the upper most region, lyrately bipinnate, primary segments or pinnae petiolate, 2.5 x 1.2 cm, ovate, lyrately pinnatifid to pinnate; ultimate segments crenate-mucronate. Inflorescence subfoliate to aphyllous, cymes 7-5-flowered, first pair of cymes opposite; peduncle 1.4-1.8 cm; pedicel 6.5-14 mm, densely glandular; bracteoles narrowly oblong, acute, glabrous, 4.5-7 mm, smaller than the pedicel. Calyx segments 3.5 - 4 x 1.8-2.2 mm, ovate to obovate, glabrous, scarious margin white, 1.5-2 mm wide. Corolla pale pinkish brown, 9 mm long, stamens exserted, filament glands of oblong type; staminode reniform. Capsules unknown

*Fl.* 4-?

**Type:** *Turkey C4 Içel*: prov. Mersin, distr. Gûlnar; Bozaç-Ahirini, between Gûlnar and Gîlnûre, 700 m. On limestone-rocks in deciduous oak forest.

Perennial. Flowers pale pinkish brown. 14 April 1956, Davis 26041 (Holo: E; iso, K).

**Distribution in Turkey.** - **S. Anatolia**

Endemic; only known from the type. Related to *S. lucida* L. from which it differs in its elongate pedicels (6.5-14 mm) which are longer than the bracteoles, and the calyx segments with a wider scarious margin.
Davis 26, 041, 046, Selinin.
Scrophularia magnum L. 

Turkey, Prov. Erein, dist. Selinar; between Selinar and Silindire, 700 m. On limestone rocks in deciduous oak forest.
Perennial, Fls. pale pinkish brown, 14 April 1956.

Plate 1.20


Biennial or perennial, 30-40 cm, several-stemmed, glabrous except in the floral region. Stem ascending or erect, purple to blackish, quadrangular, simple or branched. Leaves 3.4-8 cm, pinnate (petiole 1.2-3.8 cm), green to purplish-black, bi-tripinatissect, segments narrow, 1-3.5 x 0.3-0.7 mm, upper subsessile; the floral leaves gradually becoming small, sessile, linear, and entire-marginated. Cymes 6-3-flowered, upper 2-1-flowered; peduncle 0.7-2 cm; pedicel 1-6.5 mm; bracteoles 2-10 mm. Calyx segments ovate to obovate, glabrous, 1.8-3 x 2.3-2.5 mm, scarious margin white, 0.3-0.5 mm wide. Corolla 4.5-6 mm, upper lobes (C-type) maroon, lateral and the median greenish to maroon; stamens included or shortly everted, filament glands of oblong type; staminode reniform. Capsules 5x5 mm, apiculate, globular, 2-2.5 times longer than calyx. Fl. 5-8.

Habitat: Dry rocky places, igneous slopes, screes, 2100-2300 m.

Type: Turkey Ch. Antalya: Hab. in rigione Superiori montis Gheidagh Cheyik Da., Tauri Isaurici, 1829 m, Hessler (K).

Distribution in Turkey: NW. & SW. Anatolia.

A3-4: Bolu: Ala Da., 2100-2200 m, Davis 37394!

Ch. Antalya: Geyik Da., 2200-2300 m, Davis 14364!

External Distribution: Greece.

Approaching some forms of *S. lucida* L. in general facies but differing in its extremely narrow ultimate leaf segments and elongate pedicels which are longer than the bracteoles. Also related to *S. subaequiloba* Lall which can be easily distinguished from it by the subequal corolla lobes and the staminode with a dorsal canal.
Boissier distinguished \textit{S. laxa} from \textit{S. myriophylla} by its thicker leaf segments and longer (twice as long) flowers. Since these distinctions break down I have reduced the former to a synonym of the latter.

Biennial, 30 cm, minutely glandular-puberulent throughout. Stem subsimple, red, ± terete, ascending. Leaves small alternate, petiolate in the lower region, becoming gradually sessile in the upper region, 2.5 cm long (including petiole); liratately pinnatisect, pinnae elliptical, margin sharply dentate. Lower 1-3 floral leaves lanceolate deeply pinnatifid, gradually becoming narrowly linear, entire-margined. Cymes shortly pedunculate (peduncle 1 cm long); pedicel 4.5 mm, glandular, longer than the bracteoles; bracteoles oblong-linear, acute, glandular 2.5 mm. Calyx segments glabrous, 3 x 2.5 mm, ovate-obtuse to obovate; scarious margin white, 0.7-1 mm wide. Corolla 6.5-7 mm, dirty brown red, upper lobes C-type; stamens included filament glands of both type; staminode + orbicular. Capsules globular, long mucronate, slightly longer than the calyx (immature).

Fl. ?

Habitat: unknown.

Type: /Turkey B8 Erzurum/ 'Prope Erzurum', Calvert 984. (G!).

Endemic. Related to S. canina and S. myriophylla from which it can be distinguished by its alternate leaves with broader segments, and also to S. variegata M.B. subsp. variegata, from which it differs in its biennial habit, simple stem, and alternate leaves.
42. *S. canina* L., Sp. Pl. 865 (1753).

