FLORAL MORPHOLOGY

IN RELATION TO

ADAPTATION AND TAXONOMY

IN

THE CARYOPHYLLACEAE

BY

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ABSTRACT

The floral morphology of several species in the 3 subfamilies of the family Caryophyllaceae has been investigated from different aspects.

The reproductive biology of the family has been examined to determine if style number and stigmatic area are in any way related to ovule/seed number, and it has been found that there is no positive relationship. The genera in the family have also been placed in groups according to the distribution of the stigmatic papillae and the degree of style fusion. Species in 4 genera, Spergula, Spergularia, Stellaria, Myosoton have been examined in greater detail but again few correlations could be found.

De-styling experiments on 3 5-styled species in the subfamily Dianthoideae have shown that pollen tubes readily cross between 'carpels' in these species and that if only 3 styles remain the number of seeds formed is the same as in 5-styled ovaries.

The vascular tissue of the ovary and the position of the transmitting tissue has been studied in species in the subfamilies Dianthoideae and Paronychioideae. This has revealed that the transmitting tissue is part of the septal tissue and confirmed the views of other authors that the ovary in this family has not evolved from the traditional 'carpel' but that the ovary is composed of a sterile part and a fertile part.

The taxonomy of the subfamily Paronychioideae has been investigated. A Key to the genera has been constructed and a description of each of the genera in this subfamily is given.

CONTENTS

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CHAPTER 1.

INTRODUCTION

The title of this thesis is 'Floral Morphology in Relation to Adaptation and Taxonomy in the Caryophyllaceae.' Morphology in the strictest sense is the examination of the form and structure of an organism, both externally and internally. In studying the structure of a plant, the morphologist has to relate his or her findings to the whole function of the plant, to the plant's environment, and how the morphology of one particular group of plants relates to another particular group. This thesis sets out to examine the taxonomy, reproductive ecology, development and evolution of certain species within this family by careful observation of the floral morphology of the plants concerned using both direct observation on whole flowers and by taking sections of flowers and staining the cells to reveal the internal arrangement of the tissue.

The family Caryophyllaceae, with its 3 subfamilies offers a wide range of species which can be investigated. From an evolutionary point of view, the family is of great importance, in having free central placentation, the homologies of the parts of the ovary have been of controversy, with those supporting the view that free central placentation is only a variation of axile placentation and those who propose the ovary consists of a sterile part forming the outer wall of the ovary and a separate fertile part bearing the ovules; thus the ovary has not evolved from the traditionally accepted carpel bearing ovules on its margins. The species within the family also vary in style number from 1 to 5 (6). Especially of interest is variation within genera and between closely related genera and why this variation should occur and if it is of any adaptive significance. The taxonomy of the family, although extensively studied since its foundation in 1759, remains controversial, especially the status of the subfamily Paronychioideae, with many genera being placed by different authors in different subfamilies and some excluding the subfamily Paronychioideae from the Caryophyllaceae. Within the subfamily Paronychioideae, although recently in part investigated by Chaudhri (1968), many problems still exist in interpretation of the structure of the flower/ ....

flower, especially in the interpretation of stamens and petals.

This thesis has 3 main aims. Firstly, to investigate style number and stigmatic area in relation to ovule and seed number to find out if, or how, style number and stigmatic area affect the ovule and seed number per 'carpel' and per ovary, firstly within the family as a whole and secondly within pairs of related genera selected so that within each pair, the genera are similar except that style number in one is 3 and in the other 5. Related to this study is a study of selected removal of styles to find out how this affects the number of seeds fertilized.

The second aim of this thesis is to investigate the septa in this family from an evolutionary point of view (whether the septa are sterile or whether the septa are fertile and bear the ovules) from a physiological point of view (to study the position of the transmitting tissue) from a taxonomic point of view. Within the 3 subfamilies the disintegration of the septa and the extent the septa grow varies, this is of particular interest in the subfamily Paronychioideae.

The third aim is to examine the subfamily Paronychioideae and investigate the taxonomy of the group, mainly using floral characters, giving a detailed description of each genus.

In order that the work that follows can be seen in perspective, a brief description of the morphology of the family is necessary as only a few genera in the other 2 subfamilies will be examined, although description of all the genera in the third subfamily Paronychioideae are given.

The family Caryophyllaceae of B. Jussieu (1759) Ordin. Nat. Ludovici 15 Hort. Trian. published in A. L. Jussieu, Gen. Plant. (1789) contained only 31 genera of which 9 are now considered to be in different families. As the family stands at present it contains between 70 and 90 genera, depending on where generic limits are made and on the inclusion or exclusion of the subfamily Paronychioideae. The Paronychioideae are considered to be part of this family in this work.

CARYOPHYLLACEAE. B. Jussieu

Annual, biennial or perennial herbs or undershrubs, erect to prostrate. Stems glabrous or pubescent, usually much branched, rarely woody/ ....

woody. Leaves opposite, rarely alternate or spirally arranged, rarely a spiral of leaves at nodes, entire, often petiolate, stipulate or exstipulate, glabrous or pubescent. Stipules when present (subfamily Paronychioideae) usually membranous occasionally connate at base, or adnate to base of leaves, rarely completely adnate to leaf margins. Inflorescence cymose, dichasial or monochasial, terminal, lax or compact, or flowers solitary, or flowers in axils of leaves solitary or in clusters, clusters sessile or on long peduncles. Bracts foliar or membranous. Flowers actinomorphic, bisexual, rarely unisexual and then with rudiments of stamens or ovary, sessile or on pedicels. Sepals 5, occasionally 4, rarely greater than 8 and then arranged in a spiral, connate at margins to form a tube, or only slightly adnate at base to a short or elongated perigynous zone, rarely completely free. Petals 5 or 4, occasionally absent, may be differentiated into a claw and limb and then often with coronal scales, usually entire or dissected if so usually bilobed, usually conspicuous, occasionally small inconspicuous (subfamily Paronychioideae). Stamens in 2 whorls of 5, the second whorl often absent or reduced to staminodes; pollen grains porate or furrowed. Secretory tissue associated with the stamens forming a ring around the base, often extending up the base of antisepalous stamen filaments to form distinct nectary glands on the abaxial surface, a secretory tissue forming a flap in front of base of petal where antipetalous stamens have been lost, tissue not always functional. Ovary superior rarely fused with walls of elongated perigynous zone, may be borne on a gynophore/ stipe, usually unilocular at maturity rarely 3 - 5 locular at base when mature but usually completely septate at an earlier stage in development, with a strand of transmitting tissue usually present from the apex of the ovary to apex of placental column/funicle at anthesis and shortly afterwards; 1 - 400 ovules, basal or arranged on a central placental column. Styles 2 - 5, free or united, stigmatic papillae on adaxial surface of style often with knob or cone of stigmatic papillae at apex or stigmatic area may be greatly reduced to just the knob at apex. Fruit usually a dehiscent capsule, dehiscing by valves or teeth equal or twice in number to carpels, occasionally a 1-seeded indehiscent fruit, rarely a berry or pseudo-berry; embryo curved, rarely straight.

Chromosone number varies greatly: x = 9: Spergula, Herniaria, Corrigiola/ ....

Corrigiola (Blackburn & Morton 1957), Spergularia (Ratter 1963 - 64), Arenaria, Cerastium (Beaman etal 1962), Cerastium Favarger (1976). x = 10: Pleconax, Sourkova 1978. x = 12: Silene (Khoshoo 1960), Agrostemma, Cucubalus, Lychnis, Petrocoptis, Silene, Viscaria, Uebelina (M. Sourkova 1978), Silene (Talavera 1976), Silene, Cucubalus, Viscaria, Lychnis, Paronychia, Agrostemma, Cerastium, Honkenya Minuartia, (Blackburn & Morton 1957.) x = 14: Saponaria, Velezia, Myosoton, Moenchia (Blackburn & J. K. Morton 1957), Saponaria, Velezia (M. Sourkova 1978.) x = 15: Drypis, Acanthophyllum, Dianthus, Vaccaria (M. Sourkova 1978) Vaccaria (Khoshoo 1960) Dianthus (Carolin 1957), with a range of other possible x valves of 5, 7, 11, 13, 16, 17, 18 19.

The family is cosmopolitan, with the genus Colobonthus being one of only 2 phanerogramous plants able to grow, flower and reproduce south of lat. 60° S. in the Antartic (S. W. Greene 1970, D. M. Greene & A. Holtom 1971). Genera are also to be found growing in almost all habitats from seashore to arid areas.

Classification. Three subfamilies, Dianthoideae, Alsinoideae and Paronychioideae are recognised. Until recently, M. Sourkova (1978), the subfamily Dianthoideae has been called Silenoideae (Asch. & Graebn. (1919), Benth. & Hook. (1862 - 67), Pax & Hoffm. (1934), Davis (1966), Komarov (1963), McNeil (1973)) but the type of the family and for this particular subfamily is Dianthus caryophyllus L. The subfamilies are usually separated on the following characters: presence or absence of stipules, sepals connate or free. A typical Key to the subfamily is that of Komarov (1936) p. 297

1. Leaves stipulate subfamily Paronychioideae.
   Leaves exstipulate 2
2. Sepals free, if somewhat connate to the middle then perianth single subfamily Alsinoideae.
   Calyx always with connate sepals, often tubular, pereanth always double subfamily Silenoideae (Dianthoideae).

The degree of fusion of the sepals is difficult to define exactly. McNeil (1973) described the case of a species, placed in the genera Gypsophila, Stellaria, and Arenaria, by various authors, which has calyx lobes usually free to base, 2 free styles, capsule dehiscing by twice as many valves as carpels, bifid petals and frequently/ ....

frequently with basal placentation, not unlike species described in Sect. Dichoglottis of Gypsophila. Gypsophila is, however, placed in the subfamily Dianthoideae whereas both Stellaria and Arenaria are in the subfamily Alsinoideae. McNeil described it in the genus Stellaria, section Oligosperma under the name S. blatteri Mattf. In the subfamily Alsinoideae most if not all the genera are to some extent perigynous, the sepals being adnate to the perigynous zone, although the zone may not be very conspicuous. The sepals can thus not be described as being free in the subfamily Alsinoideae. However, in the subfamily Danthoideae a calyx tube is usually formed rather than a perigynous zone, the stamens and petals not being adnate to the calyx tube. In the subfamily Paronychioideae a perigynous zone is always present.

Stipules are usually easily defined, but the genus Scleranthus, without having well defined stipules, has membranous margins to the base of the leaves and the flower is strongly perigynous with no petals which suggest affinities with the subfamily Paronychioideae rather than Alsinoideae.. A number of genera in the Paronychioideae also have species which do not possess stipules, but are otherwise clearly members of the Paronychioideae.

Subfamily Dianthoideae.

The subfamily contains between 15 and 18 genera with the genus Silene L. containing the largest number of species, somewhere in the region of 400. The following genera are considered to belong to this subfamily: Pleironeura Ankyropetalum Fenzl, Drypis L., Bolanthus Reichb., Allochrusa Bunge., Phryna (Boiss.) Pax and Hoffm., Cucubalus L., Silene L., Petrocoptis A. Br., Agrostemma L., Saponaria L., Viscaria Roeh., Heliosperma Reichb., Lychnis L., Petrorhagia Link, Uebelina Hochst., Acanthophyllum C. A. Mey., Velezia L.

Two tribes are usually recognised, Lychnideae and Dianthoideae, separated by the presence or absence of commissural veins on the calyx tube, a commissural vein being defined as one which is found along the line of fusion of the sepals, consisting of the lateral veins of 2 adjacent fused sepals. The Lychnideae having species which possess commissural veins. A third tribe Drypideae Fenzl is recognised by Bentham & Hooker f. (1862 - 67), Ledebour (1841) and Sourkova (1978) containing the genera Drypis and Acanthophyllum which both have spiny leaves and reduced flowers which form compact inflorescences. Sourkova/ ....

Sourkova (1978) separates this tribe from the previous 2 on the basis of reduced seed number to one, rarely 3, and irregular dehiscence of the capsule, features which can be found in species in the tribe Dianthoideae. Acanthophyllum is also very close to Gypsophila and is often difficult to separate from the Gypsophila/Saponaria/Bolanthus/Allochrusa group in the tribe Dianthoideae. Drypis, although appearing similar to Acanthophyllum has several characters which would suggest that there is no close relationship between the 2 genera.

Firstly the fused calyx of Drypis has commissural veins which would place it in the tribe Lychnideae, secondly, the petals are bifid and have coronal scales whereas in Acanthophyllum the petals are entire and usually without coronal scales. Drypis also has 2 or 3 styles, Acanthophyllum always having 2. Acanthophyllum probably should be placed in the tribe Dianthoideae and Drypis in the tribe Lychnideae in the monotypic subtribe Drypidinae (Pax and Hoffm. (1934) Asch. & Graebn. (1919)).

Subfamily Alsinoideae.

This subfamily contains between 20 and 24 genera placed in 2 or 3 tribes. The tribe Alsineae DC. is usually recognised, although it's 2 subtribes Stellariinae Pax and Sabulininae Asch. & Graebn. may be given the rank of tribe, the subtribes being separated on whether the capsules open by twice as many valves/teeth as carpels as in Arenaria in Stellariinae or the same number as carpels as in Minuartia in Sabulininae. The genus Pycnophyllum is placed in a separate tribe Pycnophylleae, although it is often placed in the subfamily Paronychioideae. Another tribe is also recognised, Merckieae Fenzl, containing the genus Wilhelmsia Reichb. (Merckia Fisch. & Cham & Schlt.) This genus appears similar to Honkenya, both having fleshy capsules. Pax & Hoffman (1934) placed the genus in the subtribe Sabulininae along with Honkenya and Minuartia. Scleranthus and Habrosia sometimes included in this subfamily are placed in the subfamily Paronychioideae. The following genera are placed in this subfamily; Moenchia Ehrh., Pseudostellaria Pax, Myosoton Moench, Brachystemma P. Don., Arenaria L., Hymenella Moc. & Sesse, Welhelmsia Reehb., Lepyrodicilis Fenzl, Moehringia L., Minuartia L., Bufonia L., Honkenya Ehrh., Pentastemonodiscus Reching., Colobanthus Bartl., Thurya Boiss., Schledia Cham. & Schlecht., Sagina L., Thylacospermum Fenzl, Holosteum L., Cerastium L.

Subfamily Paronychioideae

This subfamily is discussed in greater detail in a later chapter. Six tribes are recognised here; Paronychieae, Pollichieae, Pterontheae, Polycarpeae, Scleranthea, Habrosieae. The genera Spergula, Spergularia, Telephium, Habrosia and Scleranthus are considered to be in this subfamily.

Morphology. The main emphasis in this work is on floral morphology, thus only the floral structures are discussed here.

Calyx. There are usually 5 sepals, occasionally 4, and only in the genus Krauseola Pax & Hoffmann, are there somewhere between 5 and 11 sepals arranged in a spiral rather than a whorl. The genera Dianthus and Petrorhagia also have a number of spirally arranged structures around the base of the sepals, but these are considered to be bracts and separate from the calyx.

In the subfamily Dianthoideae, the sepals are always fused into a calyx tube, sometimes with commissural veins, sometimes the line of fusion being membranous. The lobes of the calyx usually have a membranous margin, are occasionally hooded, and sometimes extended by a short spine or mucro. The calyx tube often becomes swollen and is usually persistent in fruit. The petals, stamens and carpels are not adnate to the calyx tube.

A perigynous zone is usually present in the subfamily Alsinoideae to which the sepals are adnate, usually totally but always at least by the central area of the sepals. It is unlikely that in any of the species the sepals are completely free. The sepals again usually consist of a central green area with membranous margins. The 3 veins are usually very prominent and in some genera where the perigynous zone is greatly extended, commissural veins are evident; Thurya, Minuartia, spp. The apex of the sepal is rarely hooded or extended by a short spine or mucro except in Thylacospermum sp.

In the subfamily, Paronychioideae, the perigynous zone is often greatly extended; Lochia, Gymnocarpos, Scleranthus, so that it appears to be a'calyx tube'to which the stamens and petals have become adnate. Commissural veins are again evident e.g. Achyronychia cooperi, in a number of genera. The perigynous zone, however, in all genera in this subfamily is far more conspicuous than in the Alsinoideae.

The/ ....

The apex of the sepals is often hooded and extended by a long spine or mucro, both characters being used in a number of instances to separate genera and to separate species e.g. to separate the subgenera in Paronychia.

Petals. Petals are usually equal in number to the sepals and alternate with them. In Krauseola, the petal number is, however, less than the sepal number and they are not arranged so as to alternate with the sepals. As the sepals are spirally arranged and the petals are in a whorl, the petals tend to be evenly distributed around the rim of the perigynous zone and not positioned in regard to the sepals. The petals are usually large and conspicuous but are occasionally much reduced and shorter than the sepals.

In the subfamily Dianthoideae the petals are very conspicuous, being pink, red or white. The petals are often differentiated into a claw and limb with ligules or coronal scales at the junction. The apex of the limb is often dissected or emarginate, occasionally distinctly trilobed, Ankyropetalum, or bilobed, Drypis, Silene sp., Lychnis sp. The claw often has 2 membranous wings along its length, between which is found the antipetalous stamen filament; Silene sp., Dianthus sp., Bolanthus sp., Allochrusa sp., Phryna sp., Saponaria sp., Petrorhagia sp. The differentiation of the petal into a limb and a claw would appear to be because of the narrowness of the calyx tube. An androginophore is often present, lifting the apex of the petals, stamens and styles above the neck of the calyx tube.

The petals in the subfamily Alsinoideae tend to be white or yellow, entire, emarginate or bilobed, larger than or of equal length to the sepals. They are ovate to lanceolate in shape and are never differentiated into a distinct claw and limb, although the base is often narrowed. At the base, the petals are adnate to the rim of the perigynous zone at the same level as the sepals or slightly above.

In the subfamily Paronychioideae, petals are either present or absent. The genera can be divided into 2 groups, those which possess petals and usually lack antipetalous stamens, and those which lack petals but which possess alternisepalous stamens in the form of staminodes. Petals are usually white but are pink/red in Spergula/Spergularia species and except in a few genera are small, inconspicuous and shorter than the sepals, and are adnate to the rim of the perigynous zone/ ....

zone.

It was suggested by Mattfeld (1938) that the petals in this family are homologous with the secretory glands and are stipule-like basal parts of alternisepalous stamens. However, Arber (1939) points out that glandular tissue is present in Lychnis vespentina Sibtn. against the antipetalous stamens as well as the antisepalous stamens and that the glands are present on the adaxial surface in the Dianthoideae, not the abaxial surface as in some of the species in Alsinoideae which were studied by Mattfeld. Petals may have originated from leaf-like organs and are similar to sepals or they may be staminal in nature.

Stamens. The stamens in this family have often been described as being obdiplostemonous. It is certainly true that in a number of genera in both the subfamilies Dianthoideae and Alsinoideae the antipetalous stamens appear to be the outer stamen whorl: Velezia sp. Dianthus sp. Sagina sp. or for both stamen whorls to be at the same level: Silene sp. Arenaria Sp. Minuartia sp. Honkenya. However, in most of the genera the outer whorl or first stamen whorl, does appear to be the antisepalous one: Dianthus sp., Acanthophyllum sp. Pleinoneura sp. Silene sp. Welhelmsia, Bolanthus sp.

Stroebl (1925) observed the arrangement of stamens in Stellaria holostea and Melandrium rubrum, (Silene dioica) and found that in the former species the antisepalous stamen primordia were initiated before the antipetalous ones and that in the latter the antisepalous stamens were the outer stamen whorl. The sequence of primordia initiation has also been examined in other species. Lyndon (1978) found in Silene coeli-rosa that the antisepalous stamens were initiated immediately after the sepal primordia, with the initiation of the petal primordia more or less at the same time, the antisepalous stamens being initiated prior to the antipetalous ones. Another Silene species, S. vulgaris, has been examined by Satter (1973) in which it was found that the antisepalous stamen primordia were initiated after the petal primordia and before the antipetalous stamen primordia. The stamen primordia are thus diplostemonous. Rohweder (1967) found that antisepalous stamen primordia were initiated before antipetalous stamen primordia in both Vaccaria pyramidata and Agrostemma githago. Further/ ....

Further evidence that the androecium is diplostamenous comes from the work of Thomson (1942) on the vascular anatomy of the flower. In Dianthus sp., Saponaria sp., Lychnis sp., Silene sp., Stellaria sp., Sagina sp., and Spergula sp. it was found that the antisepalous stamen traces arise lower than the antipetalous stamen traces and that in Dianthus sp., Gypsophila sp., Lychnis sp., Silene sp., Cerastium sp., and Arenaria sp. the traces for both sets of stamens arise at the same level. From all this evidence it would appear to be that although in some species the antipetalous stamens may appear to be the outer stamen whorl this is not due to the androecum being obdiplostemanous but to some other cause such as the petals "pulling" the antipetalous stamens towards the outer margin of the flower especially as these 2 structures are often very close together.

In the subfamilies Dianthoideae and Alsinoideae most of the species have both antipetalous and antisepalous stamens, and where the stamens are reduced to a single whorl, it is usually the antisepalous stamens which are retained, except in Colobanthus species, where it is the antipetalous ones. In the subfamily Paronychioideae, the antipetalous stamens are lost in most of the genera which have petals, but in those which lack petals both stamen whorls are present, with the antipetalous stamens reduced to filiform or rarely petaloid staminodes. The antisepalous stamens in the family as a whole tend to mature before the antipetalous ones, although both filaments may reach the same final height. Antipetalous staminodes, however, are usually shorter than the fertile antisepalous stamens in the subfamily Paronychioideae.

Two types of pollen grain are found in the family, those which are porate and those which are furrowed. In the subfamilies Dianthoideae and Alsinoideae, the pollen grains are usually porate, varying in pore number from 12 in Gypsophila (Faegri & Inversen 1964: 198) to 35 - 45 in Agrostemma githago Chanda (1962) and in pollen grain size from 10,/um. to 60,/um. (Erdtman (1952): 101.) In a few species the pollen grains have been found to be furrowed; Silene moorcroftiona Wall., Lychnis himalayensis Edgeur. Arenaria festucoides Benth., Lychnis nutans Benth., Cucubalus baccifer (Vishnu-Mittre & Guptra (1963)).

In the subfamily Paronychioideae both types are found, and in the genus Corrigiola some of the species appear to be 3-porate and others 3/ ....

what agrees with the interpretation of the petals of Mattfeld (1938). (see p. 9)

Carpels. The structure of the carpels, including the styles, will be discussed fully in the following chapters.

CHAPTER 2

REPRODUCTIVE BIOLOGY

2.1 Introduction

In the family Caryophyllaceae, as in other Angiosperm families, the number of styles per ovary is often used to help separate otherwise similar genera, e.g. Spergula from Spergularia, Myosoton from Stellaria. The adaptive significance of style number is unclear, although in simplest terms it might be expected that the more styles present, the more 'carpels', therefore potentially the more ovules and thus the greater the reproductive capacity of the plant. The ovule and seed number of any one species is, however, related to a number of factors, as well as style or 'carpel' number. These factors include:

i. Stigmatic area, in this family related to style length, as the stigmatic papillae are often present on the entire adaxial surface of the style.

ii. Pollen grain number, viability and size.

iii. Number of flowers, produced on each plant per year.

iv. Seed weight, related to the habitat of the species.

v. Environmental factors.

vi. Pollination mechanisms, self-pollinating or out-crossing.

The stigmatic area will determine the number of pollen grains able to germinate and produce pollen tubes per style. Two factors have to be considered in relation to stigmatic area; the first is the density of papillae, and the second is how much of the stigmatic area can realistically be expected to be involved in pollen 'capture'. The density of the stigmatic papillae and size of papillae is likely to be reflected in the size of pollen grains of that particular species. Pollen tubes grow through the cuticle or wall of the papillae/ ....

papillae and in a few cases through the papillae, to the transmitting tissue of the style, the papillae collapsing after the passage of the pollen tube. The papilla number is thus directly related to the maximum number of pollen grains able to germinate and produce pollen tubes, and thus to the maximum number of ovules that can be fertilized. The total stigmatic area may not be involved in pollen grain 'capture'. In a number of species in this family where the stigmatic papillae reach the base of the style it is unlikely that pollen grains are ever found in this area. This is, in part, also related to the pollination mechanism of the species which will be discussed below, where in self-pollination only the very apex of the styles may be involved in 'capture' of the pollen grains, as only the apex touches the anthers.

The size of pollen grains will determine, physically, how many pollen grains can cover the stigmatic area. The pollen grains tend to be larger than the stigmatic papillae, but those species with large pollen grains tend to have larger stigmatic papillae, e.g. Agrostemma githago. The number of pores on each grain may also be relevant; the more pores, the more pollen tubes can be produced from each pollen grain. Should the first pollen tube to grow fail to penetrate the papillae, then another pollen tube may grow until one is successful in penetrating a papillae. Only one pollen tube per pollen grain will be able, however, to grow further and into the transmitting tissue.

The pollen to ovule ratio is often quoted (Ratter 1976) for species when discussing reproductive biology. The greater the number of pollen grains in relation to ovules, the more likely it is that all the ovules will be fertilized. However, a low pollen to ovule ratio does not, in itself, indicate that the opposite is true. In Onagraceae, pollen grains are held together by viscin threads (R. W. Cruden & K. G. Jensen 1979) and thus efficiency is high; the low number of pollen grains produced is enough to fertilize the ovules present, even in Epilobium species. The production of pollen grains may well reflect the pollination mechanism more than anything else. With this in mind, it may be that the amount of pollen produced in each anther will vary in some species. There may well be more pollen produced by antisepalous stamens, which shed pollen grains first, prior/ ....

prior to the style becoming receptive, than in the antipetalous stamens which often shed pollen at about the time the styles become receptive and are thus more likely to be involved in self-pollination than the pollen grains of antisepalous stamens.

Where a large number of flowers are produced on each plant, the number of ovules produced in the first flower will be greater than the number produced in the last flower (Salisbury 1942 p. 61) although there may be no difference in the average number of seeds or ovules formed between plants producing a large number of capsules and a small number except at the lower extremes where ovule/seeds per capsule will be reduced. The number of ovules/seeds in this case is not related to the number of styles, although style length may decrease as the flowering season progresses, but to the nutritive state of the flower. The weight of the seed may also have a direct bearing on the number of ovules/seeds formed. The greater the weight of the seed, related to the amount of nutrient in the seed, will be determined, to a certain extent by the type of habitat in which the seedling and/or mature plant is found growing, whether the community is closed or open. Where the species is found growing in a closed community or a more advanced succession, the greater the likelihood of the seed having a large food reserve (Salisbury 1942 p. 229), whereas those plants growing in an open community are likely to produce seeds with a small food reserve and to produce more seeds.

Geographical variations may also occur between species. A detailed work by Thompson (1973) on populations of Agrostemma githago from different parts of Europe demonstrated the different number of seeds/ovules formed due to the different environmental factors and/or other external factors. Plants grown at high density may also have a reduced seed output (Harper 1977 p. 196) by reducing the amount of basal branching, the number of flowers per plant, the number of seeds per ovary and the mean seed weight. B. A. Schaal (1980), working on Lupinus texensis, found that there was no correlation between seed weight per plant and total number of seeds per plant or seeds per legume per plant, but that seed weight did vary according to the position of the seed in the legume; those nearest the styles weighing the least. Other environmental factors such as the amount of nutrient available to the plant and fungal or viral attack/ ....

attack will also effect the final reproductive capacity of the plant.

In this family, the species are thought to be self compatible (Ratter 1976) and thus self-pollination can occur; but self-sterility has been noted by Knuth (1908) in Dianthus species. Cross-pollination does, however, readily occur, especially in the larger flowers of the subfamily Dianthoideae. A number of insect pollinators have been noted: night flying moths are said to pollinate Silene alba (Baker 1947, Percival 1965), S. otites (Brantjes 1976), Silene species (Knuth 1908); butterflies to pollinate Silene dioica (Baker 1947, Percival 1965), Dianthus barbatus (Percival 1965), Dianthus species (Knuth 1908), Vaccaria (Knuth 1908), Viscaria (Knuth 1908), Lychnis species (Knuth 1908), Agrostemma (Knuth 1908); bees often making holes at the base of the calyx tube in species in the subfamily Dianthoideae to 'rob' the flower of nectar but at the same time pollinating Silene dioica (Baker 1947, Knuth 1908), Spergula arvensis (New 1961, Knuth 1908); mosquitoes in Silene otites (Brantjes 1976) and flies are said to pollinate a number of species in the subfamily Alsinoideae. Cleistogamy has also been recorded in this family in the genera Silene, Sagina and Stellaria (Knuth 1908). In species in which cross-pollination by insects has been recorded, self-pollination is also said to readily occur, especially in those species in which the flower remains open for only a short period of time as occurs in species in the subfamily Alsinoideae. Flowers tend to be protandrous or homogamous and only rarely protogynous in the family. In only a few species is self-pollination impossible. Agamospemy has not been recorded to occur in the Caryophyllaceae.

Style number has been used as a stable taxonomic character because it is thought to be less variable than other floral characters such as stamens, and petals. Variation in stamen number has been noted in a number of species: Myosoton aquaticum (Matzke 1929), Stellaria media (Matzke 1929, Haskell 1949), Spergularia media (Sterk 1969, Ratter 1976), Silene coeli-rosa (Lyndon 1979). Petal number has also been found to vary in Carnation c.v. Dianthus by Garrod & Harris (1974). Variations in stamen and petal number are thought to be induced in some cases by temperature. Style variation has been found to exist not only between species in the same genus; Silene, Arenaria, Cerastium, but also between plants in the same species/ ....

species. In Silene alba (as lychnis alba) Dean (1963) found that in N. American plants 66.6% had flowers with 5 styles and the remaining plants had flowers with styles varying in number from 0 - 4, 6 - 13; each plant having a range of style numbers but not observing any one plant with the total range. The presence of up to 8 styles had previously been noted by Baker (1947), for Melandrium species, a genus in which Silene alba was originally placed and now included in Silene. Warming in 1920 also found Stellaria borealis Bigel to have a range of styles from 3 - 5, Honckenya peploides Ehrh. 3 - 6 styles and Silene furcata Rafin. (as Melandrium affine J. Vahl) 4 - 6 styles.

This chapter discusses the importance of style number, stigmatic area, and pollen grain number and size in relation to ovule and seed number. Three separate, although related studies have been carried out.

The first involved the use of herbarium specimens to observe the number of styles and the extent of fusion of the styles, the stigmatic area of each style and the number of ovules per ovary in the flowers of at least one species of all genera available in the family Caryophyllaceae, some 75 genera (App. 1). As a result of these observations and measurements it was possible to construct a Key to the genera examined using only these characters and to come to some conclusions about the relation of style number, stigmatic area and ovule number in the family.

The second study, involved only a few species in 4 genera. It was felt that a detailed study on a smaller group of genera may either confirm or repudiate the conclusions reached in the first study. In the species examined in this part, a detailed study of the reproductive biology was carried out. The 4 genera were chosen because of the ease in which seeds were produced under greenhouse conditions and, more importantly, because of the similarities between the pairs of genera, differing within each pair in style number. The 2 groups of genera studied were Spergularia/Spergula and Stellaria/Myosoton, the first genus in each group having 3 styles and the latter having 5 styles.

Several observations were made on species in each of the 4 genera above: length of styles, area of stigmatic papillae, number of ovules, number of seeds, the time the flowers remained open, sequence/ ....

sequence of stamen and style development, number of pollen grains in antipetalous and antisepalous stamens. As well as these observations, but related to them, the variation of sepal, petal, stamen and style number was also recorded. Where the styles were found to vary in number from the 'normal' number for the species the number of ovules in that ovary was also recorded to see how 'natural' style variation affected ovule number.

The third study involved de-styling experiments to try and determine the importance of style number to the number of ovules fertilized in a few species in this family. Varying numbers of styles were removed in the species Agrostemma githago, Lychnis coronaria and Silene coeli-rosa. This study is also related to the chapter on carpel morphology.

2.2. Materials and Methods.

In the general survey of styles and ovule number in the family Caryophyllaceae, only herbarium specimens were examined. All the herbarium material was obtained from the Royal Botanic Gardens, Edinburgh (App.1). The flowers were boiled and then dissected, choosing as far as possible flowers that were at anthesis and from the middle of the inflorescence rather than the first formed flower of the cyme. It was not possible, however, in all cases to be sure that the flower was at anthesis, especially where material was limited and where flowers lacked petals and/or were very small. Measurements of the style and stigmatic area were made using a dissecting microscope or microscope with a micrometer eye-piece unit. The number of ovules of the ovary from which the style was taken was also noted. Only 1 flower was in general examined for each species.

In the other 2 parts of the work, all the results are from plants grown from seed in the greenhouse in the Botany Department of Edinburgh University. In the section dealing with Spergula/Spergularia and Stellaria/Myosoton the following plants were used:

Stellaria media

Acc. 30 Aberdeen, Scotland, planted 13.10.78.

Acc. 270 Botanic gardens of Nantes, France, planted 28.11.78 & 9.11.80.

Acc./ ....

Acc. 290 Botanic gardens of Gembloux, Belgium, planted 8.1.79.

Stellaria graminea

Acc. 366) Botanic Gardens, University of Union in Katu, Helsinki,
Acc. 364) Finland, planted 8.1.80.

Myosoton aquaticum

Acc. 332 Karl Marx University, Germany, planted 27.2.79.
Acc. 235 Moscow, U.S.S.R., planted 5.2.79.
Acc. 82 Gembloux, Belgium, planted 28.9.78, 28.11.78.

Spergula arvensis

Acc. 20 Falkirk, Scotland, planted 21.2.78 & 2.11.78 & 19.1.79.
Acc. 320 Botanic Gardens of Copenhagen, Denmark, planted 15.2.79.
Acc. 258 Botanic Gardens of Karlsruhe, Germany, planted 15.2.79.

Spergula morisonii

Acc. 124 Botanic Gardens of Hamburg, Germany, planted 15.2.79 & 8.1.80.
Acc. 157 Botanic Gardens of Oldenburg Germany, planted 8.1.80.
Acc. 139 Botanic Gardens of Helsinki, Finland, planted 15.2.79 & 8.1.80.

Spergularia rubra

Acc. 142 University of Sienna, Italy, planted 10.11.78, 19.1.79.
Acc. 287 Gembloux, Belgium, planted 9.1.80.
Acc. 314 Botanic Gardens of Copenhagen, Denmark, planted 8.12.78.

Spergularia media

Acc. 376 Moscow, U.S.S.R. planted 26.3.79.
Acc. 321 Botanic Gardens of Copenhagen, Denmark, planted 7.11.78, 8.12.78, 3.4.79, 9.1.80.

Spergularia marina

Acc. 387 Coimbra, Portugal, planted 9.1.80.

In addition to these plants grown from seed in separate pots 5" square in John Innes potting compost no. 1, some flowers of Stellaria/ ....

Stellaria species were obtained from plants in natural habitats. In these plants it was impossible to obtain separate plants and the measurements were taken using 'branches' rather than whole plants.

Stellaria holostea

Kippford, Dumfriesshire.

Blackford Glen, Edinburgh.

Roslin Glen, near Edinburgh.

For each accession, in this section of the work, the following observations were made:

i. 5 plants, 10 flowers, from each
   a) style length
   b) style width

ii. 5 plants, 1 flower from each
   a) pollen grain width
   b) number of pores per pollen grain

iii. 5 plants, 50 flowers from each
   a) sepal number
   b) petal number
   c) antisepalous stamen number
   d) antipetalous stamen number
   e) style number

iv. 5 plants, 10 capsules from each
   a) seed number
   b) non-fertilized ovule number
   c) total ovule number

v. 2 plants, 5 flowers from each plant, 2 anthers from each flower
   a) number of pollen grains in antipetalous anthers
   b) number of pollen grains in antisepalous anthers

vi. 2 plants, mixture of pollen grains of flowers from each plant
   a) viability of antipetalous pollen grains
   b) viability of antisepalous pollen grains.

In addition, for each species, except Stellaria graminea, S. holostea and Spergularia marina, the number of seeds, non-fertilized ovules/ ....

ovules and total number of ovules per capsule formed on 5 plants were determined. The seed weight for most accessions was also found. Results were obtained from the same 5 plants in i., ii., iii., v. and vi. but separate plants were grown for part vi. The seeds and non-fertilized ovules of the first 10 flowers were counted as this both standardised which capsules were used and because it was felt that the first capsules formed the most seeds and ovules although this may not have been true for Myosoton aquaticum and some of the Spergula and Spergularia species where the first-formed flowers were often found to be male sterile. The capsules were not removed from the plants as it was felt that this may have altered the results, but were instead 'bagged' using tape to seal each capsule and each capsule being numbered so that the sequence of flowering could be determined.

In order to determine style length and width, all the styles of each flower examined were removed and measured under a microscope using a micrometer unit. The style was measured at the base to give the maximum width. In most of the species, these measurements were representative of the stigmatic area of the style, as stigmatic papillae were found on the entire adaxial surface of the style, except in Stellaria graminea and S. holostea where the stigmatic papillae did not reach the base of the style. All measurements are given in millimetres.

To determine the number of pores per pollen grain and the diameter of the grains, pollen grains were taken either from the styles or from open anthers. Pollen grains were mounted in glycerin jelly which had been melted. Pore number was calculated by counting the number of pores observed and doubling this number, results are thus likely to be higher than the actual number of pores per pollen grain. The width of the pollen grain was determined by viewing the grains magnified 400 times and using a micrometre eye piece unit. In both pollen grain width and pore number, 10 pollen grains were examined per flower.

In all the species examined it was possible to count the number of seeds and the number of non-fertilized or aborted ovules in each capsule so that the total number of ovules per capsule could be determined. Error may have occurred as it was often difficult to distinguish/ ....

distinguish non-fertilized ovules from the swollen funicles of other seeds, especially in those species in which the non-fertilized ovules remained white.

It was felt necessary to separately count the number of pollen grains in antisepalous and antipetalous anthers as it was thought that the pollen of antisepalous stamens was more likely to pollinate the same flower (be involved in self-crossing). Antipetalous stamens in all species examined matured later than antisepalous stamens and styles tended to only become receptive after antisepalous stamens had been shedding pollen for some time. Mature, but unopened, anthers were placed in a drop of water on a slide and squashed using a small metal rod. A coverslip was then placed on the slide and the pollen grains were counted with the aid of a microscope.

Two methods were used to determine the viability of antisepalous and antipetalous pollen grains. In all cases pollen grains used to determine viability were obtained from the same plants used to determine pollen grain number. A mixture of pollen grains was used, usually obtained from anthers from 5 flowers for each of the 2 methods.

METHOD 1

Lactophenol and cotton blue

Open anthers were placed in a drop of 0.6% solution of cotton blue in lactophenol on a slide and squashed using a metal rod. A coverslip was then placed over the sample and the pollen grains were viewed with a microscope. Viable pollen grains were considered to be those of uniform shape which stained dark blue, non-viable pollen grains were considered to be those which did not stain or only stained a very light blue.

METHOD 2

Fluorescein diacetate

A drop of glycerin jelly was melted on a slide and allowed to cool, open anthers were then placed in the glycerin and squashed as before. Drops of a solution containing fluorescein diacetate were then added to the glycerin until the glycerin became milky. The slide with the stained pollen grains was then viewed with a U.V. microscope. The fluorescein diacetate solution consisted of 2 mg. of fluorescein/ ....

fluorescein diacetate per ml. of acetone. The method outlined above was modified from the method of J. Heslop-Harrison and Y. Heslop-Harrison (1970). The brightly fluorescing pollen grains were considered to be viable.

This method is thought to test how permeabile and functional the cell membrane is, fluorescein accumulating intracellularly in cells with intact cell membranes but where the cell membranes are damaged the fluorescein diffuses back into the solution.

In each method, 2 groups of 100 pollen grains were examined, and the average found. The results obtained from these 2 methods were not always the same, due in part to the differences of the stain and also to differences in the samples of pollen grains used. The only way to determine pollen viability accurately would have been to germinate the pollen grains. In order to obtain pictures of the stigmatic papillae and pollen grains, fresh material was fixed with gluteraldehyde, first being placed in a 1% solution for 1 hour and then in a 3% solution for 4 - 5 days. The material was kept during this time in a fridge at 4°C. and solutions of the gluteraldehyde were made in a phosphate buffer at p.H 7.0. The material was then washed several times, with distilled water before being dehydrated using a graded series of acetone solution, 50%, 60%, 70%, 80%, 95%, the material being placed in each solution for half an hour. The material was then placed in 100% acetone and changed 4 times. The material was then dried by a critical point drying method using carbon dioxide. Specimens were then mounted using a water soluble glue onto the scanning electron stubs, thinly coated with gold and viewed with a Cambridge Scientific Instrument Stereoscan 150 at levels of magnification ranging from x100 to x2000.

In the de-styling expermiments the following plants were used:

Agrostemma githago

Acc. 76 Botanic Gardens of Karlsruhe, Germany.

Lychnis coronaria

Acc 42 A. Baytop 38094, Turkey.

Silene coeli-rosa

Acc 37 Botany Department, King's Buildings, Edinburgh, Dr. Lyndon.

The three species used in the de-styling experiments were chosen because the flowers were large and thus the styles could be easily removed, the flowers remained open for long periods and this allowed hand pollination to be carried out and a better chance of self-pollination occurring, and lastly because Agrostemma githago and Lychnis coronaria have uniloculor ovaries at maturity which could be compared with the basally septate mature ovaries of Silene coeli-rosa.

Agrostemma githago and Silene coeli-rosa are both annual species, the former producing a limited number of flowers, up to 11 per plant and the latter a large number of flowers. In the former species all the flowers of one plant were used, but in the latter species only up to 30 flowers were used per plant. In both species, the number of styles removed per flower was the same for all the flowers of each plant. In Agrostemma githago, 5 plants were used for each style number, but in Silene coeli-rosa only 2 plants were used for each style number.

Lychnis coronaria on the other hand is a long-lived perennial, with a basal rosette of leaves, producing a large number of flowering branches. In this species instead of using all the flowers of a plant for one style treatment, each of the flowering branches were used separately. Each flowering branch produced up to 24 flowers. In all, 6 plants were used with up to 4 branches for each style treatment.

Two groups of experiments were carried out on each of the 3 species; in the first group of experiments the flowers were allowed to self-pollinate and in the second group the flowers were artificially pollinated. It was felt necessary to artificially pollinate the flowers because a) Silene coeli-rosa appeared to be an out-crossing species which was not well adapted to self-pollination under greenhouse conditions and b) to ensure that all styles were covered with the maximum amount of pollen grains so that 'capture' of pollen grains was not variable between the style treatments.

In all 3 species the calyx is fused to form a distinct calyx tube, which before anthesis completely conceals the developing styles. The following procedure was carried out to remove the styles: the calyx tube was carefully slit and the desired number of styles removed/ ....

removed with a pair of forceps, the calyx tube was then 'repaired' with a piece of tape and the flower allowed to develop normally. The styles were always removed prior to their emergence from the calyx tube, and before the anthers were open. In all 3 species, all the styles of all the flowers of 1 plant or flowering branch were removed and no seeds were observed to form in these flowers, even although in Agrostemma githago the ovary did enlarge. As in the previous section of work, all the capsules were left on the plant until all the capsules were mature, the capsules being 'bagged' with tape to prevent seed loss.

In this work only basic statistical methods have been used, S.D. and S.E. figures are given. To determine if differences between treatments were significant, the technique of analysis of variance or partitioning of the total sum-of-squares was used to find values of F. The level of significance $p = 0.01$ or $p = 0.05$ is given in most cases where it is stated that there is or is not significant difference between treatments.

2.3 Styles, stigmatic area and ovules in the family Caryophyllaceae.

Within the family Caryophyllaceae, style number ranges from 1 to 13 with most species having 2, 3 or 5 styles. Style fusion occurs sporadically in the subfamily Alsinoideae: Myosoton, with Pycnophyllum having 3 totally fused styles (the position of this genus both within this subfamily and within the family Caryophyllaceae is however in some doubt). In the subfamily Paronychioideae most of the genera have fused styles although within some genera all the species may not: Corrigiola, Telephium, Hernaria, and in Spergula and Spergularia (in which most of the species never have fused styles) in some species, and some plants of other species, the styles are fused. There is no style fusion in the subfamily Dianthoideae in which the largest flowers are placed. A list of genera giving the 'normal' number of styles in each is given in Table 1, although some of the genera may appear in more than one category where style number is found to vary between species and where within a single species number is found to vary to such an extent that it has been impossible to determine which style number is the 'normal' style number for that species.

The/ ....

TABLE 1

Genera listed according to the number of styles and whether the styles are free or fused.