Perennial, 30-100 cm or more, woody at the base, many-stemmed, nearly glabrous. Stem simple or branched, quadrangular, purple or purplish-green, especially in the lower region, striate. Lower leaves petiolate, upper subsessile gradually becoming sessile in the floral region; 1-2-pinnatisect; primary segments oblong to lanceolate, entire-margined or variously dentate to pinnatisect especially in the lower region. Lower floral leaves pinnatisect, usually tridentate, upper lanceolate to linear, entire-margined. Cymes distant, alternate, 11-3-flowered, usually once rarely twice dichotomous, with 2-4 resulting straight or slightly zigzag monochasia; pedicel 1-2 mm; bracteoles 4-8 mm. Calyx segments ovate to orbicular, 1.3-2.5 x 1.8-2 mm, glabrous, scarious margin white, entire-margined to lacerate, 0.5-0.7 mm. Corolla 2.5-5 mm, maroon, upper lobes (of C-type) with or without a white or yellow border; stamens short to long exserted, filament glands of oblong type, staminode narrowly oblong to oblong-lanceolate. Capsules globular, 3.5 x 4 mm, apiculate, twice as long as calyx. Fl. 4-7.

Habitat: Sandy shores, salt marshes, cultivated fields, dry rocky slopes and also on hard, dry clay and shale near streams, 0-1500 m.

1. Upper corolla lobes without a white or yellow border ...... i. subsp. *canina*

1. Upper corolla lobes with a yellow or white border ...... ii. subsp. *bicolor*

i. Subsp. *canina*

Syn: *S. pinnata* Mill., Gard. Dict. ed. 3: 15 (1768);
*S. multifida* Lam., Fl. Fr. 2: 336 (1778);
*S. pinnatifida* Brot., Fl. Lusit. 1: 292 (1804);
*S. lucida* Pall. ex Bieb., Fl. Taur.-Cauc. 2: 78 (1808);
*S. atropurpurea* Moretti, in Bibl. Ital. 12: 372 (1818);
S. ramosissima Uriv. in Mém. Linn. Soc. 1: 331 (1822);
S. juratensis Schleich ex Wydler in Mém. Soc. Phys. Genév. 2: 164 (1838);
S. pyramidalis Wydler in Mém. Soc. Phys. Genév. 2: 164 (1838);
S. pubescens Hort. ex Sweet, Hort. Brit. ed. 2: 392 (1830);
S. hoppii Mert. et Koch., Deutschl. Fl. 4: 410 (1839-45);
S. ruta-canina Bubble in Fl. Pyr. 1: 345 (1847);
S. tenuisecta Jord. ex Nym., Consp. 1: 534 (1881);
S. humifusa Timb. ex Nym., Consp. 1: 534 (1881);

Described from Italy (hb. Cliff., BM)

Distribution: C. & S. Europe, Crimea, S. Russia, N.W. Iran, N.W. Africa.

None of the specimens seen from Anatolia is referrable to S. canina subsp. canina, and it seems that the taxon in question does not grow in Turkey.

ii. Subsp. bicolor (Sibth. & Sm.) Greuter in Chloris Kythereia (Boissiera13) 109 (1967).

Syn: S. bicolor Sibth. et Sm., Fl. Graec. Prodr. 1: 437 (1806);
S. chrysanthemifolia Willd., in Hort. Berol. 1: 59 (1816);
S. canina L. var. bicolor (Sibth. & Sm.) Vis., Fl. Dalm. 2: 159 (1847);
S. heldreichii Boiss., Diagn. 2 (3): 158 (1856);
S. floribunda Boiss. et Balansa in Boiss., Diagn. 2 (3): 158 (1856);
S. canina L. var. floribunda (Boiss. et Bal.) Boiss., Fl. Cr. 4: 419 (1879);

Type: in Sicilia, Sibthorp.

A1(E) Tekirdağ: on the way from Naiphy to Isiklar, 30.4.1967, Baytop 10876.
A2(E) İstanbul: Rumelihisari-Bosphore, 26.6.1918, Post.
A2(A) İstanbul: Rumelihisari-Bosphore, 26.6.1918, Post.
A4 Kastamonu: Daday to Azdavay, 10 km from Daday, 1200 m, Davis 38643.
A5 Sinop: Boyabat to Sinop, Davis 38068.
A6 Samsun: Ladik, 900 m, 26.6.1965, Tobey 1166.
B1 İzmir: Çeşme, 10-50 m, Davis 41816.
C1 Muğla: near Selimiye, 170 m, Davis 40722.
C3 Isparta: Eğridir, 29.5.1955, Baytop 4251.
C4 Konya: Ermenek, 10.6.1948, Reese.
Islands: Lesbos, K.H. Rechinger fil. 5862; Khios, Khios-Epos, 600 m, Huber-Morath 5651; Samos, K.H. Rechinger fil. 3860; Kalimnos, Forsyth Major 25; Kos, Kephalos, K.H. Rechinger fil. 8068.

External Distribution: Crimea!, Balkan-Peninsula!, Austria!, Switzerland!, Sicily!, Corsica!, Hungary!, Germany!

Related to S. xanthoglossa, from which it differs in its white or yellow bordered upper corolla lobes and the staminode shape. In the absence of the flowers it is impossible to separate the two species.

S. canina is perennial but can flower in the first year, and some of the plants collected in the first year look annual or biennial. Boissier's S. heldreichii, which was distinguished from S. canina only by its biennial habit, probably represents one of the plants of S. canina subsp. bicolor collected in the first year. In the absence of any other difference, I do not see any justification for keeping it as a separate species.

Perennial, 30-45 cm, many-stemmed, woody at the base, glabrous. Stem woody, slender, erect, quadrangular, simple or branched. Leaves pinnatisect with 1-3 pairs of primary segments, the terminal segment longest, 8-30 x 0.6-2 mm, the laterals 3-20 x 0.6-1.5 mm, entire-margined; upper leaves long, linear, entire-margined, up to 60 x 2 mm; gradually diminishing in size in the floral region. Peduncle 1.6-2.3 cm, cymes distant, 5-3-flowered, upper 2-1-flowered. Calyx segments ovate to orbicular, 2.2-2 x 1.8-2 mm, glabrous, scarious margin white, lacerate, 0.5-0.6 mm. Corolla 4-4.5 mm, maroon, upper lobes (of C-type) purple, the laterals and the median lobes with a white border; stamens long exserted, filament glands of oblong type; staminode narrowly oblong. Capsules ovate, apiculate, 3.5-4 x 2.8-3.5 mm, twice as long as calyx. Fl. 4-6.

Habitat: Rocky places, basalt ruins, etc., 1500 m.


Distribution in Turkey: E. Anatolia.

A7 Gümüşane: distr. Gümüşane, Gümüşane-Bayburt, 31 km. S. of Gümüşane, 1500 m, Huber-Morath 14003!

External Distribution: Caucasus.

Approaching some forms of *S. striata* Boiss. in general facies but can be readily distinguished by its linear staminode; also related to *S. canina* L. but differing from it in its delicate stems, and pinnatisect leaves with 1-3 pairs of long and extremely narrow, entire-margined leaf segments.

The Turkish specimens differ from the Caucasian plants in having the upper corolla lobes with a yellow border showing an affinity with *S. canina* L. subsp. *bicolor* (Sm.) Greuter which is common in Turkey. Boissier (Fl. Cr. 4: 413) has transferred the Iranian syntype of *S. thesioides* (Buhse 1339).
44. S. striata Boiss., Fl. Cr. 4: 413 (1879).


Perennial, 30-60 cm, many-stemmed, sparingly glandular-puberulent. Stem erect or ascending, simple to much branched, quadrangular, usually thin and woody, green to purplish-green. Lower leaves petiolate, upper subsessile gradually becoming sessile in the floral region; pinnatisect, segments usually narrow entire-margined to dentate, occasionally broad (especially in the lower leaves in the first year); rarely some of the lower leaves bipinnatisect but the segments extremely narrow (4.5-12 x 0.8-1.2 mm). Lower floral leaves pinnatisect to dentate, upper narrowly oblong to linear, entire-margined. Cymes alternate, distant, 9-5-flowered, (rarely up to 25-flowered if the cymes twice dichotomous); peduncle 1-2.2 cm; pedicel 1-1.8 mm; bracteoles 4-8 mm, glabrous to sparingly glandular. Calyx segments oblong or ovate to obovate, 1.8-2.5 x 1.2-1.5 mm, glabrous, scarious-margin 0.5-0.6 mm wide. Corolla 4-5 mm long, maroon, lateral and the median lobes with a white border, upper lobes of C-type; stamens short-, to long-exserted, filament glands of round type; staminode orbicular, nearly as large as the upper lip, white to pale, margin usually crenate. Capsule 4 x 4.5 mm, globular to subglobular, mucronate, 2-2.5 times longer than calyx. Fl. 4-6.

Habitat: Fallow fields, limestone ridges, slopes, clay and volcanic rocks, 700-1300 m.

Syntypes: Hab. in montibus prope Jezd Persiae orientalis ad Pagum Deh Ballo (Buhse 1339), in Persia loco non notato sub S. bicolori (Kotschy 871, Derderian), prope Ichredabad, Kerman, Ispahan (Bunge). Pennell cited the following specimen as 'topotype': Persia Yesd, Bornmüller 4997.

Distribution in Turkey: E. (Southern) & C. Anatolia.
B5 Niğde: Hasan Da. above Taşpinar, 1300 m, Davis 27947!
C6 Gaziantep: distr. Nisib; Nisib-Birecik, 400 m Davis 27947!
C6 Urfa: Urfa-Akçakale, 450 m, Davis 28163!
C8 Siirt: 15 km S.W. of Siirt on the way to Erüh, 500 m, 17 5 1966, Eiselt!
C9 Mardin: Hessana at foot of Cudi Da., 900 m, Davis 4281!

External distribution: Iran, Afghanistan, W. Pakistan, India, C. Asia (Turkmenistan, Pamir-Alai).

Related to S. xanthoglossa Boiss. from which it differs in more numerous and delicate stems, pinnatisect leaves with a median to broad primary segments, and perennial habit. S. xanthoglossa can be either biennial or perennial.

Extreme forms of S. xanthoglossa and S. striata are very distinct, but intermediates occur (Coode & Jones 247, from C5 Adana; Davis 28367, from C8 Mardin, and Sintenis 472 from C6 Urfa). Extreme forms of S. striata approach S. thesioides in habit but can be easily distinguished by their staminode shape.
45. *S. xanthoglossa* Boiss., *Diagn.* ser. 1 (12): 38 (1853)

Syn:  
*S. decipiens* Boiss. et Ky. in Boiss., *Diagn.* ser 2 (3): 156 (1856);  
*S. hispidula* Boiss. et Bal. in Boiss., *Diagn.* ser. 2 (6): 157 (1859);  
*S. aintabensis* Boiss. et Hausss. ex Boiss., *Fl. Cr.* 4: 413 (1879);  
*S. expansa* Reut. ex Boiss., *Fl. Cr.* 4: 413 (1879);  
*S. orientalis* Ehrenb. ex Boiss., *Fl. Cr.* 4: 413 (1879);  
*S. xanthoglossa* Boiss. var. *genuina* Boiss., *Fl. Cr.* 4: 413 (1879);  
*S. xanthoglossa* Boiss. var. *decipiens* Boiss., *Fl. Cr.* 4: 413 (1879);  
*S. xanthoglossa* Boiss. var. *hispidula* Boiss., *Fl. Cr.* 4: 413 (1879);  