2 Styles

FREE : Acanthophyllum, Allochrusa, Ankyropetalum, Arenaria, Bolanthus, Brachystemma, Bufonia, Dianthus, Drypis, Gypsophila, Habrosia, Herniaria, Lepyrodiclis, Moehringia, Pentastemondiscus, Petrorhagia, Phyria, Pleirneura, Pseudostellaria, Saponaria, Sclernathus, Silene, Thurya, Thylacospermum, Vaccaria, Velezia, ? Illecebrum, ? Silene, ? Paronychia.

FUSED : Achyronychia, Cardionema, Cerdia, Chaetonychia, Herniaria, Illecebrum, Paronychia, Pollichia, Pteranthus, Sclerocephalus, Sphaerocoma.

3 Styles

FREE : Arenaria, Corrigiola, Cucubalus, Drypis, Holosteum, Honckenya, Minuartia, Moehringia, Sagina, Schieda, Silene, Spergularia, Stellaria, Stipulicida, Telephium, Welhelmsia.

FUSED : Achyronychia, Cardionema, Chaetonychia, Cometes, Corrigiola, Dicheranthus, Drymaria, Gymnocarpos, Haya, Illecebrum, Lochia, Loeflingia, Microphyes, Ortegia, Polycarpaea, Polycarpon, Pteranthus, Pycnophyllum, Sclerocephalus, Scopulophila, Spergula, Stipulicida, Telephium.

4 Styles

FREE : Arenaria, Colobanthus, Silene

5 Styles

FREE : Agrostemma, Arenaria, Cerastium, Lychnis, Moenchia, Myosoton, Petrocoptis, Sagina, Silene, Spergula.

FUSED : Krauseola, Spergula

TABLE 2/ ....

TABLE 2

Percentage of genera in each subfamily with 2, 3, 4, 5 free or 2, 3, 5 fused styles.

Style No.	Subfamily	Dianthoideae	Alsinoideae	Paronychioideae
Free	2	63.6%	28.6%	7.2%
	3	13.7%	35.7%	7.2%
	4	9.0%	17.85%	-
	5	13.7%	17.85%	2.5%
Fused	2	-	-	26.2%
	3	-	-	52.4%
	5	-	-	4.7%

The distribution of style number between the 3 subfamilies is found to be different. From Table 2, in the subfamily Paronychioideae over 50% of genera have 3 free or fused styles. The most common style number in the subfamily Dianthioideae is found to be 2, whereas in the Alsinoideae it is 3, in both cases the styles being free. However, these figures are for genera and not for species. In the subfamily Dianthoideae, for instance, the genus Silene has about 500 species, the majority of which have 3 styles and in the subfamily Paronychioideae, the genus Paronychia has about 107 species, all of which have 2 styles. However, in all the subfamilies most species have either 2 or 3 styles. It would be expected that the more styles or the more carpels present then the more ovules and seeds produced and that, therefore, 'species' would tend to have a large style number. However, this does not seem to occur, 2 and 3 styles appearing to have some advantage.

Within the family the stigmatic papillae are usually found on the adaxial surface of the style, in a single strip or scattered towards the base of the style and with a knob or cone at the apex. Rarely the stigmatic papillae are confined to the apex of the style or are found on all surfaces. At an immature stage, the papillae appear as small protuberances on the surface, as the style mature and lengthen, the length of the papillae and the distance between papillae increases. In some species, the mature papillae appear to have a vertical base with a horizontal apex (Plate 1.a). It is unusual to find, except sometimes towards the base, epidermal cells which have not developed into stigmatic papillae among those that have.

In order to try to determine the stigmatic area of the style, the length of the stigmatic area was measured and the presence or absence of a knob or cone recorded. Originally it was hoped that more accurate measurements of the stigmatic area could be made taking into account the density of the papillae and the width of the stigmatic area, but this prooved impossible to do accurately where such a large number of species was involved and where only herbarium specimens were available.

The length of the papillae was found to vary from less than 0.01 mm to 0.1 mm. The longest papillae on any style were found at the apex and the shorter at the base, although in some species, at maturity/ ....

maturity the length of the papillae was more or less the same along the whole stigmatic strip.

The value of having a knob or cone at the apex of the style, covered in stigmatic papillae is obvious. In most species, as already stated, the flowers are protandrous, thus pollen grains are shed when the styles are still erect and the papillae immature. As the styles start to spread and the papillae become receptive, the chances of self-pollination is greatly increased by there being stigmatic papillae on all surfaces at the apex. In Myosoton aquaticum the tips of the styles, which have a knob of stigmatic papillae touch the antipetalous stamens, soon after the styles have started to spread open. In other species, especially those with short styles and thus a small stigmatic area, or long styles but a reduced stigmatic area, a knob or cone of stigmatic papillae greatly increases the surface area. In other species with long styles the stigmatic area was effectively increased by at least the apical part of the style becoming twisted (Vaccaria pyramidata, Lychnis coronaria). Of all the herbarium specimens examined, 48% were found to have either a cone or knob of stigmatic papillae at the apex. This included species in which the stigmatic papillae extended to the base of the style and where the stigmatic papillae were confined just to the apex, with a whole range between. A knob or cone of stigmatic papillae were also found at the apex of 'fused' or free styles. It should be stated that in only a few genera were the styles completely fused into a single 'style': in most, only the base of the styles became fused.

In order to try to group the variation observed in style fusion and stigmatic area, 10 categories were devised using only these characters into which all the genera examined could be placed, some being placed in more than one category.

Key to Style Categories

1. Styles fused; apex entire, bifid, trifid, pentafid or dentate
   2. Styles totally fused, apex entire with stigmatic knob at apex ..... A.
   2. Styles not totally fused, apex bifid, trifid, pentafid or dentate

3./ ....

3. All surfaces of lobes covered in stigmatic papillae; knob or cone of stigmatic papillae at apex..... B.

3. Stigmatic papillae confined to adaxial surface; knob or cone absent or present

4. Stigmatic papillae to base of lobes on adaxial surface only ..... C.

4. Stigmatic papillae to base of lobes on adaxial surface but with knob or cone at apex covered in stigmatic papillae ..... D.

1. Styles not fused

5. Stigmatic papillae found on all surfaces of styles, knob or cone at apex absent or present ..... E.

5. Stigmatic papillae confined to adaxial surface of style, knob or cone at apex absent or present

6. Stigmatic papillae only on adaxial surface, no knob or cone at apex

7. Stigmatic papillae extending to base of style .... F.

7. Stigmatic papillae not extending to base ..... G.

6. Stigmatic papillae on adaxial surface of style, knob or cone at apex

8. Stigmatic papillae extending to base of style .....H.

8. Stigmatic papillae not extending to base of style

9. Stigmatic papillae more than 60% length of style but not to base ..... I.

9. Stigmatic papillae less than 60% length of style or confined to knob or cone at apex only ..... J.

In each of these categories, species of the following genera are found, Table 3.

TABLE 3

Genera arranged in 10 categores according to distribution of stigmatic papillae and degree of style fusion.

Category A

Styles totally fused with stigmatic papillae confined to knob or cone at apex:

Haya/ ....

Haya, Polycarpon, Pycnophyllum.

Category B

Styles fused; apex of fused style bifid, trifid, or dentate; all surfaces of lobes covered in stigmatic papillae; knob or cone at apex present or absent:
Chaetonychia, Dicheranthus, Drymaria, Gymnocarpos, Herniaria, Illecebrum, Loeflingia, ? Microphyes, Paronychia, Sclerocephalus.

Category C

Styles fused; apex of fused style bifid, trifid, pentafid or dentate; stigmatic papillae to base of lobes on adaxial surface only:
Achyronychia, Cardionema, Cerdia, Cometes, ? Krauseola, Lochia, Ortegia, Polycarpon, Pollichia, Pteranthus, Scopulophila, Spergula, Spergularia, Stipulicida, Telephium.

Category D

Styles fused; apex of fused style bifid, trifid; stigmatic papillae to base of lobes on adaxial surface but without a stigmatic knob or cone at apex:
Corrigiola, Paronychia, Sphaerocoma

Category E

Styles free; stigmatic papillae found on all surfaces of styles; knob or cone present or absent:
Colobanthus, Herniaria.

Category F

Styles free; stigmatic papillae to base of style on adaxial surface only; no knob or cone at apex:
Bolanthus, Lychnis, Minuartia, Moenchia, Petrocoptis, Silene, Spergularia, Stellaria, Telephium, Velezia.

Category G

Styles free; stigmatic papillae not to base of style on adaxial surface; no knob or cone at apex:
Dianthus, Petrorhagia, ?Thurya, Vaccaria

Category H/ ....

Category H

Styles free; stigmatic papillae to base of styles on adaxial surface; knob or cone present at apex:

Arenaria, Agrostemma, Cerastium, Corrigiola, Cucubalus, Holosteum, Honckenya, Minuartia, Myosoton, Petrorhagia, Sagina, Schiedea, Scleranthus, Silene.

Category I

Styles free; stigmatic papillae covering more than 60% of adaxial surface but not all of surface; knob or cone at apex:

Arenaria, Brachystemma, Cerastium, Lepyrodicilis, Minuartia, Phryna, Saponaria, Silene, Stellaria

Category J

Styles free; stigmatic papillae covering less than 60% of adaxial surface of style; knob or cone at apex:

Allochrusa, Ankyropetalum, Arenaria, Acanthophyllum, Bufonia, Drypis, Gypsophila, Habrosia, Lychnis, Minuartia, Moehringia, Pentastemondiscus, Pleironeura, Pseudostellaria, Welhelmsia.

Using these data it is possible to construct Table 4 which indicates the percentage of genera in each of the 3 subfamilies in each of the 10 categories. The majority of genera in the subfamily Paronychioideae have fused styles with lobes either totally covered in stigmatic papillae or confined to the adaxial surface, with or without a knob or cone at the apex. In the subfamily Alsinoideae, the majority of genera fall into the last 3 categories, stigmatic papillae on adaxial surface of style either to base, to cover 60% of adaxial surface or less than 60% with or without a knob or cone at the apex. However, in the subfamily Dianthoideae most of the genera fall into categories F and J; the stigmatic papillae to the base of the styles on the adaxial surface or the stigmatic papillae confined in this subfamily to a knob or cone at the apex of the styles and usually just slightly below, although a large number of genera also have stigmatic papillae to the base of the style on the adaxial surface with a knob or cone at apex (category H).

TABLE 4/ ....

TABLE 4.

Percentage of genera in each subfamily in each of the 10 categories.

Category / Subfamily	A	B	C	D	E	F	G	H	I	J
Paronychioideae	10.7	35.7	56.25	10.71	3.57	10.71	-	7.14	-	3.57
Alsinoideae	3.6	-	-	-	3.6	10.7	3.6	3.2	17.5	28.5
Dianthoideae	-	-	-	-	-	23.8	14.2	19.0	9.0	33.0

In order to compare style number and stigmatic area in relation to ovule number, 3 factors have to be considered, a) if an increase in style number increases the number of ovules per 'carpel' b) if increased stigmatic area per style allows an increase in ovule number per 'carpel' and c) if style length has any effect on ovule number. Rather than making comparisons at the genus level, in order to compare the factors above compairsons have been made at the species level and Table 5 constructed. Table 5 shows the style number compared to the mean average number of ovules per ovary and per 'carpel' and the mean average style length.

TABLE 5

Style number compared to average style length and average number of ovules per ovary.

Character Style Number		n.	Average no. of ovules per ovary	S.D.	S.E.	Average no. of ovules per carpel	Average style length	S.D.	S.E.
Fused	2	16	2.688	6.226	1.556	1.34	0.552 mm	0.364	0.091
	3	17	15.471	17.861	4.332	5.16	0.828 mm	0.583	0.206
Free	2	44	19.2	28.624	4.261	9.6	5.27 mm	4.523	0.698
	3	29	49.0	51.07	9.32	16.3	4.439 mm	4.66	0.897
	4	9	40.0	15.52	8.96	10.0	5.143 mm	3.827	1.447
	5	16	89.5	124.56	31.14	17.9	5.128 mm	5.352	1.298

Surprisingly, there is no significant difference in style length or in ovule number per 'carpel' in plants with 2, 3, 4 or 5 free styles although there is significant difference in ovule number between 2 and 3 fused styles. However, this difference can be explained because the majority of genera/species with 2 fused styles only have a single ovule and are in the subfamily Paronychioideae in which in a number of genera only have one ovule. This is apparently related to some evolutionary factor rather than to style number or length. The greatest factor affecting ovule number per ovary is style number which also affects the total stigmatic length, i.e. the stigmatic length of all the styles added together, but an increase in style number does not increase the number of ovules formed per carpel or increase the length of the styles.

In order to try and estimate the effect of stigmatic area on ovule number, the species with the same style number were arranged in each of the 10 stigmatic area categories and the average ovule number per ovary and style length were found for each category. For each style number, the percentage of genera in each of the categories was also recorded. Tables 6 to 11 record these data.

TABLE 6

Two Fused Styles

Character / Style Category	% of genera	n.	Ovule no. per ovary	S.D.	S.E.	Average style length	S.D.	S.E.
B	41.7%	9	1	0	0	0.472 mm	0.305	0.102
C	41.7%	5	5.33	10.13	4.137	0.477 mm	0.139	0.062
D	4.8%	1	2	0	0	0.730 mm	-	-

TABLE 7

Three Fused Styles

Character / Style Category	% of genera	n.	Ovule no. per ovary	S.D.	S.E.	Average style length	S.D.	S.E.
A	15%	4	17	26.746	13.373	0.606 mm	0.288	0.144
B	30%	5	8.6	7.369	3.295	1.028 mm	0.650	0.291
C	55%	8	19	18.501	6.541	1.103 mm	1.287	0.455

TABLE 8

Two Free Styles

Character / Style Category	% of genera	n.	Ovule no. per ovary	S.D.	S.E.	Average style length	S.D.	S.E.
F	8%	8	10.875	4.912	1.737	3.763 mm	2.123	0.751
G	16%	10	28.728	38.317	8.791	9.126 mm	5.430	1.717
H	12%	2	1	0	0	1.350 mm	0.919	0.650
I	16%	6	22.667	32.684	13.343	6.067 mm	5.766	0.714
J	44%	16	6.313	5.237	1.309	3.9 mm	3.194	0.854

TABLE 9

Three Free Styles

Character / Style Category	% of genera	n.	Ovule no. per ovary	S.D.	S.E.	Average style length	S.D.	S.E.
F	23.8%	12	75.917	63.952	18.461	4.688 mm	4.501	1.299
H	42.8%	13	35.214	33.582	8.975	3.547 mm	3.802	1.054
I	14.3%	2	20.5	6.364	4.5	8.75 mm	10.960	7.750
J	19.1%	2	23.5	9.899	7	2.1 mm	1.556	1.1

TABLE 10

Four Free Styles

Character / Style Category	% of genera	n.	Ovule no. per ovary	S.D.	S.E.	Average style length	S.D.	S.E.
E	12.5%	1	39	0	0	0.6 mm	0	0
F	25%	4	80.75	83.072	41.536	8.925 mm	1.533	0.766
H	25%	2	22.5	3.536	2.5	1.450 mm	0.354	0.233
I	25%	1	32	0	0	3.312 mm	0	0
J	12.5%	1	75	0	0	2.8 mm	0	0

TABLE 11

Five Free Styles

Character / Style Category	% of genera	n.	Ovule no. per ovary	S.D.	S.E.	Average style length	S.D.	S.E.
F	45.4%	7	133.429	183.975	69.536	4.179 mm	4.079	1.542
H	45.4%	8	52.875	27.331	9.663	6.892 mm	6.5	2.298
J	9.9%	1	75	0	0	2.8 mm	0	0

Except for 2 and 4 free styles, there is no significant difference at p = 0.01 in ovule number or style length between any of the style categories; suggesting that stigmatic area may not be the limiting factor. In 2 free styles there is significant difference in ovule number and style length between categories G, I, and F, J and E, H but not between these pairs of categories. Style length appears to be related to ovule number in that those categories with the longest style length also have the largest number of ovules per ovary. However, the percentage of stigmatic papillae on those styles with ovaries with the most ovules is not as 'great' as those with ovaries with the least number of ovules; in category E, stigmatic papillae cover the entire surface of the styles and in category H, stigmatic papillae cover the entire adaxial surface of the style and a knob of stigmatic papillae is present at the apex, whereas in category G stigmatic papillae do not reach the base of the style on the adaxial surface and no knob is present. In category I, although a knob of stigmatic papillae is present at the apex of the style, the stigmatic papillae do not reach the base of the style on the adaxial surface. Although significant difference was found in ovule number between categories with four free styles, no significant difference was found in style length. From the other Tables, there would appear to be no tendency for those ovaries with the longest styles to have the most ovules, or for those styles that have the greatest stigmatic area to have the greatest number of ovules according to the 10 categories, or for there to be any relation between style length and area of stigmatic papillae, i.e. where stigmatic papillae cover a small percentage of/ ....

of the style, style length is not increased. Also the percentage of the style covered in stigmatic papillae does not increase when style number is low; if anything the percentage of the style covered in stigmatic papillae increases with style number.

The following statements can thus be made:

i. It is possible to separate genera in this family solely on style and stigmatic papillae cover characters.

ii. Most species/genera in the family have 2 or 3 styles either fused or free.

iii. In species with free styles, the number of free styles does not affect the number of ovules per 'carpel'.

iv. There is no significant difference in style length between species with 2, 3, 4 or 5 free styles or 2 or 3 fused styles.

v. Stigmatic area does not appear to be directly related to style length or ovule number per ovary.

vi. There is some evidence that the more styles present the greater the stigmatic cover per style.

vii. Stigmatic area (number of styles and stigmatic cover per style) does not appear to be a limiting factor in ovule/seed number per ovary/capsule.

However, this survey was carried out on a large number of species which varied greatly in flower size, habitat, probably pollen production, type of pollination mechanism and other biological factors which make comparisons very inaccurate. No variation between flowers of the same species was examined, neither was the 'age' of the flower on the plant considered. The measurements of style length may themselves not be accurate as only herbarium material was used - styles are likely to shrink on being dried and pressed and may not expand to the same length, as when fresh, on being rehydrated (App. 2). Although/ ....

Although species were placed in 10 stigmatic categories, the actual area of stigmatic papillae was not examined and therefore stigmatic area, or density of stigmatic papillae may still be a limiting factor. However, perhaps the greatest error is in only counting ovule number per ovary. It is by no means certain that all the ovules produced in an ovary under ideal conditions will be fertilized; in the genus Acanthophyllum, although 4 ovules are usually formed, only 1 seed is produced. The difference between ovule number and seed number may account for the lack of observed connection between stigmatic area, style length and ovule number.

In order to try and overcome some of these problems a small number of species in related genera were examined.

2.4 Comparisons between Genera with Three and Five Styled Species

This section, as stated in the introduction, sets out to explore the reproductive capacity of species of 4 genera and the relations between several factors: style number and length, stigmatic area, pollen grain number, size and viability, ovule and seed number, seed weight. From the first section: styles, stigmatic area and ovules in the family Caryophyllaceae, there would appear to be no correlation between stigmatic area/style length and ovule number. However, as discussed above these results are unsatisfactory. In this section comparisons will be made within species, within genera and between genera to try and establish if there is any relationship between the above factors and how this relates to the reproductive capacity of the species examined.

Stellaria L and Myosoton Moench

The genus Stellaria is large and cosmopolitan, containing in the region of 100 species which are either annual or perennial, although often shortly so. Many of the species are weedy and all have 2 - 3 styles. Myosoton is a monotypic genus found in most of Europe and temperate Asia. The species is perennial, but is probably only short lived and is often weedy, having 5 styles. In the Flora of Turkey Vol. 2, p.15 (1966) and in Flora Europea Vol. 1, p.116 (1964) the 2 genera are separated by the capsule valves being equal in number to styles in Myosoton and double in Stellaria.

Stellaria/ ....

Stellaria L.

The following species have been examined: Stellaria media (L.) Vill., Stellaria graminea L. and Stellaria holostea L.

Stellaria media (L.) Vill.

This is an annual or shortly lived perennial, weedy herb which often spreads over large areas. The flowers are small, about 8 mm in diameter at anthesis, white, and numerous, often flowering all year round. The flower usually has 5 sepals, petals and antisepalous stamens lacking antipetalous stamens, although a few may be found. The stigmatic papillae are found to cover the entire adaxial surface of the style with no knob of stigmatic papillae at the apex (Plate 1.d). The main stem is terminated by a central flower and 2 lateral leafy flowering branches, in the 3 accessions the average number of leaves to this first central flower varied, in Acc. 30, 8.8 leaves, in Acc. 270, 7 leaves, and in Acc. 290, 20.5 leaves. Four main lateral branches are formed from the first leaf of the main stem, each branch terminating in a dichotomous cyme inflorescence, the first central flower of 2 of these lateral branches flowering shortly after that of the main stem. Shorter lateral flowering branches are also formed from the other leaves of the main stem and leaves of the 2 main lateral branches formed on the first leaf of the main stem. In general, it took 2 to 3 months from time of planting to flowering in all 3 accessions.

Table 12 gives the results of observations on style length and width, seed number and total ovule number per capsule, pollen grain number in antisepalous stamens, pollen grain viability, diameter and pore number and the average number of sepals, petals, stamens and styles for each accession. The average for each of these characters was first determined for each plant and from these figures the average for each accession was found. The averages for the species as a whole were determined using the average figures per plant rather than per accession. A whole seed count was done on Acc. 30, the figures entered in Table 12 for ovule number and seed number for this accession are for the first 10 flowers to flower on each plant and not the average of all the capsules examined, these figures are as follows:

TABLE 13/ ....

TABLE 13

Acc. 30 Stellaria media Total Seed Count Results

Character / Plant Number	Number of capsules counted	Average number of seeds per capsule	Range	Average number of ovules per ovary	Range
1	85	7.6	0 - 15	12.7	5 - 15
2	33	8.3	0 - 16	12.3	3 - 16
3	100	5.2	0 - 14	8.4	3 - 12
4	33	6.9	0 - 15	10.9	2 - 13
5	58	7.5	0 - 15	10.7	3 - 15

For the 5 plants : average number of capsules counted = 61.8

S.D. 30.294
S.E. 13.548

average number of seeds per ovary = 7.1

S.D. 1.173
S.E. 0.524

average number of ovules per ovary = 11.0

S.D. 1.691
S.E. 0.756

TABLE 12

Results for Stellaria media

Character / Acc.	Acc. 30	Acc. 270	Acc. 290	Total for Stellaria media
n.	5	4	4	13
style length	0.978 mm	1.019 mm	0.853 mm	0.942 mm
S.D.	0.036	0.069	0.064	0.076
S.E.	0.016	0.035	0.032	0.021
style width	0.100 mm	0.111 mm	0.095 mm	0.102 mm
S.D.	0.012	0.013	0.004	0.012
S.E.	0.005	0.006	0.002	0.003
seed no per capsule	10.6	9.4	12.484	10.142
S.D.	1.203	1.151	0.809	3.250
S.E.	0.538	0.515	0.362	0.839

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TABLE 12 (contd)

Acc. / Character	Acc. 30	Acc. 270	Acc. 290	Total for Stellaria media
Total ovule no. per ovary	12.72	12.073	14.600	13.131
S.D.	1.186	1.344	0.997	1.560
S.E.	0.531	0.601	0.446	0.403
n.	2	2	2	6
No. of pollen grains per antisepalous stamens	197.05	166.30	190	184.45
S.D.	3.182	15.697	25.45	19.71
S.E.	2.250	11.1	18.0	8.047
Pollen grain viability method 1	85.75%	66.25%	80.75%	77.58%
S.D.	3.182	6.010	0.353	9.557
S.E.	2.25	4.25	0.250	3.902
pollen grain viability method 2	68.5%	34%	64%	55.5%
S.D.	2.12	9.899	6.36	17.607
S.E.	1.50	7.0	4.5	7.188
Average of method 1 and method 2	77.125%	50.125%	72.375%	66.54%
n.	5	4	4	13
pollen grain diameter	34.320 /um	31.633 /um	32.25 /um	32.958 /um
S.D.	2.035	0.750	0.957	1.834
S.E.	0.910	0.433	0.478	0.529
pollen grain pore no.	18.24	14.4	12.0	15.200
S.D.	1.45	0.6	1.070	3.04
S.E.	0.649	0.346	0.535	0.878
petal no.	5.06	4.999	5.010	5.023
S.D.	0.432	0.02	0.02	0.038
S.E.	0.086	0.01	0.01	0.011

(contd next page)

TABLE 12 (contd)

Character \ Acc.	Acc. 30	Acc. 270	Acc. 290	Total for Stellaria media
sepal no.	5.055	5	5.020	5.018
S.D.	0.443	0	0.02	0.054
S.E.	0.0221	0	0.04	0.015
Antisepalous stamens	4.536	4.205	4.26	4.272
S.D.	0.672	0.912	0.738	0.719
S.E.	0.301	0.456	0.326	0.200
Antipetalous stamens	0.024	0.015	0.005	0.015
S.D.	0.026	0.019	0.010	0.020
S.E.	0.012	0.009	0.005	0.006
style no.	3.072	3	3.010	3.031
S.D.	0.067	0	0.02	0.053
S.E.	0.03	0	0.01	0.015
weight of 100 seeds	0.045 g.	0.039 g.	0.035 g.	0.040 g.

The average number of seeds per ovary for the total seed count of Acc. 30 is, as expected, less than the average for the species where only the first 10 capsules per plant were examined. The average number of ovules per ovary is also less in both cases, this reflects the decrease in the number of ovules formed per ovary as more flowers are produced, the last flower having less ovules than the first flower.

On examination of the figures in Table 12 there would appear to be little correlation between seed number and style length/stigmatic area: Acc. 290 has on average the shortest styles but the most seeds per capsule, and Acc. 270 on average the longest styles but the smallest number of seeds per capsule. Seed number would appear to be more related to ovule number per ovary with roughly 2 ovules per ovary failing to develop into seeds. Variation between accessions on style/ ....

style length and width, and seed number and ovule number is small and of no significant difference. There is also little variation in the number of pollen grains per antisepalous stamen and viability is high except in Acc. 270. Petal and sepal number vary little from the 'accepted' number with most flowers also having 5 antisepalous stamens and only a few producing any antipetalous stamens. Style number was also found to vary little from the 'accepted' number and where variation occurred the style number always increased to 4. In Acc. 30, 3 flowers had 4 styles and in Acc. 290, 2 flowers had 4 styles. The number of ovules was recorded in these flowers and the results given in Table 14.

TABLE 14

Results for Those Ovaries with 4 Styles, Stellaria Media.

Character / Accession	n.	Average no. of ovules per ovary	S.D.	S.E.
Acc. 30	3	18.333	0.577	0.333
Acc. 270	2	12.500	3.535	2.500
Total	2	15.417	4.125	2.917

There would thus appear to be some increase in ovule number in these ovaries but not by as much as would have been expected. The average number of ovules per ovary for the species as a whole is 13.131 or 4.377 ovules per carpel. The number of expected ovules for a 4-carpellate ovary is thus 17.508, more than the actual figure observed.

Stellaria graminea L.

Unlike Sellaria media, this is a perennial species which is much branched. Although several accessions were grown in the greenhouse, only 2 accessions successfully flowered and results are incompleted due to lack of material. The flowers are usually slightly larger than those of Stellaria media being up to 1 cm in diameter. They are scented and produce nectar, remaining open for about 4 days. In nature the flowers are probably out-crossing and this has resulted in/ ....

in a low seed production in greenhouse conditions. The styles remain inrolled while the antisepalous stamens are shedding pollen grains and are often not receptive until after the antipetalous stamens have shed their pollen grains. Self-pollination is thus very restricted.

There are usually 5 sepals, petals, antisepalous stamens and antipetalous stamen. Male sterility is common, sometimes whole plants being male sterile although this was not found in the flowers examined. The stigmatic papillae are found on the adaxial surface of the styles but do not extend to the base. A knob of stigmatic papillae is present at the apex. As there were only a few plants producing flowers no total seed count was carried out. Table 15 records the results for this species, the figures were arrived at as described for Stellaria media.

TABLE 15

Results for Stellaria graminea

Character \ Accession	Acc. 366	Acc. 364	Totals for Stellaria graminea
n.	5	1	6
style length	2.50 mm	3.135 mm	2.604 mm
S.D.	0.099	-	0.270
S.E.	0.044	-	0.110
style width	0.128 mm	0.116 mm	0.126 mm
S.D.	0.005	-	0.007
S.E.	0.002	-	0.003
length of area with stigmatic papillae	1.57 mm	1.78 mm	1.675 mm
seed no. per capsule	0.68	4	1.233
S.D.	0.968	-	1.608
S.E.	0.433	-	0.657
Total ovule no. per ovary	21.26	18.8	20.883
S.D.	1.071	-	1.380
S.E.	0.479	-	0.564

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TABLE 15 (contd)

Character \ Accession	Acc. 366	Acc. 364	Totals for Stellaria graminea
n.	2	1	3
no. of pollen grains per antisepalous stamen	476	196.8	382.933
S.D.	29.13	-	162.507
S.E.	20.66	-	93.823
no. of pollen grains per antipetalous stamen	321.8	180.4	274.733
S.D.	40.59	-	86.589
S.E.	28.78	-	49.993
pollen grain viability method 1, antisepalous stamens	76.6%	94.5%	82.5%
S.D.	9.138	-	12.258
S.E.	6.48	-	7.077
pollen grain viability method 2, antisepalous stamens	72.25%	-	72.25%
S.D.	3.888	-	-
S.E.	2.75	-	-
Average of method 1 and method 2 antisepalous stamens	74.42%	94.5%	77.37%
pollen grain viability method 1, antipetalous stamens	79.75%	90.5%	71.833%
S.D.	4.59	-	16.921
S.E.	3.26	-	9.770
pollen grain viability method 2, antipetalous stamens	62.5%	-	62.5%
S.D.	7.07	-	-
S.E.	5.02	-	-
Average of method 1 and method 2 antipetalous stamens	68.46%	90.5%	67.17%

(contd next page)

TABLE 15 (contd)

Accession / Character	Acc. 366	Acc. 364	Totals for Stellaria graminea
n.	5	1	6
pollen grain diameter	32.04 /um	31.2 /um	31.90 /um
S.D.	1.084	-	1.029
S.E.	0.485	-	0.420
pollen grain pore no.	17.36	15	16.967
S.D.	0.792	-	1.196
S.E.	0.354	-	0.488
petal no.	5	5	5
S.D.	0	-	0
S.E.	0	-	0
sepal no.	5	5	5
S.D.	0	-	0
S.E.	0	-	0
Antisepalous stamens	5	5	5
S.D.	0	-	0
S.E.	0	-	0
Antipetalous stamens	4.76	5	4.8
S.D.	0.055	-	0.110
S.E.	0.025	-	0.045
style no.	3	3	3
S.D.	0	-	0
S.E.	0	-	0
Weight of 100 seeds	0.10 g.	0.023 g.	0.017 g.

As/ ....

As these figures are incomplete it is difficult to come to any clear decisions. About one third of the styles are covered in stigmatic papillae but because of the low seed production on comparison can be made between accession. The average number of seeds per ovary in Acc. 364 was only 4 but up to 12 seeds were observed in a single capsule. The maximum number is, however, not known. Pollen grain number varied greatly between the 2 accessions, Acc. 36 producing nearly double the number as Acc. 364, even although the latter produced the most seeds. Pollen grain viability, however, appeared to be higher in Acc. 364 than in Acc. 366. Sepal, petal and antisepalous stamen number did not divert from the accepted values with fewer than 5 antipetalous stamens being produced in a few of the flowers. Style number was found to be constant.

Stellaria holostea L.

This is also a perennial species, producing a large number of branches. Although a number of plants were grown in the greenhouse, only 1 plant flowered and not very successfully. It was therefore necessary to collect plants from natural habitats which, unfortunately, made it impossible to collect whole plants, as branches from different plants became entangled. Collections of flowers were made from 2 sites in and around the Edinburgh area, 1 site near Kippford. Results are very incomplete. In each site 50 capsules were examined to determine seed number per capsule and the total number of ovules per ovary. At least 14 flowers were examined from each site for style length and width and sepal, petal antisepalous stamen, antipetalous stamen and style number.

Usually there are 5 sepals, petals, antisepalous stamens and antipetalous stamens. The flowers are up to 1.5 cm in diameter, produce large quantities of nectar and and remain open for about 4 days. This would appear to be an outcrossing flower, especially as the styles mature after the stamens have shed or started to shed their pollen. As in Stellaria graminea stigmatic papillae fail to reach the base of the style on the adaxial surface but a knob of stigmatic papillae is present at the apex. In general pollen grains were only observed at the apex of the styles. Table 16 records the results of observations on this species.

TABLE 16/ ....

TABLE 16

Results for Stellaria holostea

Character \ Accession	Kippford	Blackford Glen	Roslin Glen	Totals for Stellaria holostea
n.	105	132	61	3
style length	3.377 mm	2.493 mm	3.614 mm	3.161 mm
S.D.	-	-	-	0.591
S.E.	-	-	-	0.341
style width	0.126 mm	0.128 mm	0.148 mm	0.134 mm
S.D.	-	-	-	0.012
S.E.	-	-	-	0.007
length of area with stigmatic papillae	2.627 mm	-	2.539 mm	2.583 mm
n.	50	50	50	3
seed no. per capsule	1.94	2.68	2.44	2.353
S.D.	1.49	1.33	1.692	0.377
S.E.	0.211	0.188	0.239	0.218
Total ovule no. per ovary	9.521	10.54	10.92	10.327
S.D.	1.368	1.265	1.259	0.723
S.E.	0.197	0.179	0.178	0.417
n.	5	4	0	2
no. of pollen grains per antisepalous stamen	2280	1945.25	-	2112.625
S.D.	445.011	416.225	-	236.7
S.E.	199.015	208.112	-	167.37
no. of pollen grains per antipetalous stamen	1519.2	1546.75	-	1532.97
S.D.	409.79	256.48	-	19.48
S.E.	183.26	128.24	-	13.775

(contd next page)

TABLE 16 (contd)

Character \ Accession	Kippford	Blackford Glen	Roslin Glen	Totals for Stellaria holostea
n.	10	-	-	1
pollen grain diameter	32.7 /um	-	-	32.7 /um
pollen grain pore no.	17.60	-	-	17.6
S.D.	1.838	-	-	-
S.E.	0.581	-	-	-
n.	39	45	21	3
petal no.	4.95	5	5	4.983
S.D.	0.224	0	0	0.029
S.E.	0.036	0	0	0.017
sepal no.	4.95	5	5	4.983
S.D.	0.224	0	0	0.029
S.E.	0.036	0	0	0.017
Antisepalous stamens	4.95	5	4.952	4.967
S.D.	0.224	0	0.218	0.028
S.E.	0.036	0	0.048	0.016
Antipetalous stamens	4.95	4.978	4.952	4.960
S.D.	0.224	0.149	0.218	0.015
S.E.	0.036	0.022	0.048	0.009
style no.	2.744	3	2.905	2.883
S.D.	0.442	0	0.301	0.129
S.E.	0.071	0	0.066	0.075
weight of 100 seeds	0.220 g.	-	-	0.220 g.

Even although the information is not complete, there would appear to be little correlation between stigmatic area and seed or ovule number/ ....

number. The number of seeds produced per capsule was very small but the seeds were large. The maximum number of recorded seeds per capsule was 5 in capsules collected from Roslin; in the other 2 sites the maximum number was 4 with a large number of capsules with no seeds being found in all 3 sites. The total number of ovules per ovary is therefore about double the number of seeds, i.e. 50% of ovules are 'wasted'. Petal, sepal, antisepalous stamen and antipetalous stamen varied little from the expected figure of 5 but a few flowers had a reduced style number of 2. The number of ovules per ovary in those ovaries with 2 styles was recorded, Table 17.

TABLE 17

Results for ovaries with 2 styles, Stellaria holostea.

Character / Accession	n.	Average no. of ovules per ovary	S.D.	S.E.
Roslin Glen	2	8	0	0
Kippford	9	7.778	0.833	0.278
Total	2	7.889	0.025	0.111

The expected number of ovules per ovary for a 2-carpellate ovary is 6.88 ovules, therefore one ovule more on average has been formed in these ovaries.

Myosoton Moench

Myosoton aquaticum (L.) Moench

This is a perennial species, which under greenhouse conditions produced 2 flowering periods, the second immediatly after the flowers of the first flowering period have withered and produced seeds. The plants are large and covered in glandular hairs. As seedlings this species is indistinguishable from Stellaria species. There is extensive branching, at the first node there are up to 6 branches, producing flowers and fruits, the second and third node often produce up to 4 branches with only 1 flowering/fruiting branch formed at subsequent nodes. The number of leaves to the first flower on the main stem/ ....

stem varies little between the 3 accessions examined; Acc. 332, 14.4 leaves, Acc. 235, 12 leaves, Acc. 82, 14.8 leaves. A total seed count, up to the end of the first flowering period, was carried out on 5 plants of Acc. 82, the results are recorded in Table 18. In Table 19, the figures for ovule number and seed number for these accessions are for the first 10 flowers to flower on each plant.

TABLE 18

Acc. 82, Myosoton aquaticum results for total seed count.

Character / Plant Number	No. of capsules counted	Average no. of seeds per capsule	Range	Average no. of ovules per ovary	Range
1	235	14.58	0 - 73	52.56	18 - 79
2	268	18.645	0 - 81	57.813	24 - 97
3	274	29.72	0 - 93	61.488	33 - 98
4	110	7.036	0 - 38	59.482	20 - 110
5	194	22.70	0 - 76	53.22	30 - 90

For the 5 plants : average number of capsules counted = 216
S.D. 67.359
S.E. 30.124

average number of seed per ovary = 18.536
S.D. 8.520
S.E. 3.810

average number of ovules per ovary = 56.913
S.D. 3.903
S.E. 1.745

The flowers are large, up to 15 mm in diameter, and produce large quantities of nectar. Under greenhouse conditions the flowers remain open for 4 - 5 days. Pollen grains from both antisepalous and antipetalous stamens tend to be shed when the styles are still erect and immature, and there is some evidence that the antisepalous stamens may start to shed pollen grains at the bud stage. This species is, therefore, probably out-crossing but self-pollination readily occurred under greenhouse conditions. There are usually 5 sepals, petals, antisepalous and antipetalous stamens and styles, although male sterility is common. In Acc. 332 about 50% of plants were male sterile/ ....

sterile, anthers being formed but with no pollen grains. In this accession only those plants producing pollen grains were used to find seed counts per capsule although male sterile flowers were used to determine style length and width and the variability of floral structures. In 3 flowers in Acc. 235 where style number was increased to 6, some of the styles were fused at the base. In all the styles the stigmatic papillae extended, to the base on the adaxial surface with a knob of stigmatic papillae at the apex.

TABLE 19

Results for Myosoton aquaticum

Accession / Character	Acc. 332	Acc. 235	Acc. 82	Total for Myosoton aquaticum
n.	5	5	5	15
style length	2.45 mm	2.739 mm	2.390 mm	2.642 mm
S.D.	1.037	0.234	0.145	0.270
S.E.	0.464	0.104	0.064	0.067
style width	0.201 mm	0.207 mm	0.170 mm	0.193 mm
S.D.	0.004	0.016	0.005	0.019
S.E.	0.001	0.007	0.002	0.005
seed no. per capsule	21.120	32.2	42.240	31.86
S.D.	12.320	18.599	20.322	18.437
S.E.	5.509	8.317	9.088	4.760
Total ovule no. per ovary	81.120	86.9	77.0	81.607
S.D.	12.845	5.483	12.823	10.887
S.E.	5.744	2.452	5.735	2.811
n.	2	2	2	6
no. of pollen grains per antisepalous stamen	1392.7	1427.9	1483	1434.533
S.D.	154.29	8.826	248.901	137.199
S.E.	109.1	6.1	176.0	56.011

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TABLE 19 (contd)

Accession / Character	Acc. 332	Acc. 235	Acc. 82	Total for Myosoton aquaticum
no. of pollen grains per antipetalous stamen	1150	1145	1235.4	1176.833
S.D.	170.412	9.899	311.975	165.530
S.E.	120.5	7.0	220.6	67.577
pollen grain viability method 1	77.5%	84.75%	78.0%	80.083%
S.D.	1.414	3.181	15.556	7.996
antisepalous stamens S.E.	1.0	2.250	11.0	3.264
pollen grain viability method 2	70.75%	81.25%	82.0%	78.0%
S.D.	3.181	8.131	1.414	6.877
antisepalous stamens S.E.	2.25	5.750	1.0	2.807
Average method 1 & 2 antisepalous stamens	74.125%	83.0%	80.0%	79.04%
pollen grain viability method 1	73.875%	90.50%	78.0%	80.792%
S.D.	10.429	9.192	5.656	10.247
antipetalous stamens S.E.	7.375	6.5	4.0	4.183
pollen grain viability method 2	76.75%	77.75%	69.5%	74.667
S.D.	1.767	18.031	17.677	12.015
antipetalous stamens S.E.	1.250	12.75	12.5	4.905
Average method 1 & 2 antipetalous stamens	75.312%	84.125%	73.75%	76.7%
pollen grain diameter	31 µm	34.5 µm	35.2 µm	33.8 µm
S.D.	1.732	0.989	0.836	2.213
S.E.	1.0	0.7	0.374	0.699
pollen grain pore no.	11.4	24.65	16.920	14.840
S.D.	0.2	11.398	0.742	2.585
S.E.	0.115	5.699	0.332	0.817

(contd next page)

TABLE 19 (contd)

n.	5	5	5	15
Petal no.	5.008	5.004	5	5
S.D.	0.10	0.008	0	0.008
S.E.	0.004	0.004	0	0.002
Sepal no.	5.004	5	4.996	5.00
S.D.	0.008	0	0.008	0.008
S.E.	0.004	0	0.004	0.002
Antisepalous stamens	5.068	5.004	5	5.024
S.D.	0.041	0.008	0	0.039
S.E.	0.018	0.004	0	0.010
Antipetalous stamens	5.012	5.004	5	5.005
S.D.	0.10	0.008	0.014	0.012
S.E.	0.004	0.004	0.006	0.003
style no.	5.276	5.096	5.024	5.132
S.D.	0.186	0.065	0.051	0.155
S.E.	0.083	0.029	0.023	0.039
Weight of 100 seeds	0.020 g.	0.022 g.	0.027 g.	0.023 g.

Style length and width varied little between accessions with no evidence of style length correlating with seed number, but some correlation with total ovule number. Petals, sepals, antisepalous stamens, antipetalous stamens, and styles varied little in number from the expected value of 5. Where variation did occur, the number of floral structures tended to increase rather than decrease. In all 3 accessions flowers with 6 styles were found, the number of ovules found in these flowers is recorded on Table 20, but some flowers with 4 styles and 7 styles were also found. Except for 6 styles, the average number of ovules per ovary found in ovaries with 4 or 7 styles is as expected; 4 styles - 65.284 ovules per ovary, 6 styles - 97.926 ovules per ovary, 7 styles - 114.247 ovules per ovary.

TABLE 20

6 Styles

Character / Accession	n.	Average no. of ovules per ovary	S.D.	S.E.
Acc. 332	57	107.895	12.835	1.700
Acc. 235	22	105.864	14.587	3.110
Acc. 82	3	116.667	61.076	35.263
Totals	3	110.142	5.741	3.315

TABLE 21

7 Styles

Character / Accession	n.	Average no. of ovules per ovary	S.D.	S.E.
Acc. 332	11	123.818	10.935	3.297
Acc. 235	2	110.500	3.536	2.500
Totals	2	117.159	9.417	6.59

TABLE 22

4 styles

Character / Accession	n.	Average no. of ovules per ovary	S.D.	S.E.
Acc. 332	3	74.0	6.245	3.606
Acc. 235	4	72.0	15.427	7.714
Acc. 82	7	60.143	4.298	1.625
Totals	3	68.714	7.490	4.324

In order to compare the results of different species Table 23 has been constructed. This Table shows the stigmatic area as the total style length and style width multiplied by the number of styles the species has on average. The pollen grain number per antisepalous and antipetalous stamens are represented as the total amount of viable/ ....

TABLE 23

Total Results for Stellaria/Myosoton

Species / Character	Stellaria media	Stellaria graminea	Stellaria holostea	Myosoton aquaticum
Style no.	3.031	3	2.883	5.132
Total stigmatic length	2.855 mm	5.025 mm	7.445 mm	13.559 mm
Total stigmatic width	0.309 mm	0.378 mm	0.386 mm	0.990 mm
Total no. of antisepalous pollen grains	787.97	1914.665	10493.408	7207.094
Total no. of viable antisepalous pollen grains	524.315	1481.376	?	5696.487
Total no. of antipetalous pollen grains	-	1318.718	7603.531	5890.049
Total no. of viable antipetalous pollen grains	-	885.783	?	4517.668
Pollen grain diameter	32.958 µm	31.90 µm	32.7 µm	33.8 µm
No. of pores per pollen grain	15.20	16.967	17.6	14.840
No. of seeds per ovary	10.142	1.233	2.353	31.86
No. of ovules per ovary	13.131	20.883	10.327	81.607
Breeding system	Self-pollination	Probably predominantly outcrossing	Probably predominantly outcrossing	Probably predominantly outcrossing
Seed weight	0.040 g.	0.017 g.	0.220 g.	0.023 g.
Pollen grain to ovule ratio	39.929	113.209	1752.391	125.163
Pollen grain to seed ratio	51.646	1919.837	7691.007	320.595

viable pollen grains likely to be produced by each flower, taking into account the number of stamens usually present and the percentage of viable pollen grains. No S.D. or S.E. values are given, to simplify the table.

If comparisons are made within Stellaria, the style length/stigmatic length would appear to have no relationship with either seed number or ovule number per ovary/capsule; S. holostea has on average the longest styles but on average the smallest number of ovules per ovary. The seeds of S. holostea are the largest of the 3 Stellaria species examined, 5 times heavier than those of S. media and 10 times heavier than those of S. graminea. Interestingly the average number of seeds per capsule of S. media is also about 5 times that of S. holostea. The seed number for S. graminea cannot be compared with the other 2 species because of the small number of seeds produced, probably due to lack of pollination under greenhouse conditions rather than to the 'true' number of seeds usually formed in this species. There may, therefore, be some relationship between seed number and seed weight.

Of the 3 Stellaria species, S. media is probably the only one which is regularly self-pollinated, cleistogamy may in fact occur. Therefore, the number of pollen grains per flower is greatly reduced in this species, and the antipetalous stamens are lost. Both Stellaria graminea and S. holostea are predominantly out-crossing with the styles in both species remaining immature until both antisepalous and antipetalous stamens have at least started to shed pollen grains. The number of pollen grains produced in both these species is, therefore, very large but why the number should be so large in S. holostea is unclear. Pollen grain number is not, therefore, related to either seed number of ovule number per ovary; Stellaria holostea produces the largest amount of pollen but has the smallest number of ovules per ovary.

Myosoton aquaticum has a greater stigmatic area than any of the Stellaria species examined, both per ovary and per style. If Stellaria graminea and Myosoton aquaticum are compared, both having seeds about the same weight, the stigmatic area/length of Myosoton aquaticum is about $2\frac{1}{2}$ times that of Stellaria graminea but the ovule number per ovary is more than $2\frac{1}{2}$ times that of Stellaria graminea. So/ ....

So even where seed weights are about the same there is no positive relationship between stigmatic area length. Style width is also greater in Myosoton than in Stellaria graminea, and this combined with the greater length in fact makes the stigmatic area of Mysoton about 6 times that of Stellaria graminea. If there was a direct relationship between stigmatic area and ovule number, taking into account seed weight, the number of ovules per ovary in Myosoton aquaticum should be about 120. However, only 81.6 are found but the seeds of Myosoton aquaticum are slightly heavier than those of Stellaria graminea. Myosoton aquaticum, like Stellaria graminea and S. holostea, is a predominantly out-crossing species, but self-pollination readily occurs. Pollen grain number is, therefore, larger and the pollen grain to ovule ratio is about the same as that of Stellaria graminea. In all the out-crossing species, pollen grain number is high and there is a large wastage, with not as high a percentage of ovules being 'fertilized' or at least seeds being formed as in the very efficient, self-pollinating Stellaria media.

Spergularia (Pers.) J. & C. Presl and Spergula L.

These 2 genera are very similar, having leaves in whorls at each node and similar flowers. They are usually separated on style number, Spergula having 5 styles and Spergularia 3 styles, and on the fusion of stipules, fusion occurring in Spergularia but not in Spergula. The genus Spergula contains only about 5 species which are usually annual but may occasionally be perennial. Spergularia is a much larger genus with about 40 species, mainly perennial but occasionally annual. Both genera have a wide geographic distribution being found in most of Europe, N. & S. America, Africa, India, Australia, New Zealand, and Asia.

Spergularia (Pers.) J. & C. Presl

Three species were examined, although 2 of them, S. marina and and S. media, are very closely related, indeed J. Szujko-Lacza et al (1979) considered, that in Hungary S. salina (S. marina)is a hybrid between S. media and S. rubra. The following species were examined: S. media (L.) C. Presl, S. marina (L.) Griseb., S. rubra (L.) J. & C. Presl.

Spergularia media/ ....

Spergularia media (L.) C. Presl

This is a perennial species predominantly found in salt marshes. The flowers are quite large, about 8 mm in diameter, pink to white in colour. There are usually 5 petals and sepals with a varying number of antisepalous and antipetalous stamens, usually there are more antisepalous than antipetalous stamens. The 3 styles may be free or united, fusion may occur just between the margins at the base of the styles or a distinct area of fusion may occur. The vascular tissue of the style, however, remains separate. In the flowers in which fusion occurred 2 measurements were taken, firstly the length of the fused area and secondly the length of the free lobes or styles. The second measurement represents the length of the stigmatic area present, the stigmatic papillae covering the whole adaxial surface of the style with no knob at the apex. The flowers remain open for about 4 days and large amounts of nectar are produced, all suggesting a flower adapted to outbreeding, the flowers also being scented. Under greenhouse conditions, self-pollination, however, readily occurred.

Only 2 accessions were examined, the number of leaves to the first flower on the main stem varied little: Acc. 376, 17.2 leaves; Acc. 321, 15.4 leaves. The first node of the main stem tended to produce a large number of branches, up to 10 branches being recorded, each of these producing further branches all of which produced terminal cymes. The second and subsequent nodes of the main stem tended to produce only 1 branch which tended not to produce a large number of branches, but these branches also flowered. A whole seed count was carried out on Acc. 321. The results are recorded in Table 24; in Table 25, the first 10 flowers were used to obtain the figure for the average ovule and seed counts.

TABLE 24

Acc. 321, Spergularia media, total seed count results.

Character / Plant no.	no. of capsules counted	Average no. of seed per capsule	Range	Average no. of ovules per ovary	Range
1	104	80.37	18 - 123	85.29	44 - 123
2	35	55.32	0 - 124	76.57	33 - 136
3	98	84.03	20 - 143	85.91	30 - 143
4	171	83.17	22 - 119	87.78	47 - 119

For the 4 plants : average number of capsules counted 102.0

S.D. 55.588
S.E. 27.794

average number of seeds per ovary 75.723

S.D. 13.691
S.E. 6.846

average number of ovules per ovary 83.888

S.D. 4.992
S.E. 2.496

The average number of seeds and ovules per ovary in the whole seed count is only slightly less than for the first 10 flowers, seed number does not appear in this species to decrease to any great extent the more flowers/capsules are formed, i.e. the last capsule does not produce on average less seeds than the first capsule.

TABLE 25

Results for Spergularia media

Character \ Accession	Acc. 376	Acc. 321	Totals for Spergularia media
n.	5	4	9
style length lobes	0.908 mm	0.698 mm	0.803 mm
S.D.	0.063	0.102	0.136
S.E.	0.028	0.045	0.043
style width lobes	0.112 mm	0.106 mm	0.109 mm
S.D.	0.011	0.007	0.009
S.E.	0.005	0.003	0.003
fused style length	0.201 mm	0.086 mm	0.144 mm
S.D.	0.105	0.046	0.098
S.E.	0.047	0.020	0.031
seed no. per capsule	89.86	85.95	88.122
S.D.	31.695	13.77	24.034
S.E.	14.175	6.885	8.011

(contd next page)

TABLE 25 (contd)

Character \ Accession	Acc. 376	Acc.321	Totals for Spergularia media
Total ovule no. per ovary	105.434	90.225	98.674
S.D.	21.054	8.542	17.699
S.E.	9.416	4.271	5.900
n.	2	2	4
No. of pollen grains per antisepalous stamen	4715.6	5886.6	5301.1
S.D.	322.724	426.244	743.208
S.E.	228.20	301.400	371.604
No. of pollen grains per antipetalous stamen	3844.9	4824.1	4334.45
S.D.	330.502	471.923	656.014
S.E.	233.7	333.70	323.007
Pollen grain viability method 1, antisepalous stamens	79.250%	84.75%	82.0%
S.D.	10.253	11.667	9.513
S.E.	7.250	8.250	4.757
Pollen grain vibaility method 2, antisepalous stamens	63.25%	88.5%	75.875%
S.D.	5.303	9.899	15.955
S.E.	3.750	7.00	7.978
Average of method 1 and 2, antisepalous stamens	71.25%	86.625%	78.938%
Pollen grain viability method 1, antipetalous stamens	77.5%	90.75%	84.125%
S.D.	12.728	3.182	10.765
S.E.	9.00	2.250	5.383
Pollen grain viability method 2, antipetalous stamens	74.0%	89.25%	81.625%
S.D.	17.678	2.475	13.555
S.E.	12.500	1.750	6.777

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TABLE 25 (contd)

Character \ Accession	Acc. 376	Acc. 321	Totals for *Spergularia media*
Average of method 1 and 2, antipetalous stamens	75.75%	90.0%	82.875%
n.	5	4	9
Pollen grain diameter	18 µm	18.2 µm	18.1 µm
S.D.	0.707	0.837	0.738
S.E.	0.316	0.374	0.233
Petal no.	5	5	5
S.D.	0	0	0
S.E.	0	0	0
Sepal no.	5	5	5
S.D.	0	0	0
S.E.	0	0	0
Antisepalous stamens	5	4.912	4.956
S.D.	0	0.078	0.07
S.E.	0	0.035	0.022
Antipetalous stamens	4.984	4.888	4.936
S.D.	0.017	0.048	0.061
S.E.	0.007	0.022	0.019
Style no.	3	3	3
S.D.	0	0	0
S.E.	0	0	0
Weight of 100 seeds	0.007 g.	0.009 g.	0.008 g.

Of the 2 accessions, Acc. 376 had a higher proportion of flowers with fused styles and the length of the fused area was greater. The total/ ....

total length of the styles, i.e. the fused region plus the lobes was also greater in Acc. 376 than in Acc. 321, fusion had not decreased the stigmatic length of styles; in fact, in this case the stigmatic length had increased. There was, however, little variation in the number of seeds and the number of ovules per ovary formed between the 2 accessions or in the number of pollen grains. Fusion of styles is thought to discourage inbreeding by preventing the anthers of the same flower touching (J. A. Ratter 1976 p. 416), but this does not appear to be the case in this species. Self-pollination readily occurred, under greenhouse conditions in those flowers with fused styles. Sepal, petal, antisepalous stamen and antipetalous stamen number varied little from the expected figure of 5: all flowers examined had 3 styles.

Spergularia marina (L.) Griseb.

This annual, biennial or perennial species is found in the same type of habitat as S. media, salt marshes, although this species tends to be slightly more weedy. Only 1 accession was examined and a total seed count was not carried out. The branching pattern of the plant is as described for Spergularia media, with on average 11 leaves to the first flower on the main stem. The flowers are large, about 7 mm in diamter, usually with 5 sepals and petals. Stamen number is reduced with a range of 1 - 5 antisepalous stamens, and 0 - 3 antipetalous stamens. In this accession anthers were also found attached to the petals, the petal sometimes remaining otherwise 'normal' in shape or differentiating into a 'stalk' and expanded lamina to which the anthers were attached. The 2 pairs of loculi of the anthers were usually found on opposite margins of the petals and sometimes only 1 pair was present. The styles were all free although in 1 flower, 4 styles were observed. Stigmatic papillae cover the entire adaxial surface of the style with no knob at the apex. The flowers remained open for only a day and although producing large amounts of nectar were not scented. This species is probably predominantly self-pollinated.

The results obtained for this species are given in Table 26. Pollen grain number and viability for the anthers attached to the petals are given and also the number of petals with and without anthers.

TABLE 26

Acc. 387, Spergularia marina Results

Character \ Results	Average	S.D.	S.E.
n.	5		
style length	0.569 mm	0.026	0.012
style width	0.096 mm	0.013	0.006
seed no. per capsule	72.775	5.138	2.569
ovule no. per ovary	75.4	3.774	1.887
n.	2		
No. of pollen grains per antisepalous stamen	1694.7	322.016	227.7
No. of pollen grains per antipetalous stamen	1605.9	432.608	305.900
No. of pollen grains per petal anther	715.415	136.351	96.415
Pollen grain viability Method 1, antisepalous stamens	81.25%	1.768	1.250
Pollen grain viability Method 2, antisepalous stamens	82.5%	14.500	10.500
Average of Method 1 & 2 antisepalous stamens	81.875%	-	-
Pollen grain viability Method 1, antipetalous stamens	75.25%	3.889	2.750
Pollen grain viability Method 2, antipetalous stamens	73.5%	2.828	2.00
Average of Method 1 & 2, antieptalous stamens	74.375%	-	-
Pollen grain viability Method 1, petals	72%	5.657	4.00
Pollen grain viability Method 2, petals	66%	30.406	21.5

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TABLE 26 (contd)

Character \ Results	Average	S.D.	S.E.
Average method 1 & 2 petals	69%	-	-
n.	5		
Pollen grain diameter	18.4 µm	0.548	0.245
Petals without anthers	3.772	0.573	0.256
Petals with anthers	1.192	0.543	0.243
Sepals	5	0	0
antisepalous stamen	1.928	0.244	0.109
antipetalous stamen	0.605	0.134	0.060
styles	3	0	0
weight of 100 seeds	0.009 g.		

Spergularia rubra (L.) J. & C. Presl

This is a very varied annual to perennial species found throughout Europe. The flower consists of 5 sepals, petals and antisepalous stamens, and a reduced number of antipetalous stamens with a range of 1 - 5. There are usually 3 free styles, but flowers with 2 styles were found in 2 of the accessions, and evidence of style fusion especially in Acc. 142 (Plate 1.c). Stigmatic papillae cover the entire adaxial surface of the style with no knob at apex. Flowers are about 6 mm in diameter and remain open for less than a day, usually opening in the morning and closing by mid-afternoon. Nectar is produced, but the flowers would appear to be predominantly self-pollinating, because of the short period the flower remains open. Male sterility was also noted in this species, usually in the central flower of the cyme, anthers being formed but not producing pollen grains.

The first node of the plants produced up to 13 branches but usually about 8 branches which further branches all terminating in a lax dichotomous cyme. Subsequent nodes on the main stem produced only/ ....

PLATE 1

1.a Myosoton aquaticum (L.) Moench, S.E.M. photograph of stigmatic papillae of style with pollen grain.

1.b Spergula arvensis L. S.E.M. photograph of pollen grains germinating on style, note some of pollen grains with more than 3 apertures.

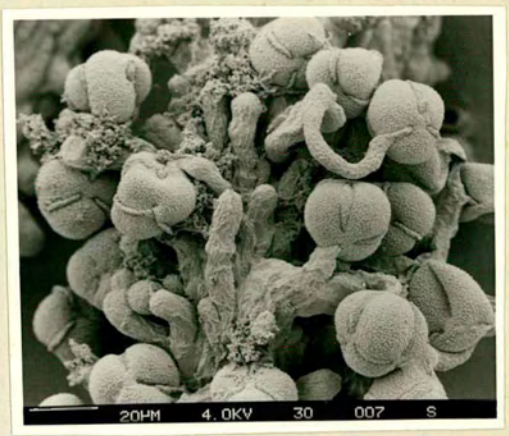
1.c Spergularia rubra (L.) J. & C. Presl, S.E.M. photograph of the fused styles.

1.d Stellaria media (L.) Vill. S.E.M. photograph of the styles.

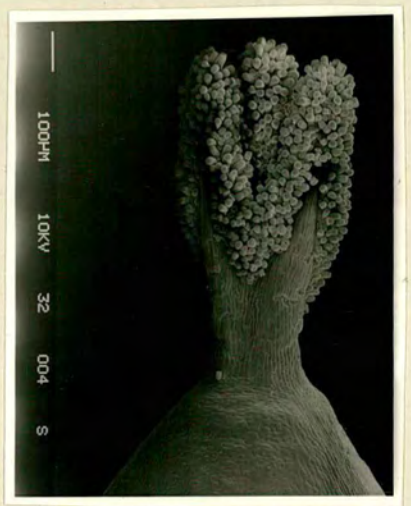
1.e Myosoton aquaticum (L.) Moench, S.E.M. photograph, ovary wall removed, with septal arrachments still intact, demonstrating continuity of transmitting tissue of style with that of ovary and also the papillae of styles.

PLATE 1

1.a

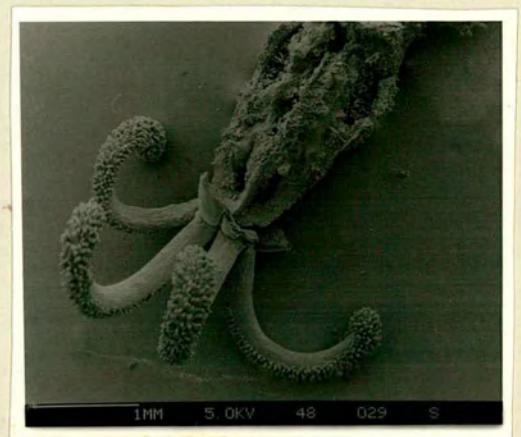


1.b



1.c

1.d



1.e

only a single flowering branch. The number of leaves on the main stem to the first flower varied little between accessions 287 and 142; Acc. 287, 12.4 leaves, Acc. 142, 12.2 leaves, but in Acc. 314 there were on average 20.6 leaves to the first flower. Acc. 314 and 142 were planted within one month of each other and flowered at the same time. A total seed count was carried out on Acc. 314 and the results given in table 27, in table 28 the results for this accession are for the first 10 flowers.

TABLE 27

Acc. 314, Spergularia rubra, total seed count results.

Character / Plant no.	n.	Average no. of seeds per capsule	Range	Average no. of ovules per ovary	Range
1	129	96.03	0 - 150	107.03	55 - 155
2	149	90.82	0 - 135	107.73	55 - 152
3	83	74.69	22 - 143	92.49	35 - 143
4	112	82.81	0 - 140	98.54	49 - 143
5	105	92.01	0 - 144	97.69	35 - 158

For the 5 plants : average number of capsules counted 115.6
S.D. 24.916
S.E. 11.143

average number of seeds per capsule 87.272
S.D. 8.514
S.E. 3.808

average number of ovules per ovary 100.696
S.D. 6.531
S.E. 2.921

The average number of ovules and seeds per ovary in the total seed count is slightly less than in the species as a whole. As in Spergularia media, the lobes of fused styles are equal in length if not slightly longer than the total length of styles that are not fused. The number of seeds per capsule was, however, reduced in Acc. 142 where style fusion occurred, even though ovule number was slightly higher than in other accessions examined. The fusion of styles/ ....

styles may therefore have reduced self-pollination as suggested by Ratter (1976). The diameter of pollen grains surprisingly varies between accessions with Acc. 142 having large pollen grains than the other 2 accessions; this would certainly reduce the number of pollen grains physically able to cover the styles. Antipetalous stamens were also less reduced in number in Acc. 142 than in the other 2 accessions and the number of pollen grains per anther in antipetalous stamen was higher in Acc. 142.

TABLE 28

Results for Spergularia rubra

Character \ Accession	Acc. 142	Acc. 287	Acc. 314	Totals for Spergularia rubra
n.	5	5	5	15
style length or length of lobes	0.785 mm	0.726 mm	0.741 mm	0.751 mm
S.D.	0.058	0.039	0.012	0.045
S.E.	0.026	0.017	0.005	0.012
style width or width of fused area	0.249 mm	0.084 mm	0.089 mm	(style width) 0.086
S.D.	0.057	0.004	0.006	0.006
S.E.	0.026	0.002	0.003	0.002
Fused style length	0.196 mm	0	0	
S.D.	0.219	0	0	
S.E.	0.098	0	0	
Seed no. per capsule	42.072	89.42	99.860	77.117
S.D.	21.702	9.188	19.535	30.743
S.E.	9.705	4.109	8.737	7.938
Ovule no. per ovary	125.160	95.712	115.140	112.004
S.D.	8.668	5.895	10.145	14.864
S.E.	3.876	2.636	4.537	3.838
n.	2	2	2	6

(contd next page)

TABLE 28 (contd)

Character \ Accession	Acc. 142	Acc. 287	Acc. 314	Totals for Spergularia rubra
No. of pollen grains per antisepalous stamen	1478.8	1321.7	1393.4	1397.967
S.D.	68.165	173.807	219.486	146.814
S.E.	48.2	122.9	155.2	59.937
No. of pollen grains per antipetalous stamen	653.1	286.6	450.7	463.467
S.D.	77.075	0.849	112.430	175.153
S.E.	54.5	0.600	79.500	71.506
Pollen grain viability method 1 antisepalous stamen	79%	86.75%	87%	84.25%
S.D.	0.707	14.496	2.828	7.764
S.E.	0.5	10.250	2.00	3.170
Pollen grain viability method 2 antisepalous stamen	80%	72.25%	90.25%	77.595%
S.D.	0.354	8.132	11.667	7.591
S.E.	0.250	5.750	8.250	3.099
Average of method 1 & method 2, antisepalous stamen	79.5%	79.5%	88.625%	82.542%
Pollen grain viability, method 1 antipetalous stamen	70%	91%	93%	84.667%
S.D.	0.707	10.607	5.657	12.604
S.E.	0.500	7.500	4.00	5.146
Pollen grain viability, method 2 antipetalous stamen	73%	46.95%	85%	68.317%
S.D.	2.121	8.415	5.657	18.005
S.E.	1.500	5.950	4.00	7.351
Average of method 1 & method 2, antipetalous stamen	76.25%	63.225%	86.813%	76.492%
n.	5	5	5	15
Pollen grain diameter	24 /um	18.25 /um	20.24 /um	21.014 um
S.D.	0.707	0.957	0.550	2.543
S.E.	0.316	0.479	0.246	0.680

(contd next page)

TABLE 28 (contd)

Character \ Accession	Acc. 142	Acc. 287	Acc. 314	Totals for Spergularia rubra
Petal no.	5	5	5	5
S.D.	0	0	0	0
S.E.	0	0	0	0
Sepal no.	5	5	5	5
S.D.	0	0	0	0
S.E.	0	0	0	0
Antisepalous stamen	5	5	5	5
S.D.	0	0	0	0
S.E.	0	0	0	0
Antipetalous stamen	4.972	2.10	3.976	3.68
S.D.	0.033	0.21	0.407	1.26
S.E.	0.015	0.09	0.182	0.32
Style no.	2.996	2.996	3	2.997
S.D.	0.009	0.009	0	0.007
S.E.	0.004	0.004	0	0.002
weight of 100 seeds		0.002 g.	0.002 g.	0.002 g.

Spergula L.

The following species have been examined: S. arvensis L., S. morisonii Boreau.

Spergula arvensis L.

This is an annual herb, widely found as a weed in disturbed habitats and areas of cultivation. The flowers are about 6mm in diameter and usually consist of 5 petals, sepals and antisepalous stamens with a reduced number of antipetalous stamens from 0 - 5 with no plant examined being found to have 5 antipetalous stamens in all

50/ ....

50 flowers examined. Flowers usually have 5 styles but 6 and 4 styles were recorded and style fusion was observed in flowers of 2 plants of Acc. 20. Stigmatic papillae extended to the base of the styles, covering the whole adaxial surface, with no knob at the apex. Under greenhouse conditions most flowers opened at noon and closed in the evening of the same day. Pollen grains were observed at the base of the styles. As in other species examined, the antisepalous anthers shed pollen grains before the antipetalous anthers. As the flowers remain open for less than 1 day, the flowers are probably self-pollinated even although nectar is produced. Self-pollination certainly readily occurred under greenhouse conditions. Male sterility occurred in all accessions examined, especially the central flower of the cyme, and in latter central flowers the flowers often did not develop beyond the bud stage. Stamens were found in these flowers but the anthers were shrivelled and no viable pollen grains were produced.

The first node produced 8 - 13 branches, with subsequent nodes producing only 1 branch. The branches of the first node in themselves branching, all terminating with a lax dichotomous cyme. In the 3 accessions examined the number of leaves on the main stem to the first flower was found to vary little between accessions, in Acc. 320 6.8 leaves, Acc. 258, 6.9 leaves, Acc. 20 7.8 leaves. A total seed/ovule count was carried out on accession 20 and the results are given in Table 29, as before the first 10 flowers were used for the results in Table 30.

TABLE 29

Acc. 20, Spergula arvensis, total seed count results

Character / Plant no.	n.	Average no. of seeds per capsule	Range	Average no. of ovules per ovary	Range
1	530	10.725	0 - 35	14.398	5 - 35
2	225	8.507	0 - 22	11.406	3 - 26
3	195	11.154	0 - 30	15.0	6 - 31
4	388	12.704	0 - 36	16.208	6 - 36
5	368	8.394	0 - 28	12.287	5 - 28

For/ ....

For the 5 plants : average number of capsules counted 341.2

S.D. 135.491
S.E. 60.593

average number of seeds per capsule 10.297

S.D. 1.840
S.E. 0.823

average number of ovules per ovary 13.86

S.D. 1.975
S.E. 0.883

The average seed and ovule number in the whole seed count varies little from the average for that of the first 10 flowers, suggesting the seed and ovule number do not decrease in later formed flowers. Style length varied little between accessions although in Acc. 320 the styles were on average slightly longer than in the other 2 accessions and both seed and ovule number was also higher. Pollen grain number per antisepalous and antipetalous stamens was higher in Acc. 258 but this did not increase the number of seeds produced. Petal, sepal and antisepalous stamen number varied little from the expected figure of 5 but the number of antipetalous stamens was again much reduced. Style number was also found to vary with there being a reduction in style number to 4 in some of the flowers of Acc. 20 and Acc. 258. Surprisingly seed weight was found to vary considerably between accessions. The seeds of Acc. 258 were found to be double the weight of the seeds of the other 2 accessions; seed number per capsule was, however, the same between Acc. 20 and Acc. 258, suggesting that seed weight may not be as important in determining seed number as previously thought. The number of ovules per ovary of ovaries with only 4 styles are given in Table 30A. As expected, ovule number per ovary is slightly lower than for the species as a whole, but if the results for the accessions with flowers with 4 styles are compared then there is no difference. Decrease in style number to 4 in this species does not appear to effect the number of ovules formed per ovary.

TABLE 30/ ....

TABLE 30

Results for Spergula arvensis

Character \ Accession	Acc. 20	Acc. 320	Acc. 258	Totals for Spergula arvensis
n.	5	5	5	15
style length	0.625 mm	0.680 mm	0.578 mm	0.628 mm
S.D.	0.089	0.090	0.084	0.092
S.E.	0.040	0.040	0.038	0.024
style width	0.066 mm	0.082 mm	0.079 mm	0.076 mm
S.D.	0.007	0.004	0.007	0.009
S.E.	0.003	0.002	0.003	0.002
seed no. per capsule	10.26	14.511	9.693	11.487
S.D.	3.480	0.887	2.107	3.147
S.E.	1.556	0.397	0.942	0.812
Total ovule no. per ovary	13.240	17.300	14.773	15.105
S.D.	2.291	0.751	1.205	2.253
S.E.	1.024	0.336	0.539	0.582
n.	2	1	2	5
No. of pollen grains per antisepalous stamen	447.9	586.0	727.7	587.44
S.D.	195.303	-	0.990	170.613
S.E	138.1	-	0.700	76.30
No. of pollen grains per antisepalous stamen	226.5	288.4	363.1	293.52
S.D.	125.158	-	51.619	96.205
S.E.	88.5	-	36.5	43.024
Pollen grain viability, method 1 antisepalous stamen	71.25%	91.5%	77.75%	78.1%
S.D.	15.203	-	10.96	12.366
S.E.	10.750	-	7.75	5.530
Pollen grain viability, method 2 antisepalous stamen	62%	88.5%	71.25%	71.0%
S.D.	11.314	-	1.768	12.242
S.E.	8.00	-	1.250	5.475

TABLE 30 (contd)

Character \ Accession	Acc. 20	Acc. 320	Acc. 258	Totals for Spergula arvensis
Average method 1 & 2 antisepalous stamen	66.625%	90%	74.500%	77.042%
Pollen grain viability, method 1	60.75%	78%	57.5%	62.90%
antipetalous stamen S.D.	4.596	-	14.142	11.366
S.E.	3.250	-	10.00	5.083
Pollen grain viability, method 2	57.75%	79.5%	84.0%	72.6%
antipetalous stamen S.D.	6.01	-	4.243	14.166
S.E.	4.25	-	4.00	6.335
Average method 1 & 2 antipetalous stamen	62.188%	78.75%	70.75%	75.396%
n.	5	5	5	15
Pollen grain diameter	26.8 µm	26.50 µm	27.75 µm	26.873 µm
S.D.	1.997	1.756	0.500	1.542
S.E.	1.153	0.878	0.250	0.465
Petals	4.996	5	4.996	4.997
S.D.	0.009	0	0.009	0.007
S.E.	0.004	0	0.004	0.002
Sepals	4.996	5	4.996	4.997
S.D.	0.009	0	0.009	0.007
S.E.	0.004	0	0.004	0.002
Antisepalous stamens	4.98	5	4.996	4.992
S.D.	0.024	0	0.009	0.017
S.E.	0.011	0	0.004	0.004
Antipetalous stmaens	2.960	2.504	4.044	3.169
S.D.	1.389	1.187	0.445	1.207
S.E.	0.621	0.531	0.199	0.312

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TABLE 30 (contd)

Character \ Accession	Acc. 20	Acc. 320	Acc. 258	Totals for Spergula arvensis
Styles	4.964	5	4.988	4.984
S.D.	0.059	0	0.030	0.039
S.E.	0.026	0	0.014	0.010
Weight of 100 seeds	0.032 g.	0.042 g.	0.084 g.	0.053 g.

TABLE 30A

4 Styles

Character / Accession	n.	Average no. of ovules per ovary	S.D.	S.E.
Acc. 20	7	12.286	2.498	0.944
Acc. 258	4	14.0	1.414	0.707
Totals	2	13.143	1.212	0.857

Spergula morisonii Boreau

This species is very similar to S. arvensis, separated by the seeds in S. arvensis being almost round, and the leaves channelled beneath, whereas in S. morisonii the seeds are compressed and distinctly winged and the leaves are not channelled. This is an annual species, the flowers consisting of 5 sepals, petals and antisepalous stamens with a reduced number of antipetalous stamens ranging from 0 - 5. In 2 plants in the 3 accessions examined flowers with 4 styles were found. Styles were not found to be fused in any of the flowers examined; the stigmatic papillae covering the entire adaxial surface of the style with no knob at the apex. Flowers are about 6 mm in diameter. As in S. arvensis, flowers opened around noon and closed later the same day, some flowers appearing to remain open for only 4 hours. Nectar is produced in this species but because of the short period the flower remains open it is likely to be predominently a self-pollinating species. Male sterility was noted in only a few flowers/ ....

flowers of 2 plants in 1 accession and there did not seem to be a tendancy for the central flower of the cyme to be male sterile as in S. arvensis.

As in S. arvensis a number of branches are formed at the first node, up to 13 branches with 1 or 2 branches in subsequent nodes. The plant as a whole was very similar to Spergula arvensis. In the 3 accessions examined, the number of leaves to the first flower of the cyme on the main stem were found to vary little between 2 of the accessions, Acc. 157 6.25 leaves, Acc. 124 6.01 leaves but to vary in the other accession, Acc. 139 10.6 leaves. A whole seed count was carried out on plants in Acc. 124, the results of this are given in Table 31, as before the results for this accession in Table 32 are for the first 10 flowers.

TABLE 31

Acc. 124, Spergula morisonii, total seed count results.

Character Plant no.	n.	Average no. of seeds per capsule	Range	Average no. of ovules per ovary	Range
1	81	36.24	7 - 63	38.3	14 - 63
2	105	37.25	13 - 66	38.61	17 - 66
3	38	37.13	11 - 59	49.1	13 - 60
4	134	38.54	8 - 66	40.34	15 - 66
5	121	31.86	6 - 63	34.12	10 - 63

For the 5 plants : average number of capsules counted 95.8

S.D. 37.877
S.E. 16.939

average number of seeds per capsule 36.204

S.D. 2.563
S.E. 1.146

average number of ovules per ovary 40.094

S.D. 5.529
S.E. 2.473

TABLE 32/ ....

TABLE 32

Results for Spergula morisonii

Character \ Accession	Acc. 124	Acc. 157	Acc. 139	Totals for Spergula morisonii
n.	5	5	5	15
style length	0.716 mm	0.716 mm	0.812 mm	0.753 mm
S.D.	0.074	0.027	0.090	0.081
S.E.	0.037	0.013	0.040	0.023
style width	0.089 mm	0.082 mm	0.100 mm	0.091 mm
S.D.	0.007	0.003	0.004	0.009
S.E.	0.004	0.001	0.002	0.003
seed no. per capsule	42.733	31.11	55.32	43.054
S.D.	5.371	10.031	2.87	12.003
S.E.	2.402	4.486	1.284	3.099
Total ovule no. per ovary	44.620	39.561	56.6	46.936
S.D.	5.092	6.726	2.262	8.730
S.E.	2.277	3.008	1.011	2.254
n.	2	2	2	6
No. of pollen grains per anti-sepalous stamen	595.7	290.85	843.7	576.75
S.D.	106.773	65.549	150.331	262.685
S.E.	75.500	46.350	106.300	107.241
No. of pollen grains per anti-petalous stamen	320.625	98.9	311.50	243.675
S.D.	88.919	42.002	197.283	149.368
S.E.	62.875	29.700	139.500	60.979
Pollen grain viability method 2	92.75%	95%	94.25%	94%
antisepalous stamens S.D.	6.010	0.707	1.768	3.00
S.E.	4.250	0.500	1.25	1.225

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TABLE 32 (contd)

Character \ Accession	Acc. 124	Acc. 157	Acc. 139	Totals for Spergula morisonii
Pollen grain viability method 1 antisepalous stamens	88.75%	93.25%	74.75%	85.583%
S.D.	5.303	3.889	13.081	10.832
S.E.	3.750	2.750	9.25	4.423
Average method 1 & 2 antisepalous stamen	90.75%	94.125%	84.5%	89.79%
Pollen grain viability method 1 antipetalous stamens	80.25%	92.75%	78%	83.667%
S.D.	13.081	0.354	9.192	10.083
S.E.	9.25	0.250	6.500	4.116
Pollen grain viability method 2 antipetalous stamens	95.25%	95.75%	90.25%	93.75%
S.D.	0.354	1.061	1.061	2.806
S.E.	0.250	0.750	0.75	1.146
Average method 1 & 2 antipetalous stamen	87.75%	94.25%	84.125%	88.708%
n.	5	5	5	15
Pollen grain diameter	19.75 µm	20.5 µm	18.6 µm	19.538 µm
S.D.	1.500	1.00	1.140	1.391
S.E.	0.750	0.500	0.510	0.386
Petals and Sepals	5	5	5.004	5.002
S.D.	0	0	0.009	0.006
S.E.	0	0	0.004	0.002
Antisepalous stamen	5	5	5	5
S.D.	0	0	0	0
S.E.	0	0	0	0
Antipetalous stamen	4.77	3.165	4.344	4.112
S.D.	0.370	0.615	0.728	0.878
S.E.	0.185	0.308	0.325	0.244

(contd next page)

TABLE 32 (contd)

Character \ Accession	Acc. 124	Acc. 157	Acc. 139	Totals for Spergula morisonii
Styles	4.995	4.995	5	4.997
S.D.	0.010	0.010	0	0.008
S.E.	0.005	0.005	0	0.002
Weight of 100 seeds	0.017 g.	0.011 g.	0.019 g.	0.016 g.

The number of ovules and seeds formed in the first 10 flowers are only slightly higher than those for all the flowers formed on 1 plant. Therefore, there would appear to be little change in ovule and seed number in later formed flowers.

Style length and ovule and seed number per ovary was found to vary little between Acc. 124 and Acc. 157 but in Acc. 139 styles were longer and ovule and seed number greater. In Acc. 157 the number of pollen grains produced both in antisepalous and antipetalous stamens was lower although the number of stamens per flower varied little between accessions. Unfortunately Acc. 157 was grown at about the same time as the other 2 accessions, being planted in January/February, but Acc. 157 was grown in 1980 and the other 2 accessions in 1979, therefore the reason for the low pollen grain count could have been environmental, but even if this was the case it is still of interest that Acc. 124 and Acc. 157 have similar style length and ovule and seed number per ovary and yet Acc. 157 produced less than half the number of pollen grains. Therefore there are more pollen grains produced in Acc. 124 and Acc. 139 than are required suggesting that pollen grain number does not have a great effect on the number of ovules fertilized, even in a self-pollinating flower. Seed weight appeared not to correlate with seed number; Acc. 139 on average had the heaviest seeds and on average the most seeds per capsule and Acc. 157 had on average the lightest seeds and the fewest seeds per capsule. The number of petals, sepals and stamens was as expected, with a reduced number of styles being found in flowers in Acc. 124 and Acc. 157. The number of ovules per ovary in ovaries with 4 styles is given in Table 33. Only 2 flowers were found to have 4 styles.

TABLE 33

4 Styles

Character / Accession	n.	Average no. of ovules per ovary	S.D.	S.E.
Acc. 124	1	42	0	0
Acc. 157	1	12	0	0
Totals	2	27	21.213	15.0

Little can be made of the results although the first figure falls within the range of ovules per ovary found in flowers with 5 styles in Acc. 124.

As for Stellaria and Myosoton, Table 34 compares the results for species of Spergularia and Spergula. The term 'total stigmatic length' in this table does not refer to total style length where the styles are fused, as in Spergularia media, but to total non-fused length; the area of the styles covered in stigmatic papillae. If comparisons are first made within the same genus, within Spergularia species, the species, with an average, the longest styles also has the greatest number of seeds and the species, with an average the shortest styles has the smallest number of seeds but there is great variation within species. In all 3 Spergularia species, however, there is a high percentage of ovules fertilized, developing into seeds. Seed weights do not appear to affect seed number; Spergularia rubra has the lightest seeds but not the most seeds per capsule although it has the most ovules per ovary. However, the seeds of S. rubra are a quarter of the weight of seeds of S. media but S. rubra does not have, on average, 4 times as many ovules per ovary as S. media. Pollen grain number is as expected, with the predominantly out-crossing Spergularia media producing more pollen grains per ovule and seed than the predominently in-crossing S. rubra and S. marina. The differences within the genus Spergula are slightly different. Spergula arvensis produces much heavier seeds than S. morisonii, and also for fewer seeds and ovules per ovary/capsule. The stigmatic length and width per flower of Spergula morisonii is greater than that of S. arvensis but again the difference is not in proportion to the/ ....

the difference in the number of seeds produced per flower/ovary by the 2 species. The stigmatic area does not therefore appear to be the limiting factor in seed production in Spergula arvensis. Pollen grain production in both Spergula species is low, as expected of predominently self-pollinating flowers, with that of S. arvensis being slightly higher than expected.

TABLE 34

Total results for Spergularia/Spergula.

Species.. Character	Spergularia media	Spergularia marina	Spergularia rubra	Spergula arvensis	Spergula morisonii
Style no.	3	3	2.997	4.984	4.997
Total stigmatic length length	2.409 mm	1.707 mm	2.251 mm	3.13 mm	3.768 mm
Total stigmatic width	0.327 mm	0.288 mm	0.258 mm	0.378 mm	0.454 mm
Total no. of antisepalous pollen grains	26272.251	3267.382	6989.835	2932.5	2883.75
Total no. of viabile anti-sepalous pollen grains	20738.789	2675.169	5769.55	2259.256	2589.32
Total no. of antipetalous pollen grains	21394.845	971.569	1705.558	930.165	1001.992
Total no. of viable anti-petalous pollen grains	17730.977	722.605	1304.615	701.307	888.847
Total no. of petal pollen grains	-	852.777	-	-	-
Total no. of viable petal pollen grains	-	588.414	-	-	-
Pollen grain diameter	18.1 µm	18.4 µm	21.014 µm	26.873 µm	19.538 µm

(contd next page)

TABLE 34 (contd)

Species / Character	Spergularia media	Spergularia marina	Spergularia rubra	Spergula arvensis	Spergula morisonii
No. of seeds per ovary	88.122	72.775	77.117	11.487	43.054
No. of ovules per ovary	98.674	75.4	112.004	15.105	46.936
Breeding system	Probably predominently out-crossing	Probably predominently self-pollinated	Probably predominently self-pollinated	Probably predominently self pollinated	Probably predominently self-pollinated
Seed weight	0.008 g.	0.009 g.	0.002 g.	0.053 g.	0.016 g.
Pollen grain to ovule ratio	389.867	52.867	63.16	196.0	74.104
Pollen grain to seed ratio	436.551	54.774	91.733	257.732	80.786

When the 2 genera are compared it is found that both seed and ovule number is greater in Spergularia species than in Spergula species, i.e. those species with only 3 styles are producing more than those with 5 styles. However, Spergularia media, S. marina, S. rubra, and Spergula morisonii appear to produce less flowers per plant (according to data from whole seed counts) than Spergula arvensis. Spergula arvensis and S. morisonii, however, still have a greater stigmatic area per flower than the Spergularia species, style length/stigmatic length of the 3-styles species has not limited the number of seed/ovules produced. The length of each style in Spergula and Spergularia species is about the same, however.

Comparisons between Spergularia/Spergula and Stellaria/Myosoton are difficult to make, a few comments can, however, be made. Firstly the pollen grain diameter of Stellaria/Myosoton is greater than that of Spergularia/Spergula and the styles tend to be longer as well, seed/ovule number is, however, less than that of Spergularia/Spergula species (except Spergula arvensis). Seed weight is on average less in the Spergularia/Spergula species than in the Stellaria/Myosoton species and this may in part be the reason for the reduced number of seeds and ovules in the latter 2 genera. Also as pollen grain diameter/ ....

diameter is greater in Stellaria/Myosoton less pollen grains can physically cover the styles, this may be related to the increased length of the styles and again to the low seed/ovule number. Pollen grain production in both pairs of genera tends to reflect the type of breeding system found in the species, with Stellaria media being the most efficient of all the species examined.

Some general conclusions can be made:

i. The number of pollen grains per anther is always less in antipetalous stamens than in antisepalous stamens.

ii. The greatest variation in number in floral structures is in the number of stamens.

iii. Reduction of, to total loss of antipetalous stamen occurs more frequently than antisepalous stamen reductions or total loss.

iv. Floral structures tend to be reduced in number rather than increased in number, although this does occur.

v. Style number is variable, both in species with 3 and those with 5 styles.

vi. Within species fusion of styles does not always lead to a reduced number of seeds or ovules per capsule/ovary; length of stigmatic area is also not reduced.

vii. Within genera, species with the longest styles/stigmatic length do not necessarily produce the most ovules/seeds.

viii. Style length may, or may not, be longer in 5-styled species than 3-styled species.

ix. Seed weight does not always effect ovule number, i.e. ovaries with many seeds do not necessarily have lighter seeds than ovaries with fewer seeds.

x./ ....

x. Pollen grain number is related to pollination mechanism, predominantly out-breeding species produce more pollen grains per ovule or seed than predominantly self-pollinating species.

Even although point vii. states no relation between style length or stigmatic length and ovule and seed number, there is 1 factor which has not been considered in this study; this is the density, or number of stigmatic papillae per style or per flower. The number of papillae has to limit the total number of pollen grains able to 'germinate' as often passage of a pollen tube destroys the papillae. Plate 1 illustrates the styles of some of the species examined and certainly the papillae in some Spergularia species are denser than Stellaria/Myosoton species, and the pollen grains of Spergula/Spergularia are smaller than those of Stellaria/Myosoton. It would appear that all the factors outlined in the introduction to this chapter play a part in determining ovule/seed number and that no one factor is more important than any other.

2.5 De-styling Experiments

The above section of this chapter has shown there to be little correlation between stylelength/stigmatic area and either ovule number or seed number per capsule. This section attempts to examine the effect of style number/stigmatic length on the number of ovules fertilized and forming seeds, by the removal of styles. In section 2.4 style number was constant within genera but style length varied and density of stigmatic papillae was not known, between species, making comparisons between seed/ovule numbers difficult. In this section, experiments on seed number can be carried out on a uniform group of plants with roughly the same number of ovules but with varying numbers of styles and thus varying stigmatic lengths. Two factors were therefore examined in this section:

i. The effect of decreases in style number/stigmatic area, on the total number of ovules fertilized.

ii. The distribution of fertilized ovules within capsules in which styles have been removed.

Three/ ....

Three species were used in this part of the work: Silene coeli-rosa, Agrostemma githago, Lychnis coronaria. The methods used are described in the materials and methods section of this chapter.

Silene coeli-rosa (L.) Godron

This is an annual plant which produces either a large number of flowers per plant or a small number, in these experiments only plants producing a small number of flowers were used. Four to five styles were found to be produced, only those flowers with 5 styles were used in these experiments. The base of the ovary remained septate at anthesis and in the mature capsule. No seeds were produced when all the styles were removed, 'capsules' tended to be small but hard in these plants, with septal attachments from the apex of the ovary to the apex of the placental column remaining intact.