Perennial or biennial, 2-120 cm, a few to many-stemmed, glabrous, rarely glandular-puberulent. Stem erect, thick and fleshy or thin and somewhat woody, quadrangular, simple or branched, green or reddish to purplish, especially in the lower region. Lower leaves petiolate, 4-12 cm, bipinnatifid to tripinnatisect; primary segments ovate elliptic to lanceolate or oblong in outline 10-38 x 5-18 mm; dentate to bipinnatisect especially towards the base, upper leaves shortly petiolate, usually becoming sessile. Floral leaves lanceolate to linear, pinnatisect to dentate, gradually diminishing in size and becoming entire-margined. Peduncle 8-33 mm; cymes alternate, 2-5-flowered, once, rarely twice, dichotomous, branches of dichotomy modified into straight or occasionally into zigzag monochasia; pedicel 1.5 mm; bracteoles 4-10 mm, nearly glabrous. Calyx segments ovate to obovate, rarely oblong, 2-4.5 x 1-4.5 mm, broadly scarious-margined, glabrous. Corolla 5-6 mm long, maroon, lateral and the median lobes with a white to yellowish border, upper lobes of C-type; stamens short- to long-exserted filament-glands of oblong type; staminode orbicular, yellowish, nearly as broad as the upper lip, margin usually crenate. Capsules globular, mucronate, 4-5 x 3.5-4.5 mm, twice as long as the calyx. *Fl.* 4-7.
Habitat: Rocky slopes, gorges, Artemisia-Astragalus steppe, edges of wheat- and corn-fields and water courses, 50-1700 m.

Type: Circa Hierosolyman frequens, Boissier. (K!)

Distribution in Turkey: Nearly all over Turkey.
A2 Bilecik: Bilecik, 300 m, Davis 42136.
A7 Gümüşane: Kelkit, 1600 m, 18.5.1960, Stainton 8427.
B4 Ankara: Tuz Gölü, 10 km, south of Sereflikoçhisar, 64-32-84.
B5 Nevşehir: 8 km S E Urgüp, 1200 m, 1.6.1964, Sorger 64-32-84; 950 m, 29.4.1965, Coode & Jones 159.
B6 Malatya: near Akçadağ, 1000 m, Davis 27665.
B7 Elazığ: Maden, 1000 m, Davis 28874.
C4 Konya: 14 km S W of Konya, 6.6.1948, Reese.
C4 Ispı: 50 km W of Mut (Ermenek), 1000 m, 7.6.1966, Sorger 66-29-5.
C5 Adana: Kozan (Anti-Taurus), 300 m, Davis 26606.
C6 Adana: distr. Misis: Nur Da. above Kızıldere, 50 m, Davis 26721.
C6 Maraş: Andirin, 900 m, 17.5.1965, Coode & Jones 1173.
C6 Gaziantep: Dülük Baba, 1100 m, Davis 27877.
C6 Hatay: 5 miles from Belen towards Antakya, 600 m, Coode & Jones 527.

External Distribution: Egypt, Arabia, Palestine, Syria, Iraq, Iran and Caucasus.

Perennial, 65 cm or more, woody at the base, many-stemmed. Stem quadrangular, rigid, branching almost from the base with intricate spreading panicles. Leaves petiolate (the upper subsessile gradually becoming sessile), 1-2 pinnatisect, primary segments narrowly linear 8-35 x 1-2.5 mm, secondary segments smaller, linear. Lower floral leaves pinnatisect, gradually becoming linear and entire-margined in the upper region. Cymes alternate, distant, once or rarely twice dichotomous, branches of dichotomy straight, 2-12 cm long, rigid, monoachasia, each usually bearing 10-30, subsessile flowers. Peduncle 2-4 cm; pedicel 1-2.5 mm; bracteoles 4-8 mm, linear. Calyx segments obovate to orbicular, 1.5-1.8 x 1.5-1.8 mm, scarious margin 0.2-0.4 mm, white. Corolla 4 mm long, upper lobes (of C-type) and the tube purplish maroon, lateral and median lobes white; stamens included, filament glands of both round and oblong type; staminode small, ovate-oblong, base cordate, pale yellow. Capsule 2.5-3 x 3-4 mm, globular, mucronate, twice as long as calyx. *Fl.* 5-7.

**Habitat:** Steep marly bank, dry slopes, rock crevices and waste places, 600 m.

**Type:** *Syria:* Hab. in fissuris ripum prope Beirut; Post 113.

**Distribution in Turkey:** S.E. Anatolia.

**C7 Urfa:** Urfa-Hilvan, 5 km from Urfa, 600 m, Davis 28205!

**External distribution:** Syria, Lebanon, Palestine.

Related to *S. xanthoglossa* from which it differs in smaller flowers, relatively longer median corolla lobe, very long monoachasia branches with 10-many flowers, stem branching into intricate spreading panicles almost from the base, and small, ovate, staminode usually with a cordate base and entire margin and situated just below the point of junction of the upper corolla lobes.