Two separate experiments were carried out in consecutive years; in the first experiment flowers were allowed to self-pollinate under greenhouse conditions and in the second experiment flowers were artificially pollinated.

Experiment 1

Plants were allowed to self-pollinate under greenhouse conditions, seeds were planted in February and flowers first opened at the beginning of June, capsules were harvested at the end of July.

There is no significant difference at $p = 0.01$ in the average total number of ovules per ovary in any of the treatments and it is therefore valid to compare directly the number of ovules fertilized per ovary between treatments. At $p = 0.05$ there is significant difference in the number of seeds per capsule between treatments but not at $p = 0.01$ level. However, the number of capsules with seeds is low in plants with flowers with only 1 or 2 styles but is almost 100% in plants with flowers with 3, 4 or 5 styles. This alters the mean averages of those flowers with 1 or 2 styles if only those capsules with seeds are included from 21.8 to 37.6 seeds per capsule in flowers with 1 style and to 8.6 and 22.0 seeds per capsule respectively for plant 1 and 2 with flowers with 2 styles. These figures still remain slightly below the average for those plants with flowers with 3, 4 or 5 styles. Although there is great variation in the results obtained in all treatments there would appear to be a dividing line between flowers/ ....

TABLE 35

Experiment 1, Silene coeli-rosa

Character / Style no.	No. of plant	No. of flowers	Average no. of ovules	S.D.	S.E.	Average no. of seeds	S.D.	S.E.	Average % fertilized	% of capsules with seeds
1	1	10	297.5	23.77	7.52	21.8	33.58	10.62	10.62	50
2	1	7	270.28	17.08	6.46	6.14	4.95	1.86	1.86	71.4
	2	4	239.2	56.01	14.97	12.78	31.21	8.29	8.29	50
3	1	7	242.8	47.55	17.97	59.8	87.4	33.06	33.06	85.7
	2	5	286.2	10.4	4.65	101.2	112.8	50.4	50.4	100
4	1	11	269	61.44	18.52	32	33.34	10.05	10.05	100
	2	5	259.4	33.17	14.83	59.4	46.87	20.96	20.96	100
5	1	3	203	19.67	11.36	57.66	73.04	42.17	42.17	100
	2	5	268	70.05	31.33	92.2	109.81	49.11	49.11	100

flowers with 1 or 2 styles and those with 3, 4 or 5 styles. Flowers with only 3 styles are able, on average, to produce as many seeds as those with 5 styles.

The position of the seeds in the capsule is of interest. In all the capsules examined the seeds tended to be in the top half of the capsule, above the level that the capsule becomes septate. If no crossing of pollen tubes from 1 carpel to another occurred, then the seeds would be expected to be found only in those 'carpels' in which the style had not been removed. This, however, was not the case in all capsules examined. In 71.7% of capsules with seeds, the seeds were evenly distributed throughout the capsule and only in 5.6% were the seeds restricted to the carpel or carpels with styles. Of the remaining capsules with seeds, seeds were sometimes restricted to 1 'carpel' because only 1 seed was formed or seeds were in the 'carpel' with the style/styles and adjacent carpels. In those flowers with only 1 or 2 styles, distribution of seeds tended to be restricted. Crossing/ ....

Crossing-over readily occurred, but less so where style number was reduced to 1 or 2 styles beyond adjacent carpels.

Experiment 2

Flowers were artificially pollinated with pollen grains from different flowers, usually from different plants, using a fine brush. Seeds were planted in March and the first flowers opened in July. The capsules of all the treatments were harvested at the end of August.

TABLE 36

Experiment 2, Silene coeli-rosa

Character / Style no.	No. of flowers	Average no. of ovules per ovary	S.D.	S.E.	Average no. of seeds per ovary	S.D.	S.E.	Average % of ovules fertilized	S.D.	S.E.	% no. of capsules with seeds per plant
1	9	166.78	27.4	9.13	33.2	41.07	13.69	18.93	24.76	8.25	44.4
2	9	200.89	30.63	10.21	93.3	27.7	9.24	46.74	12.31	4.10	100
3	7	236.14	17.4	6.58	98.43	48.01	18.17	41.85	20.44	7.72	85.7
4	7	81.8	30.218	11.421	28.85	42.7	16.16	29.65	36.83	13.92	57.14
5	3	156.67	35.92	20.74	37.0	38.69	22.34	20.90	19.78	11.42	100

Unfortunately, although the plants were all grown from the same seed accession, and only plants producing a small number of flowers were selected for the treatments, the average total number of ovules per ovary was found to be significantly different at $p = 0.01$ between treatments. The plant used for treatments with 4 styles produced a small number of ovules per ovary. It is, therefore, impossible to compare, directly, the seed number per capsule between treatments. In each treatment, the percentage of ovules fertilized per capsule, for each capsule was found and an average obtained for each treatment, and these averages were used to compare results between treatments. The figures are tabulated in Table 36 along with the rest of the results.

Using the percentage of ovules fertilized at p = 0.01, there is no significant difference between treatments, but those flowers with only 1 style or 4 styles, tended to produce only about 50% of capsules with seeds per plant. In this experiment all seeds were evenly distributed within the capsule, even in those with only 1 or 2 styles. There was no significant difference in seed production in flowers with 1 or 2 styles and those with 3, 4 and 5 styles as found in Experiment 1, indeed flowers with 2 styles had the highest number of seeds per capsule on average.

Agrostemma githago L.

This is an annual plant, producing between 3 and 11 flowers with the average being 6.5 flowers for plants used in these experiments. Although the flowers are large and remain open for 4 - 5 days, indicating adaptation to out-crossing, seeds were readily formed under greenhouse conditions by self-pollination. Two separate experiments were again carried out in this species, with 5 plants being used per treatment in both experiments; in the first experiment flowers were artificially pollinated and in the second experiment flowers were allowed to self-pollinate.

Experiment 1

Seeds were planted in August with the first flowers opening in November. All capsules were removed in December. Flowers were artificially pollinated using a fine brush. The results are given in Table 37. The average for each plant was found and then using these figures the average for the treatment. Except for the plants with flowers with 2 styles, there is no significant difference in the average number of ovules per ovary between treatments. If the results for the average number of fertilized ovules are compared there is no significant difference at p = 0.05 between flowers with 2, 3 and 5 styles, or flowers with 1 and 4 styles although there is significant difference between these 2 groups. However, the actual number of ovules not fertilized is small, only about 9 ovules between the highest and lowest figure and even with only 1 style 46.82% of ovules are still fertilized per capsule. The difference between treatments is thus small.

TABLE 37

Experiment 1, Agrostemma githago

Character Style no.	n.	Average no. of ovules per ovary	S.D.	S.E.	Average no. of ovules per ovary	S.D.	S.E.	% of ovules fertilized per capsule
1	5	47.99	3.38	1.49	22.47	2.71	1.19	46.82
2	5	54.88	1.09	0.48	31.26	3.04	1.34	56.96
3	5	45.31	3.65	1.61	28.38	1.44	0.63	62.63
4	5	49.08	2.54	1.12	24.84	3.52	1.55	50.6
5	5	49.33	3.55	1.56	28.01	4.95	2.18	56.78

In all treatments, all capsules contained seeds and all the seeds were evenly distributed between the carpels. The amount of pollen-tube crossing-over is therefore great, with pollen tubes from 2 styles being able to fertilize the same number of ovules as those from 5 styles. As the results would indicate that all 5 styles are not really required, it was decided to allow the flowers to self-pollinate and see if this altered the results obtained.

Experiment 2.

Seeds were planted in January and the first flowers opened in the middle of March with all capsules being removed at the beginning of June. Flowers were allowed to self-pollinate under greenhouse conditions. Five plants were again used per treatment and the average figures for ovule number and seed number per ovary obtained as in Experiment 1. Results are given in Table 38.

Surprisingly, the per centage of ovules fertilized is higher in this experiment than in the previous one in which flowers were artificially pollinated. As in Silene coeli-rosa, there would appear to be a difference between flowers with 1 or 2 styles and those with 3, 4 or 5 styles, although in fact there is no significant difference at $p = 0.01$ in the number of seeds per capsule between the 5 treatments. All capsules examined contained seeds, and all the seeds were as in the first experiment, evenly spread thoughout the capsule.

TABLE 38

Experiment 2, Agrostemma githago

Character Style no.	n.	Average no. of ovules per ovary	S.D.	S.E.	Average no. of seeds per ovary	S.D.	S.E.	% of ovules fertilized per ovary
1	5	46.67	0.55	0.24	27.05	3.36	1.48	57.96
2	5	47.68	9.77	4.36	30.47	8.08	3.6	63.9
3	5	50.79	5.05	2.25	36.65	1.60	0.71	72.16
4	5	49.81	4.56	2.03	35.44	3.75	1.67	71.1
5	5	49.45	4.83	2.16	35.84	3.31	1.48	72.48

Lychnis coronaria (L.) Desr.

This is a perennial species. The plants used in this experiment were originally grown from seeds planted in February of 1978 which flowered in May of that year. A second flowering occurred in September 1978 and it was these flowers that were used in the experiment. Only 1 experiment was carried out on this species, using the flowering branches of 6 plants. At least 3 flowering branches, usually from different plants were used in each treatment. The average seed and ovule number was determined for each plant, and using these figures the average for each style treatment was determined. Results are given in Table 39.

From these results there would appear to be a difference again between flowers with 1 or 2 styles and those with 3, 4 or 5 styles in the number of seeds formed per capsule. Indeed there is significant difference in average seed number per capsule between the treatments at $p = 0.01$, but no significant difference between 1 and 2 style treatments or between 3, 4 and 5 styles treatments at $p = 0.01$.

Although seeds were found in almost all capsules examined, the seeds were not evenly distributed in the treatment with only 1 style, being more or less evenly distributed in the other treatments. In the treatments with 1 style, 17.1% of capsules had seeds mostly in 1 'carpel', 11.4% mostly in 2 'carpels' and 5.7% mostly in 3 'carpels'. Although crossing-over of pollen tubes occurred in this treatment, most of the pollen tubes only crossed to adjacent 'carpels'.

TABLE 39

Results for Lychnis coronaria.

Character / Style no.	Plant no.	n.	Average no. of ovules per ovary	S.D.	S.E.	Average no. of seeds per capsule	S.D.	S.E.	% of ovules fertilized per ovary	% capsules with seeds per branch
1	5	9	249	28.0	9.33	65.11	53.72	17.91	26.15	88.9
	6	2	227	21.21	15.00	134	101.82	72.0	59.03	100
	6	24	224.3	34.8	7.11	96.92	59.49	12.14	43.21	91.6
	Average	3	233.43	13.54	9.88	98.68	34.48	19.93	42.27	
2	2	6	261.5	30.07	12.28	222.3	29.18	11.91	85	100
	6	6	244.17	28.42	11.61	158.0	72.25	29.5	64.7	100
	3	3	244.67	52.01	30.03	66.67	44.88	25.91	27.25	100
	Average	3	250.1	9.86	5.70	148.99	78.21	45.2	59.57	100
3	2	8	263.13	25.33	8.95	201.37	82.7	29.22	76.53	100
	6	6	240.83	31.15	12.72	216.33	42.87	17.5	89.82	100
	5	5	267.2	42.96	19.21	240.4	50.98	22.8	89.97	100
	3	5	192.4	65.06	29.09	107.2	85.9	38.43	55.7	100
	Average	4	240.89	34.34	19.85	191.33	58.34	33.72	79.43	100
4	2	5	245.4	29.25	13.08	210.0	42.77	19.11	85.57	100
	5	3	265	24.06	13.89	240.3	39.37	22.73	90.68	100
	3	4	220.5	48.02	24.01	178.5	64.72	32.36	81.14	100
	6	10	215.4	71.53	22.62	195.5	83.28	26.33	90.76	100
	Average	4	236.45	23.16	13.39	206.07	15.14	15.14	87.15	100
5	1	4	257.25	27.84	13.92	192	58.44	29.22	74.64	100
	5	7	254.86	43.06	16.28	228.57	57.8	21.84	89.68	100
	6	5	253.2	19.37	8.66	235.4	23.14	10.35	92.97	100
	Average	3	255.1	2.03	1.17	218.66	13.49	13.49	85.71	100

The following statements can be made about the effect of the removal of styles on the number of ovules fertilized in these 3 species:

i. In all experiments there was no significant difference in the average number of seeds formed per capsules in treatments with 3, 4 or 5 styles, and usually no significant difference between the number of seeds formed in each capsule in any of the treatment: 1, 2, 3, 4 or 5 styles.

ii. Artificial pollination tended to increase the number of seeds formed in treatments with 2 styles, although the number of seeds in 1 style treatments still remained lower than the other treatment even if the difference was not significant.

iii. Except for Agrostemma githago, the percentage of capsules containing seeds per plant/flowering branch was low for 1 style treatments and sometimes 2 style treatments, and distribution of ovules also tended to be restricted in these 2 treatments often to only the 'carpel' with the style or styles and the adjacent carpels.

iv. In all treatments of Agrostemma githago and in treatments with 3 or more styles, seeds were evenly distributed between carpels, regardless of the position of the styles.

From these statements it would appear that for these 3 species only 3 styles are required to allow the fertilization of the maximum number of ovules. There would appear to be a decrease in the number of ovules fertilized where only 1 or 2 styles remained, but in the case of 2 styles this difference can be slightly eleviated by artificial pollination, suggesting that the decrease in seeds in flowers with 2 styles is due not to inadequate stigmatic area but to inefficient pollen grain 'capture'. This being the case, why do these

3/ ...

3 species produce '5-carpellate' ovaries and not '3-carpellate' ovaries? The reason may well be that '3-carpellate' ovaries contain fewer ovules than '5-carpellate' ovaries. This can be stated because of results found in the previous 2 sections of this chapter. Table 40 indicates the expected number of ovules per ovary in '3-carpellate' ovaries and the average number of seeds in '5-carpellate' ovaries with 5 styles for these 3 species.

TABLE 40

The number of ovules in '3-carpellate' ovaries compared to the number of seeds in '5-carpellate' ovaries.

Character Species	n.	Average no. of ovules in 5-carpellate ovary	S.D.	S.E.	Average no. of ovules in 3 carpels	Average no. of seeds in 5-carpellate ovary	S.D.	S.E.
Agrostemma githago	52	9.83	1.84	0.25	29.49	31.52	10.44	1.45
Silene coeli-rosa	11	43.98	13.78	4.15	131.94	68.27	82.25	24.79
Lychnis coronaria	16	50.99	6.39	1.59	152.97	221.56	49.81	12.45

Except for Silene coeli-rosa 3-carpellate ovaries would not contain the same number of ovules as can be fertilized with 3 - 5 styles in a 5-carpellate ovary.

In most capsules/ovaries except some of those with only 1 or 2 styles, there would appear to be a large number of pollen tubes crossing-over between 'carpels'. This crossing-over not only occurred to adjacent carpels but also to 'carpels' on the opposite side of the ovary from the carpel with the style, especially Agrostemma githago. In all these experiments it should be emphasised that styles that were removed were always adjacent to each other, a fact which certainly affected results, especially for ovaries with only 2 styles.

C. C. Doak (1937) removed 2 opposite stigmatic lobes of cotton (in cotton the ovary is completely septate at maturity, placentation is axile, 5 styles are fused with 5 stigmatic lobes at the apex) and found that in the 400 carpels of which the styles had been removed only/ ....

only 378 seeds were formed, less than 1 per carpel, each carpel having, on average, 9.3 ovules. Crossing-over has also been reported in the 2-carpellate Umbellifer Daucus carota, by H. A. Borthwick (1931). The crossing-over found in these Caryophyllaceous species is, however, greater than in these studies and must be due to the position of the transmitting tissue which will be discussed in the next chapter.

However, all these conclusions can only be reached on the assumption that the seed number counted represents the total number of ovules fertilized, which in turn represents the total number of pollen tubes reaching the ovary (to some extent). It may be that in all 3 species examined there is a high rate of abortion of fertilized ovules. If this is the case, then this factor has to be taken into account when considering the results. If there is a maximum number of fertilized ovules that can develop into seeds, then there may be more ovules fertilized in 5-styles ovaries than in 3-styles ovaries. The viability of the ovules may also limit seed production. However, the facts remain that a) crossing over between carpels readily occurs and b) that in all the experiments, there was no significant difference in the number of seeds formed in 3, 4 or 5 styles ovaries and therefore that 3 styles per ovary could achieve the fertilization of the maximum number of ovules likely to develop into seeds.

2.6 Discussion

The connection between style length/stigmatic area and ovule/seed number remains unclear. Both section 3 and section 4 of this chapter would seem to indicate that style number and length have little relation to the number of seeds formed or the number of ovules per ovary. Other factors, such as pollen grain number appear to be related to different things, pollen grain number to the particular breeding system of the species, and not to the number of ovules per ovary. Stamens would appear to be the most variable floral structures, especially the antipetalous stamens. Seed weight may be related to seed number but this is not always so. Surprisingly the destyling experiments confirmed the lack of relationship between style number, length of stigmatic area to seed number. This study also showed that the minimum number of styles required to fertilize the maximum number of ovules in a 5-carpellate ovary is 3, and it is therefore not surprising/ ....

surprising that the most common style numbers found in this family are 3 and 2. The study also confirmed that in this family all styles should be considered to function as a single unit, with each style having the capacity to 'capture' pollen grains which produce pollen tubes, capable of fertilizing ovules in different 'carpels'. Style length/stigmatic area should not be examined per style or 'carpel' but per ovary in this family.

CHAPTER 3.

OVARY MORPHOLOGY

3.1 Introductory Review

The free central placentation, often said to be present in this family although septa are in fact formed in a large proportion of the genera, has been of great controversy and importance in the study of the origin of the Angiosperm ovary. Allied to the problem of interpreting how the ovary of present day Angiosperms was formed is the equally important problem of how the pollen tubes reach the ovules to achieve fertilization, now and during the process of ovary closure in early pro-Angiosperms. The present work deals with aspects of carpel/ovary morphology, mainly on the presence or absence of septa and the importance of the septa in several species: Agrostemma githago L., Lychnis coronaria (L.) Desv., Cucubalus baccifer L., Silene coelirosa (L.) Gordon, Silene conoidea L., Spergularia media (L.) C. Presl., Polycarpon tetraphyllum (L.) L., Drymaria cordata Willd. ex Roem. et Schult., Corrigiola sp., Herniaria sp., Illecebrum verticillatum L., Paronychia sp.

In Agrostemma githago a detailed study has been made of the placental column with the observation that vascular tissue exists in the upper levels of the septa, not previously noted by other authors. Also in this species a careful examination of the route of pollen tubes has been made using both histological methods and direct observation of the pollen tubes in the tissue. In all the other species listed above, an attempt has been made to follow the route of the pollen tubes using the same methods. With these observations it is hoped to try and state the adaptive significance of the septum in this family and to tentatively suggest the composition of the ovary from an evolutionary point of view.

It is, therefore, important to consider the several theories as to the origin of the carpel in Angiosperms, before discussing the morphology of carpels/ovaries in the Caryophyllaceae. The main theories are: the Classical theory or Sporophyll theory, Carpel polymorphism, the Anthocorm theory, the Gonophyll theory, Stachyospory/Pachyospory/ ....

Pachyospory. These theories may help to understand the form of the carpel in the Caryophyllaceae and to interpret the new observations which will be discussed.

Two main methods have been used to investigate the carpel. In the earliest works on carpel morphology the authors observed present day plants, mainly the vascular tissue arrangement of the floral axis, and from this postulated the origin and homology of the carpels. More recent authors have examined the fossil record and the morphology and anatomy of present day lower plants and from this have tried to find the earliest Angiosperm carpel which will agree with the structure found in living Angiosperm plants. That is to say some have followed the New Morphology as opposed to the Old Morphology. Another group, Sattler (1974), Wardlaw (1968), have taken a totally different view, considering the morphology of present angiospermous ovaries to be a result of changes at the primordia level, without consideration of the fossil record. The vascular system has been used by most investigators. There are those who support the use of the vascular system in this way: A. Arber (1937), Moseley (1967), Puri (1951) and those who repudiate it: Carlquist (1969). The latter author considers that: vascular anatomy is not necessarily conservative; vascular traces can be gained as well as lost; the vascular sytem of present day flowers should be viewed from their functional role rather than from a supposed historical one.

The classical concept is that the carpel is a modified folded leaf, a sporophyll, to which the ovules are attached. This interpretation of the carpel was first put forward by Goethe in his 'Essay on the Metamorphosis of Plants' (1790) points 78, 79 and 80 in which he envisages the change from the leaf-producing vegetative axis to the floral axis with the "leaves" being transformed into sepals, petals, stamens and carpels (pistils). Many present day authors support this view with modifications: Arber (1937), Cutter (1971), Eames (1961), Esau (1965). Mamay (1969), after the discovery of 2 new genera of Cycad-like fossils from the late Palaeozoic period, postulated the development of the "classical carpel" from the megasporophyll from one of them, the genus B.

The ovules are considered to be borne either on the margins of the leaf-like carpels or on the lamina. The leaf-like carpel or sporophyll is envisaged as folding longitudinally, with the margins curving/ ....

curving inwards so that the ovules are turned towards the inside of the ovary, the margins thus being involute. Bailey and Swamy (1951), after examination of carpels of Degeneriaceae and Winteraceae species, postulated that the ovules are not borne on the margins but are borne on the lamina of the Sporophyll and that the carpel is thus a conduplicately folded structure, without involving involution of the margins of the sporophyll (Swamy & K. Periasamy 1964). The primitive Sporophyll has been described by A. Eames (1931) as having palmate venation and to be slightly 3-lobed. H. H. Thomas (1931) also suggested that the primitive sporophyll may have been palmate and K. W. Hunt (1937), although considering the leaf and carpels to have evolved from a primitive branch system, considered a palmately 3-lobed structure as being a possible intermediate stage in evolution. However, it has been suggested that 3 traces are not primitive as only 2 traces have been found in a number of fossil plant leaves (Marsden & Bailey 1955). The carpel has also been interpreted as arising from a peltate organ. Troll (1933) considered this to be the case after studying both the mature ovary and the initiation of the carpels in Aquilegia sp., Nigella sp. and Helleborus sp.

Controversy has existed between the axial or appendicular origin of the placentae/ovules. In the New Morphology the distinction between axial and appendicular is not valid as it is considered that all appendicular organs evolved from a branched, axial system. The appendicular nature of the placentae/ovules is basically the classical theory, the ovules being borne on a specialized leaf, the sporophyll. The axial theory, however, envisages an axial origin of the placentae/ovules with the "carpellary" leaves being sterile and forming the wall of the carpel/ovary around the fertile branches.

Payer in 1857, writing on the problems surrounding the axial or appendicular nature of parts of the carpel, considered that in unilocular ovaries with a central placental column (Amaranthaceae, Plumbaginaceae, Primulaceae) the pistil consisted of an axial part, the central placental column bearing the ovules, and another part of leaf-like carpels which formed the ovary wall and the styles. In multi-locular ovaries with axile placentation such as Coriaria, each carpel is also proposed to be of 2 parts, an appendicular exterior part, and an axial internal part to which the ovules are attached. The styles in such ovaries are usually appendicular in origin. Other ovaries/ ....

ovaries, both inferior and superior, are also examined and stated to consist of an axial part bearing the ovules and an appendicular part, the leaf-like components of the ovary wall. He thus states, p. 723 "Le carpelle de De Candolle est donc forme par une partie appendiculaire, la feuille carpellaire in seriee par sa base sur les deux branches d'un axe bifurque qui parte les ovules." Hagerup (1936) also considered in ovaries with central placentation that the placental veins were an extension of the apex of the floral axis and thus axial in origin and that the placental column was surrounded by sterile leaves. Later in 1938, in ovaries with parietal placentation using Salix sp. as an example, he concluded that the ovules were like "leaves" inserted on the floral axis, completely independent from the sterile "carpels" which formed the ovary wall. J.Mc.Thompson, in a series of papers from 1932, also supported the view that ovules were borne on the floral axis and surrounded by sterile structures, even in such families as the Leguminosae. Finally Gregoire (1938) in a detailed work also concluded that the placenta was axial in nature.

The other point of view is to consider that both axial and appendicular placentae are to be found in the Angiosperm families. Lam in 1948 proposed the terms Phyllospory and Stachyospory placentae which were respectively appendicular and axial in origin. These terms were first used in respect to lower plants by Sahni (1921): Phyllospermae and Stachyospermae. Lam proposed in his work 2 groups defined as follows p. 129 "Stachyospermae: Plants in which the sporangia being axis-borne originally are not or hardly connected with the sterile telomes or syntelomes other than be secondary processes; accordingly there are no true sporophylls; and Phyllosporae: plants in which the sporangia are essentially borne on many-telomed sterile fronds, which therefore deserve the denotion of sphorophylls.'

All plants, fossil and present forms, are envisaged as being able to be placed in either of these 2 groups. However, Lam adds that all land plants must originally have been Stachyosporous and that only with the development of telome leaves could phyllospory have arisen. The distinction between the 2 groups is, therefore, not great, and may merely be one of time. He also proposed that Angiosperms arose from at least 2 lines. In a later paper (1955) Lam considered that "perhaps only the "Polycarpicae" and the Liliiflorae/ ....

Liliflorae with their derivatives are answering the classical concept and are, therefore, phyllosporous," p. 425; all other families of Angiosperms are thus probably stachyosporous. A detailed table of which groups belong to the stachyosporous and which to the phyllosporous is contained in an earlier paper (1950), including an evolutionary time scale.

In a further paper (1959) Lam proposed the following structures: structures consisting of a dichotomy with fertile (male and female) and sterile parts - Mixed Protective Bifurcating Units, M. P. B. units; Mixed Bifurcating units, M. B. units, the basic type in the phyllosporous groups; Sterile Protective Bifurcating units, S. P. B. units, of leaf and axillary sterile shoot, confirming the interpretation of an axillary flower as a modified shoot. In many ways these structures are similar to those proposed later by Meeuse and Melville, being especially similar to Melville's ideas of the origin of the axillary bud of leaves. Lam states in the same paper p. 130, point 18, "It is suggested that integuments belong to the same morphological category as the cupule of the Pteriodospernales, arilli in many groups, and in some cases pseudocarpels," thus agreeing with the later work of Meeuse. The nature of the Bifurcating unit is further explored in 2 papers. In 1961, Lam criticised the Gonophyll Theory of Melville's as being too narrow.

Some other theories have tried to maintain the carpel or the sporophyll by envisaging that the "carpel" as seen in present day plants consists of a number of components, mainly based on the fact that most "carpels" have 3-traces (although many have more, or less). The vascular anatomy of the carpel is usually described as consisting of a central mid rib vein, the dorsal vein, which may branch to give laterals, and 2 ventral veins which may also branch and which supply the ovules. The ventral veins are usually larger than the dorsal veins and also may arise at a slightly higher level than the dorsal veins.

Saunders, in a series of papers from 1925, postulated, with a number of illustrations, carpel polymorphism which was based solely on the vascular anatomy of present day flowers. She envisaged that as in other floral structures, there could be more than one whorl of carpels and type of carpel, recognising 3 forms; valve carpels, solid carpels, semi-solid carpels, which could be combined in a number of ways/ ....

ways to form a syncarpous ovary. In the families Rutaceae, Zygophyllaceae, Meliaceae and Stachyuraceae for instance, 2 carpel whorls are thought to be present, the outer sterile, the inner fertile so that each "carpel" consisted of a sterile carpel with half an adjacent fertile carpel on either side (Saunder 1934). The carpel types are considered to be either leaf-like, or in the case of the solid carpel to consist only of a vascular cord. Each individual vascular trace was envisaged as supplying a single organ. Ovules were presumably considered to be borne on lateral organs. Eames (1931) greatly criticised this paper, using the floral anatomy of a number of plants to show discrepancies in Saunder's theory.

In 1931, H. H. Thomas also postulated that the carpel or sporophyll was compound, from studying fossil plants (Caytoniales, Palaeozic Pteridosperms). He envisaged that from the megasporophyll of the Gristhorpia type, which consists of a branch with opposite pairs of cupules containing ovules by a series of reductions in the number of cupules, a shortening of the axis/branch and eventually fusion of the 2 remaining opposite cupules, a follicle of the Caltha type could be reached. In this theory, the dorsal vein would correspond to the vein in the axis/branch and the ventral veins to those found in the cupules. The wall of the carpel would thus correspond to part of the axis/branch and part of the two cupules, with the 2 rows of ovules appearing along the ventral surface, where the cupules fused. In the following year the same author wrote a detailed paper on the merits of the study of fossil plants in determining the nature of the carpel. He stated that leaves may be separated into "...simple microphylls and the branched systems or telomes which later evolved into the megaphylls of higher plants" p. 26, "the fertile branches long remained as relatively narrow terminal structures, either as separate branch systems or associated with foliage development ..... carpels of the Angiosperms ..... homologous with leaves they are equally homologous with branches." p. 27. Various later authors have expanded and altered both the origin of ovaries from cupules and the origin of ovaries from the branched system or telome.

The origin of the cupule and of the 2 integuments of the ovule in the Lyginopterid Pteridosperms has been examined in 2 papers by W. H. Camp & M. H. Hubbard (1963)[a, b]. These authors postulated that the integuments of these ovules originated from dichotomously branched/ ....

branched "lateral trusses" or telomes which surrounded the megasporophyll and that the cupule was similarly derived. The aril of present day Angiosperms such as Paeonia is tentatively suggested to be derived from the cupule. The connection between these ovules and those of Angiosperms is only suggested and not clearly stated.

A year later Meeuse (1964) in reviewing the papers of Camp and Hubbard takes the view that the first integument of the ovule in these Pteridospermous plants originated from sterile adjacent sporangia and not from telomes, based on the work of Benson (1904), but agrees that the cupule in these fossil Pteridosperms originated from the telomes enclosing one or more ovules. Meeuse also considered the true aril of Angiosperms to be derived from the cupule. The origin of ovaries from fused cupules, as is suggested by Thomas (1931), is dismissed. In a detailed account of floral morphology (1965) Meeuse postulated the Anthocorm Theory of the angiosperm flower. The prototype of the Angiosperm reproductive regions is considered to consist of a central branch with lower sterile branches (which may become perianth lobes) with a number of fertile branches above, each subtended by bract-like phyllomes. The lower fertile branches, androclads, bearing clusters of stalked microsporangia and the upper branches, gynoclads, bearing stalked cupulate ovules. This whole structure is termed an anthocorm, although only part of the above structure may be present, for instance, the structure could be unisexual. From the cupules, the ovary of Angiosperms is envisaged to have developed along 3 lines. First the cupule may become the ovary wall, enclosing a single ovule, the first integument of which elongates and eventually closes the "ovary", the second integument may be involved in this or may fuse to the third integument or cupule to form part of the ovary wall, the extended integument/s becoming the style. The following groups are cited as having this type of ovary: Cyperaceae, Urticales, Juglandales, Piperaceae, Chloranthaceae, Myricales. In the second type, the ovary wall is formed from a number of sterile organs enclosing the fertile gynoclads: Centrospermae. The final type of ovary is found in the Polycarpicae and is similar to the latter type, formed from the ovuliferous axis, the gynoclad, forming the placental area in the ovary on which the cupulate ovules are borne, the rest of the ovary being composed of the sterile bract which subtended the ovuliferous/ ....

ferous branch. The third integument, the cupule, or as Meeuse terms it, the true aril has been lost in most of the advanced Angiospermous families. Meeuse has continued to write a series of papers based on this theory, modifying this original work. In 1975, for instance, he discussed 2 routes of evolution within the Angiosperms, one in which all the Anthocorm and one in which only part, became the functional reproductive unit. E. J. H. Corner (1966) dismissed the concept of the aril as being equivalent to the third protective layer of the ovule, as he considered the aril to be a post-fertilization development of the ovule. This paper also criticised the form that the Anthocorm takes in that the branches, androclads and gynoclads have internodes between the cupules and the microsporangia but no leaves or bracts at these nodes.

A. G. Long (1965) states that "a carpel may therefore be considered to be a dorsiventral divalved cupule, appendicular in nature but not derived from a conduplicate leaf," considering the ovary wall to be the cupule not the cupule to be enclosed within the ovary wall as in Meeuse's interpretation of the ovary (except in a very few cases where the ovary contains a single ovule).

A few years before Meeuse proposed his theory, Melville (1960) proposed the Gonophyll Theory. The basic unit, the gonophyll consisted of a leaf with either one or a number of epiphyllous fertile branches of either one sex or both. Gonophylls with either male or female reproductive units were termed respectively androphylls and gynophylls and those with both androgynophylls. The leaf which bore these fertile branches was termed the tegophyll when sterilization of the fertile branches occurred. Like Meeuse, Melvile envisaged that by repeating this basic unit in a branch system, a 'gonophyll of gonophylls' p. 7, specialization of this system would lead to an inflorescence or flower. This branch system he termed a synogonium. Melville cites fossil evidence of the existance of a leaf-branch system in the Coenopterid ferns of the Carboniferous period, Ankyropteris grayi, and in other fossil plants such as the Glossopteridales (Pteridospermales?) found at the end of the Carboniferous or early Permian period. Two further papers followed in 1962 and 1963, the first describing how carpels/ovaries evolved and the second on how the androecium evolved.

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The basic unit from which the components of the ovary are said to have evolved consisted of a leaf with a single epiphyllous dichotomous fertile branch. The fertile branches bearing secondary gonophylls, the leaves of which Melville terms bracts. From this basic unit, by a number of reductions, the ovaries of Anglosperms are thought to have evolved. Fossil Plants such as Glossopteris and the Cordaitales are thought to have evolved their reproductive structures from bracteate fertile branches whereas present Angiosperms are thought to have evolved their ovaries by the loss of the foliar organ of the secondary gonophylls giving an ebracteate fertile branch. From this structure, a leaf bearing a dichotomous, epiphyllous ebracteate fertile branch, the following reductions are said to have occurred: the fertile branch may move into an axillary position; by hormonal control during the vegetative stage the fertile branch system either in an axillary or epiphyllous position, can be suppressed and in a reproductive stage the leaf may be suppressed; ovule number may be reduced even to a single ovule attached to the midrib of the leaf. To reach the Angiosperm condition from these derivates it is envisaged that the leaf of the gonophyll unit may have folded around on the axillary placed fertile branch bearing one to many ovules. The 'syncarpous' ovary either arose by fusion of these units or by fusion of a number of tegophylls and separate fertile branches to give the different types of placentation now found. The paper goes on to describe how the ovary in a number of Angiosperm families is believed to have arisen.

Melville carries his theory slightly further in suggesting that the partial suppression of the fertile branch has led to the leaf with with an axillary bud, and that in Ranunculus sp. the petal plus the nectary flap may also have evolved in a similar manner. Melville is reminiscent of Goethe in his ideas of transformation of the vegetative axis to the reproductive axis by hormonal control of the suppression of the vegetative or fertile part of the gonophyll. No indication is given as to how the integuments of the ovule were formed. The leaf plus fertile branch is the same structure as proposed by Meeuse, except that the branches in Meeuse's thoery bear cupules and not ovules, and the branch is single and not dichotomous. Meeuse (1965) criticises Melville on the grounds of these 2 differences and that there is no fossil evidence of a dichotomous fertile branch system.

Finally/ ....

Finally, it is interesting to go back to the work of Goebel (1905) who states p. 55 'the essential points in dispute are to what extent the carpel (megasporophyll) and the flower axis (torus) share respectively in the construction of the gynoecium and in particular what is the correct interpretation of the placenta.' In syncarpous ovaries he recognises 2 categories, those in which the floral axis does share in development and those in which it does not, and that this affects the type of placentation found. Both categories can, however, be found in the same ovary. Goebel states p. 556 'Hitherto morphologists have considered leaf-borne and axis-borne organs as having different morphological value and have therefore endeavoured to avoid tracing to the same place of origin, organs which in their other peculiarities appear as evidently similar.'

According to the classical theory or phyllosporous theory the stigmatic papillae or tissue in the primitive open carpel occupied the margin of the leaf-like carpel on the inner adaxial surface and occasionally the abaxial surface. The style is envisaged as a sterile extension of the apex of the leaf-like carpel. Thus folding of the leaf-like carpel and fusion of several of these structures would result in the transmitting tissue being found next to the ovules/ placentae in 2 groups, one from each margin of the 'carpel.'

In Saunders polymorphic theory of the origin of the 'carpel', a single style may consist of a number of prolongations from different carpel types or may result from only one carpel type. The inner transmitting tissue presumably occupied the same position as that envisaged in the classical theory, with some of the carpel types losing this function as fusion occurred. Hunt (1937), who supported Eames' view that the primitive carpel had palmate venation and was a 3-lobed structure, envisaged that where the central lobe was larger than the 2 lateral lobes the central lobe became the style and where all 3 lobes developed equally, then all 3 would be involved in the formation of the style. There is no indication of where the transmitting tissue in the primitive ovary would have been. Thomas (1931) considered the 'carpel' to consist of 2 lateral cupules and the sterile axis to which they are attached. The original cupules are thought to have had basal styles attached to the hood-like structure of the cupule, fusion of the 2 cupules with the axis resulted in the axis coming in contact with these and becoming stigmatic and elongating/ ....

ing into the style. This interpretation is similar to that of Hunt and no explanation of the position of the internal transmitting tissue is given or how it is connected to this centrally placed style.

A very different view was proposed by Joshi (1934). Working on species in the Centrospermae he concluded that the stylar canal (transmitting tissue) occupied the same position as the ventral bundles of the carpel and considered the transmitting tissue to be derived from this vascular tissue. A. Arber (1937) and Thompson (1934) criticised this view, and in 1947 Joshi withdrew this theory.

In the Gonophyll theory of Melville, the leaf of the gonophyll is suggested to have had hydathodes on the margins, as in the bracts of Mercurialis. On the fertile branches as the complex began to reduce the ovules at the apex of the branches became sterile and were 'replaced by glandular tissue functioning as hydathodes' p. 20. As the leaf closed around the fertile branches, a liquid path along which the motile microspores could swim to the ovules was complete. The closure of the carpel and the development of the pollen tube, probably originally as an anchoring device, would occur at about the same time. The gonophyll leaf and the fertile branch would thus have both contributed to the formation of the style and the transmitting tissue depending on the way in which the fertile branch fused to the leaf.

Meeuse (1965) in those ovaries where the wall is equivalent to the cupule, fused or not fused with the integuments of the ovule, the inner integument of the ovule is proposed to have formed the style, the transmitting tissue thus consisted at an early stage of a hollow stylar canal joining the microphyle of the ovule to the outer surface of the 'ovary'. This hollow canal would eventually have closed and thus formed the transmitting tissue. In those ovaries in which the ovary wall is envisaged as being formed by the sterile bracts or the sterile bracts and the axis of the ovuliferous branch, the ovuliferous branch forms terminal styles which fuse together or remain separate as the ovuliferous branches and the sterile bracts fuse to form the syncarpous or apocarpous ovary. Thus in Meeuse's interpretation it is part of the ovuliferous branch which becomes stigmatic, whereas in Melville's Stachyosoporous ovaries the stigmatic tissue appears to be derived from both the sterile leaf of the gonophyll and the fertile branch.

The/ ....

The ovary as found in the family Caryophyllaceae consists of 2 or possibly 3 types. The first is multiovulate and completely septate or nearly so at an early stage in development, with the septa almost totally disintegrating prior to anthesis in most of the species except in some Silene species which remain multilocular at the base at maturity. These septa are formed between the styles at the traditional line of fusion of the 'carpels'. The subfamilies Dianthoideae, Alsinoideae and the tribe Polycarpeae in the subfamily Paronychioideae have species with this type of ovary. In the second type of ovary, usually only 1 ovule is present, although there may be up to 4, the inner wall of the ovary often has a distinct ridge of tissue between the styles, i.e. in the same position as the septa in the first type of ovary, and at anthesis strand/strands of tissue are evident from the apex of the style to the apex of the funicle/placental column. However, at no time is it evident that these ovaries are completely septate. The genera Scleranthus, Pollichia, Achyronychia and Scopulophila have ovaries in this category. The final type of ovary always has a single ovule with no evidence of a strand uniting the apex of the style to the apex of the funicle/placental column and with little evidence of remains of septa on the ovary walls. The ovary would appear not to be completely septate at any time, although the base of the ovary may be septate. Species in the tribes Paronychieae and Pterantheae in the subfamily Paronychioideae have ovaries of this type.

The vascular tissue of the wall of the ovary consists of dorsal bundles equal in number to the styles with lateral bundles between. Occasionally other vascular bundles may arise between the lateral and dorsal bundles. The dorsal bundles always extend into the styles, only rarely do the lateral bundles, and then only for a short distance. The placental bundles are usually described as consisting of ventral bundles opposite the dorsal bundles of the ovary wall, supplying the lower ovules, with the upper ovules being supplied by an originally central vascular system opposite the lateral bundles of the ovary wall. The placental tissue will be more fully discussed in the 'results' section.

The following problems thus arise about the ovary of the Caryophyllaceae species:

i./ ....

i. The septa, which disintegrate at an early stage resulting in most genera having a unilocular ovary, may indicate that the ovary is modified from a 'classical' axile placentation type, or the septa may be secondary and formed by sterile 'pseudocarpels' not involved with the placentae.

ii. The vascular tissue which supplies the uppermost ovules could be appendicular or axial in origin and could be separate or part of the ventral system.

According to Goebel (1905) the axis shares in the development of the ovary. The classical view is taken that the placentae are borne on the margins of carpels which unite with the floral axis, the placentation is considered to be axile. Disintegration of the septa leads to free central placentation with the placental column being made up of the margins of the carpel plus part of the floral axis. The formation of free central placentation from the traditional axile placentation is also the view of Puri (1952) p. 614.

In the other main theories concerning the origin of carpels, Saunder (1925), after studying Dianthus species and Lychnis vesperina Sibth., concluded that there were 2 carpel whorls, valve carpels and solid carpels; the valve carpels forming part of the ovary wall including the dorsal bundles, and the solid carpels with the lateral bundles of the ovary wall and the septa, to which are attached the placentae. Therefore, in this view the ovules on either side of the septum have originated from the same 'carpel', whereas in the classical theory the ovules within 1 locule, opposite the dorsal bundle are considered to be from the same 'carpel'. No mention is made of the inner vascular bundles supposed to supply the uppermost ovules. Lam (1948) believed the Centrospermae to be in the group Stachyosperme, i.e. to have outer sterile leaf-like carpels which enclosed the fertile ovule bearing branches. Melville (1962) considered the ovary in Caryophyllaceae to consist of sterile gonophylls, tegophylls, fused together to form the outer wall and alternating with the ovuliferous branches. He failed to recognise that septa were formed and that there was any direct connection, therefore, between the apex of the placental column and the base of the styles. Melville, therefore, proposed a complex theory as to how the transmitting tissue of the styles/ ....

styles connect with the inner transmitting tissue of the ovary leading to the ovules. Using Dianthus species he postulated that the alternating ovuliferous branches bifurcated at the base of the ovary, 1 branch supplying the ovules and the other, the stigmatic branch, running along the tegophyll blades where the blades ('leaves') would fuse. At the apex of the ovary, the stigmatic branch breaks into 2, each fork now going into adjacent styles, but only for a short distance. Although it is unclear from both the text and the diagrams, it would appear that the stigmatic branches, to which Melville refers are normally termed the median laterals, Thomson (1942) p. 366, and are in no way connected to the ventral or placental bundles. It is not clear as to whether Melville considers the transmitting tissue to run along the inner wall of the ovary opposite the lateral bundles, i. e. in the position of the septa, or not.

Lastly, according to Meeuse (1965) the Caryophyllaceous ovary can be interpreted as consisting of ovuliferous axes or gynoclads and a number of lateral structure, the bracts which subtend the gynoclads. He also states that these sterile bracts may produce septa which may fuse with the apex of the placental column, but gives no indication of what effect this would have on his theory.

An extensive study on the floral morphology of the Caryophyllaceae was carried out by B. Thomson (1942) on species in the subfmailies Dianthoideae and Alsinoideae from a 'classical' point of view. She concluded, from the large number of species studied, that the 'carpel' consists of 5 or 3 traces, with the median laterals of adjacent 'carpels' more or less completely fused; the ventral traces being fused in pairs and often forming a central mass in the placental column and are situated opposite the dorsal bundles of the carpel. Of the bundles which supply the uppermost ovules, she refers to them as follows "where the septa pull apart from the centre, the ventral traces separate, one standing in the edge of each septum and each probably composed of the strands of adjacent carpels which have coalesced" p. 347. She also recognised the presence of axial tissue in the centre of the placental column and of the ovaries being nearly completely septate at an early stage in development, and thus considered the ovary to represent axile placentation becoming free central.

In an early paper on the origin of the placentae by G. Lister (1884)/ ....

(1884), she gives a detailed account, from the primordia initiation, of the development of the carpels in Lychnis, Dianthus, Sagina, Spergula, Arenaria, Cerastium and Stellaria species, recognising that the ovary is septate at an early stage and that on disintegration of the septa the part uniting the apex of the placental column to the base of the styles remains intact until after fertilisation. From her observations the upper ovules are formed first, on the margins of the septa, then the lower ovules in 2 rows between the septa, although the very uppermost ovules appear to develop slightly after those immediately below. The ovary arises as primordia equal in number to 'carpels' around the base of the slightly raised central part of the floral apex, and shortly after initiation form pockets, thus the septa, ovary wall, and the central column all arise together from an early stage. The outer part of the ovary wall grows faster than the inner part, the septa and the central column, and eventually overtops these structures as the ovary closes; the ovules appear before the ovary closes. In some species it was noted that the area above the central placental column did not always become totally septate, although the strands were still present between the apex of the column and the apex of the ovary, but not as a single fused structure but as separate strands equal in number to the styles/'carpels' (Sagina sp., Spergula sp., Arenaria sp.) In the species examined from the subfamily Alsinoideae the ovules were formed on the septa first, as described above, but formed between the septa on the placental column. From these observations, Lister concluded that in Lychnis 'the first developed ovules are developed along the unattached margins of the dissepiments (septa) in the upper unilocular portion of the capsule, it must be admitted that the placenta are carpellary' p. 428, and from this statement concludes all the ovules/placentae to be carpellary in the other species she examined. The differences in the position of the ovules are due to the different growth rates of the central column and the 'carpels'/septa.

Later authors have also studied the development of the carpel from the primordia stage. I. Roth in 1963 described the development of the ovary in Cerastium species, Sattler in 1973 described Silene and Cucubalus species and R. F. Lyndon (1978) described Silene coelirosa. All found no evidence of the septa fusing postgenitally and the former/ ....

former 2 authors concluded that the septa, central placental column and the ovary wall arose together, although at different rates, agreeing with the earlier work of Lister. I. Roth (1962) also studied the ovary of Herniaria species which only have a single ovule. She concluded that the ovule was 'derived directly from the residual apical meristem of the floral axis' p. 194, the ovule primorida then becomes postgenitally attached to one of the 2 'carpels' although it would appear that she still supports the phyllosporous origin of placentae. She also noted 2 ridges on the ovary wall. Eckardt (1955) also observed these ridges which appeared to fuse slightly at the base with funicle in Herniaria species. These outgrowths were also found in Scleranthus by Eckardt (1955). In this same paper Eckardt states that these outgrowths, or septa, may be transmitting tissue. Rohweder (1967) studied the ovaries of Vaccaria pyramidata, Silene dioica, and Lychnis viscaria and concluded that the septa fused congenitally to the placental column, that the species belonged to the phyllosporous group, that in the upper part of the ovary, i.e. beyond the level of the placental column, ovules could be formed in a parietal position, and that the septa did not completely fuse in this region, a small hole being left immediately above the area to which the ovules are fromed on the septa. In longitudinal sections of the ovaries in all these 3 species, the ovules at the very top of the placental column, i.e. the ones usually fused to the septa, are shown as having a different vascular supply from the rest. In 1965, using Uebelina, a genus in the subfamily Dianthoideae with a single ovule, Rohweder concluded that the septa were fused to the funicle in the lower part of the ovary and are only partially evident in the upper part of the ovary, above the funicle/placental column. The ovule is said to form from an axile placenta. At anthesis, the septa disintegrate, the separated parts becoming papillate and forming the transmitting tissue. Postgenital fusion of septa in the upper part of the ovary results in the completion of the transmitting tissue from the apex of the ovary to the apex of the funicle/placental column. In a further paper (1970) on species in all the subfamilies, Rohweder indicates that the transmitting tissue is associated with the septa; in 2 distinct areas on either side of the remains of the septa on the placental column in Telephium species, Sagina species, Myosoton and Spergularia species/ ....

species; and that the transmitting tissue is attached to the strands of tissue, that are remnants of the septa, in the area between the apex of the ovary and the apex of the placental column. Moeliono (1959), in a preliminary paper on the placentation of Stellaria species, concluded that there is a distinct difference between the septa and the placental tissue and that the septa or margins of the 'carpel' are not forming the placentae. He thus concluded the placentae to be axial, with the 'carpels' being sterile leaves.

K. Buell (1952) studied the development of the pistil of Dianthus chinensis L. She recognised 2 rows of transmitting tissue on either side of the septa in that part of the ovary still completely septate, with no indication of what occurs when the septa disintegrate. The placentae were considered to be part of the septa; thus axile placentation becoming free central placentation on disintegration of the septa. A few years later in 1959 G. Bocquet discussed the ovary of Melandrium (Silene) species. He found that the ventral strand supplied the lower-most ovules, forming 2 rows of ovules opposite the dorsal bundles of the ovary wall, and that in the centre of the placental column, a first separate then a united strand of vascular tissue, extended above the level of the lower ovules supplied by the ventral strands and separated into 5 strands which supplied the uppermost ovules. These strands were opposite the lateral bundles of the ovary wall. However, he concluded that the strands which supplied the uppermost ovules were 'nothing more than a portion of the placental vascular system. ..... not a relic of the axis.' p. 221. He also concludes that those ovules formed in 2 rows opposite the dorsal bundles are from the same 'carpel', whereas those ovules formed on either side of the septa, with a vascular supply from the central strands described above, are from different, adjacent 'carpels'. There is no indication that the central vascular strands extended above the last pair of formed ovules. In the interpretation of the vascular strands and of the grouping of the ovules this work agreed with the previous work of J. Dickson (1936). Later, in 1960, Bocquet and Bersier, working on Silene species, reaffirmed that the central vascular bundles were not a prolongation of the floral axis but part of the placental ventral vascular system, and disagreed with the interpretation of B. M. Moeliono (1959) that the septa fused post-genitally to the placental column.

A/ ....

A very detailed and extensive work on the morphology of the ovary of species in the family Caryophyllaceae and other families in the Centrospermae appeared in 1970. In this work B. M. Moeliono concentrates mainly on 2 aspects; the growth of the septa: whether the septa fuse with the placental column and are part of the sterile carpels, or whether the septa bear the placentae and thus the central placental column is carpellary in nature, thus axile placentation becoming free central placentation; the nature of the central vascular strands of the placental column; part of the ventral bundle system or a residue of the vascular tissue of the floral axis. He examined the morphology of the ovary in the following species in detail: Silene alba (Miller) Kraues, S. vulgaris (Moench) Garke, Lychnis flos-cuculi L., L. viscaria L., Myosoton aquaticum (L.) Moench, Stellaria holostea L., S. graminae L., S. media (L.) Vill. and to a less extent Corrigiola litoralis. By studying histologically the ovaries in these species, Moeliono concluded that the septa grew independently of the placental column, and that during the development of the ovary fused postgentially with the column. Each septum is further described as representing the congenitally fused margins of adjacent sterile 'carpels' or phyllomes which form the ovary wall. The placental column is considered to be a direct outgrowth/extension of the floral axis and can be separated into 2 parts, the first part, here termed the placentae inferiors opposite the dorsal bundles, supply the ovules of the central column 'sensu stricto', and the second part, the placentae superiores, opposite the median lateral bundles and septa which supply the uppermost ovules, those which form on the 'margins' of the free septa during development. Vascular bundles which supply these 2 placentae systems are further described as being independent of each other. Reduction of ovule number to one, as is found in a number of genera in the subfamily Paronychioideae, is interpreted as reduction in the number of placentae to a single 'placenta superior'.

B. M. Moeliono thus considers the ovary in the Caryophyllaceae to consist of 2 parts, a sterile abaxial part and a fertile axial part, the fertile axial part consisting of 2 alternating axis, corresponding to the 'placentae inferiores' and 'placentae superiores'. The family thus belongs to the Stachyosporous group of Lam (1948). The sterile phyllomes can be considered to be leaf-like, each consisting/ ....

sisting of a dorsal bundle and 2 laterals, in the 'syncarpous' ovary the lateral bundles of adjacent phyllomes fusing congenitally to form the median laterals.

The transmitting tissue in the ovary in species in the family Caryophyllaceae appear from the work of Rohweder and others to be either on the septal ridges of the ovary wall, or to be on the septal ridges of the placental column and the septal strands or attachments connecting the apex of the ovary to the apex of the funicle/placental column. A great deal of work has been done on the transmitting tissue of the style in Angiosperms but not as much on the inner transmitting tissue of the ovary.

Styles are classified as being either wet or dry according to the presence or absence of stigmatic exudate, secreted by specialised sub-epidermal cells, and as being open, closed or sometimes half-closed (Hanf 1935) according to the type of transmitting tissue. Styles in the family Caryophyllaceae are both dry and closed, although, as will be discussed in the next chapter, some of the species with fused styles do have holes within the transmitting tissue of the style. The stigmatic papillae do, however, have a protein coating or pellicle outside the cuticle and this may be involved in penetration and recognition of pollen tubes (J. Heslop-Harrison & Y. Heslop-Harrison 1975, O. Mattsson. R. B. Knox, J. Heslop-Harrison & Y. Heslop-Harrison 1974). Where stigmatic exudate is present it contains lipids phenolic substances and small amounts of sugars (Vasil 1974, M. Sedgley & M. S. Buttrose 1978, F. W. Martin 1969) but proteins are not present in significant amounts (F. W. Martin 1969). The exudate is probably involved in nutrition of the developing pollen tubes and may inhibit germination of foreign pollen grains (I. K. Vasil 1974, M. Sedgley et al 1978, J. Heslop-Harrison 1979, F. W. Martin 1969). Dry styles are associated with sporophytic incompatibility systems and wet styles with gametophytic incompatibility systems (K. R. Shivanna & D. C. Sastri 1981). The transmitting tissue in solid styles consists of a specific area in the style, variously described as consisting of cells with thick lateral walls composed of pectic substances and hemicellulose (cotton: I.K. Vasil 1974, W. A. Jensen et al 1969) or consisting of cells which may appear collenchymatous but in fact have no cell wall thickening/ ....

ing but produce a secretory product similar in function to that found in the stylar canals of open type styles, outside the primary wall in the intercellular space (Lythrum, Salicara: M. M. A. Sassen 1974, Pavonia zeylanica, Zephyranthes ajax: I. K. Vasil & M. M. Johri 1964, tobacco: J. Bells & G. Hicks 1976, Lycopersicon peruvianum: M. Cresti et al 1976). In Agrostemma githago I hope to show that the transmitting tissue in the styles of this species are thin walled, and smaller than the surrounding cells.

The pollen tubes grow either intercellularly in those styles with mucilage between the cells of the transmitting tissue, or within the cell wall in cotton, or through the cell walls and into the cells (H. J. Wilms 1980). The transmitting tissue tends to be found in the centre in fused styles, between the vascular bundles (I. K. Vasil & M. M. Johri 1964). Within the ovary, the pollen tubes either grow over the surface of the transmitting tissue (ectotropic pollen tube growth) along the papillate cells to the funicles and eventually to the micropyle of the ovule (Vasil & Johri 1964, M. Sedgley 1979) or between the cells of the transmitting tissue (endotropic pollen tube growth). Buell (1952) working on Dianthus chinensis found that the pollen tubes grew between the cells of the transmitting tissue of the style and the placental column. The nature of the growth of the pollen tubes will also be discussed in the species examined here, as well as the position of the transmitting tissue. In cotton (Doak 1937) the pollen tubes are described as growing between the placental ridges and then turning to the micropyles or growing along the groove between the placental ridge and the septum. Gore (1932), however, described the pollen tubes of cotton as both growing within and along the tissue of the placenta.

3.2 Materials and Methods

All material used in this section of the work was obtained from plants grown from seed in the greenhouse of the Botany Department in King's Buildings, Edinburgh. During the winter months, lighting was maintained at 16 hours per day and the greenhouse heated to a temperature of 15°C. Plants were grown individually in pots either

5/ ....

5 inches square for the larger species or 3½ inches square for the smaller species in John Innes Potting Compost no. 1. All seeds were obtained from Botanic Gardens or Institutes, most collected from plants growing in natural habitats. The following species were used, obtained from the following places and the identification checked:

Agrostemma githago L.

Acc. 76. Collected in the gardens of the Botanic Gardens, Germany, Karlsruhe.

Acc. 90. Switzerland, Birgisch.

Acc. 284. Sweden, Stockholm.

Acc. 286. Belgium, Gesves.

Acc. 346. Belgium, Brussels.

Acc. 380. Turkey, Ankara.

Corrigiola litoralis L.

Acc. 327. East Germany.

Corrigiola telephifolia Pouret

Acc. 104. Portugal.

Cucubalus baccifer L.

Acc. 78. Collected in the gardens of the Botanic Gardens, Germany, Karlsruhe.

Drymaria cordata Willd. ex Roem & Schult.

Acc. 123, Germany, Berlin.

Acc. 188. Seeds of Acc. 123 which had been grown in the greenhouse of the Botany Department.

Herniaria glabra L.

Acc. 135. France, Strasbourg.

Acc. 154. Germany, Kuckrutz, Oldenburg.

Illecebrum verticillatum L.

Acc. 105. Portugal, Coimbra.

Lychnis/ ....

Lychnis coronaria (L.) Desv.
Acc. 42. Turkey, Gungormez, Tekirdas Al(E).

Paronychia echinulata Chater
Acc. 103. Portugal, Coimbra.

Polycarpon tetraphyllum (L.) L.
Acc. 96. Portugal, Coimbra.
Acc. 175. Italy, San Bernardino di Trana.

Scleranthus annuus L.
Acc. 75. Collected in the gardens of the Botanic Gardens, Germany, Karlsruhe.

Scleranthus perennis L.
Acc. 343. France.

Silene coeli-rosa (L.) Godron
Acc. 394. Collected from plants in garden in Botany Department of King's Buildings.

Silene conoidea L.
Acc. 281. Sweden, Stockholm.
Acc. 326. W. Germany.

Silene gallica L.
Acc. 229. Russia.

Spergularia media (L.) C. Presl.
Acc. 376. Russia, Moscoa.

Spergularia rubra (L.) J. & C. Presl.
Acc. 314. Denmark, Vesterlyug.

Most of the material, either whole plants or just the flowers, was fixed in F. A. A. (90 ml 50% ethanol, 5 ml glacial acetic acid, 5 ml formalin) for at least 2 days. Some fresh material was used in studying/ ....

studying the route of pollen tubes in Agrostemma githago and although it gave the same results as the fixed material it was found more convenient to use fixed material.

Method 1.

In order to observe the vascular tissue of the flower, either flowers, or ovaries, or placental columns with the seeds/ovules removed, were cleared using a method slightly modified from that of Fuchs (1963).

i. Material rehydrated slowly, 8 - 5 hrs in 50%, 30% ethanol and finally into water overnight.

ii. Placed for 6 - 7 hrs at 60°C in a solution of basic fuschin and NaOH.
Solution, 1 gram of basic fuschin, 10 grams of solid NaOH in 100 ml of water.

iii. Washed overnight in water, with frequent changes the following day and then left in water overnight.

iv. Dehydration of material in a series of ethanol, 30%, 50% 70% leaving material in each solution until no more of the red dye came out of the material.

v. Material placed in absolute ethanol for 1.5 hrs.

vi. Placed in a solution of ethanol and conc. H.Cl. 3:1 for about 15 minutes.

vii. Material placed in absolute ethanol for about 20 hrs, xylem vessels now purple in colour.

viii. Material placed in a solution of 0.5% fast green in ethanol of 10 minutes, so that the outer edges of the material can be distinguished.

ix. Placed in absolute ethanol overnight.

x. May be required to rehydrate slightly because of loss of green colour in 70% ethanol and then to dehydrate in 100% ethanol again.

xi. Two washes in xylene, and material mounted in Canada Balsam, xylem vessels now stained a purple to red colour.

Method 2.

The ovaries of a number of species were examined to identify the presence or absence of septa. Ovaries and, in the case of the smaller flowers, the whole flower were embedded in wax using the paraffin method as outlined in 'Plant Microtechnique' by D. A. Johansen (1940) p. 130 - 131, with a few drops of the red dye eosin added to the final alcohol solution so that the smaller material could be seen more easily in the wax after embedding. Only transverse sections were made of the material using a microtome, sections being 10 µm in thickness. The sections were then stained with safranin or a combination of safranin and light green. In some cases the wax sections were observed directly without staining for quicker results.

i. Wax removed by placing sections in xylene for about 15 minutes.
ii. Fifteen minutes in xylene and absolute ethanol, 1:1.
iii. Absolute ethanol for c. 5 minutes.
iv. Five minutes in safranin, 1% safranin in 70% ethanol.
v. Rinse in 70% ethanol.
vi. Absolute ethanol for 15 minutes.
vii. Wash in xylene.
viii. Mount in Canada Balsam.

OR

i. to v.
vi. Series of dehydration steps, 70%, 90% to absolute ethanol.
vii. Light green for c. 2 minutes, concentrated solution of light green in clove oil.
viii. Rinse in clove oil.
ix. Wash in xylene.
x. Mount in Canada Balsam.

Method 3.

In order to obtain details of the remains of the septa on the placental column, the placental column of a number of ovaries, with or/ ....

or without the removal of the seeds or ovules, were viewed with a scanning electron microscope. As the material in this part of the work was fresh, it had first to be dried before observation.

Fresh material was first dissected to remove the placental column from the ovary, and then fixed with gluteraldehyde, first being placed in a 1% solution for 1 hour and then with a 3% solution for 4 - 5 days. The material was kept during this time in a fridge at 4°C, and solutions of the gluteraldehyde were made in a phosphate buffer pH 7.0. The material was then washed several times with distilled water before being dehydrated using a graded series of acetone solutions, 50%, 60%, 70%, 80%, 95%, the material being placed in each solution for half an hour. Finally the material was placed in 100% acetone and changed 4 times. The material was then dried by a critical point drying method using carbon dioxide. Specimens were then mounted using a water-soluble glue on to the scanning electron stubs, thinly coated in gold and viewed with a Cambridge Scientific Instrument Stereoscan 150 at levels of magnification ranging from 100 to 2000 .

Method 4.

Most of the work to determine the route of the pollen tubes was done using flowers of Agrostemma githago, Acc. 76, as in this species the placental column is comparatively large and the plants flowered readily and were easily self-pollinated within 2 months of planting the seeds.

Several methods were examined to determine the stain best suited to the pollen tubes in the material. Pollen tubes are usually stained using substances which will indicate the presence of callose. Callose is said to be formed both within the pollen tubes themselves in the form of callose plugs and on the walls of the tube, and within the transmitting tissue through which the pollen tubes have travelled. The callose plugs and the walls of the pollen tubes also contain pectins and cellulose (N. V. Tsinger & T. P. Petrovskaya-Baranova 1967). Traditionally cotton blue (analine blue, methyl blue) or lacmoid have been used in conjunction with some method of clearing the tissue. The first method tried was that of Muntz (1971) using cotton blue and with lactophenol as the clearing agent. All the tissue of styles, ovary walls and placental columns stained dark/ ....

dark blue with darker blue areas evident. These darker blue areas on the ovary wall appeared to be vascular tissue, although in the styles stained pollen tubes were observed on the papillate surface. In the placental column all the tissue stained blue, especially the xylem vessels, with dark blue areas on the septal ridges which were probably due to the nature of the tissue and not, necessarily, to the presence of pollen tubes. If the material was left in lacto-phenol for a number of days, the tissue became transparent except for the xylem vessels. This method did not, therefore, appear to be a satisfactory way of following the pollen tubes.

Fresh material of placental columns, with the seeds/ovules removed were stained with lacmoid following the method of E. Gurr (1963). In both fertilized and non-fertilized ovaries, the septal attachments, septal ridges and the apex of the funicles became deeply stained blue, while the rest of the material remained green. This would again indicate that the nature of septal tissue allows it to take up stain readily. Longitudinal sections of the placental column of a fertilised flower were also stained with lacmoid using the method of D. W. Ramming & H. A. Hinrick (1973) but only the vascular tissue stained blue; the rest of the tissue remained unstained or only faintly blue. The final method tried was that of Martin (1959) using fixed material of whole styles, placental columns and ovary walls. Results were very poor, probably because this method used 8 N. Na.OH, which dissolves callose, and also due to the inadequate storage of the analine blue solution; the solution should have been stored in dark containers in a fridge at 4°C. However, a a modified method of Martin's was used for both sections and whole tissue, styles, dissected open ovaries and placental columns.

Method 4a.

For whole tissue.

i. Fixed in F. A. A. for at least 24 hours.

ii. Placed in a solution of 1 N. Na.OH. for 3 to 4 hours.

iii. Washed several times in water for at least 24 hours.

iv. Placed in a solution of o.2% methyl blue (T. Gurr 17900 0582) in a 0.1M. K_3PO_4 (D. P. H.) for about 1 week and kept in a fridge at 4°C.

The/ ....

The longer the material was left in the stain the better the results. Material remained usable for several months.

v. The material was then observed under UV light using a Vickers Instruments M41 Photoplan Fluorescence Microscope. Pollen tubes fluoresced bright yellow, the rest of the tissue dark blue or slightly green, the tissue being kept moist by applying the 0.2% methyl blue solution to the surface while being viewed.

Method 4b.

For transverse sections of ovaries, placental columns and flowers, the sections being made using the paraffin method of embedding as in 'Plant Microtechnique' by D. A. Johnston and microtomed, thickness being 10,/um.

i. Xylene for c. 10 minutes to remove the wax.

ii. Xylene and absolute ethanol, 1:1, for c. 10 minutes.

iii. Absolute ethenol 5 minutes.

iv. A series of alcohol solutions to rehydrate the material, 70%, 50%, 30% for c. 5 minutes in each solution.

v. Water for 5 minutes.

vi. Placed in a solution of 0.2% methyl blue (G. T. Gurr 17900 0582) in 0.1M K_3PO_4 for 2 - 3 hours in the case of large sections but for small sections only for c. 5 minutes, otherwise sections tended to float off the surface of the slide.

vii. Removed from the solution and stored dry without a coverslip in a fridge at $4^{\circ}C$, material remaining usuable for several months.

Note: After these 2 methods outlined above had been successfully used for some time, it was discovered that formalin is known to fluoresce both by itself and when combined with ethanol and acetic acid (F. A. A.)/ ....

(F. A. A.), and that the use of formalin in work with fluorescense is not recommended (J. D. Reynold & W. V. Dashek 1976). In a later paper I. E. Hughs & B. E. S. Gunning (1980) described callose deposition occurring in immature nectaries and trichomes fixed in gluteraldehyde or formaldehyde, but if fixed in a range of other solutions, including F. A. A., this did not occur. The type of callose deposition caused by aldehydes described by I. E. Hughs et al (1980) is of wall deposition which would not be mistaken for pollen tubes. Reynold & Dashek also used F. A. A. as a fixative and did get fluorescence of pollen tubes using aniline blue, similar to that found using other chemical fixatives such as Carnoy's fixative and absolute ethanol and acetic acid 3:1. It would, therefore, appear that although formalin by itself should not be used in fluorescent work, F. A. A. may still be acceptable.

3.3 Results.

The results section is divided into the 2 subfamilies examined in this chapter, Dianthoideae and Paronychioideae. Within each of the subfamilies the results for each species are given separately.

Subfamily Dianthoideae

Agrostemma githago L. K(5) C5 A5 + 5 G(5)

Plates 2, 3, 4

Figures 1, 2

This species in the subfamily Dianthoideae is closely related to the genus *Silene*. The pistil consists of 5 free styles with stigmatic papillae covering the entire length of the adaxial surface. The abaxial surface is covered in long sharp hairs which extend onto the surface of the ovary wall for a short distance as 5 distinct lines of hairs parallel to the styles. Among these hairs on the styles are also found papillate structures, more or less equal in length to the hairs, with about 5 being found on each style. (Plate 2.a) The function of these structure is unknown. The syncarpous ovary consists of 5 ovary components or 'carpels' which extend into the ovary cavity as 5 septa making the ovary, at an early stage in development, completely septate except probably for a small 'hole' above/ ....

above the placental column. The septa breakdown, except for the strands of tissue from the apex of the ovary to the apex of the placental column, before anthesis to form septal ridges on the ovary wall and the placental column. These septal ridges on the ovary wall run along the suture line of adjacent 'carpels' along the median lateral veins, between the styles, the septal ridges on the placental column being opposite those of the ovary wall. The placental column fills about two thirds of the ovary at anthesis. Ovules are arranged in 2 rows between the septal ridges. On average 51.7 ovules are formed each ovary of which 29.9 ovules are fertilized and develop into seeds.

Under greenhouse conditions, the flower remains open for about 5 days, suggesting that the flowers may well be out-crossing. However, self-pollination readily occurred.

The septal tissue is very fragile and white in colour at anthesis, becoming brown as the seeds mature. The placental column appears to be composed of the fused funicles of the ovules and at anthesis is distinctly fleshy and green in colour, the septal attachments at anthesis appearing as a 5-spoked solid papillate structure. (Plate 4a,b).

Several abnormalities were noted in this species. A fully formed ovary with style containing 'ovules' was produced at the apex of the placental column in a number of ovaries. In some, at the base of the ovary, the funicle elongated and a callus formed in place of an ovule. Occasionally 'ovaries' with papillate styles were also found to develop at the base of the ovary, but no ovules were found inside these structures. Such abnormalities may have been induced by fungal invasion.

Description of vascular tissue in the placental column and septa.

In this work only open flowers were examined. It was not possible due to staining difficulties to examine very young ovaries, although this has been done in other species discussed later. The description of the morphology of the ovary is as found in flowers from the time the stamens start to shed pollen grains until pollination and fertilization, when the septal attachments begin to break, some 4 to 5 days.

Acc./ ....

Acc. 76.

Transverse sections of the placental column with the septal ridges and attachments, but without the seeds or ovules, were examined using either method 2 or 4b to prepare the material. It would have been impossible to section the material with the seeds/ovules attached. The septal attachments were separated from the apex of the ovary but the styles were left attached to the apex of the septal attachments.

In all sections examined, the apex of the septal attachments appeared as a solid, 3-sided structure, sometimes round, the margins often ragged and possible papillate (level 1), certainly this would seem to be the case after examining the placental column with septal structures with the Scanning Electron Microscope, method 3 (Plate 4.a). About one quarter of the way down the septal attachements, the structure began to become a solid 5-pointed star in transverse section (level 2). Each of the points appears to consist of 2 areas, separated by a lighter staining area; sometimes this tissue contained small holes. The points were not opposite the median lateral bundles of the ovary wall but opposite the dorsal bundles. Very shortly after this level, each point separated down the centre, along the lighter tissue, and at the same time fusion occurred between the adjacent havles of the original points. It appeared that the tissue from adjacent points was 'pulled' together and fusion occurred. Firstly, the tips of the tissue fused, leaving a hole in each of the 5 new points, but by about halfway down the septal attachment, these 'holes' disappeared and the septal attachment now became a 5-pointed star again (level 3) but the points of the star were not as prominent as at level 2, and each point was now opposite the septal ridges on the ovary wall, and parallel to those of the placental column, occupying the position as the 'space' between the original 5 points at level 2.

Each individual septal ridge and attachment thus consists of 2 parts. If the ovary wall is said to consist of 5 components or 'carpels', considering the above description, the following statements can be made:

i. The septal attachments, the 5 separate points, at the apex of the ovary consists of the margins of the same 'carpel' unit and the points are parallel to the styles (level 1 and 2).

ii./ ....

ii. The septal ridges of the ovary wall and the placental column, consist of the fused 'margins' of adjacent 'carpels'.

iii. The septal attachments, the 5 points, halfway down the structure from level 3 consist of the 'margins' of adjacent 'carpels'.

There is no evidence, that even at the apex of the ovary, the septal ridges of the ovary wall are not between the dorsal bundles. This would suggest, therefore, that at the apex of the ovary there is a downward growth of the septa at an early stage in development as the apex of the ovary closes; thus results in the margins of the same 'carpel' becoming fused. Indeed, the styles are set in a slight depression at the apex of the ovary, the slight downward growth of the septa being supported by Moeliono (1970). The apex of the ovary is also probably completely solid at an early stage in development (see results of Silene coeli-rosa). Thus it is the manner in which this solid area breaks down which results in the configuration of the septal tissue at the apex of the septal attachments.

The tips of the 5 points became papillate at this level and vascular strands appeared in the tissue of the septal attachments Only xylem vessels have been identified in groups of 2 to 5. Lignin autofluoresces a greenish yellow colour, individual xylem vessels can thus be readily identified by the distinct shape of the cell in transverse section, the walls fluorescing. Each group of xylem strands is situated opposite the points of the septal attachment, not in the centre of the structure or in the point itself but more in the centre. All 5 groups of xylem strands do not appear at the same time, the number and the exact level at which the xylem vessels are evident vary between ovaries examined, although even in the youngest ovaries (taken from day 1 flowers) xylem vessels were evident sometime between the septal attachment appearing as a solid 5-pointed star (level 3), structure and the hole appearing in the centre of the septal attachment (level 4).

The 5 points then begin to elongate into spokes, and as this occurred the margins of the spokes as well as the tips became papillate. About three quarters of the way down the septal attachments a 'hole' developed in the centre of the tissue, the margin of which was also papillate (level 4). The 'hole' quickly increased in size and the/ ....

the five spokes eventually separated from each other to become the 5 separate septal attachments, all the margins of which were papillate (level 5). Each septal attachment consists of the congenitaly fused margins of adjacent carpels. Even at level 2, where the septal attachments are completely fused, the 5 separate septal attachments can already be identified when the tissue has been stained with cotton blue. The tissue, which will form the 5 separate septal attachments, is darker stained than the tissue which will eventually break (Plate 3.a).

The 5 separate septal attachments now spread further away from each other. The 'ends' where the groups of xylem vessels were situated, i.e. towards the centre, became rounder and the rest of the septal attachment became longer and narrower. At the rounded end, about seven eighths of the way down the structure, a different tissue 'fused' with the septal attachments (level 6). This tissue was much denser than that of the septal tissue and was part of the placental column. The margins of this tissue do not become papillate. Very soon after this tissue appears, the xylem vessels cross from the tissue of the septal attachments into the tissue of the placental column (in transverse sections of 8-day flowers longitudinal sections of xylem vessel were observed rather than transverse at this level). Funicles of ovules were now evident in the sections. The placental tissue increased in size, both the original tissue that fused to the septal attachments and funicles of other ovules 'fusing' with the structure from the adaxial side until eventually the hole in the centre disappeared.

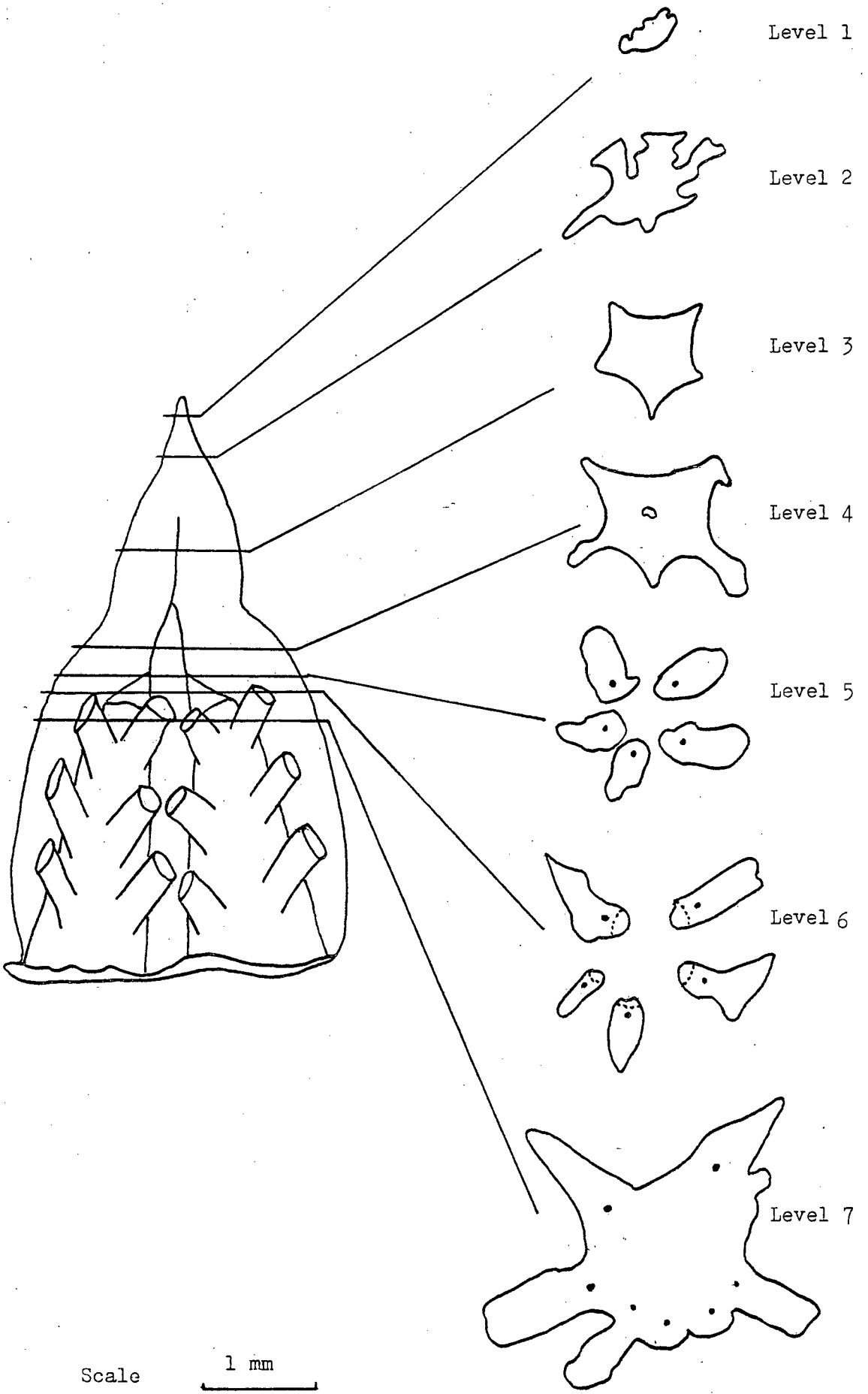
The septal attachments now became completely 'fused' with the placental column (level 7) and are now termed septal ridges. The septal ridges continue to the base of the placental column, gradually decreasing in size. At early stages in flowering, the septal ridges are papillate but in later stages become very disorganised and distinct papillae are not evident. Figure 1 , illustrates the septal attachments at the different levels outlined above, in a day 4 flower.

The xylem vessels which first appeared above the area of separation of the septal attachments and crossed over before total fusion of the septal attachments to the placental column into the placental/ funicle tissue continue as 5 separate strands in the centre of the placental/ ....

FIGURE 1

Agrostemma githago L. : Placental column with septal ridges and septal attachments with the ovules removed, to show the different levels of the septal tissue in a day 4 flower.

FIGURE 1


Level 1
Level 2
Level 3
Level 4
Level 5
Level 6
Level 7
Scale
1 mm

placental column, eventually fusing with the rest of the placental vascular tissue to form a 10-spoked structure, although the discrete xylem vessels could still be distinguished. Moeliono (1970) has described these central strands in other species as supplying the upper pair or pairs of ovules which are inserted/fused with the free septal attachments above the placental column. In Agrostemma githago species examined, these upper ovules were not present. O. Rohweder (1967) in describing Agrostemma githago, however, shows in his fig. 24d a pair of ovules attached to each septal attachment in a manner which suggests that the septal attachments bear the placentae according to the view that the carpel margins bear the ovules. The figure shows the occurence of these ovules before total fusion of the placental column. The inner part of the septal attachments is swollen and triangular in shape, suggesting this represents the area described above into which the vascular tissue 'moves' and is placental tissue, not part of the septal attachments as is suggested by Rohweder's figure. These sections have been taken from a young ovary and it is possible that a hole does occur in the centre of the placental column at this stage, just before total fusion, as will be discussed in Silene coeli-rosa. However, what appears to happen is that the septa fuse with the placentae/funicles of the upper ovules, but in this species ovules are not formed and the vascular tissue (at least the xylem vessels) instead 'pass' from the placental tissue into the tissue of the septal attachments. The vascular tissue, however, has not been observed to extend to the apex of the septal attachments or into the styles. Growth of this vascular tissue into the septal attachments appears to occur at a late stage in floral development. It may be that in other species where the upper ovules are not formed, that vascular tissue will also continue into the septal attachments.

As described above the vascular tissue becomes a 10-spoked solid structure. The 10 spokes are in 'pairs', each pair between the septal ridges, opposite the dorsal bundles of the ovary wall. Further down the placental column the solid vascular tissue appears as a central, round-shaped structure with 5 'V' shaped structures attached, each 'V' being opposite the dorsal bundles of the ovary wall. What appears to happen is that as the separate vascular tissues of/ ....

of the funicles fuse, the 5 central strands also fuse, and it appears from some sections that these strands 'fork', 1 fork going to each of the 'V' structures now formed but this may not be the case. At the angle of 'V' structure is a large group of xylem vessels, equivalent to the ventral bundle, giving off bundles in 2 rows to supply the ovules. The central area consists of a number of xylem vessels which appear to cross, with no evidence that the xylem vessels occupy any particular position, although these strands of xylem may be a continuation of the 5 central strands. The vascular tissue of a Day 8 flower is illustrated in figure 2 .

Route of pollen tubes.

The pollen grains with up to 48 pores are readily observed germinating on the stigmatic surface of the styles. The opercula of the pores appeared to open by a hinge mechanism, In a number of instances more than 1 pollen tube was seen to be produced by each pollen grain. The growth of more than 1 pollen tube has also been observed, but rarely, in Silene alba (R. E. Crang & C. M. Miles 1969). According to P. Maheshwari (1950), this condition regularly occurs in species in the Balvaceae, Cucurbitaceae and Campanulaceae, and in Clarkia elegans (G. W. Johnston 1959). In Agrostemma githago the pollen tubes (Plate 2) penetrate the papillae (Hanf 1935) rather than running through the wall or cuticle as in a number of other species in this family. Pollen tubes of Dianthus chinensis have also been found to penetrate the papillae (K. Buell 1952).

The transmitting tissue within the style consists of a narrow strip of tissue between the single central vascular bundle of the style and the stigmatic papillae (Plate 2c, d). The cells of this tissue being smaller than the cells of the surrounding tissue, with large intercellular spaces. Within the ovary the transmitting tissue may either have been found on the ovary wall or as in other species (O. Rohweder 1970) on the septal attachments and the septal ridges of the placental column.

Using several flowers, 4 - 5 days old in which the septal attachments had just broken, using method 4a fluorescing pollen tubes could be seen on the part of the septal attachments still attached with the apex of the ovary wall. A continuous fluorescing line was also observed along the line of fusion of the ovary wall components/ ....

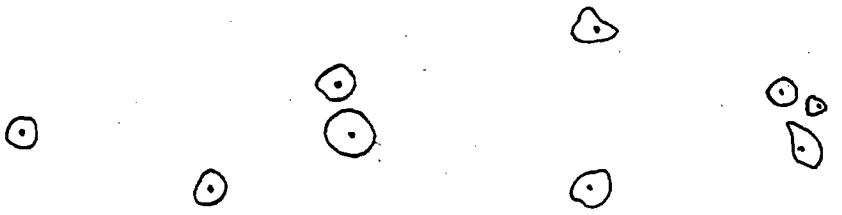
FIGURE 2

Transverse sections of the placental column of a day 8 flower of Agrostemma githago L.

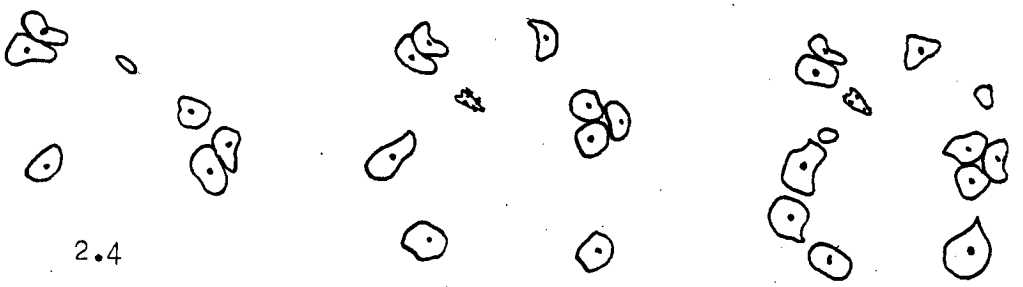
2.1 One funicle
2.2 Three funicles
2.3 Five funicles
2.4 Six funicles and the apex of the septal attachment.
2.5 Nine funicles and a section through the apex of a solid septal attachment with five groups of xylem vessels.
2.6 Twelve funicles with a solid septal attachment.
2.7 Eighteen funicles with septal attachment at level 4.
2.8 Large number of funicles now evident all very close to the septal attachment still at about level 4.
2.9 Septal attachments now at level 5 with funicles beginning to appear as two rows between each septal attachment.
2.10 Septal attachments at level , the vascular tissue originally in the septal tissue now in the placental tissue, with the funicles clearly in two rows between the septal attachments and fusion occuring on the right side.
2.11 Septal attachments at level 7, septal ridges on the placental column now small, the vascular tissue of each funicle evident in the placental column, with the vascular tissue originally in the septal tissue now evident opposite each septal ridge.
2.12 Vascular tissue of funicles now fused although xylem tissue can still be distinguished, about the middle of the placental column.
2.13 Very near the base of the placental column, arrows indicating the position of the septal ridges which are now no longer evident. Groups of xylem vessels evident in centre of placental column with distinct 'V' of vascular tissue between the position of the septal ridges.

ov - ovules
o - xylem vessels
x - xylem vessels originally found in septal tissue

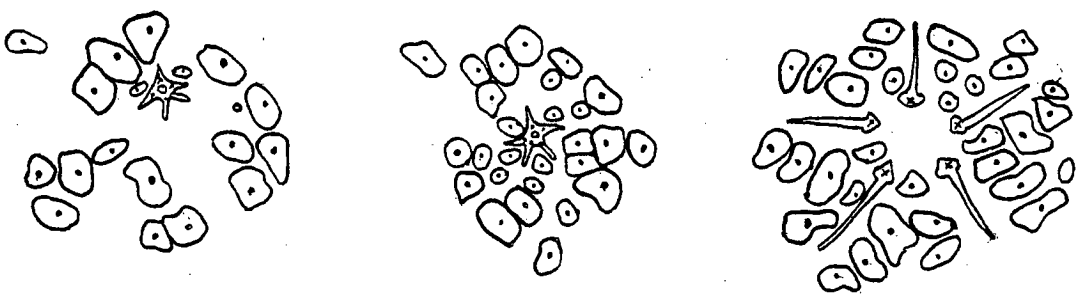
FIGURE 2



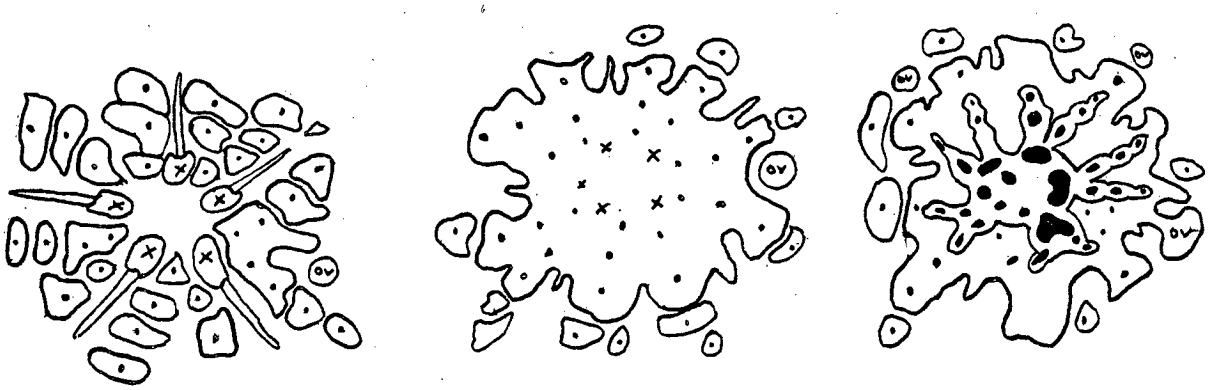
2.1 2.2 2.3



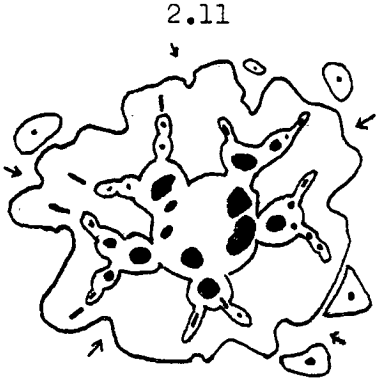
2.4 2.5 2.6



2.7 2.8 2.9



2.10 2.11 2.12



2.13

Scale 1 mm

PLATE 2

Agrostemma githago L.