Biennial or perennial, 25-53 cm, or more, erect, many-stemmed, glandular-puberulent, subangular, simple or branched. Leaves pale-green, coriaceous, bipinnatisect with three types of pinnae on the rachis; large pinnatisect, smaller toothed and small, oblong to elliptic, acute, entire-margined. Lower leaves petiolate (petiole up to 2.3 cm long), rarely subsessile; upper subsessile, gradually becoming sessile. Inflorescence aphyllous, bracts linear, acute, entire-margined (rarely the first bract pinnatisect). Cymes 9-4-flowered; peduncle 6.5-11 mm; pedicel 0.5-4.5 mm; bracteoles narrowly oblong to linear, 1.5-7 mm. Calyx segments sparingly glandular, oblong to obovate, scarious margin white, entire to denticulate. Corolla maroon, 6 mm, upper lobes of C-type; stamens shortly exerted, filament glands of oblong type; staminode ovate-acute to oblong obtuse. Capsule globular, 4.5x 4.5 mm, apiculate, 1.5-2 times longer than calyx. Fl. 5-7.

Habitat: Gravel and rocky igneous slopes, 1600-2000 m.

Type: [Azerbaijan]: distr. Lerik, prope P. Zarengy, in Zuvand, 1600 m, in glareosis, 20.5.1946, A. Grossheim et M. Kirpiznikov. (LE).

Distribution in Turkey:

A9 Erzurum: Horasan-Karaargan, 17 miles from Horasan, 2000 m, Davis 29501!

External distribution: Caucasia.
**S. gypsicola Hub.-Mor., sp. nov.**

Biennial, 30 cm, several-stemmed, minutely densely glandular-puberulent. Stem simple, erect, purplish in the lower region, quadrangular. All leaves opposite, purplish-green, lower petiolate (petiole purple, 1.8 cm), upper sub-sessile gradually becoming sessile; bipinnatisect, primary segments 6-9 mm long, secondary 3.5-4.5 x 2-2.5 mm, densely glandular. Inflorescence aphyllous, floral leaves 4 mm long, subulate, glandular, diminishing in size higher up. Lower 1-2 pairs of cymes opposite, upper alternate, distant, 5-3-flowered; peduncle 9-10 mm; pedicel 1-2 mm, glandular; bracteoles 1.5-2.5 mm, glandular. Calyx segments obovate to orbicular, 2-2.5 x 2.5 mm, sparingly glandular, scarious margin white 0.4-0.5 mm wide. Corolla 4 mm long, bright yellow, upper lobes (of C-type) purple inside; staminode long exserted, filament glands of oblong type; staminode round, margin crenate. Capsule globular, 4.5-4.5 mm, mucronate, purplish, twice as long as calyx. Fl. 4-6.

Type: Turkey B6 Sivas: distr. Kangal, Tecer-Gärün, Gipsschutt 37 km S von Tecer, 1570 m, 27 June 1955, Huber-Morath 14004!

Distribution in Turkey: C. Anatolia.

Endemic. Related to the Caucasian *S. olgae* Grossh. from which it differs in staminode shape and bright yellow corolla.
Plate 1.21
256


Perennial, 20-30 cm, many-stemmed at the base, the whole plant thickly covered with whitish-grey, lepidote scales. Stem simple with a few vegetative dwarf basal shoots, each terminating in a single floral stem the following year; basal portion of the stem thick with persistent leaf-bases. Leaves alternate, thick, oblong to linear-spathulate, 3-7 x 0.3-0.7 cm. (including petiole); petiole long, attenuate; tip obtuse, or slightly to deeply tridentate; margin entire, some of the leaves slightly to deeply 5-dentate. Lower floral leaves small, deeply tridentate, upper oblong linear, acute, sessile, diminishing in size. Peduncle 0.8-0.9 cm long; cymes 5-1-flowered; pedicel 1-2 mm, much shorter than the calyx. Bracteoles 2-3 mm, oblong-linear obtuse to subulate, longer than the pedicel. Calyx segments densely covered with lepidote scales and the glandular-hairs, ovate to obovate, 3.5-4 x 3.5-4.5 mm, scarious margin yellow, lacerate, ± plicate, 1.2-2.5 mm wide. Corolla glabrous, greenish, brownish-mauve within, upper lobes of C-type, all the 5 lobes with a yellow border; stamens shortly exserted, filament glands of oblong type; staminode ovate to roundish, acute, margin ± lobed, larger than either of the individual upper lobes. Capsules glabrous, globular, apiculate 4-4.5 x 4-4.5 mm, slightly larger than the calyx. Fl. 5-6.

Habitat: Dry gypseous hillsides, 1200-1500 m.

Type: Armenia, Aucher 2437.

Distribution in Turkey: C. Anatolia.

B6 Sivas: Sarkisla, 1500 m, Davis 32717!

B6 Sivas: 17 km S.W. of Sivas on the way to Sarkisla, 15.vi.1939, Reese!

B6 Sivas: Sivas, 1200 m, Stainton & Henderson 5369!

Endemic. A very distinct species of doubtful affinity. The species is unique in being thickly covered with lepidote scales and is extremely xerophytic in habit.
Species imperfectly known or wrongly recorded


Willdenow described **S. heterophylla** from Crete, and gave the description of the leaf as follows: Lower leaves opposite, fleshy, glabrous, trifoliate, the lateral leaflets oblong, obtuse, six times smaller than the terminal lobe; the terminal lobe deeply divided into 3 unequal lobes, and incised-dentate, obtuse in the upper part, and the upper leaves trilobed or elliptic with an attenuate base and incised-dentate upper part.