2.a S.E.M. phdtograph of style showing papillate structures among hairs of styles.

2.b S.E.M. photograph of germinating pollen grains, note the 'hinge' opening of pollen grain pore operculum.

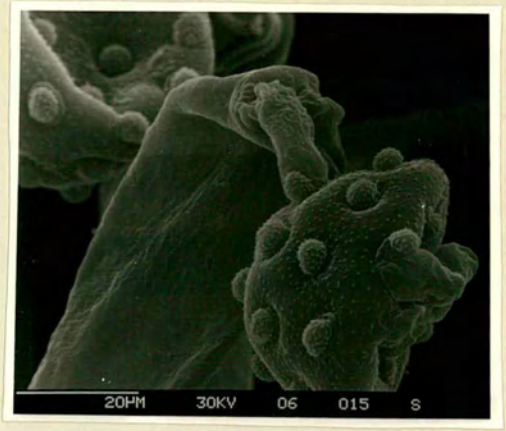
2.c S.E.M. photograph of T.S. of style showing transmitting tissue.

2.d T.S. of styles, showing transmitting tissue with fluorescing pollen tubes. X 200.

2.e Pollen grains germinating on styles, many pollen grains with more than one pollen tube. (Fluorescing microscope.)

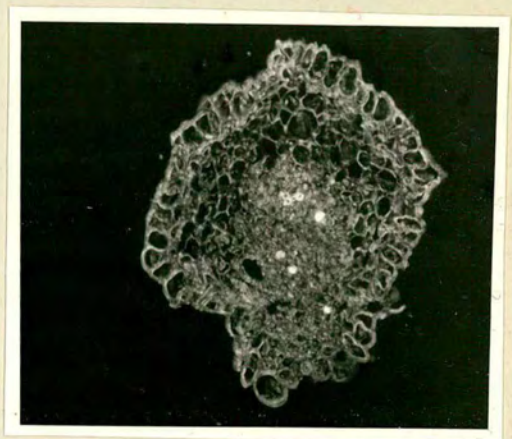
PLATE 2

2.a



2.b

2.c



2.d

2.e

components or 'carpels' but this was found to be due to the xylem vessels in this region, rather than to the presence of pollen tubes. On the placental column of pollinated flowers, broken fluorescent lines were observed on the septal attachments and the septal ridges. The pollen tubes often appeared to be within the tissue (endotropic growth) rather than on the surface. Some of the pollen tubes on the septal ridges of the placental column were also seen to be branched , a condition also found in other species. H. J. Wilms (1974) found the pollen tubes of Spinacia oleracea to be often branched and concluded that the branching was due to the production of a hormone by the female tissue after the ovule had been fertilized, causing changes in the direction of growth of the pollen tubes. No pollen tubes were observed on any other part of the placental column, i.e. no pollen tubes were observed between the 2 rows of ovules as has been described for cotton (C. C. Doak 1937). On the septal ridges of some of these placental columns, the pollen tubes appeared to be running over the surface, and in others to be internal. It was difficult using this tissue to be sure if pollen tube growth was ectotropic or endotropic, as differences observed could have been due to the transmitting tissue being in different stages of disintegration.

Using method 4b, sections of the styles and the placental column confirmed observations made using whole tissue, that pollen tubes grow either within or along the transmitting tissue in the septal attachments and ridges of the placental column. In non-pollinated flowers of the same age (styles being removed as soon as the flower opened when the styles were still not receptive) no pollen tubes were observed or fluorescence in the position that pollen tubes were found in known pollinated flowers. In transverse sections of the placental column only the xylem vessels were observed to fluoresce in the septal attachments; no fluorescence was observed within the septal ridges.

In order to determine when pollen tubes first appeared in the tissue and to try and determine the exact route of pollen tubes, a series of flowers was examined from the first day the flowers opened until the tenth day, flowers usually closing on day 4 or 5. By doing this it could also be determined if the septal attachments broke/ ....

broke prior to the appearance of pollen tubes. If this occurred the route of the pollen tubes could not be as suggested above. All flowers were removed in the morning to try and obtain flowers of uniform age.

Description of flowers on each day.

This information is also given in table form, table 41.

Day 1.

At this stage, the petals had started to open (originally petals were twisted together, upright) and spread apart but not yet flat against the 5 teeth of the calyx tube. The stamens, both antipetalous and antisepalous, were usually above the level of the neck of the calyx tube and in some flowers, only a few of the anthers were shedding pollen grains although in some flowers only a few of the anthers were open. The styles remained below, or just at the level of the neck of the calyx tube. The stigmatic papillae were not receptive but pollen grains were observed on some of the styles. The ovary was about 4 mm in length at this stage, the septal attachments still being intact although the rest of the septal tissue had already disintegrated.

Day 2.

By day 2, the petals were almost touching the spreading teeth of the calyx tube but the flowers were not yet completely open; all the anthers in all the flowers examined were, however, now shedding pollen grains, with some grains still present in most of the anthers. The styles were now above the level of the neck of the calyx tube but were still erect so that the adaxial stigmatic surface was not exposed, the stigmatic papillae being still small and not receptive. The ovary had slightly increased in size to about 5 mm in length but the septal attachments were still intact.

Day 3.

The flowers were now fully open, the limb of the petals were now totally horizontal, the tips slightly curving downwards. The stamens were still shedding pollen grains, the styles were no longer erect but/ ....

but were flat against the petals, in contact with the anthers. The stigmatic papillae had increased in size and were now easily seen and must now be considered to be receptive with pollen grains observed on the styles. The ovary remained about 5 mm in length with the septal attachments still intact.

Day 4.

By day 4, the flowers had closed, the petals had become erect and twisted together again and were beginning to wither slightly. The ovary had increased in length to about 7 mm, the ovary wall had now become slightly hard, but the septal attachments remained complete, although disintegration was evident.

Day 5 - Day 6.

The petals were now very shrivelled and no longer attached to the receptacle. The ovaries were now quite hard and had increased in length to about 9 mm, but the ovary still did not reach the neck of the calyx tube, with the septal attachments now no longer complete in most flowers.

Day 7 - Day 10.

Ovules were now clearly fertilized, developing seeds being clearly evident in older flowers.

Four ovaries were fixed in F. A. A. for each of the 10 days. Two were observed using method 4a, the ovary wall being removed so that observations could be made on the placental column intact, and also the styles. The other 2 ovaries were also dissected open and the placental column removed. Transverse sections using method 4b were made of the placental column (with the ovules or seeds removed) and the styles.

Whole tissue results using method 4a.

From day 1, the septal attachments and the septal ridges on the placental columns were clearly papillate, the papillae increasing in length up to about the fourth day. After the fourth day, the tissue of the septal ridges on the placental column and the septal attachments began to disintegrate and became less organised. Pollen grains were/ ....

TABLE 41.

Development stages of flowers of Agrostemma githago, day 1-10 of flowering.

Character / Day of Flowering	Petals	Stamens	Styles	Septal attachments	Ovules	Pollen tubes in styles	Pollen tubes in septal attachments	Pollen tubes in septal ridges of placental column
1	Open	Shedding pollen grains	Below neck of calyx tube, papillae not receptive	Intact	Not fertilized	Little evidence of pollen tubes except next to papillae	Little evidence of pollen tubes	No evidence of pollen tubes
2	Open	Shedding pollen grains	Above neck of calyx tube, papillae not receptive	Intact	Not fertilized	Little evidence of pollen tubes except next to papillae	Little evidence of pollen tubes	No evidence of pollen tubes
3	Open	Shedding pollen grains	Spread open, papillae receptive	Intact	Not fertilized	Little evidence of pollen tubes except next to papillae	Little evidence of pollen tubes	No evidence of pollen tubes
4	Closed	Empty	Papillae receptive	Beginning to disintegrate	Probably fertilized	Dull areas of fluorescence in transmitting tissue	Dull areas of fluorescence at apex of septal attachments	No evidence of pollen tubes
5 - 6	Withered	Empty	Papillae receptive	Not intact	Seeds	Pollen tubes clearly seen	Pollen tubes clearly seen	Clear evidence of pollen tubes mainly with transmitting tissue
7 - 10	Withered	Empty	Papillae receptive	Not intact	Seeds	Pollen tubes clearly seen	Pollen tubes clearly seen	Clear evidence of pollen tubes

were first observed on the styles of day 3 flowers. Pollen tubes were observed penetrating the stigmatic papillae and extending into the transmitting tissue of the style but only for a short distance in day 3 flowers. By day 4, the pollen tubes were clearly evident in the transmitting tissue of the styles and by day 5 a large number of pollen tubes were observed within the transmitting tissue of the styles and the stigmatic papillae were beginning to disintegrate. The pollen tubes continued to be evident in the transmitting tissue of the style up to day 10 flowers.

Pollen tubes were first clearly observed in the septal attachments of day 5 flowers, although at day 4, a number of small dots of yellow fluorescence were observed within the tissue at the very apex of the septal attachments. Prior to this, the septal attachments and septal ridges remained stained dark blue. Pollen tubes were also observed, both on and within the tissue of the septal ridges of the placental column from day 5, reaching the base of the ridges, the rest of the tissue of the septal ridges and attachments now fluorescing bright green with the pollen tubes fluorescing yellow. By day 9, the pollen tubes were not so evident on/in the septal tissue, the tissue now fluorescing a very bright green, obscuring the pollen tubes. Plates 4 e, f, illustrate observations of pollen tubes in whole tissue.

Transverse sections results using method 4b.

In sections, whether pollen tubes were present or not, the tissue fluoresces a green colour with autofluorescent xylem vessels a greenish yellow colour. Where pollen tubes are present they fluoresce a bright yellow colour as does phloem tissue. Pollen tubes were, however, easily distinguished from phloem tissue as in the latter only small dots of fluorescence were observed, scattered over the cells of the tissue which was also associated with the easily identifiable xylem vessels, whereas pollen tubes were evident as large solid yellow fluorescing discs of callose. (M. C. Chou & D. J. Harberd 1970).

From a day 1 flower, a pollen tube was surprisingly observed at the very apex of the septal attachments at level 3, but not extending below this level. No pollen tubes were observed, however, in the sections of the 2 styles examined. In day 2 ovaries examined,

6/ ....

6 pollen tubes were observed altogether within the tissue of the septal attachments. One of the pollen tubes was observed at the very apex of the septal attachment, at level 2, appearing next to the margins of 1 of the 'halves' of the 5 points, and would at level 3 appear in the centre of 1 of the 5 points. The rest of the pollen tubes were observed after the appearance of the central hole in the septal attachment at level 4, 3 of the tubes in the solid tissue of the attachment, close to the margin of the hole, and the other 2 tubes among the papillae of the margins of the points, towards the abaxial part of the point. Again in the ovaries of day 3 flowers, a single pollen tube was observed in 1 of the ovaries, towards the abaxial part of the septal attachment. In day 4 flowers, 2 pollen tubes were observed in the septal ridges of the placental column, 1 within the tissue towards the adaxial part of the ridge and the other among the papillae towards the abaxial part of the ridge. Evidence of a large number of pollen tubes within the septal attachments, close to the centre at level 1 to level 3, was also found, but the tubes were only fluorescing very faintly.

From day 1 until day 4 there was therefore little evidence of pollen tubes within the style, although pollen grains were seen from day 1, but in day 4 styles, as in the septal attachments, there were areas of dull fluorescence observed within the transmitting tissue of the style. The situation changed dramatically by day 5. Of the 2 styles examined pollen tubes were observed within the transmitting tissue of the styles in all sections from the apex of the styles to the base. Pollen tubes were only found in this tissue, a small area from the central vascular bundle to the stigmatic papillae on the adaxial surface of the style. In the septal attachments, pollen tubes were observed from the very first sections. Within the septal attachments pollen tubes were mainly observed within the tissue, not among the papillae. At level 1, the pollen tubes were most evident on the margins of the septal attachments, i.e. in the area which at level 3 would become the centre of the points, and towards the centre of the septal attachments, but not in the area that would become the 'hole' at level 4. Further down the septal attachments pollen tubes were found in all areas but, as stated above, mostly within the tissue not among the papillae. Before fusion of the septal attachments with placental tissue (level 6), most of the pollen tubes were towards/ ....

towards the middle of the septal points, with a few at the abaxial part of the points. Within the septal ridges of the placental column, pollen tubes were evident to the base of the column, mainly towards the adaxial part of the ridges at the margins, but with a few at the abaxial part. No pollen tubes were observed in any other part of the placental column. Plate 3 , illustrates pollen tubes at all levels of the septal attachments and septal ridges on the placental column. The presence of pollen tubes in the septal attachments is also shown in plate 4.e , where the septal attachments have broken from the placental column but have remained attached to the ovary wall.

By day 7, the number of pollen tubes observed had decreased, although they were still seen up to day 10 within the tissue of the septal attachments, ridges and the styles.

From these results, the following statements can be made about the route of pollen tubes in this species:

i. Pollen tubes grow within the style in a special tissue, between the adaxial surface with the stigmatic papillae and the central vascular bundle (Plate 2.c). The cells of this transmitting tissue are small with either thick cell walls or large 'liquid'-filled intercellular spaces, it is unclear which is the case in this species.

ii. Pollen tubes do not grow along the inner surface of the ovary wall, either on the septal ridges or between.

iii. The septal attachments and the septal ridges of the placental column form the internal transmitting tissue of the ovary.

iv. Pollen tubes grow mainly within the transmitting tissue (endotropic pollen growth), only a few growing among the papillae on the surface of the tissue (ectotropic pollen growth). However, this observation may be due to the pollen tubes becoming detached from the tissue during preparation, but even in whole tissue observations, pollen tubes were not evident on the outer surface.

v./ ....

PLATE 3

Agrostemma githago L.

3.a T.S. of septal attachment, level 2, showing lighter area of tissue. c. X 50.

3.b T.S. of septal attachment, level 3, showing lighter area of tissue. c. X 50.

3.c T.S. of septal attachment, level 2, with fluorescing pollen tubes. c. X 70.

3.d T.S. of septal attachment, level 3, with fluorescing pollen tubes. c. X 70.

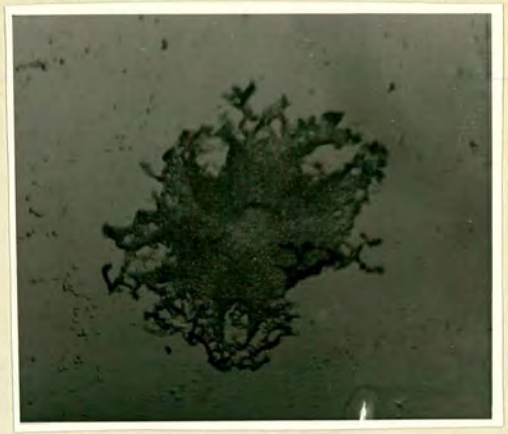
3.e T.S. of septal attachment, level 4, with fluorescing pollen tubes. c. X 50.

3.f T.S. of septal attachments, level , with fluorescing pollen tubes. c. X 50.

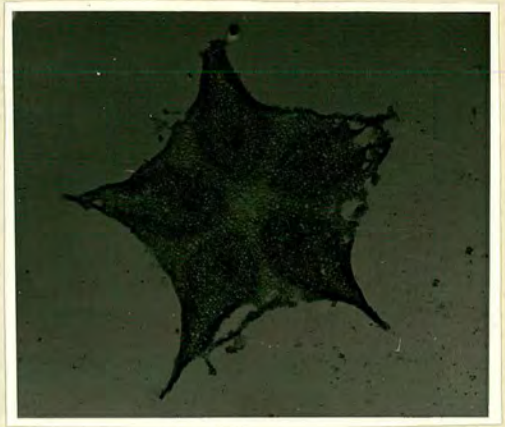
3.g T.S. of middle placental column with one septal ridge evident with fluorescing pollen tubes. c. X 20.

3.h T.S. of near base of placental column with one septal ridge with fluorescing pollen tubes. c. X 20.

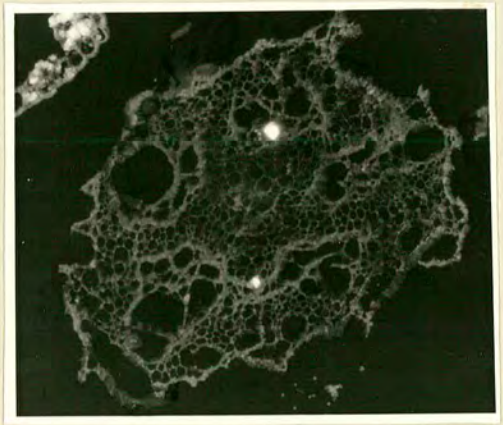
PLATE 3



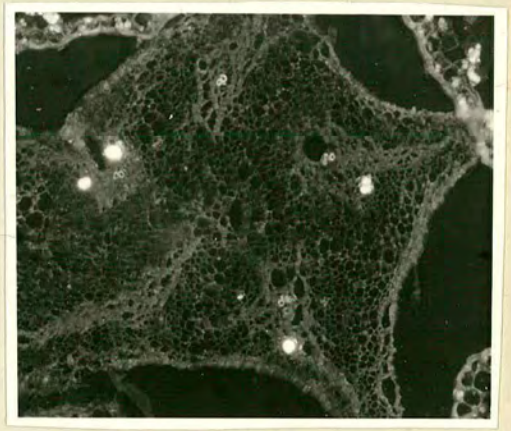
3.a



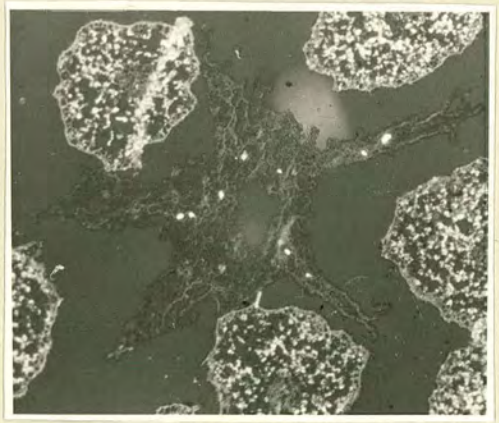
3.b



3.c



3.d



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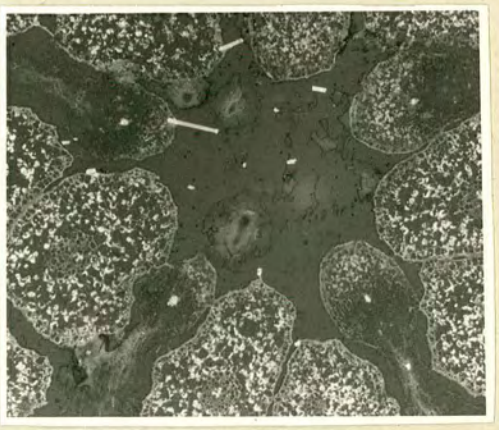

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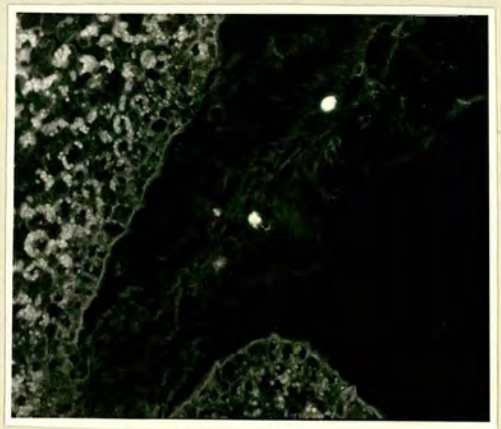

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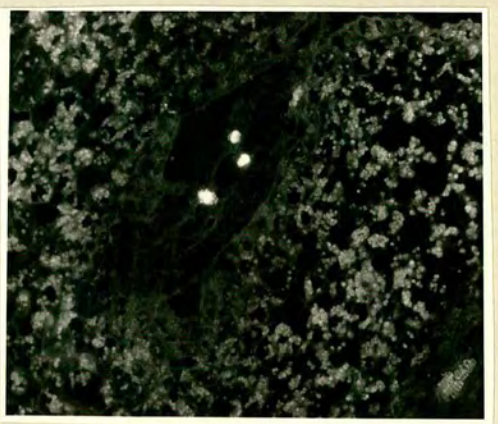


3.h

PLATE 4

Agrostemma githago L.

4.a S.E.M. photograph of apex of septal attachments.

4.b S.E.M. photograph of placental column.

4.c S.E.M. photograph of septal ridge and funicles.

4.d S.E.M. photograph of apex of ovary with styles removed showing transmitting tissue of styles and papillate rows of cells inside the ovary.

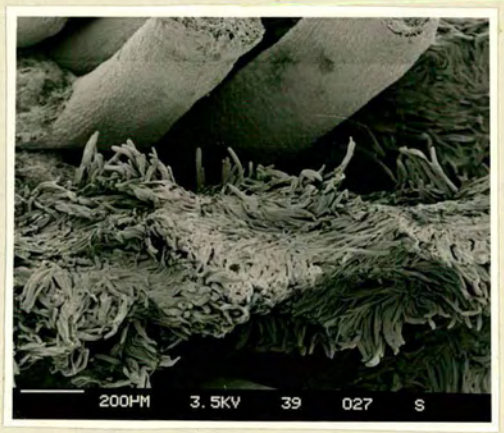
4.e Apex of ovary, part of ovary wall removed, broken septal attachment evident, with pollen tubes fluorescing on/in septal tissue. X 20.

4.f Not a very clear photograph, septal ridge of placental column with funicles on either side and evidence of pollen tubes fluorescing in septal tissue. X 20.

PLATE 4

4.a

4.b



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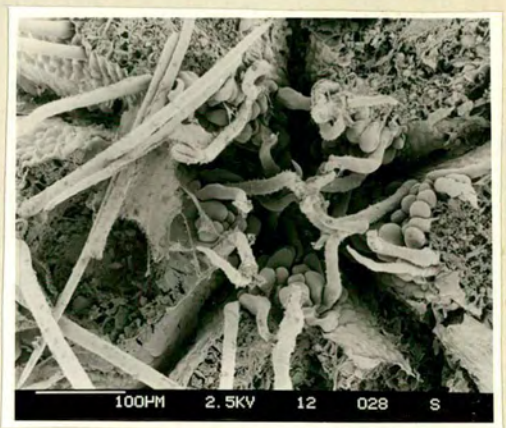

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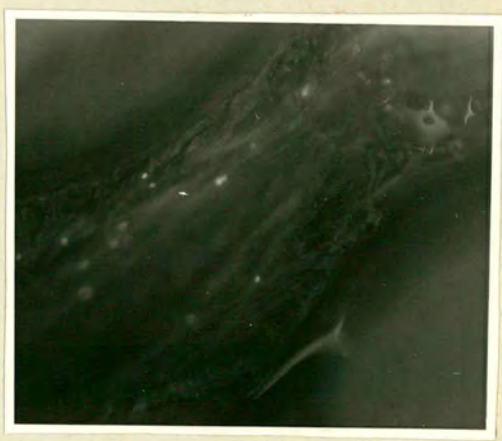
4.e



4.f

v. Pollen tubes were first observed in the septal attachments and ridges before the septal attachments break or just after on day 5 (many observations). As in this work, the method used to identify the pollen tubes, was the presence of callose plugs which fluoresce when stained with cotton blue, the presence of pollen tubes is likely to be observed later than the tubes themselves penetrate the tissue. As callose plugs are formed after the pollen tubes have grown some distance within the tissue, pollen tubes were only faintly observed on day 4 ovaries and then only at the very apex of the septal attachments.

Lychnis coronaria K(5) C5 A5 + 5 G (5)

Plate 5.a

In Lychnis coronaria Acc. 42, the route of the pollen tubes using method 4a was found to be the same as that out-lined for Agrostemma githago. The septa disintegrate entirely at maturity so that the capsule is unilocular as in Agrostemma githago. Transmitting tissue is borne on the septal attachments and the septal ridges of the placental column. This was found using whole tissue, method 4a (Plate 5.a). The route of the vascular tissue is unclear because firstly no sections were made using method 4b, and secondly because of the large number of funicle vascular strands as there are 4 rows of ovules between the septa which makes observations using method 1 difficult. What is clear is that the upper ovules are supplied with vascular tissue from the central vascular strands. These central vascular strands appear to 'come' from the 'main' vascular bundles which supply the lower ovules, the ventral bundles, 2 strands appearing to separate from the ventral bundles supplying a row of ovules on either side of the septum of adjacent septum. Four or five pairs of ovules are supplied with vascular tissue from these central strands. Thus unlike Agrostemma githago where the central strands fuse to give 5 strands opposite the septa, in Lychnis coronaria there are 10 strands at the apex of the placental column, a pair of strands lying on either side of the septa, although fusion of these pair of strands may occur at the apex of the 'ventral' bundles before splitting again to fuse with the ventral bundles. There is no/ ....

no evidence that the central strands extend into the septal attachments as in Agrostemma githago or that these strands are anything but part of the ventral vascular supply.

Cucubalus baccifer K(5) C5 A5 + 5 G(3)

Plate 5.b

Figure 3

Using method 1, method 2 and method 4b, the route of the pollen tubes and the vascular tissue were examined in this species. As in Agrostemma githago the fruit, in this species a pseudo-berry which looks like a fleshy berry but in fact the ovary wall does not become fleshy, is unilocular with a central placental column. It is likely that at an early stage in development the ovary is completely septate, except perhaps for a small 'hole' above the placental column. In young flowers in which sections of the whole ovary were made using method 4b, the apex of the ovary was observed to be completely septate, with 3 loculi containing ovules, but with no funicles present. In the next sections a 'hole' appeared in the centre of the 3 fused septa, the margins of which were observed to be papillate. In the next few sections, this central 'hole' increased in size and each septum broke so that there were now 3 separate septal attachments and 3 septal ridges opposite these attachments on the ovary wall. The margins of the septal attachments and the apex of the septal ridges of the ovary wall were papillate. Funicles then became evident in the centre of the ovary, between the 3 septal attachments. A pair of funicles then fused with each of the 3 septal attachments with a small hole still remaining in the centre which soon disappeared to give an ovary with a solid placental column with 3 septal ridges and 3 septal ridges on the ovary wall opposite these. Towards the base of the ovary the 3 septa became complete again to give a 3 locular ovary. These different stages are illustrated in fig. 3 .

The route of the vascular tissue and the transmitting tissue were more easily observed in mature ovaries. Seeds or ovules were removed before observations were made using the 3 methods stated above so that only the placental column was examined. In these placental columns, the apex of the septal attachments first appeared as a solid 3-sided structure with no evidence of vascular tissue, equivalent to level/ ....

FIGURE 3

Cucubalus baccifer L.

3.1 - 3.5 Transverse sections through a young ovary in which the apex is still septate.

3.1 Apex of ovary septate.

3.2 Hole appearing in centre of septal tissue and in the middle of each septa.

3.3 Three separate septal attachments with fusion of funicle tissue.

3.4 Total fusion to give solid placental column and three large areas of septal ridges/transmitting tissue. Vascular tissue solid 3-armed structure incentre.

3.5 Base of ovary, completely septate with little evidence of septal ridges/transmitting tissue.

3.6 - 3.12 Transverse sections of mature placental column with ovules removed.

3.6 Solid septal attachment.

3.7 Three separate septal attachments with pairs of funicle fusing to septal tissue.

3.8 Total fusion with transmitting tissue/septal ridges at points of 3-arms. Vascular tissue in two rows opposite each septal ridge.

3.9 Vascular tissue fused to give a group of vascular tissue opposite each septal ridge.

3.10 Three arcs of vascular tissue oppoiste each septal ridge.

3.11 Fusion of vascular tissue to give a triangle of tissue in centre. Transmitting tissue/septal tissue occupying a larger portion of placental column.

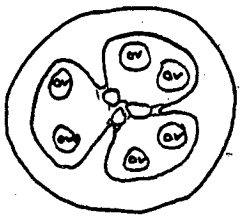
3.12 Base of placental column, transmitting tissue/septal tissue occupying most of the placental column.

ov - ovules

● - vascular tissue

FIGURE 3

3.1



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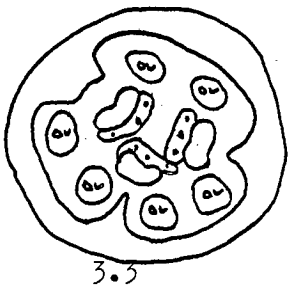

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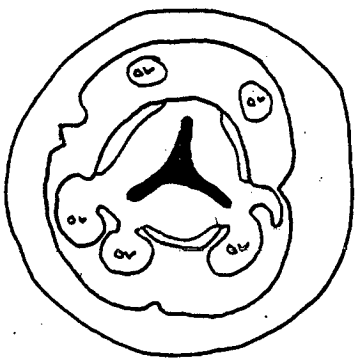

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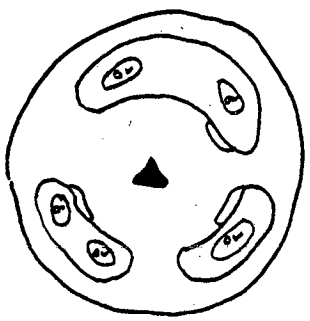

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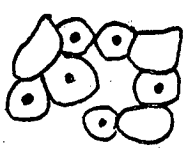
3.6



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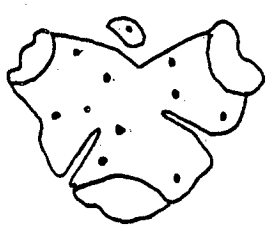

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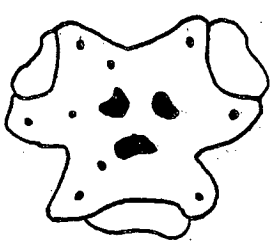

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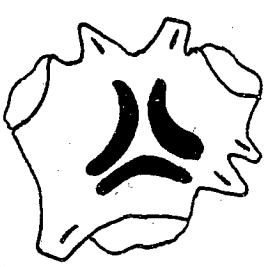

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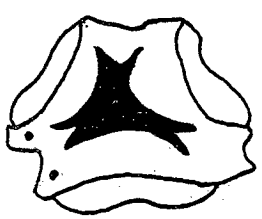

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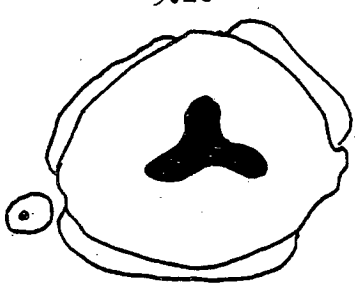


3.12

Scale 1 mm

level 2 of Agrostemma githago. This solid septal attachment then separated into 3 separate septal attachments each of which fused on the inner surface with a pair of funicles. Another pair of funicles then fused with each of the septal attachments, fusing between the first pair of funicles and the septal attachments, leading to the fusion of all the original funicles in the centra of the ovary to give a solid placental column with 3 septal ridges. The placental column in transverse section still appeared to have 3 points with the septal ridges at the apex of each point and ovules being given off on either side of the septal ridges.

A few sections onwards the placental column became triangular in shape with the points of the triangle being where the funicles were attached and the sides being totally covered in the transmitting tissue of the septal ridges. The transmitting tissue was observed to be made up of 2 parts, i.e. the margins of adjacent carpels, or ovary wall components. The transmitting tissue continued to the base of the placental column, increasing in size until almost all the placental column margin was covered in transmitting tissue. Pollen tubes were observed throughout on the papillate surface of the septal attachments and septal ridges. The route of the pollen tubes is thus along the surface of the fused septal attachments, then the surface of the free septal attachments, and eventually the surface of the septal ridges of the placental column. Vascular tissue was not observed within the tissue of the septal attachments at any stage presumably because the vascular tissue of the 'central ' strands supplied at least the 2 pairs of uppermost ovules in each loculi as in Lychnis coronaria. Plate 5.b shows pollen tubes among the papillae of the transmitting tissue, about half-way down the placental column.

The vascular tissue is similar in many ways in this species as in Agrostemma githago. At the apex of the placental column, which appears 3-starred in transverse section, there are 12 separate vascular strands arranged in 6 rows of 2, 2 parallel rows in each of the 3 points and each vascular strand supplying the 12 upper funicles (ovules) which fused with the septal attachments. Further down the placental column, more funicles are given off in pairs between the septal ridges, at this stage the 4 vascular strands of each point described above had become fused to give a single vascular strand opposite/ ....

opposite each septal ridge. As more funicles were given off the vascular tissue took on the appearance of 3 arcs of vascular tissue, with the centre of each arc being opposite the septal ridges and the 'tips' of the arc being where the vascular tissue supplying the funicles was given off. Shortly after this fusion of the vascular tissue occurred, it appeared that the 2 rows of vascular tissue, between each septal ridge fused, and the centre of the placental column, which had originally not contained vascular tissue now did. The vascular tissue now appeared as a solid triangle of vascular tissue, with the points between the septal ridges, giving off vascular strands to the funicles with a group of xylem vessels in the centre of the triangle of vascular tissue, the 3 fused central strands. This pattern of vascular tissue continued to the base of the placental column, decreasing in size after ovules ceased to be formed on the placental column. Towards the base, the vascular tissue became less triangluar and more like 3 circles fused together, each 'circle' being between the septal ridges but stil with a group of xylem vessels.

At the top of the placental column, where most of the ovules are, the main vascular strand would appear to be opposite the septal ridges, giving off vascular strands to the ovules. This is very similar to the apex in Agrostemma githago. Further down the placental column the main fascular bundle appears to be between the septal ridges. Using method 1, 3 groups of vascular strands are evident between each septal arrachment, in the position of the traditional ventral bundles. There did not appear to be central vascular tissue in the placental column although from the sections there was a central strand of xylem. Figure 3 illustrates both the vascular tissue and the septal ridges.

Silene coeli-rosa K(5) C5 A5 + 5 G (3 - 5)

Plates 5,6

Figure 4

Unlike the other species examined, in Silene coeli-rosa the ovary remains partially septate at maturity. The base of the capsule is 5-locular, the transmitting tissue in this species, at the base can not be the same as in the other species described. Transverse sections/ ....

sections were made of both young and mature ovaries to determine the position of the transmitting tissue and also to determine the course of the vascular tissue. Methods 4b and method 2 were used successfully but using method 1 the results were not good, because of the large number of strands. Using method 4a, pollen tubes were not observed even although several flowers were examined.

In buds, the ovary was removed and examined using method 4b and method 2. In both cases the results were the same. In all the ovaries examined at this stage, the apex of the ovary was not closed, in some styles were evident but not in all. The following is a description of an ovary with 5 carpel wall components although ovaries with 3 and 4 carpels were also examined and found to be the same. The apex of the ovary appeared almost solid with 5 projections, the septa, evident extending into the centre of the ovary but not quite meeting. Further down the ovary the ends of the septa became slightly bulbous and almost immediately after these sections, 2 ovule primordia were observed on either side of each septum. A 'hole' remained in the centre of the ovary, between the septa. Each septum, still attached to the ovary wall thus appeared fused to one of the faces of a triangular-shaped tissue. This resembles 'true' parietal placentation, i.e. the septum bearing the ovules. However, this is not the case as will be discussed below.

The 3 triangular-shaped tissues in the centre of the ovary fused together, to give a solid central placental column. The width of the central placental column continued to increase in size towards the base of the ovary with little evidence of other ovule primordia being formed, the ovary remaining totally septate. As has been discussed, several authors have noted the presence of ovule primordia at the apex of the placental column on the septa first, prior to total closure of the ovary. Plate 5c,f illustrates the septal tissue in young ovaries.

In mature ovaries and styles, the course of the transmitting tissue could easily be seen using method 4b. In the styles the transmitting tissue occupied the same position as in Agrostemma githago, a narrow area between the central vascular tissue of the style and the adaxial surface which is covered in stigmatic papilae. At the base of the style, apex of the ovary, the strip of transmitting tissue/ ....

PLATE 5

5.a Lychnis coronaria (L.) Desv., pollen tubes fluorescing on septal attachments at apex of ovary. c. X 20.

5.b Cucubalus baccifer L. T.S. of placental column, pollen tubes fluorescing among papillae of septal ridge of placental column. c. X 50.

Silene coeli-rosa (L.) Godron 5.c - 5.f.

5.c T.S. through apex of ovary, fusion of margins of styles just occurring, apex of ovaryopen. c. X 50.

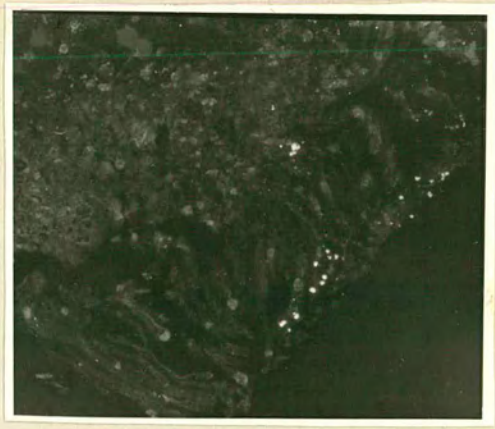
5.d T.S. through apex of ovary, septa beginning to fuse in centre. c. X 50.

5.e Ovary now completely septate, tissue in centre probably septal rather than placental in nature. c. X 50.

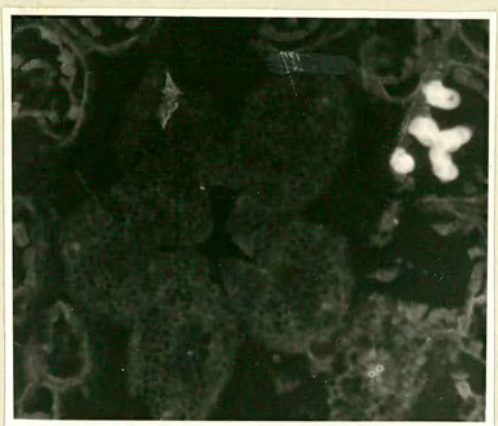
5.f Towards base of ovary, xylem vessels now evident in centre of placental column, and ovule primordia being formed in pairs between septa. c. X 50.

PLATE 5

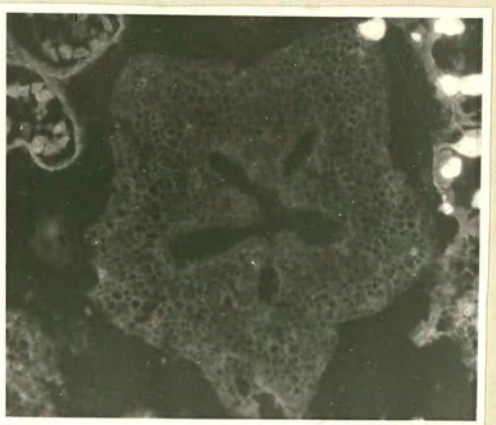
5.a



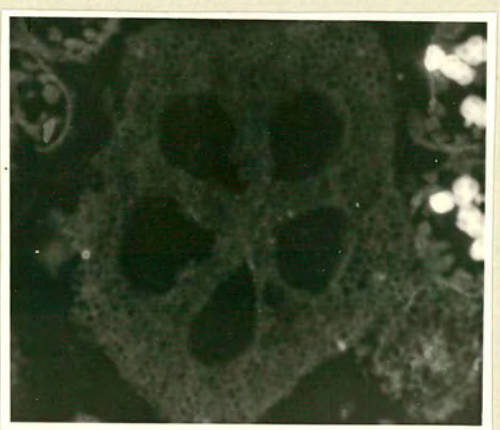
5.b



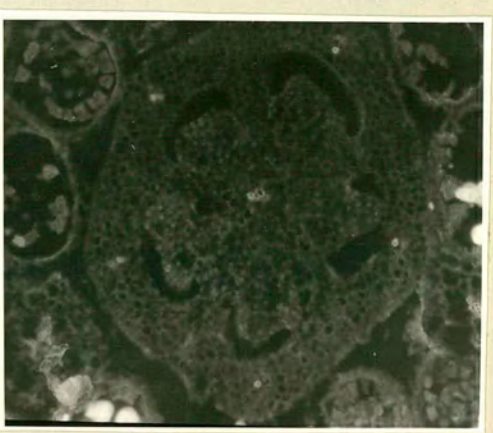
5.c



5.d



5.e



5.f

tissue became narrower so that at the apex of the solid ovary, the transmitting tissue consisted of a central area with 5 radiating spokes, each spoke being situated opposite the dorsal bundles of the ovary wall, parallel to the transmitting tissue of the style. Further down the ovary, 5 holes appeared opposite the dorsal bundles, separating the transmitting tissue into 2 parts. The holes increased in size until eventually the connection between the ovary wall and the central tissue broke so that there was now a solid septal attachment in the centre with 5 septal ridges on the ovary wall, not quite reaching the septal attachments.

In Agrostemma githago the apex of the septal attachments is described as consisting of a solid structure, a 5-pointed star, level 2, each point consisting of the fused margins of the same ovary wall component or carpel. In level 3, the 2 margins moved apart fusing with the margins of the adjacent ovary wall component or carpel so that the newly formed 'spoke' was now opposite the septal ridges of the ovary wall, not between them. The above observations of the apex of Silene coeli-rosa explains how this has come about. The importance of this observation is that the transmitting tissue of the style is continuous with that of the septal attachments and ridges.

If in the style, the pollen tubes were growing through the transmitting tissue close to the stigmatic papillae, on the adaxial surface, the pollen tubes then are likely to grow within the centre of the transmitting tissue of the apex of the septal attachments. It would therefore be possible for these pollen tubes to 'cross' from the transmitting tissue of 1 'style' to that of another. However, even if the pollen tubes were growing in the centre of the transmitting tissue of the styles, within the ovary, as the transmitting tissue separates into 2 components (the 2 margins of the same ovary wall component or carpel) going into 2 different, adjacent septal attachments and eventually 2 different septal ridges. The pollen tubes originally growing within one style or 'belonging' to one 'carpel' are able to fertilize ovules within at least 3 locules, i.e. the locule parallel to the original style and the 2 locules on either side.

In Silene coeli-rosa, further down the ovary, the length of the septal/ ....

septal ridges decreased and the solid septal attachments now became a 5-pointed star, the points being opposite the septal ridges of the ovary wall. Ovules started to be observed within the locules and in the septal attachment a small hole developed in the centre with a lighter tissue now observed within the septal attachments, opposite the dorsal bundles of the ovary wall. This light tissue eventually broke, separating the original single septal attachment into 5 separate septal attachments, each opposite the septal ridges of the ovary wall. The margins of the septal attachments were papillate. Soon after the separation of the septal attachments, placental tissue containing a single vascular strand fused to each septal attachment on the adaxial side, towards the centre of the ovary as in Agrostemma githago. The placental tissue increased in size with the fusion of more placental tissue/funicles so that soon afterwards there was a solid placental column, with 5 septal ridges in the centre of the ovary. The vascular tissue (xylem vessles) of the original placental tissue 'moved' towards the centre of the placental column to give 5 spearate strands, opposite the septal ridges. Further down the ovary the placental column increased in size with more funicles being given off in pairs between the septal ridges. The vascular tissue now consisted of a solid 5-pointed star in the centre of the placental column (the points between the septal ridges of the placental column) composed of the 5 original vascular xylem strands in the centre of the 'star' opposite the septal ridges with 5 radiating spokes of groups of xylem strands opposite the dorsal bundles of the ovary wall, between the septal ridges. Eventually the 5 original vascular xylem strands fused to give a single group of xylem strands in the centre of the placental column with 5 groups of xylems vessels between the septal ridges supplying vascular tissue to the funicles. This arrangement continued to the base of the placental column.

In this species the ovary becomes completely septate at the base of the mature ovary. Above the level of complete septation, the transmitting tissue is a single papillate tissue opposite the septal ridges of the ovary wall in the septal ridges of the placental column, below the level of complete septation the transmitting tissue is in 2 discrete areas on either side of the septum. Within each locule there is thus 2 separate strands of transmitting tissue. Towards the/ ....

the base, the transmitting tissue decreases in size and eventually disappears. It is very difficult to be sure, but it would appear that the transmitting tissue in the septate part of the ovary is not part of the placental column, but part of the septa. Figure 4 illustrates the transmitting tissue in this species and plate 6 , clearly shows the position of the xylem vessels and transmitting tissue in sections stained with cotton blue.

Throughout, the septal attachments and the septal ridges were very papillate. Pollen tubes were observed to be present among these papillae except at the apex of the septal attachments where there is some evidence that pollen tubes grow within the transmitting tissue rather than on the surface of it. Vascular tissue was not observed within the septal attachments, even although there appeared to be no terminal upper ovules, as in Agrostemma githago. The parietal placentation seen in younger flowers of Silene coeli-rosa thus represents the placental tissue plus the first pair of funicles/ ovules formed, not the funicles fused to the septa. This also explains the parietal placentation of Agrostemma githago observed by O. Rohweder, the first ovule primordia being formed on the placental tissue prior to fusion of this tissue to form the solid placental column. Growth and fusion of the septa in the upper part of the ovary thus continues after the formation of the first ovule primordia.

Silene conoidea K(5) C5 A5 + 5 G(3)
Plate 7
Figure 5

As in Silene coeli-rosa the mature ovary of S. conoidea is completely septate at the base. From mature flowers, using method 4b (method 2 was also used, the same results being found as in method 4b), the following description of the septal attachments and ridges in this species can be made. The ovary wall was only partially removed, but the seed/ovules were removed before sections were made.

The apex of the septal attachment consisted of a solid 3-pointed star structure, the points being opposite the septal ridges of the ovary wall. Below this level the septal attachment separated into 3 separate septal attachments with papillate margins, each remaining opposite the septal ridges of the ovary wall, and even at this level a large number of funicles were already evident. A pair of funicles then/ ....

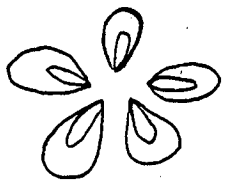
FIGURE 4

Silene coeli-rosa (L.) Gordon. T.S. of ovary.

4.1 T.S. of 5 styles with transmitting tissue outlined.
4.2 Styles almost fused.
4.3 Apex of ovary, solid, with transmitting tissue outlined.
4.4 Locules now evident with solid septal attachment in centre.
4.5 Septa now no longer as pronounced.
4.6 Septal tissue in centre now 5-pointed with ovule evident.
4.7 Five separate septal attachments with evidence of placental tissue.
4.8 Placental column now evident with five septal ridges.
4.9 Septal ridges now much reduced in size.
4.10 Septa of ovary wall now close to septal ridges/transmitting tissue of placental column.
4.11 Ovary completely septate, transmitting tissue on either side of septum.
4.12 Near base of ovary, transmitting tissue still close to septa but not as prominent.

ov - ovule

FIGURE 4



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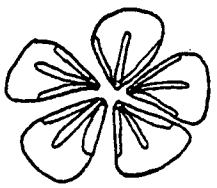

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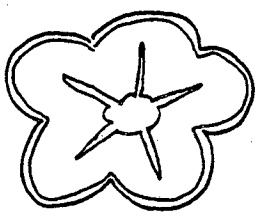

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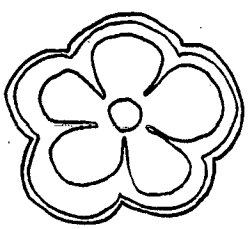

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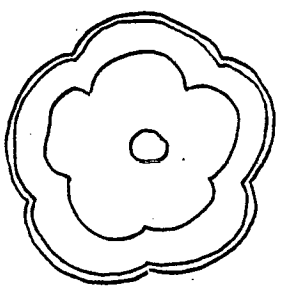

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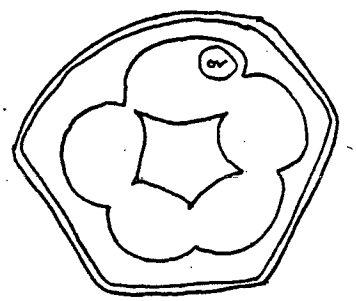

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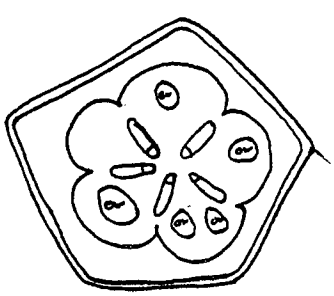

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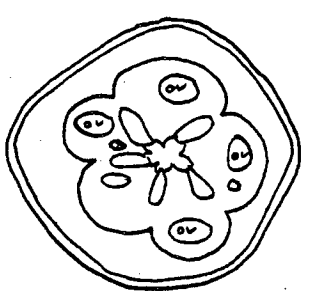

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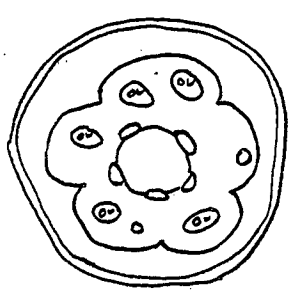

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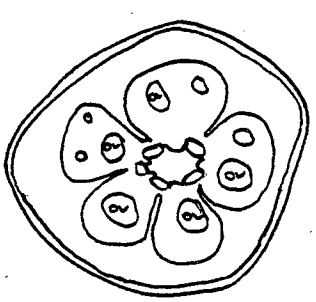

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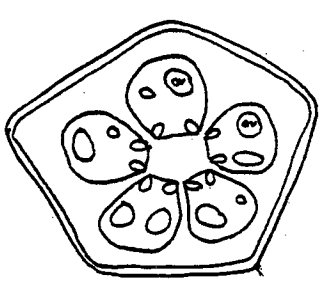

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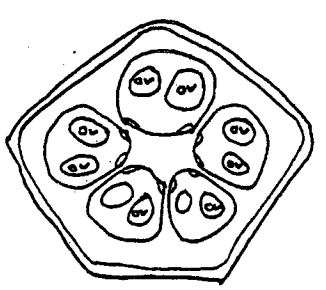


4.12

Scale

1 mm

PLATE 6

Silene coeli-rosa (L.) Godron.

6.a T.S. through septal attachment with fluorescing pollen tubes on margins. c. X 50.

6.b Five separate septal attachments with placental tissue evident (bright fluorescing areas). c. X 50.

6.c Septal ridges evident on placental column with fluorescing pollen tubes. Groups of xylem vessels also evident. c. X 50.

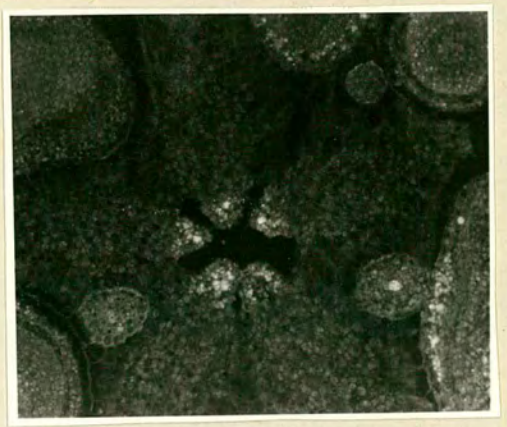
6.d Ovary now completely septate with evidence of transmitting tissue on either side of septum with fluorescing pollen tubes. c. X 50.

6.e Close up of 6.d, transmitting tissue on either side very evident. c. X 70.

6.f Ovary completely septate, towards base of ovary, areas of transmitting tissue becoming much smaller. c. X 70.

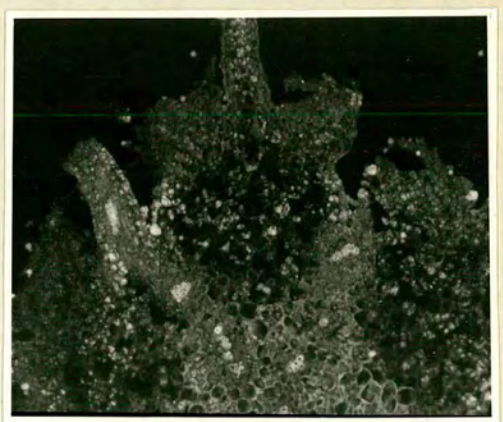
PLATE 6

6. a

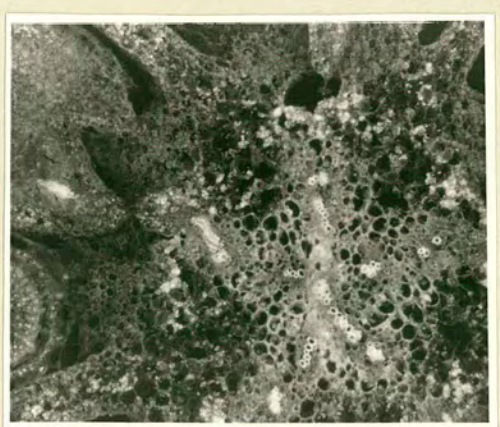


6. b

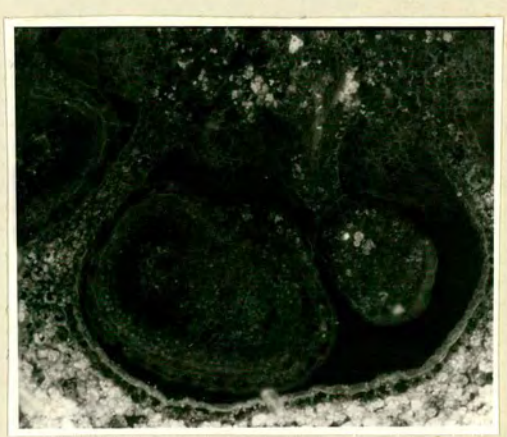
6. c



6. d



6. e



6. f

then fused with each septal attachment on the adaxial or inner surface. The placental tissue gradually increased in size, 2 further funicles fused on either side of the septal ridges, the xylem vessels (vascular tissue) of the original pair of funicles having already fused to give a single strand opposite the septal ridges. The placental column eventually totally fused in the centre to give a solid placental column with 3 septal ridges and a pair of funicles being given off between the septal ridges. Below this level the vascular tissue appeared triangular in shape, with funicles being given off at the points. The xylem vessels at this level consisting of 3 spokes with groups of xylem vessels occupying the centre of the placental column, probably from the vascular tissue which was originally opposite the septal ridges. Fusion of the vascular tissue occurred after the septa had fused to the placental column again to give a septate ovary. Above this level the transmitting tissue was present on the placental column in 3 slight depressions opposite the septal ridges of the ovary, i.e. within the septal ridges of the placental column. The septal tissues of the ovary wall increased in length, eventually 'touching' the transmitting tissue of the placental column, separating the transmitting tissue into 2 parts as the septa fuse.

In the septate part of the ovary, the transmitting tissue, was thus divided into 2 discrete parts on either side of septum as in Silene coeli-rosa. The width of the septum increased in size towards the base of the placental column, 'pushing' the 2 'bits' of transmitting tissue further apart towards the funicles. Towards the base of the placental column the transmitting tissue decreased in size and evenutally disappeared before the base of the ovary. From the apex of the ovary to the base, the transmitting tissue remained papillate, although no pollen tubes were observed in the 2 ovaries examined. At no point did vascular tissue appear in the septal tissue. The vascular tissue changed towards the base of the ovary, xylem vessels now moved to the periphery of the area of fused vascular tissue to form a triangle of xylem vessels with no xylem vessels in the centre. The points of the triangle giving off funicles and the faces being opposite the septal ridges and probably the xylem vessels making up the faces of the triangle may have come from the original strands/ ....

strands opposite the septal ridges at the apex of placental column. Figure 5 and plate 7 illustrate the transmitting tissue on this species and to some extent the position of the groups of xylem vessels.

In this subfamily, using the examples above, the following statements about the transmitting tissue and the vascular tissue (xylem vessels) can be made:

i. The septal attachments and septal ridges of the placental column and ovary wall consist of the congenitally fused margins of adjacent carpels or ovary wall components, except at the apex of the septal attachments where they consist of the fused margins of the same carpel or ovary wall components.

ii. The transmitting tissue within the style, consists of a narrow area between the central vascular tissue and the stigmatic papillae on the adaxial surface.

iii. The internal transmitting tissue of the ovary is found on/within the septal attachments and septal ridges of the placental column, the surfaces of which are papillate.

iv. The transmitting tissue of the style is continuous with that of the septal attachments and septal ridges of the placental column.

v. The arrangement of transmitting tissue means that pollen tubes from one style are able to fertilize ovules in 3 locules.

vi. Pollen tubes grow within the transmitting tissue of the styles and the apex of the septal attachments and over the surface of the transmitting tissue of the septal ridges of the placental column, except in Agrostemma githago where pollen tubes were also found to grow within the tissue of the septal ridges of the placental column.

vii. The vascular strands which supply the lower ovules consist of/ ....

FIGURE 5

T.S. of placental column of Silene conoidea L. with part of ovary removed and ovules/seeds removed.

5.1 Three free septa with a solid triangular shaped septal attachment in centre (no vascular tissue) and a number of funicles.

5.2 Septal attachments now separate each fused to 1 pair of funicles.

5.3 Septal attachments and placental tissue now more evident.

5.4 Solid placental column with 3 septal ridges/transmitting tissue.

5.5 Septa now beginning to fuse with septal ridges/transmitting tissue of placental column. Vascular tissue solid triangular shape in centre of column.

5.6 Ovary now completely septate, transmitting tissue occupying two small areas on either side of septum.

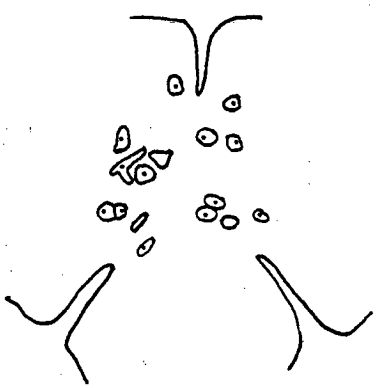
5.7 Near base of ovary, transmitting tissue now far from base of septum, close to funicles.

5.8 Vascular tissue of placental column now with a discontinuous ring of groups of xylem vessels in centre.

5.9 Base.

• - vascular tissue.

FIGURE 5



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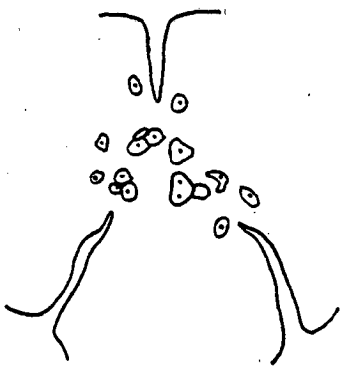

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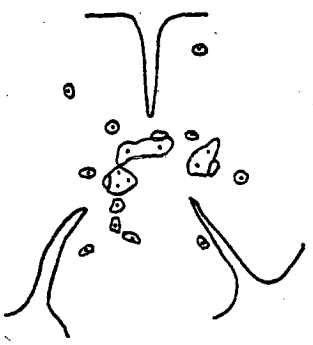

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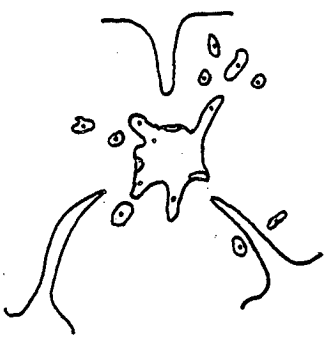

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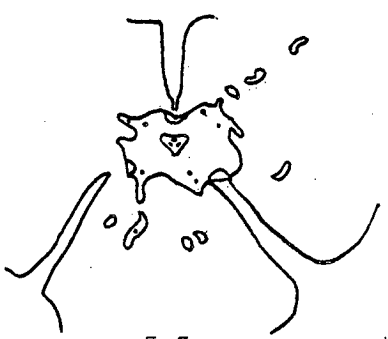

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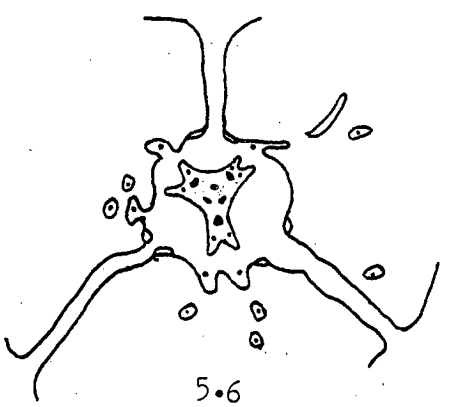

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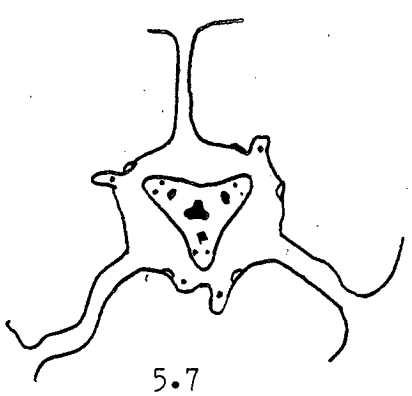

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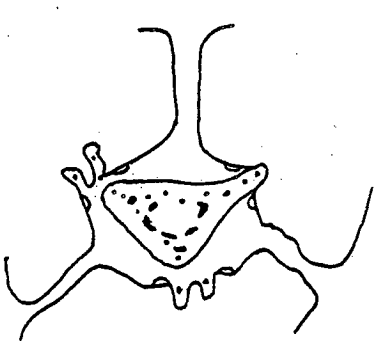
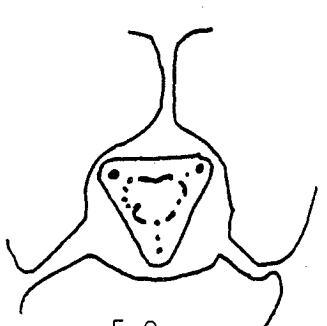


5.8

Scale 1 mm



5.9

PLATE 7

Silene conoidea L.

7.a T.S. through septal attachment - 3-spoked structure. c. X 50.

7.b Three septal attachments fused with 3 - 5 funicles. c. X 50.

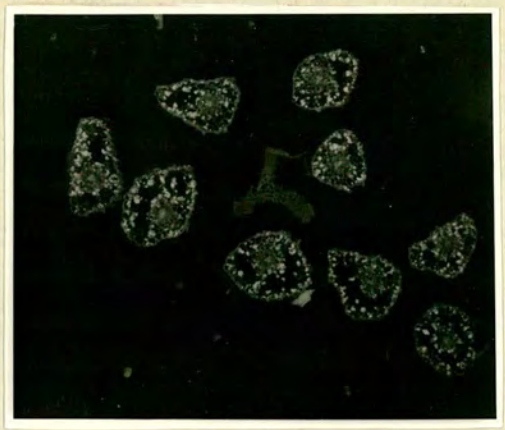
7.c Total fusion to give placental column with 3 septal ridges. Vascular tissue in 3 'arcs' opposite each septal ridge. c. X 50.

7.d Septa of ovary wall beginning to fuse with septal ridge/ transmitting tissue of placental column (top left-hand corner). c. X 70.

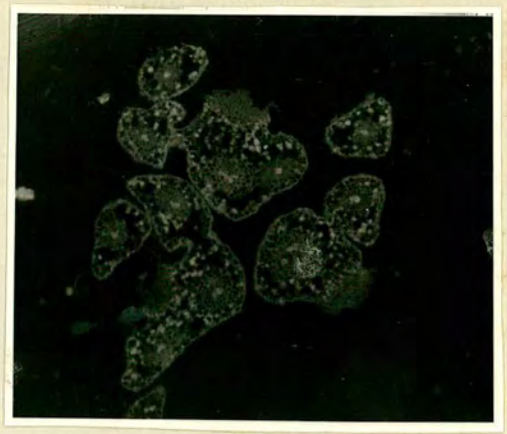
7.e Total fusion of septa to give to completely septate ovary, transmitting tissue evident on either side of septum. c. X 100.

7.f Quite far down the placental column, transmitting tissue now separate, close to funicles. c. X 100.

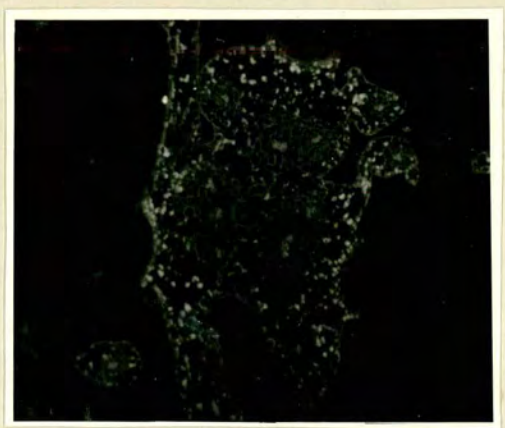
PLATE 7



7.a



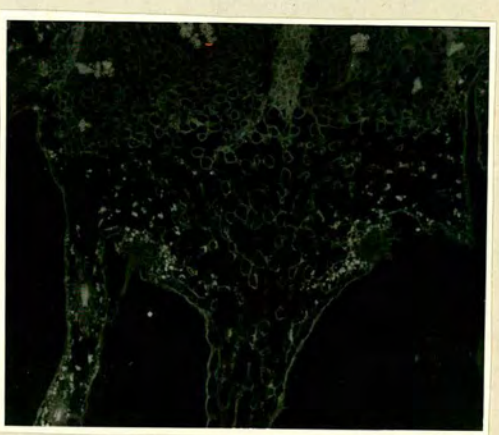
7.b



7.c

7.d

7.e



7.f

of 3 to 5 strands equal in number to the styles which alternate with the median lateral bundles of the ovary wall and are thus in the position of the traditional 'ventral' bundles.

viii. As well as these bundles there are either groups of xylem vessels in the centre of the placental column as in Agrostemma githago, Cucubalus baccifer and Silene conoidea, or a single group of xylem vessels in the centre as in Silene coeli-rosa and S. gallica.

ix. These central xylem strands either supply the vascular tissue of the uppermost ovules as in Silene conoidea and Cucubalus baccifer, or continue into the placental tissue which fuses at the apex of the placental column to the septal attachments as in Silene coeli-rosa and Agrostemma githago. Only in Agrostemma githago, of the species examined, does this central xylem tissue continue into the septal tissue.

x. At the apex of the placental column in all species examined the 'main' vascular tissue, represented by the xylem vessels, appears to opposite the septal ridges, between the dorsal bundles of the ovary wall. Further down the placental column the vascular tissue occupies the centre of the column with the 'main' vascular tissue, again represented by the xylem vessels, appearing to be between the septal ridges, opposite the dorsal bundles of the ovary wall. The main vascular tissue being that which appears to give off vascular tissue to be funicles/ovules.

Subfamily Paronychioideae

In this subfamily all 3 types of ovary described in the introduction are found: 1. ovaries which are at one stage completely septate except for a small hole at the apex of the placental column; 2. ovaries in which there is evidence of a strand of transmitting tissue from the apex of the ovary to the apex the placental column/ funicle but little evidence that the ovary is ever completely septate; 3./ ....

3. ovaries in which there is no evidence of a strand of transmitting tissue and little evidence of septal ridges on the ovary walls. Species belonging to each of these 3 categories were examined in the hope of discovering the route of the pollen tubes and if septal ridges are present. No attempt was made to study in detail the route of the vascular tissue in most of the species below. The following species were examined in the first ovary category: Spergularia media, Spergularia rubra, Polycarpon tetraphyllum, Drymaria cordata.

Spergularia media K5 C5 A5 + 5 G(3)

In this species the capsule is unilocular as in Agrostemma githago and Lychnis coronaria. However, the amount of septal tissue present as transmitting tissue on the placental column is greater (Plate 9) and the ovary appears to remain septate for a much longer time.

In young flowers of Spergularia media using method 4b, taking sections of the whole ovary, a complete picture of the transmitting tissue and the vascular system was observed. At the apex of the ovary (the ovary being closed) the transmitting tissue consisted of a 3-pointed star structure in the centre, with the dorsal bundles of the ovary wall opposite the points, the apex of the ovary being solid, the transmitting tissue being continuous with that of the styles. Three locules then appeared, opposite the points of the transmitting tissue and thus opposite the dorsal bundles of the ovary wall. The formation of these locules thus split each point of the transmitting tissue in 2, as in Silene coeli-rosa, so that the transmitting tissue was now present on the margins of the septa, the ovary being completely septate. Further down the ovary a small hole developed in the centre of the ovary and the 3 septa separated from each other in the centre, still remaining attached to the ovary wall. The free end of each septum appeared bulbous, this bulbous area being the transmitting tissue, the margins of which were papillate. Ovules also became evident in the locules at this level in the ovary.

Placental tissue now became evident between the septa in the centre of the ovary, fusing with the free ends of the septa to give 3 septa, each still 'fused' to the ovary wall with a triangular - shaped tissue at the 'free' end. Very shortly after fusion of the placental/ ....

placental tissue to the septa if not before in some of the section, 2 strands of vascular tissue appeared on either side of the placental tissue. At this level the transmitting tissue appeared as a large tissue abaxial to the placental tissue with 2 discrete areas of transmitting tissue being evident on either side of the septum, similar to the situation found in the septate base of the ovaries of Silene coeli-rosa and S. conoidea. A large number of funicles and ovules were now evident in the ovary, and fusion of the 3 triangular-shaped tissue occurred to form a solid placental column, the ovary remaining completely septate. The vascular tissue now consisted of 12 groups of xylem vessels (vascular tissue) in 6 rows, each row with 2 groups of xylem vessels (vascular tissue) on either side of each septum. Unlike the other species described, fusion then occurred of pairs of vascular tissue (xylem vessels) between the septal ridges to give 3 strands of groups of xylem vessels between the septal ridges, opposite the dorsal bundles of the ovary wall. These 3 groups of xylem vessels then 'moved' towards the centre of the placental column, to give a solid 3-spoked structure of vascular tissue with groups of xylem vessels in the centre and in all the spokes, funicles being given off at the spokes, between the septal ridges. The number of xylem vessel groups in the centre of this 3-spoked structure increased in number, but towards the base of the ovary the xylem vessel groups moved into the points of spokes of the solid vascular structure to give 3 separate groups of xylem vessels (vascular tissue) between the septal ridges, opposite the dorsal bundles of the ovary wall.

Plate 9 illustrates an older ovary, but still completely septate and plate 8a-d illustrates a younger ovary showing clearly the bulbous ends of the septa which form the transmitting tissue of the inner ovary.

In another species of Spergularia, S. rubra, the same arrangement of vascular tissue and transmitting tissue was observed, except that at the base of the ovary the vascular tissue consisted of a solid circle, with a number of groups of xylem vessels not as 3 separate groups of xylem vessels as in S. media. However, more mature flowers were examined, and using method 4b, pollen tubes were seen among the papillae of the transmitting tissue, rather than within/ ....

PLATE 8

Spergularia media (L.) C. Presl.

8.a T.S. through apex of ovary/styles, ovary still open. c. X 50.

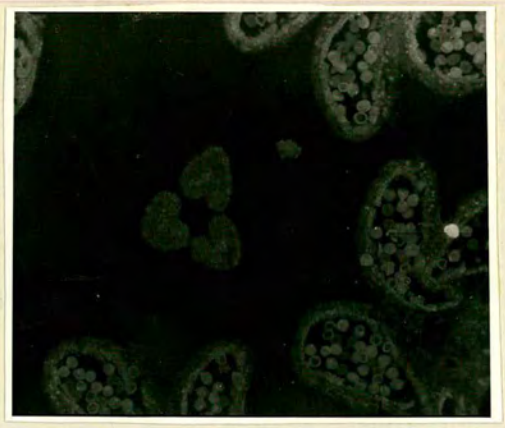
8.b T.S. through middle of ovary, ovules/funicles evident, ovary not completely septate. c. X 50.

8.c Slightly further down ovary fusion almost complete. c. X 50.

8.d Ovary completely septate, group of xylem vessels now evident in centre of placental column, c. X 50.

8.e Spergularia rubra (L.) J. & C. Presl. Mature ovary showing fluorescing pollen tubes on septal ridges of placental column. c. X 70.

PLATE 8



8.a

8.b

8.c

8.d

8.e

PLATE 9

Spergularia media (L.) C. Presl.

9.a Solid apex of ovary/base of fused styles. Transmitting evident as fluorescing tissue in centre of structure. c. X 50.

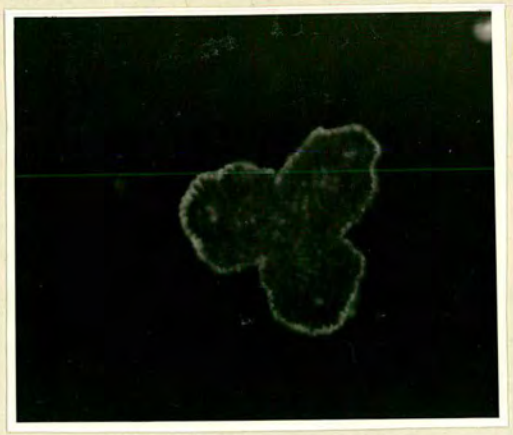
9.b Apex of ovary, completely septate with 3 locules. c. X 50.

9.c Septa still attached to ovary wall but hole now evident in centre with placental tissue fusing to inner surface of septa. c. X 70.

9.d Ovary completely septate again, with transmitting tissue evident on either side of septum. c. X 50.

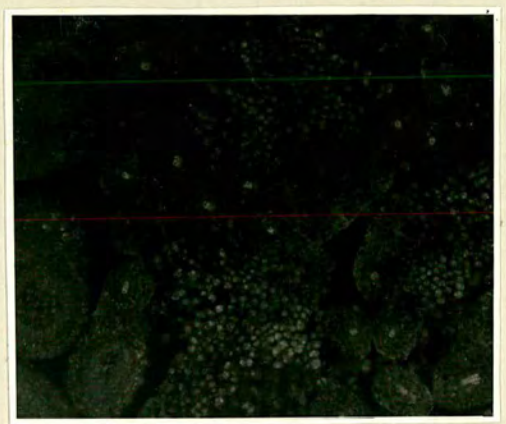
9.e Close up of septum with area of transmitting tissue on either side. c. X 70.

PLATE 9



9. a

9. b



9. c

9. d

9. e

within the transmitting tissue. Pollen tubes were observed on the surface of the transmitting tissue, of both the septal attachments and ridges, the septal ridges appearing as in other species to be in two bits in a number of sections. Plate 8.e illustrates a section clearly with pollen tubes among the papillae of the transmitting tissue of the septal ridges of the placental column.

Polycarpon tetraphyllum K5 C5 A5 G(3)

Plate 10 a,b

Flowers from 2 accessions, Acc. 96 and Acc. 175, were examined and the results using method 4b were found to be the same in both accessions. The ovary is completely unilocular at maturity as in Spergularia species. Only mature flowers were examined, mainly because of the small size of the ovary which at anthesis is about 1 mm in length. Because of the size of the ovary the identification of vascular tissue is difficult and incomplete.

In all the sections examined, the form of the septal tissue was very similar to that of Spergularia species. The apex of the ovary was solid, becoming tri-locular breaking to form 3 septal ridges on the ovary wall with a solid 3-pointed star-shaped septal attachment in the centre. Unlike other species examined, the position in Polycarpon is not as clear as there are often 6 projections of tissue into the ovary cavity from the ovary wall; thus in some sections there appears to be 6 septal ridges and not 3. Towards the base of the ovary, 3 of these projections disappear leaving only the 3 septal ridges.

The solid septal attachment separate into 3 separate septal attachments, opposite the septal ridges of the ovary wall. A pair of funicles then appear to fuse with each septal attachment, and then another pair of funicles fused, eventually forming a solid placental column with 3 large areas of transmitting tissue/septal ridges occupying a large area of the placental column. Towards the base of the ovary, the septa became complete again. The vascular tissue at the apex of the placental column consists of 2 rows between the septal ridges, consisting of 2 groups of xylem vessels. However, the xylem vessels are small and it is unclear as to what happens to these groups of xylem vessels. At the base of the ovary there is a large/ ....

large central group of xylem vessels with 3 smaller groups of xylem vessels, between the septal ridges.

Pollen tubes were clearly observed in a number of sections in the septal attachments and ridges of the placental column. There was no evidence of pollen tubes on or within the septal ridges of the ovary wall. It would appear that in this species pollen tubes grow within the tissue, at least in the upper part of the septal tissue. Plate 10 illustrates the transmitting tissue, septal tissue and pollen tubes found in this species.

Drymaria cordata K5 C5 A5 G(3)

Plate 10c - e

In this species, the 3 styles are fused for about half their length. The septal attachments and septal ridges are much the same as already outlined for Spergularia species. Four ovaries were examined using method 4b.

Below the level of fusion of the 3 styles, the transmitting tissue was found in the centre of the fused style, between the 3 vascular strands. These 3 vascular strands continue into the dorsal bundles of the ovary wall. As before the apex of the ovary was solid with 3 locules being formed shortly after opposite the dorsal bundles of the ovary wall, thus (as described before) splitting the transmitting tissue into 2. Further down the ovary as the locules increase in size the septa broke in the centre to give 3 septal ridges on the ovary wall and a solid central septal attachment. At first the septal attachment appeared round then became triangular in shape with each of the points opposite the septal ridges of the ovary wall. A hole then appeared in the centre of the septal attachments, increasing in size until 3 separate septal attachments were evident, each opposite the septal ridges of the ovary, funicles and ovules being present in the ovary at this level.

Two funicles then fused on either side of each septal attachment and then another pair of funicles fused so that a solid placental column was formed with 3 septal ridges opposite the 3 septal ridges of the ovary wall. As in Polycarpon and Spergularia species, the transmitting tissue/septal ridges occupied a large portion of the placental column. Towards the base of the ovary, the septa became complete again in 2 of the ovaries examined. Throughout the margins of/ ....

PLATE 10

Polycarpon tetraphyllum (L.) L.

10.a T.S. through septal attachments with fluorescing pollen tube evident. c. X 70.

10.b T.S. through ovary with 3 separate septal attachments evident with fluorescing pollen tubes. c. X 50.

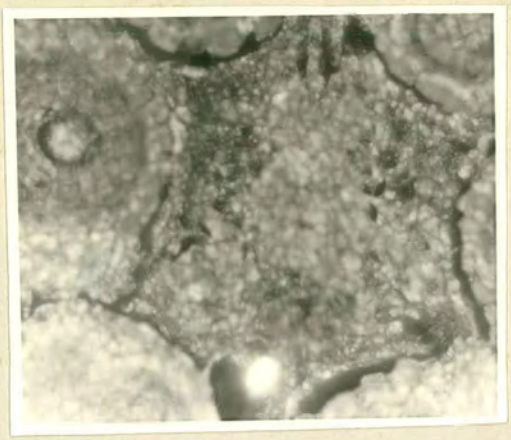
Drymaria cordata Willd. ex Roem. & Schult.

10.c Apex of ovary with fluorescing pollen tubes evident in septal tissue in centre. c. X 50.

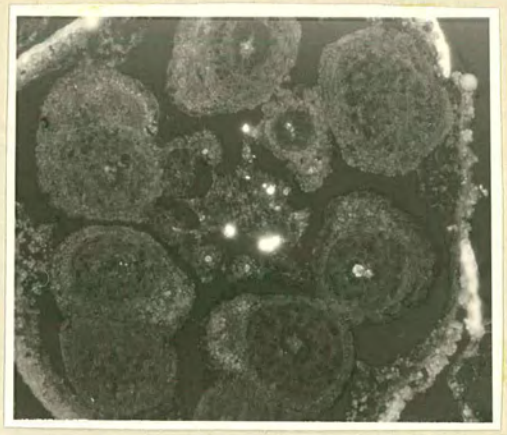
10.d Three separate septal attachments fusing with pair of funicles with fluorescing pollen tubes evident. c. X 70.

10.e Solid placental column with septal ridges evident with fluorescing pollen tubes. c. X 70.

PLATE 10



10.a



10.b

10.c

10.d

10.e

of the transmitting tissue appeared papillate as in all the other species examined.

Pollen tubes were observed within the transmitting tissue of the styles and within the transmitting tissue of the septal attachments. The route of the pollen tubes is the same as that found in species examined in the subfamily Dianthoideae. Pollen tubes were also observed on the surface of the septal ridges of the placental column. No vascular tissue was observed within the septal attachments.

At the apex of the solid placental column, soon after total fusion, there are 2 groups of xylem vessels in 2 rows on either side of the septal ridges. The inner pair of these groups of xylem vessels (from the first funicles to fuse with the septal attachments) fuse to form a single group of xylem vessels opposite each septal ridge. These 3 groups of xylem vessesl then fuse to form a single group of xylem vessels in the centre of the placental column, with 3 other groups of xylem vessels between the septal ridges giving off vascular tissue to the funicles. This arrangement of vascular tissue continues to the base of the ovary.

In the second category, only Scleranthus annuus and S. perennis were examined using method 4b. However, using method 2, the presence of septal ridges on the ovary wall and septal attachments from the apex of the ovary to the apex of the funicle/placental column was confirmed in Pollichia campestri Solander, being very similar to the situation in Scleranthus species, described below.

Scleranthus K(5) C 0 A5 + 5 G(2)
Plates 11a - c
Figure6

In both species of Scleranthus the structure of the ovary was found to be the same using method 4b and method 2. The description given below is therefore a combination of observations of sections of both S. annuus and S. perennis.

At the apex of the ovary the 2 free styles become surrounded by tissue of the ovary wall, eventually fusing with this tissue to form the solid apex of the ovary. The 2 separate transmitting tissue areas/ ....

areas of the styles also fuse to an eliptically-shaped transmitting tissue in the centre of the solid ovary with the 2 vascular strands of the styles on either end of the transmitting tissue. These 2 strands continue into the ovary wall as the dorsal bundles. Two locules **then** appeared opposite the dorsal bundles of the ovary wall, leaving a septum running across the ovary between the dorsal bundles, the central part of this septum being wider than the rest. In some ovaries, the apex of the ovule/seed, appeared immediately after these sections, with the septal attachment (the wider section of the septum in the centre of the ovary) fused to one of the sides of the ovule/seed, the ovary no longer being septate. In other sections the septum disintegrated to leave a single strand of transmitting tissue/septal attachment in the centre of the ovary with evidence of 2 septal ridges on the ovary wall, between the dorsal bundles.

The inner surface of the ovary in these species consisted of thick-walled cells, sclerenchyma cells which autofluoresced. In some ovaries these cells were arranged in 4 areas in other ovaries in 2 areas, so that in both types of ovary a small 'gap' without these cells existed between the dorsal bundles of the ovary wall. In those ovaries with 4 areas of these cells, there were also 'gaps' without these cells opposite the dorsal bundles of the ovary wall. It was in the gaps between the dorsal bundles that the tissue, here interpreted as septal ridges, protruded into the ovary cavity.

With the appearance of the ovule/seed, the transmitting tissue or septal attachment was now evident on either side of the ovule/seed, opposite the dorsal bundles of the ovary wall. Although identified as separate tissue, this transmitting tissue or septal tissue appeared to be fused to the ovule/seed. It was impossible to separate the septal attachment/transmitting tissue from the funicle, the 2 appearing to merge into 1. Thus there would appear to be a continuous route from the apex of the ovary base of the styles to the funicle of the ovule/seed. Below the micropyle of the ovule/seed, the funicle was evident as a structure separate from the ovule/seed which eventually fused with the wall of the ovary, opposite 1 of the dorsal bundles of the ovary wall, i.e. not fusing with the base of the ovary.

After/ ....

FIGURE 6

T.S. of flower of Scleranthus annuus L.

6.1 Sepals with two free styles.

6.2 Free sepals, two free styles in centre surrounded by five anti-sepalous stamens.

6.3 Sepals and stamens fused, forming a tube with the two styles in the centre beginning to fuse and become surrounded by sclerenchyma cells.

6.4 Apex of ovary now evident, with transmitting tissue between vascular bundles.

6.5 Apex of ovary no longer solid, two locules evident with septal tissue present. Inner wall of ovary composed of sclerenchyma cells.

6.6 Evidence of septal ridges on ovary wall and single septal attachment.

6.7 Ovule evident with different tissue to one side - from septal attachment to ovule no break.

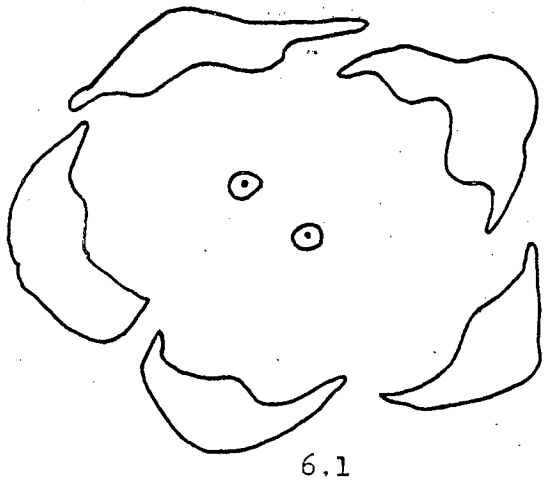
6.8 Ovule and separate funicle now evident.

6.9 Ovule with funicle fused to ovary wall, not to base of ovary.

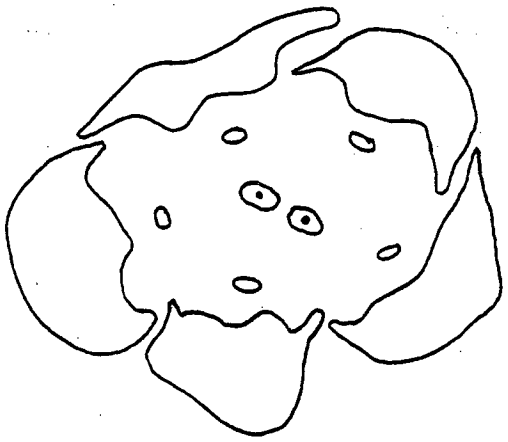
6.10 Base of flower and ovary now solid.

• - vascular tissue

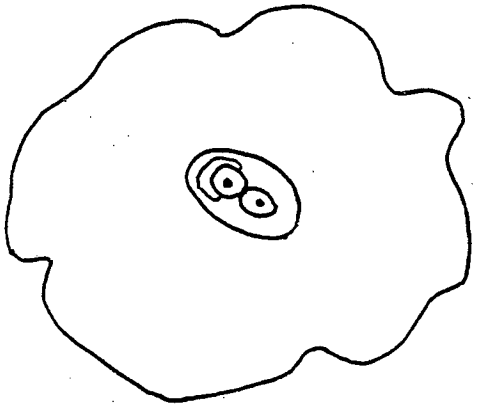
FIGURE 6



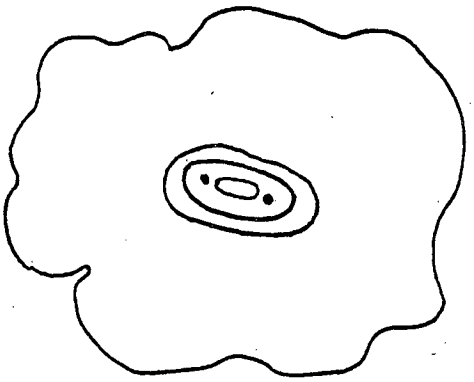
6.1



6.2



6.3



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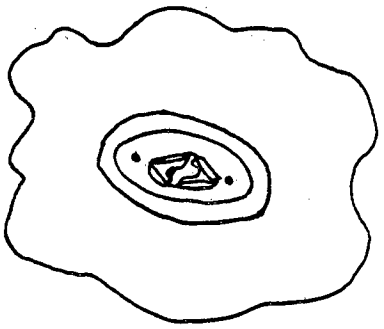
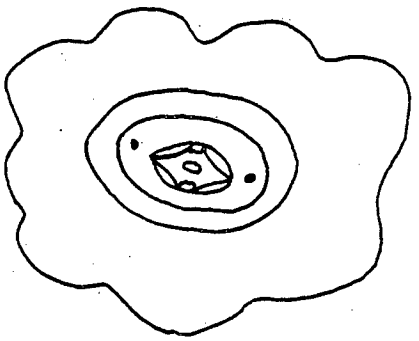
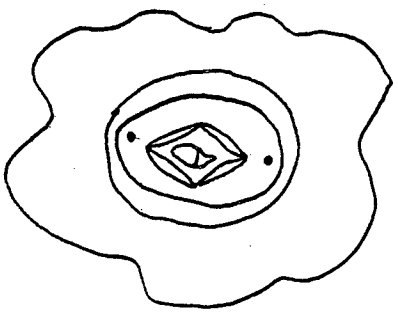


6.5



6.6



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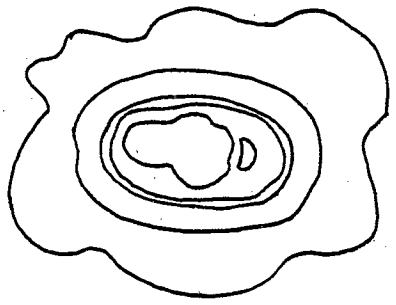

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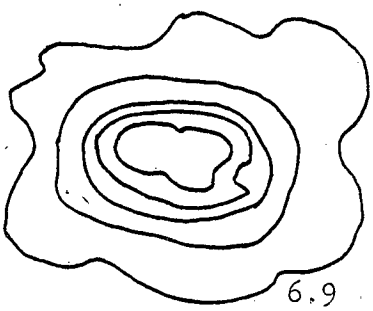

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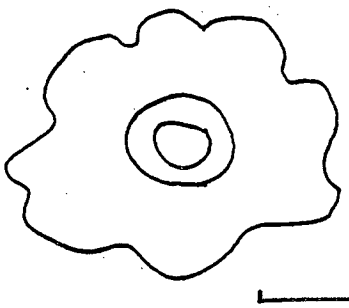


6.10

Scale

1 mm

After the appearance of the seed/ovules, septal ridges could no longer be distinguished on the ovary wall. At the base of the ovary there was no evidence in either species in the 11 ovaries examined that the base became septate. Pollen tubes were only observed in the transmitting tissue of the styles. Figure 6 illustrates the septal attachments and ridges of the ovary using method 2; plate 11a, dillustrates the results using method 4b.