However, he did not describe the staminode. Wydler (1828) took **S. heterophylla** in the sense of Willdenow, except that he included it in his subgroup with oblong-acute staminodes (probably he had the same plant in mind that Boissier later on described as **S. pinardi** from Caria). Wydler (1828) described the staminode in **S. urvilleana** and **S. oliveriana** as suborbicular.

Bentham (1846) treated **S. urvilleana** Wyd., **S. oliveriana** Wyd., and **S. micrantha** d'Urv. as synonyms of **S. heterophylla**, and cited the following specimens under it:

**Greece**: Palamide (Zuccarini).

Islands: Ferasiae, Theram (d'Urvillle); Crete (Willd.) - Sibth. et Sm. Fl. Gr. 7: 2, tab. 603.

**Turkey C5 Igel**: Kotsch 378.

**Turkey B2 Manisa**: Caria & Mesogis, 1842, Boissier.

**N. Iraq**: Mount Gara Kurdistanæ, Kotsch 316.

Orient: (Rousseau)


He described the staminode in these as orbicular and amplified the description of the leaf as follows: leaves ovate incised-crenate, obtuse or upper acute with truncate or cuneate base, several pinnatifid or subdissected at the base...
with a few ovate segments. Now S. heterophylla, in the revised sense of Bentham, included plants with an orbicular staminode and undivided to divided leaves. The illustration of S. heterophylla given by Sibthorp and Smith (Fl. Gr. 7: 2, tab. 603) agrees with the original description of this species, but they, like Willdenow did not describe the staminode.

Boissier (1879) transferred the following specimens to S. variegata var. libanotica:

\[\text{Sinai}\]: Arab Petr., mount. St.-Catharine, Bové, Shimper 350!
\[\text{N. Iraq}\]: Mount. Gara Kurdistanæ, Kotschy 316!
\[\text{Turkey C5 Icæ}\]: Kotschy 378!

He did not mention the following specimen from Turkey, although Bentham included it in S. heterophylla, considering it to be an intermediate between S. heterophylla and S. tagetetis; I consider it to be S. rimarum:
\[\text{Turkey B2 Manisa}\]: Caria & Mesogis, 1842, Boissier!

Thus the inclusion of the above mentioned 5 specimens from Sinai (Bové, Shimper 350!), N. Iraq (Kotschy 316!), and Turkey (Kotschy 378!, 1842 Boissier!) in S. heterophylla was due to the Bentham's amplified concept of S. heterophylla, although they do not agree either with S. heterophylla s.s., or with anyone of its synonyms. S. heterophylla, in fact, does not grow in Turkey, Iraq or Sinai.

Boissier accepted S. urvilleana, S. oliveriana and S. micrantha as synonyms of S. heterophylla and added S. cassia (the only genuine synonym) to the list. He described the staminode in S. heterophylla as transversely broader reniform and later workers (Halacsy 1902, Hayek 1931, Rechinger 1943) have accepted this to be typical for the species. The following specimens which conform to the original description of S. heterophylla and have a reniform staminode should be treated as S. heterophylla proper.
Greece: Akropolis, 1843, Heldreich; Spruner, (S. caesia S. & S.);
Th. Orphanides 244;
- Attica, Lycabettos, Heldreich 388 (S. heterophylla Willd. var. caesia Boiss.);
- Laconia, Davis 1153;

The following specimens from the 5 Aegean islands were examined by the author and found to belong to the taxa cited below:

Chios: 1931, Guiol, S. variegata subsp. pinardii (sub. S. heterophylla Willd.);
- K.H. Rechinger fil., 5410, S. rupestris var. libanotica (Sub S. heterophylla var. urvilleana (Wdl.) Weiss.);
- Th. Orphanides 728, S. variegata subsp. pinardii (Sub S. heterophylla Willd.);
- 1846 Heldreich, S. rupestris var. libanotica (Sub S. oliveriana Wyd.);

Ikaria: K.H. Rechinger fil. 4434, S. variegata subsp. variegata (Sub S. heterophylla var. oliveriana (Wyd.) Hay.);

Kalimnos: Forsyth Major 742, S. variegata subsp. pinardii (Sub S. heterophylla);
- K.H. Rechinger fil. 7862, S. variegata subsp. variegata (Sub S. heterophylla var. oliveriana (Wyd.) Hay.);

Samos: K.H. Rechinger fil. 4033, S. rupestris var. libanotica (Sub S. heterophylla var. urvilleana (Wyd.) Hay.);
- K.H. Rechinger fil. 5592, S. variegata subsp. pinardii (Sub S. heterophylla var. oliveriana (Wyd.) Hay.);

Kos: K.H. Rechinger fil. 8012, S. variegata subsp. pinardii (Sub S. heterophylla var. caesia (S. & S.) Weiss);
- Davis 404,75, S. variegata subsp. pinardii.

The above specimens therefore represent a mixture of S. rupestris var. libanotica, S. variegata subsp. variegata and subsp. pinardii, and none of these is S. heterophylla proper. I, therefore, exclude S. heterophylla from Aegean islands and Turkey. See fig. 16; 78-80 & fig. 17, 112-122 for the staminodes.

The true species grows in Greece, Crete and Cyclades.
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Habitat: By the waterspring, 400-500 m.

Type: *Turkey* C6 Hatay: Amanus Mts., Chaklikman, Bithias, 27.viii. 1931.

Eig, Zohary.

Eig related *S. clematidifolia* to *S. antiochia* Post from which he distinguished it by its obtuse, regularly crenate leaves. The photograph of the type suggests that it is a badly damaged form of *S. scopoli*, probably due to grazing. However, in the absence of information on floral characters it is difficult to decide about its exact affinities.
Fig. 14
Fig. 15
Fig. 16

Fig. 17
Map 13. O S. capillaris; ▲ S. ilvensis; ▲ S. chlorantha; ⬤ S. nodosa.

Map 15. F. uniflora.
Map 16. A. S. rustica var. Libocedrus; ▲ var. masogitana

Map 1. Turkish vilayets and grid system.
XII. DISTRIBUTION AND ENDEMISM
Distribution and Endemism

1. Distribution. Besides the internal distribution of the species, which is given under each species, distribution maps are also provided for all the species. In addition, 3 'summary' maps are also given; the first showing the number of widespread, as well as, the endemic species (endemic to Turkey) in each province (map 27, p.286), the second, in which the species growing in each province are indicated by initials (map 28, p.288), and the third, which is similar to the second but shows only the endemic species (map 29, p.294). Allowance, however, must be made for under-collecting in some provinces (e.g. Bingöl, Eskisehir).

A list of abbreviations of these initials is given on page 287. A table (p.283) is also provided in which all the Turkish species are arranged according to the Phytogeographical Regions in which they occur; the Phytogeographical Regions are shown on map 25, p.284, as used by P.H. Davis in Flora of Turkey vol. 1.

A summary of the external distribution of all the species is given, which, though mainly based on specimens seen, has been cautiously supplemented from the literature.
Table 6

Distribution of Species in Turkey arranged according to the Phytogeographical Regions in which they occur. E-S, Euro-Siberian Region (Euxine Province); M, Mediterranean Region (E. Mediterranean Province); I-T, Irano-Turanian Region.

& = More abundant than in other regions.

<table>
<thead>
<tr>
<th>Name of taxa</th>
<th>E-S</th>
<th>M</th>
<th>I-T</th>
<th>Name of taxa</th>
<th>E-S</th>
<th>M</th>
<th>I-T</th>
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<tr>
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<td>0</td>
<td></td>
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Map 25. Geographical areas and ethnographical regions in Turkey.

(1) North Anatolia = Provo-Provo Region
(2) Central & East Anatolia = Ireno-Ireno Region
(3) South & West Anatolia = Mediterranea Region

Caucas.
Map 27. Number of species in each province (or territory) endemic.
List of Abbreviations used in Maps 28 & 29

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<td>nd. S. nodosa</td>
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2. Endemism. Out of the 49 species accepted in the present account, 21 are endemic to Turkey. The percentage of endemism is 43% for the species, and 46% for species, subspecies and varieties combined. Most of the endemic species tend to be concentrated in E. Anatolia, the easternmost part of C. Anatolia (Sivas) and S. Anatolia. N. Anatolia is represented by two endemic species and the Western Anatolia by only one.

Out of 21 endemic species, one belongs to Sect. Ceramanthe and 20 to Sect. Scrophularia.

a) Sect. Ceramanthe. - S. cryptophila is the only endemic member of this Section in Turkey. This is a mesophytic species which grows in the forests and wet shady places in S. Anatolia but has penetrated into the dry Central Anatolian part (where it grows in damp sheltered places along the river banks, etc.) and extends as far north as Istanbul. S. kotschyanana is the nearest relative which extends from the North across the Anti-Taurus to the South as far as Içel, and shows a slight overlap in distribution with S. cryptophila in the Taurus. The two species are taxonomically well distinguished by a number of diagnostic characters (map 9, p. 265).

b) Sect. Scrophularia. - The rest of the 20 species fall into the following 3 subsection. 1. Subaequilobae, 2. Lepidota and 3. Caninæ; the first two subsections are monotypic.

1. Subsect. Subaequilobae. - S. subaequiloba, representing this monotypic subsection, is known only from the type gathering from Munzur Da. in E. Anatolia. This xeromorphic species grows on rocky limestone slopes and approaches the S. Anatolian S. myriophylla in general facies but is unique in its staminode structure. Both of these species grow on dry slopes and are somewhat similar in their ecological requirements. In corolla characters it resembles the
C. Asian *S. heucheriflora*, but is strikingly different in other features. However, the true relationship of *S. subaequiloba* is at present obscure.

2. **Subsect. Lepidotae.** - This monotypic subsection is represented by an extremely xerophytic species which is unparalleled in the genus in being densely covered by lepidote scales. *S. lepidota* grows on dry gypsum in the province of Sivas and holds a taxonomically isolated position in the genus.

3. **Subsect. Caninae.** - The rest of the 18 species fall into the following 4 taxonomic groups.

i) **Ser. Nodosae.** - This includes the following 3 endemic mesophytic species: *S. pegaea*, *S. luridiflora* and *S. capillaris*. *S. capillaris* is well separated from *S. pegaea* and *S. luridiflora*, but the latter two are closely related and differ in two diagnostic and a few differential characters. *S. pegaea* grows in E. Anatolia, while *S. luridiflora* occurs in E. Anatolia and the peripheral region of C. and NW. Anatolia. The two species are probably sympatric in E. Anatolia, but more information is needed on this point (map 11, p. 287). *S. capillaris* is endemic in Rize and is closer to the Caucasian *S. divaricata*. It represents an allopatric relative of the latter but is sufficiently different to be maintained as a separate species.

ii) **Ser. Atropatanae.** - This series is represented by 9 xeromorphic endemic species which differ from the above series in a number of correlated differential characters. *S. davisii* and *S. pumilio* are endemic in Hakkari. The nearest relative of *S. davisii* is probably the Soviet Armenian *S. atropatana*, though the two species are very well distinguished. *S. pumilio* is a small alpine plant which shows a strong tendency towards a racemose inflorescence. This species is of doubtful affinity and is probably distantly related to *S. nachitschevanica*, but differs in a number of diagnostic characters. *S. pumilio* is known only from two small gatherings and until more gatherings are available its relationship remains obscure.
S. pulverulenta and S. catariifolia are closely related endemics. S. pulverulenta is a saxatile species while S. catariifolia is more flexible in its ecological requirements, and although predominantly a saxatile species is also capable of growing along river banks; the former grows at an altitude of 1300 m, while the latter occurs from 880-2000 m. The two species are apparently vicarious but more material is required before this point can be settled. S. pulverulenta is confined to the eastern side of the 'Anatolian Diagonal' and shows a more restricted distribution.

S. serratifolia is endemic in Sivas and approaches some forms of S. rupestris var. libanotica. S. rupestris var. libanotica is widely spread in Turkey and grows sympatrially with S. serratifolia in Sivas. Both species are more or less similar in their ecological requirements and may be reproductively isolated.

S. bitlisica is closely related to S. rimarum. The two species are probably sympatric (map 15) but S. rimarum apparently grows at a higher altitude (S. rimarum 2300-3200 m; S. bitlisica 1550-1829 m). Another endemic species, S. uniflora from W. Anatolia, is probably allied to S. rimarum but is not sufficiently known.

S. hyssopifolia from the Anti-Taurus is somewhat difficult to relate. It shows an affinity with S. canina subsp. bicolor in flower structure, but differs in leaf characters. Another probable alliance is with S. serratifolia from which it differs in a number of diagnostic features. It is known only from the type gathering and its relationship remains obscure.

S. amana is the only endemic species in the Amanus. It is allied to S. variegata but is well distinguished from it. The two taxa, although sympatric in this area, are probably separated by altitude, though more information is needed on this point.

'Anatolian Diagonal': a narrow mountainous belt from the Amanus and Cilician Taurus north-eastwards to Gümüşane.
Ser. Xanthoglossae. - is represented by 5 endemic species in Turkey which are taxonomically well distinguished.

S. gypsicola from Sivas is extremely xerophytic. It is a densely glandular-puberulent biennial which grows on gypsum. The closest relative is the Caucasian S. olgae. These two taxonomically well distinguished vicariads also have different ecological requirements; S. olgae does not grow on gypsum.

S. trichopoda from Iğal is allied to S. tagetifolia but is taxonomically well separated. The latter grows along the borderline of Amanus and Syria and is probably confined to that area.

S. versicolor from E. Anatolia (N. Amanus) is related to S. myriophylla but can be readily distinguished from it. S. versicolor is known only from the type gathering. The two species are apparently vicariads.

The last two endemic species are S. candelabrum and S. mersinensis from S. Anatolia. S. candelabrum is known only from the Lycian gathering and is related to S. variegata subsp. depauperata; the latter grows in W. and C. Anatolia but does not extend as far as S. Anatolia - the two species are probably allopatric (map 19,20). S. mersinensis from Cilicia is closely allied to S. lucida. S. mersinensis is known only from the type material, and S. lucida, although common in Isaurian Taurus, is apparently absent from the Cilician Taurus. The two species are probably allopatric.

Of the 21 endemics discussed above, only 3 species, namely S. capillaris, S. gypsicola and S. davisi, have their relatives outside Anatolia (all in Caucasus). The following 4 species, S. lepidota, S. pumilio, S. hyssopifolia, and S. subaequiloba, are difficult to place and have no immediate relatives. The rest of the 14 species have their nearest allies within Anatolia, with which they are either allopatric or sympatric in distribution. Since several of these endemics
are known only from the type material, only further exploration in these areas can confirm the extent to which they are eco-geographically isolated, and the constancy of their characters.

The available evidence shows that most of the endemic species grow in different areas to their relatives. Geographical isolation may have played a dominant role in speciation. Unfortunately nothing is known about the extent of cyto-genetic barriers between these endemics and their relatives (*S. crytophila* is the only Turkish endemic in which chromosome counts are available, but nothing is known about the cytotology of its nearest relative, *S. kotschyi*). But from what we have learnt from hybridization experiments of the N. American species, it appears that genetic barriers may also be of secondary importance in our part of the world as well, but only future cytogenetic research can settle this question. Genetic or ecological barriers are probably important where endemics and their relatives grow sympatrially, but information on hybridization is totally lacking.

Only 4 species, *S. capillaris, S. luridiflora, S. pegasa* and *S. crytophila*, are mesophytic; the rest of the 17 species, if not completely xerophytic, at least show xeromorphology. Hakkari and Bitlis in E. Anatolia, Sivas in eastern part of the C. Anatolia, and the Anti-Taurus, Cilician and Lycian-Taurus in S. Anatolia, have the highest percentage of endemism. It seems that in Turkey East Anatolia (including Sivas) and South Anatolia have been the most active centres in the speciation of this genus. Some of the endemics occur only on the eastern or western sides of the 'Anatolian Diagonal'. For the distribution pattern of the endemics, see map 29.
Map 29. Distribution of Indigents (see p. 287 for abbreviations).
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XIV. INDEX TO THE SPECIES
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Index to the Species and the Infra-specific taxa

Accepted names are italicized; the first page number refers to the species' position in the synopsis, the second number to the description of Turkish species and their infra-specific taxa. Synonyms (not italicized) are only cited for the Turkish species.

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