In the genera Scleranthus and Pollichia above the level of the ovule/ovules, the ovary appears to be septate at some time in development, with a septal attachment, composed of 2 fused septal attachments fusing with the apex of the funicle/placental column, but with no evidence certainly in Scleranthus that below this level the ovary is ever septate.

In the third type of ovary described the following species were examined: Corrigiola telephiifolia, C. litoralis, Herniaria glabra, Illecebrum verticillatum, Paronychia echinulata. In all these species only 1 ovule is ever formed, and at maturity the indehiscent fruit is unilocular.

Corrigiola K(5) C 0A5 + 5 G(3)

Plate 11.d

In both C. telephiifolia and C. litoralis, using method 2 and method 4b, the structure of the ovary was found to be the same. In all the ovaries examined the 3 styles fused to form a single fused style with 3 vascular strands in between which was a triangular-shaped transmitting tissue. The 3 vascular strands continued into the ovary as the dorsal bundles of the ovary wall. The apex of the ovary was solid, being triangular in shape with the dorsal bundles of the ovary in the 'angles'. A small hole appeared in the centre of the ovary, gradually increasing in size. There was no evidence of 3 locules being formed in any of the 16 ovaries examined or of there being septal ridges or septal attachments. The ovule/seed soon appeared in the centre of the ovary cavity with a funicle. As in Scleranthus species, the funicle was found to fuse with the side of the ovary wall rather than with the base of the ovary. Below the appearance of the ovule/seed, septal ridges were not observed on the ovary/ ....

ovary walls, and the base remained unilocular.

Pollen tubes were only observed in 1 ovary. They were present in the centre of the solid tissue at the apex of the ovary and then appeared on the wall of the ovary (Plate 11.d). The pollen tubes, however, did not appear to travel in the position of the septal ridges, if they had been present, between the dorsal bundles. Pollen tubes were not observed to reach the base of the ovary. Plate11.d illustrates the structure of the ovary in Corrigiola.

Herniaria K(5) C 0 A5 + 5 G(2)

Plate 12

In both accessions of H. glabra using method 2 and method 4b, the structure of the ovary was found to be the same. In all ovaries examined, 2 septal ridges were evident on the ovary wall, from the apex of the ovary to the base, between the dorsal bundles of the ovary wall. In mature ovaries the septal ridges totally disintegrated after the appearance of the ovule, and the funicle fused at the base of the ovary however with 2 septa, the base being bilocular. In less mature ovaries septal ridges were evident from the apex to the base of the ovary. In 1 young ovary the apex of the ovary first appeared solid with the transmitting tissue in the centre of ovary, eliptical in shape. Two small holes then became evident opposite the dorsal bundles of the ovary wall leaving a complete septum across the ovary between the dorsal bundles. These 2 locules quickly increased in size, the single central septum breaking in the centre to leave 2 septal ridges on the ovary wall, between the dorsal bundles.

Pollen tubes were observed in the transmitting tissue at the very apex of the ovary and the transmitting tissue of the styles. Pollen tubes were also evident in/on the septal ridges of the ovary wall. The exact course of the pollen tubes is, however, unknown, but the septal tissue of the ovary wall is certainly involved. Plate 12 illustrate the septal ridges of the ovary wall near the apex of the ovary and fusion of the septal ridges to the funicle at the base of the ovary as well as pollen tubes within the septal tissue. In young ovaries, the septal ridges of the ovary wall were prominently papillate.

PLATE 11

Scleranthus annuus L.

11.a Solid apex of ovary. c. X 70.

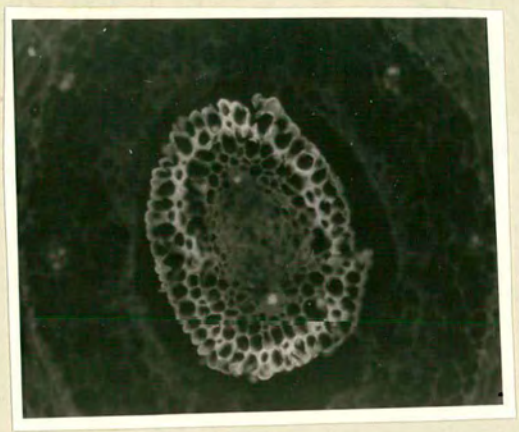
11.b Tissue beginning to break in centre. c. X 70.

11.c Septal attachment evident in centre of ovary. c. X 70.

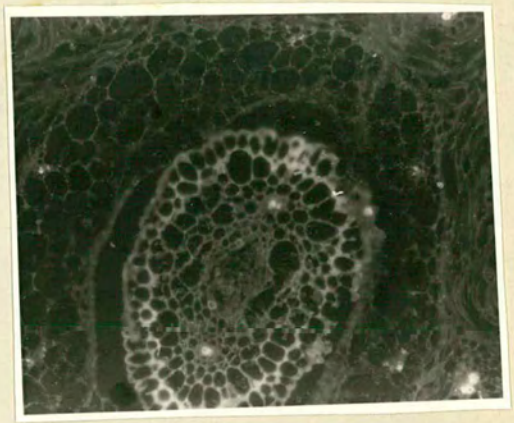
Corrigiola litoralis L.

11.d T.S. through apex of ovary with no evidence of septal tissue. c. X 70.

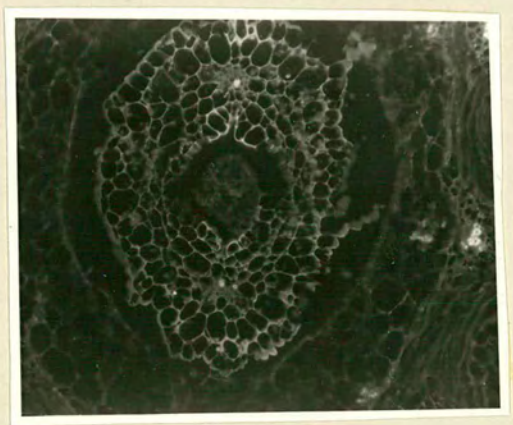
PLATE 11



11.a



11.b



11.c

11.d

PLATE 12

Herniaria glabra L.

12.a T.S. through solid apex of ovary. c. X 70.

12.b Two locules now evident. c. X 70.

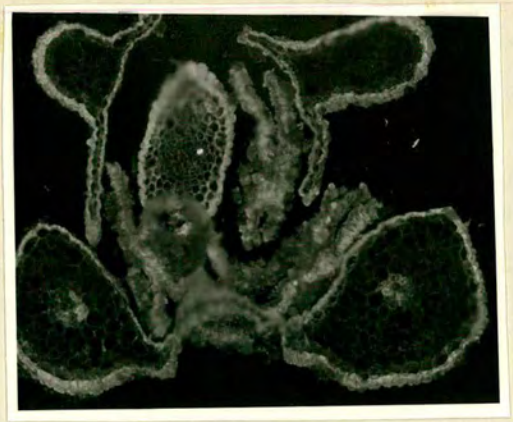
12.c Two locules increasing in size. c. X 70.

12.d Septum now broken to give two septal ridges on ovary wall. c. X 70.

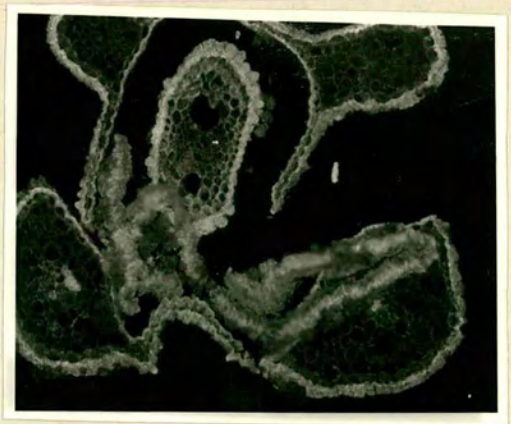
12.e Whole of flower, with ovule in centre of ovary with no evidenct of septal ridges on ovary wall. c. X 50.

12.f Base of flower, complete fusion of floral structures. Base of ovary septate. c. X 70.

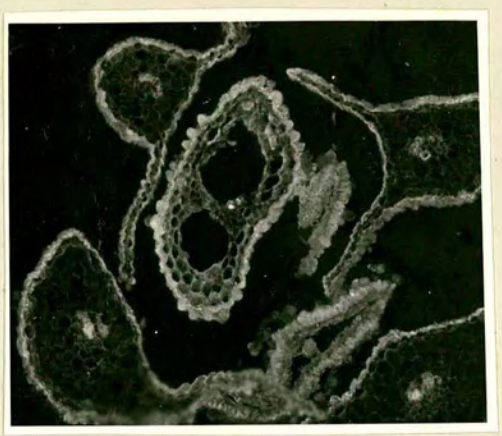
PLATE 12



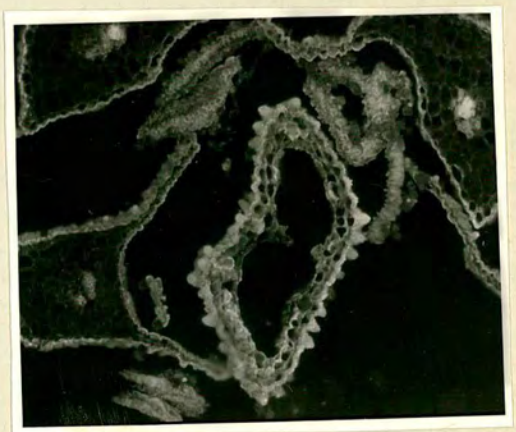
12.a



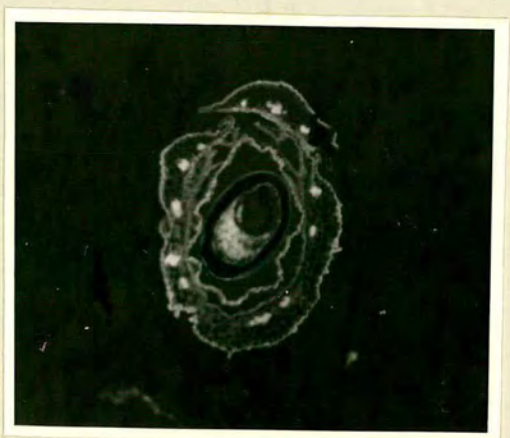
12.b



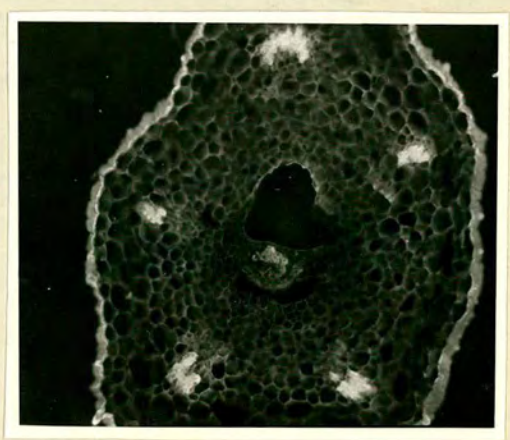
12.c



12.d



12.e



12.f

Illecebrum verticillatum K(5) C 0 A5 + 5 G(2) or G(3)

Plate 13 a - c

A number of ovaries were examined using method 4b and method 2, and it was found that the situation in this species is very similar to that in Herniaria species. Two septal ridges were observed between dorsal bundles of the ovary wall, on the ovary wall from the apex to the base of the ovary. At the base of the ovary the septa fused with the funicles to give a bilocular ovary at the base in most of the ovaries examined. A bilocular ovary was not, however, observed at the apex of the ovary as observed in Herniaria although this may occur in this genus in younger flowers. Pollen tubes were observed within the transmitting tissue of the septa ridges of the ovary wall. Plate 13 illustrates the observations made on this genus.

Paronychia echinulata K(5) C 0 A5 + 5 G(2)

Plate 13d - f

Only 7 ovaries were examined, of which 5 gave adequate results using method 4b; observations may not therefore be accurate. Of these 5 ovaries, in 3 a single septal ridge was observed, sometimes opposite the funicle, sometimes opposite the ovule. In some of the ovaries, it appeared that the ovary wall was slightly indented at this region, where the septal ridge appeared, and this indentation may have caused the inner surface to project to form what appeared to be a septal ridge. However, pollen tubes were observed in/on this tissue in one of the ovaries, but not very clearly. In a flower with 2 styles it would be expected that there would be 2 septal ridges, not 1. There is no evidence of septal attachments or of septal ridges fusing with the funicle at the base of the ovary, but the situation in this species is very unclear.

In this subfamily the results are not as conclusive as in the subfamily Dianthoideae. Much of the material was small which made it difficult to section very young ovaries. The lack of septal ridges on the ovary wall does not prove that they have not been present at any earlier stage as in other species where septal ridges on the ovary walls were evident in young ovaries but disintegrated in more mature ovaries. However, the following statements can be made about the ovaries in this subfamily using the examples above.

i./ ....

PLATE 13

Illecebrum verticillatum L.

13.a T.S. through middle of ovary with ovule in centre and evidence of two septal ridges. c. X 70.

13.b T.S. further down ovary with ovule and funicle evident and two septal ridges. c. X 70.

13.c Base of ovary, completely septate, septa fusing with funicle. c. X 70.

Paronychia echinulata Chater.

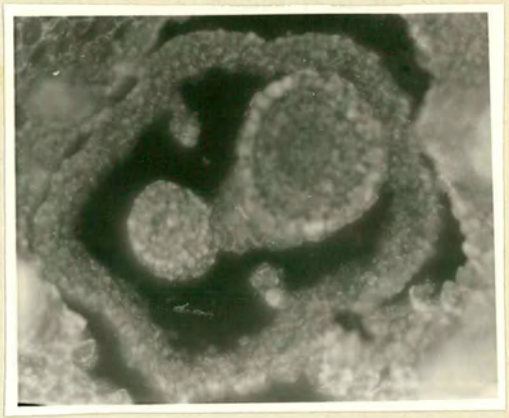
13.d Apex of ovary with single septal ridge evident. c. X 70.

13.e Ovule, funicle and septa ridge evident. c. X 70.

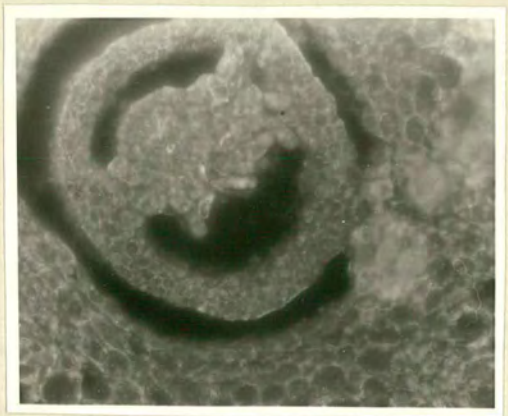
13.f Near base of ovary, funicle and septal ridge evident. c. X 70.

PLATE 13

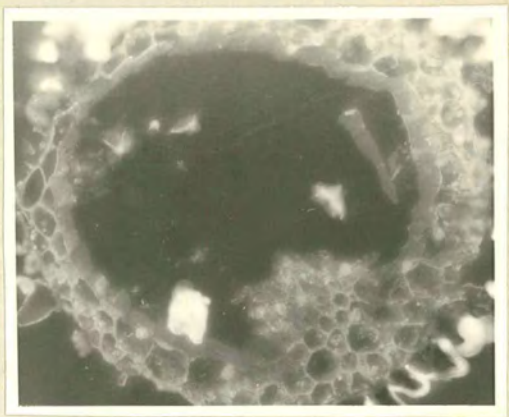
13.a



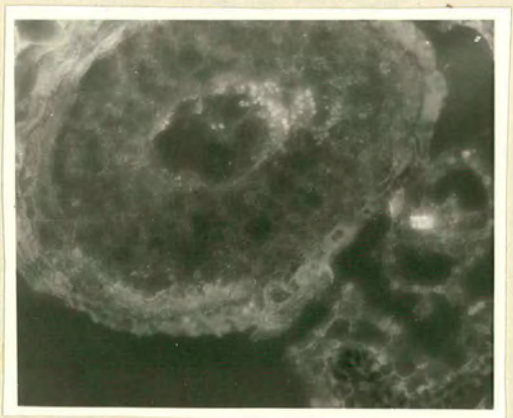
13.b



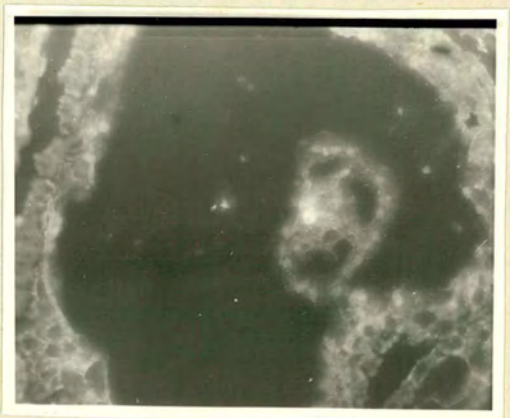
13.c



13.d



13.e



13.f

i. In Spergula, Spergularia, Drymaria and Polycarpon there is evidence that the ovary is completely septate at some stage, except probably for a small hole at the apex of the placental column.

ii. In Scleranthus, and possibly Pollichia, a strand of septal tissue/transmitting tissue from the apex of the ovary to the apex of the funicle/placental column suggests that in these genera the ovary may be completely septate at the apex of the ovary at some stage in development, but there is no evidence that the base of the ovary is septate.

iii. In Herniaria and Illecebrum there is evidence that the septa, although present in equal number to the styles, do not grow into the ovary above the level of the funicles, only septal ridges being evident on the ovary wall, but the base of the ovary would appear to be septate at some stage in development.

iv. The situation in Corrigiola and Paronychia is unclear. In Corrigiola no septal tissue have been observed and in Paronychia there is evidence of a single 'septal ridge' on the ovary wall.

v. The septal tissue, except in the 2 genera above, appear as in the subfamily Dianthoideae to 'form' the transmitting tissue.

3.4 Discussion.

The septal tissue in whatever form it is present in the species examined, is involved in the route of pollen tubes from the styles to the ovules. In the 3 categories of ovary described above (except in Corrigiola and Paronychia) the transmitting tissue is part of the septal tissue and is continuous with the transmitting tissue of the style. In the first category, a multi-ovulate ovary completely septate at some stage in development except for a small hole at the apex of the placental column, the transmitting tissue is 'carried' by the/ ....

the septal attachments which connect the apex of the placental column to the apex of the ovary, base of the styles and then by the septal ridges of the placental column. In those ovaries in which the base remaines completely septate at maturity, the transmitting tissue is still associated with the septa (compare Silene coeli-rosa and Spergularia species).

In the second category, where there is evidence of septal attachments and in some of the genera more than one ovule is formed, the situation is not clear. In Scleranthus species it would appear that the apex of the ovary is completely septate at some stage in development as there is evidence of septal ridges on the ovary wall and a single septal attachment, which could only have been formed by the fusion of the septa. At the base of the ovary the situation is unclear. In Scleranthus species there is no evidence of septa at the base, but this may have been because of the age of the ovaries examined as in other species, in which septal ridges were known to be present, they were not evident in older tissue. Also, in the other genera in this group (Pollichia, Achyronychia and Scopulophila) there is some evidence of septal ridges on the placental column from direct examination. Although the evidence is by no means conclusive, it would appear that the ovaries of these 3 genera are completely septate at some time in development and thus that these genera belong in the first category. In these genera the route of the pollen tubes is thus down the transmitting tissue of the septal attachments to the ovule or ovules as in these genera they are situated at the very apex of the placental column.

In the 4 genera in the third category of ovary type examined, in 2 of the genera, Paronychia and Corrigiola, the structure is very unclear. According to Eckardt (1955) Taf. IV fig. 3 in Corrigiola 2 septa are found at the base of the ovary between the dorsal bundles of the ovary wall, fusing to the funicle. In all Corrigiola sections examined in this work, there was no evidence of septal ridges. In the Paronychia species examined, a single septal ridge appeared to be present and in a very few of the sections 2 septal ridges. In these 2 genera the route of the pollen tubes is unclear although there is slight evidence of pollen tubes in ovaries of Paronychia on the single septal ridge and in Corrigiola on the ovary wall/ ....

wall. According to Moeliono p.116 - 117, Corrigiola represents a very reduced form in which the growth of the septa does not occur or occurs at a late stage in development, or not all the septa grow. This view probably can also be taken of Paronychia. In Herniaria and Illecebrum, the situation is clearer. In both genera, 2 septal ridges are formed in the upper part of the ovary but with no evidence that the septa grow further into the centre of the ovary cavity or fuse to give septal attachments. The base of the ovary is also septate, the septa fusing with the funicle. In Herniaria the apex of the ovary may also be bilocular at any early stage, as in species in the subfamily Dianthoideae, but the septa remain fused for only a very short time and this may not occur in all ovaries. Pollen tubes are certainly evident in/on the septal ridges of the ovary wall, confirming the link between the septal tissue and the transmitting tissue.

There would thus seem to be a reduction series in the growth of the septa from categories 1 and 2 ovaries to category 3 ovaries, although it is likely that even in Corrigiola septal ridges are sometimes formed. In all ovaries examined septal tissue and transmitting tissue are closely linked. The transmitting tissue, in the same way as the septum, is found to consist of 2 parts which correspond to the margins of adjacent 'carpels' or ovary wall components. Disintegration of the septa allows more movement of pollen tubes, the pollen tubes of pollen grains germinating on 1 style are able to fertilize ovules either from the locule immediately below that style or those from locules on either side because of the way the transmitting tissue splits at the apex of the ovary. In those ovaries in which the base of the ovary remains septate this advantage is lost, which may help to explain the lower number of ovules fertilized in Silene coeli-rosa after the removal of the styles than in other species examined in the destyling experiment described in Chapter 2.

In this work the septa are considered to fuse, at least partially, postgenitally to the placental tissue and are considered not to bear the placentae following the view of Moeliono (1970). This can be clearly observed by the manner in which fusion occurs between the septal attachments and the placental tissue at the apex of the placental column in Silene coeli-rosa, Agrostemma githago and Spergularia media. The tissue of the septa is completely different to/ ....

to that of the rest of the placental column, although it must be stated that this difference may in part be due to the fact that this tissue acts as transmitting tissue. The continuation of xylem vessels into the septa attachments in Agrostemma githago does not greatly damage this argument; the continued growth or differentiation of xylem vessels does not totally imply that the placental tissue and the septal tissue are of the same origin.

Having decided that the septal tissue and thus the ovary wall components do not bear the ovules, the origin of the ovules has to be discussed in relation to the observed vascular supply to the ovules. In all the species in which the vascular tissue was clearly examined, except in Spergularia species, there would appear to be a central vascular tissue, or groups of xylem vessels supplying the upper ovules or just extending to the apex of the placental column, and another vascular supply, often fused to the central supply, supplying the rest of the ovules and present as groups of xylem vessels, equal in number to the styles, opposite the dorsal bundles of the ovary wall in the 'traditional' position of the ventral bundles. The problem is are these '2' groups of vascular tissue (observed as groups of xylem vessels) separate, as Moeliono believes, or do they belong to the same vascular tissue as Bocquet (1959, 1960) believes?

In Spergularia media an interesting situation was observed. At the apex of the placental column, although funicles appear to fuse in pairs with the septal attachments, the vascular supply of these funicles do not fuse to form a single strand opposite the septal ridges, as observed in a number of other species, but fuse to form a single strand between the septal ridges, suggesting that in this species the central strands described above do not occur. Further, below this level groups of xylem vessels are observed in the centre of the placental column in much the same way as in species in which these central strands are thought to 'come' from a different vascular system. This could imply:

i. In this species the central strands are evident but for some reason do not extend as separate strands.

ii. The separate strands observed in other species are extensions of the 'ventral' vascular supply.

iii./ ....

iii. In this species no central vascular supply exists but for some reason the 'ventral' vascular supply merely occupies a central position.

The third explanation seems unlikely, as why should this only be observed in Spergularia species, a genus assumed to be closely related to the genera in the subfamily Alsinoideae, studied by Moelino who considered there to be 2 vascular systems present. If the first explanation is correct, it would be expected that the central strands would be evident at thebase of the ovary as in other species examined, but at the base of the ovary of Spergularia media only 3 strands are evident, each opposite the dorsal bundles of the ovary wall. The observations on Spergularia media thus tend to support the second explanation, that only a single vascular supply exists, forming both the central bundles observed and the 'ventral' bundles. However, this explanation is difficult to support when considering the vascular tissue of Cucubalus baccifer and Silene conoidea, where the central vascular strands can be traced from the apical ovules to the base of the ovary, supporting the view of Moelino of 2 separate vascular systems. If, however, there is only 1 vascular system, is this system present in the form of 3 - 5 strands opposite the dorsal bundles of the ovary wall in the traditional position of the ventral bundles, or could the main strands in fact be alternating with the dorsal bundles of the ovary wall, parallel to the upper 'central' strands? Both Saunders (1925) and Melville (1962) considered the ovules on either side of the septum to be from the same system/'carpel'. From this, is it possible that the main strands could be alternating with the dorsal bundles of the ovary wall not opposite them? Indeed in the Silene species studied by Bocquet (1959, 1960) he found that at the base of the ovary the 'ventral' strands separated to give strands alternating between the dorsal bundles. This is the situation at the apex of the placental column. In a number of species examined the main strand does appear to be alternating with the dorsal bundles, these being the central strands. All 3 possible explanations can be supported by using different examples:

i. A single vascular supply - Spergularia media, ?Agrostemma githago.

ii./ ....

ii. Two vascular supplies - Drymaria cordata, Silene conoidea, S. coeli-rosa, Cucubalus baccifer.

Although in each of the examples above it is possible to argue that the other situation exists, the main emphasis in the study of vascular tissue in this work has been the number and position of the xylem vessel groups, rather than the whole vascular bundle, and this may have made interpretation more difficult. All that can be clearly stated is that the vascular tissue of the placental column does not follow the traditional 'ventral' system, that there exists a network of vascular tissue, always with some of the tissue occupying the centre of the placental column which may or may not supply the vascular tissue of the upper ovules. Moeliono's work is very extensive, including work on other families in Centrospermae in which he has been able to interpret the ovary in all these families, as well as in the Caryophyllaceae, as consisting of originally 2 separate vascular systems and to a certain extent observations made in this work can be used to support this interpretation, even although the amount of fusion between the 'central' system and the 'ventral' system is great in all species examined. Further observation may do little to resolve the problem unless perhaps there are more species with the vascular system observed in Spergularia media.

The ovary of the family Caryophyllaceae is therefore considered to be of 2 parts, a sterile part and a fertile part. The sterile part consists of the components of the ovary wall bearing the styles and the septa. The fertile part consisting of a branched system bearing the ovules. The family Caryophyllaceae is thus a member of the stachyosporous group of plants of Lam, with sterile pseudocarpels enclosing the fertile axial branch system. This conclusion is in agreement with that reached by Melville (1962), Meeuse (1965), Lam (1948) and Moeliono (1970). As to which theory the observations made on this family lend support is unclear. This work takes the broad view of the origins of carpels, from a fertile branched system with sterile probably leaf-like components which probably evolved from a branched system, without setting out to further define the exact nature of this, as Melville and Meeuse have tried to do . However, following these 2 authors' views and that of others, it seems likely that the ovary of Angiosperms have evolved from a number of different starting points and therefore that Angiosperms have evolved from a number of different but related lines.

CHAPTER 4.

PARONYCHIOIDEAE

4.1 Introduction

The subfamily Paronychioideae consists of around 37 genera, 31 of which are discussed in this work. The genera Xerotia Oliv., Philipiella Spegazz., Polytepalum Suesseng. & Beyerle. and Kabulia Bor. & Fisch. have not been examined but may well be members of this subfamily. Robbairea Boiss. is here included in the genus Polycarpon Loefl. ex L. Among the other genera which have been included in this subfamily by other authors, Pycnophyllum Remy is here included in the subfamily Alsinoideae although this may not be its correct position as the pollen grains are 3-colpate. The genus also bears some resemblance, especially in the projections found on the outer wall of the ovary, to the genus Lyallia Hook. f. However, the interpretation of the floral parts of Lyallia by Skipworth (1961) would appear to discount any close similarity between these 2 genera. Lyallia and Hectorella Hook. f., both sometimes considered to be members of Paronychioideae, are here placed in the family Hectorelaceae Philipson & Skipworth (1961). Guilleminia H. B. & K., although similar to Scleranthus in having a distinct elongated perigynous zone and a single ovule, is placed in the family Amaranthaceae, following the view of Cavoco (1962). Dysphania R. Br. was originally described as having affinities with Chenopodium and has been placed in the Chenopodiaceae (Allen 1930), Caryophyllaceae (Engler 1889), Illecebraceae (Bentham and Hooker 1862 - 67) and in a separate family Dysphaniaceae Pax in Engler Bot. Jahrb. 61: 230 (1928) in which it is placed here as a link between the Caryophyllaceae and Chenopodiaceae.

The following genera are considered to be members of the subfamily Paronychioideae and are included in this work: Achyronychia Torrey & Gray, Cardionema DC., Cerdia Moc. & Sesse ex DC., Chaetonychia Sweet, Cometes L., Corrigiola L., Dicheranthus Webb, Drymaria Willd. ex Roem. & Schult., Gymnocarpos Forskal, Habrosia Fenzl, Haya Balf. f., Herniaria L., Illecebrum L., Krauseola Pax & Hoffm.,/ ....

Hoffm., Lochia Balf. f., Loeflingia L., Microphyes Phil., Ortegia L., Paronychia Miller, Pollichia Solander, Polycarpaea Lam., Polycarpon Loefl. ex L., Pteranthus Forskal, Scleranthus L., Sclerocephalus Boiss., Scopulophila M. E. Jones, Spergula L., Spergularia (Pers.) J. & C. Presl., Sphaerocoma T. Anderson, Stipulicida Michx., Telephium [Tourn.] L.

Subfamily Paronychioideae Fenzl in Endl. Gen. Plant.: 956 (1834)

Annual, biennial or perennial herbs, occasionally woody undershrubs, erect to prostrate. Stems glabrous or pubescent, often with swollen nodes, usually much branched. Leaves usually opposite, occasionally alternate or spirally arranged, sometimes in whorls or fascicles (due to condensing of lateral branches) at the nodes, linear to lanceolate, spathulate, ovate to orbiculate, apex obtuse or acute, often mucronate or with a short spine, sessile to subsessile, occasionally with a distinct petiole, glabrous or pubescent, often fleshy. Stipules usually present (absent in some species of Cerdia, Drymaria and Microphyes) triangular to ovate, occasionally connate at base or adnate to base of leaves, rarely completely adnate to leaf margins (Scleranthus, Habrosia, Cerdia). Inflorescence a terminal lax or compact dichasial cyme or flowers in axils of leaves, solitary or in clusters, sessile or on long peduncles. Bracts foliar or membranous, inconspicuous and shorter than flowers or longer and very conspicuous, completely obscuring the flower (Paronychia sp.), entire or lobed, often with a short spine or mucro. Flowers usually hermaphrodite, occasionally unisexual, often male sterile, rarely forming much branched sterile lateral structure (Cometes, Pteranthus, Dicheranthus), sessile to subsessile, occasionally with distinct pedicels, pedicels and peduncles often hairy, rarely glandular, rarely becoming fleshy in the fruiting stage (Pollichia) rarely peduncle a flat compressed spathulate structure. Sepals usually 5, occasionally 4, rarely 8 or more, either fused at base with other floral structures to form a short fleshy perigynous zone or a distinct pergynous tube is formed, glabrous or pubescent, lobes herbaceous or scarious/membranous, usually with membranous margins, often hooded, apex often with a short mucro or hard spine. Petals absent or present, if present usually free, rarely adnate to the stamen filaments to form a ring, triangular to ovate, entire or emarginate/ ....

emarginate, occasionally 2-lobed or 4-lobed with elaborate lateral structures, usually white, sometimes pink or red, rarely distinctly fleshy, usually with a distinct free membranous flap at base, possibly nectary gland. Stamens 1 - 10, usually reduced to 5, staminodes often found alternating with sepals when petals absent, occasionally staminodes becoming petaloid. Ovary superior, becoming unilocular when mature, sessile to subsessile, occasionally partially fused to base of perigynous zone; 1 - ∞ ovules, solitary, basal or arranged on a central placental column which is usually originally attached to ovary wall by septa which break down before/at anthesis except for a strand of transmitting tissue between the apex of the ovary and the apex of the placental column; styles free or fused, 2, 3, occasionally 5, where fused, apex lobed or entire rarely with a knob of stigmatic papillae at apex. Fruit an indehiscent, or a dehiscent capsule; 1 -∞ seeded; calyx usually persistent in fruit, occasionally several fruits dispersed as a unit; embryo straight or curved.

Distribution: Europe, N. & S. America, Australia, India, Africa, China, Japan, E. Asia.

This present work deals with the floral morphology of the genera included here in the subfamily Paronychioideae with the hope of achieving a better understanding of the grouping of the genera into tribes and subtribes. Many of the problems in this subfamily have arisen because of the small size of the flowers which require careful dissection in order to give accurate descriptions. Allied to the problem of size, making it especially difficult to count the number of lobes of the style and the number of alternisepalous staminodes, is the equally important problem of identifying the structures found in the flower, namely whether the alternisepalous structures are petals or staminodes. This distinction may appear arbritary as many consider petals to have evolved from sterile stamens, however, this may may not be the case, cf. Meeuse (1965), Melville (1962), and the fact remains that in describing the flower some distinction must be made. A description of how this distinction is arrived at is discussed in a following section.

The classification system at the tribal and subtribal levels has also had problems in this subfamily, mainly because of the isolated nature of a number of the genera. There are 12 monotypic genera, just/ ....

just over a third of all the genera in this subfamily. Six tribes are recognised, but in most a number of subtribes have had to be formed, some of which may well be separate tribes.

4.2 Floral Morphology.

This work has mainly concentrated on aspects of floral morphology, therefore the following sections will only be dealing with floral morphology in this subfamily.

Calyx. The calyx consists of 4 or 5 sepals as is found in the rest of the family, rarely with 8 or more spirally arranged sepals. There is always some kind of perigynous zone formed, however slight. A perigynous condition is also, however, evident in many species in the subfamily Alsinoideae and thus is not confined to this subfamily.

Perigynous zones are usually described as being formed either by the fusion of sepals, petals, stamens/staminodes or by the invagination of the axis or receptacle. In the Paronychioideae the former appears to be the mode of formation of the perigynous zone in most cases, although in some species of Paronychia invagination of the receptacle may also be involved. In most of the genera the perigynous zone has remained comparatively small: Cardionema, Cerdia, Chaetonychia, Cometes, Corrigiola, Dicheranthus, Drymaria, Habrosia, Haya, Herniaria, Illecebrum, Leoflingia, Microphyes, Ortegia, Paronychia sp., Polycarpaea, Polycarpon, Pteranthus, Spergula, Spergularia, Sphaerocoma, Stipulucida, Telephium. In these genera the sepals, although fused to the zone, are distinct to the base, the central area of the sepals being adnate to the zone but the margins free, or at least free in some of the sepals although occasionally the whole sepal becomes adnate to the zone, and the actual length of the zone does not usually exceed 0.5 mm (but extending to 0.7 mm in some species of Paronychia and 1 mm in Cometes). In some genera, however, the perigynous zone is greatly extended, so that the flower becomes vase or urn shaped, the whole sepal becoming adnate, i.e. the margins as well.

The following genera can be said to have a greatly extended perigynous zone: Achyronychia, Gymnocarpos, Lochia, Paronychia sp., Pollichia, Sclerocephalus, Scleranthus. In these genera the flower is/ ....

is usually vase or urn shaped with a long narrow perigynous zone with 5 lobes at the apex. The neck of the perigynous zone is usually narrowed, often with a fleshy ring to which the petals stamens or staminodes are attached. The ovary in some of these genera, Lochia, Gymnocarpos, Sclerocephalus, becomes fused to the wall of the perigynous zone, very markedly in the case of Sclerocephalus in the fruiting stage. These genera can thus be thought of as representing an intermediate state towards a truly epigynous flower.

There are usually 3 vascular strands in each sepal in both groups, i.e. those genera with a perigynous zone and those with an extended perigynous zone. The lateral veins of adjacent sepals may be fused or separate in the perigynous zone.

Petals. The subfamily is often described as lacking petals and of only possessing filiform or petaloid staminodes, but a number of genera do have petals: Achyronychia, Cardionema, Cometes, Drymaria, Habrosia, Haya, Krauseola, Loeflingia, Microphyes, Pollichia, Polycarpaea, Polycarpon, Scopulophila, Spergula, Spergularia, Sphaerocoma, Stipulicidia. Petals are defined in this work as the sterile structures composing the whorl inner to the sepal whorl. Petals may have originally been formed from sterile stamens or may be more closely related to the leaf-like sepals. The mode of formation of petals is not discussed here. In the other 2 subfamilies, Dianthoideae and Alsinoideae, the petals are well defined structures and it is appropriate to consider the petals in this subfamily as occupying the same position. The flower can thus be considered to consist of 4 basic whorls and the carpels. From the outside of the flower to the inside; sepals, petals, first stamen whorl (antisepalous), second stamen whorl (antipetalous) and carpels. The components of each of these whorls alternate with the components of the preceding and succeeding whorls. However, in many genera in the other 2 subfamilies the stamens appear either all to be at the same level or the antisepalous stamens appear to be inner to the antipetalous stamens, making the identification of petals and staminodes even more complex. Even if the structures which alternate with the sepals appear to be outer to the antisepalous stamens, this does not prove that they are petals and not staminodes. However, a number of interesting/ ....

interesting observations were made which clarify which structures are petals and which are staminodes.

In most of the genera there are only 3 whorls of structures and the carpels. The antisepalous stamens are always present but rarely are fertile antipetalous stamens. The structures which alternate with the sepals could therefore be petals or staminodes, sterile stamens of the second stamen whorl. In some species the antisepalous stamens are adnate at the base into a short tube, to which the structures alternating with the sepals are rarely fused (except Polycarpaea sp.). The structures are situated in most of the species between the stamen tube and the sepals and thus are clearly petals: Drymaria sp., Dicheranthus. In other species it has been noted that a small flap of tissue is evident in front of the base of the petaloid structures which alternate with the sepals. The presence of these flaps of tissue help to identify which of the structures are petals. Structures alternating with the sepals but not possessing these flaps of tissue are here termed staminodes.

The flaps usually consist of thin membranous tissue across the front of the base of the petal, the apex of the tissue at about the same level as the antisepalous stamens fuse to the perigynous zone. The flaps themselves are not usually adnate to the base of the petals. In some genera the flaps extend above the level of fusion of the stamens to the perigynous zone into a shortly elongated structure. Occasionally the structures are very long and fleshy and become adnate to the petals, as in Sphaerocoma. These membranous flaps could be considered as being part of the antisepalous stamen ring, the base of the stamen filaments fusing to form a membranous ring before becoming adnate to the perigynous zone. A small part of this membranous ring could remain detached from the perigynous zone and become evident as a membranous flap in front of the petals. In some genera, however, as stated, the flap of tissue appears fleshy and is often quite large and extends above the level of attachment of the stamens to the perigynous zone: Drymaria, Polycarpon, Scopulophila, Loeflingia, Microphyes, Pollichia, Polycarpaea, Sphaerocoma. In these genera, the flaps have been interpreted as nectary glands (O. Rohweder 1970, P. Zandonella 1970, 1977).

Secretory tissue is associated with the stamens in the Caryophyllaceae, usually forming a ring around the base of the stamens/ ....

stamens on the adaxial surface and occasionally also as distinct glands, usually adnate to the abaxial surface of the antisepalous stamens. In this subfamily the situation is considered to be the same. Thus in the above genera which have extended membranous flaps, the absence of antipetalous stamens has led to the extension of the secretory tissue above the level of the perigynous zone into a distinct flap in front of the petals. In many of the species, the distinct flaps often appear bilobed. This is very much in agreement with the flaps being interpreted as nectaries. The secretory tissue is usually adnate to the antisepalous stamens, in the family as a whole, often as 2 disctint areas on either side of the base of the stamen filament, the loss of the antipetalous stamen would lead to the 2 areas of secretory tissue on adjacent antisepalous stamens coming into contact, and thus forming a bilobed structure between the antisepalous stamens in front of the petals. This can be observed in a few species in the subfamily Alsinoideae where the antipetalous stamens have been lost: Arenaria sp., Colobanthus (Mattfeld 1938).

Drymaria sp., Spergula, Spergularia and Telephium do not usually have a distinct flap in front of the petals, indeed in Spergula and Spergularia some species have retained the antipetalous stamens. Thomson (1942) described the secretory tissue in Spergula arvensis as being in the form of a ring at the apex of the perigynous zone, and extending up either side of the antisepalous stamens, a situation not unlike that found in a number of species in the subfamily Alsinoideae. In 1970, Zandonella described the secretory tissue in Spergula, Spergularia and Telephium. In Spergula species without antipetalous stamens (S. arvensis), the secretory tissue is as described by Thomson, but the secretory tissue also is described as being adnate to the base of the petals, after the antisepalous stamens have separated from the perigynous zone, but the petals are at this stage still adnate to the perigynous zone. No flap of secretory tissue is therefore found in these species because of the manner in which the components of the perigynous zone separate. In Spergula and Spergularia species with antipetalous stamens the secretory tissue is described as consisting of a ring around the apex of the perigynous zone, extending to the adaxial surface of both antipetalous and antisepalous stamens. In Telephium, which lacks/ ....

lacks antipetalous stamens, the secretory tissue is similar to Spergula arvensis except that as the petals separate from the perigynous zone at an earlier stage, the tissue is not adnate to the base of the petals. The secretory tissue is adnate to the adaxial surface of the antisepalous stamens and stretches across the front of the petals as a free flap, from one antisepalous stamen to the next, instead of the tissue being fused to the base of the petals. The flap however is very small and not easily observed. A similar situation has been found to be present in Drymaria arenariodes Humb. & Bonpl. (Fig. 7) in this work.

It can thus be seen that the larger flaps observed are merely extensions of the shorter flaps observed in these 4 genera. This indicates that species which possess these flaps in front of the structures which alternate with the sepals have lost the second stamen whorl, but have retained the petal whorl.

The petals are often conspicuous: Drymaria, Spergula, Spergularia, Loeflingia, Sphaerocoma, Achyronychia, Cometes, Stipulicida, Haya, Habrosia, Scopulophila, usually white but occasionally pink, red or pale yellow. In some genera (Polycarpon, Polycarpaea sp., Microphyes, Pollichia) the petals are small and triangular and could be mistaken for petaloid staminodes, which they are not.

Stamens. Most of the genera have only an antisepalous whorl of fertile stamens, sometimes reduced to only 1 - 2 stamens: Pollichia, Scleranthus sp. Some Spergula and Spergularia species have an antipetalous fertile stamen whorl as do some Scleranthus sp. In other species where an antipetalous stamen whorl is present, the stamens are sterile and in the form of filiform or rarely petaloid staminodes. The only genus to have species which have both antipetalous staminodes and petals is Polycarpaea. The following genera have staminodes alternating with the sepals, and lack petals: Gymnocarpos, Herniaria, Illecebrum, Lochia, Paronychia, Scleranthus sp., Sclerocephalus. Staminodes are defined in this work as sterile stamens and in this subfamily are always found alternating with the sepals and thus represent the second or inner whorl of stamens. In a few species there are also some sterile stamens in the antisepalous stamen whorl.

In all the genera above said to have staminodes, it was found by/ ....

FIGURE 7

Drymaria arenarioides Humb. & Bonpl.
T.S. of flowers

7.1 Sepals, petals, stamens free, ovary in centre with placental column and ovules.

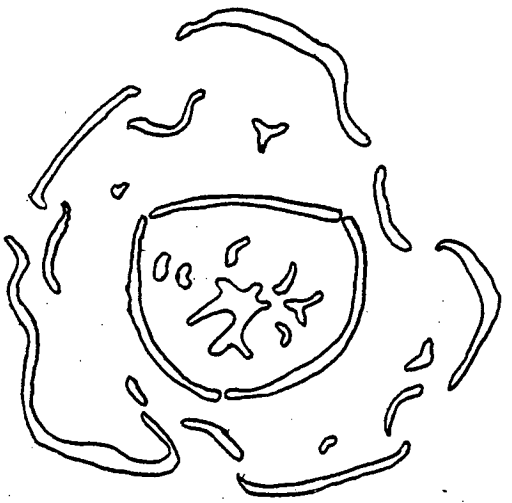
7.2 Sepals and petals close together, stamens now with evidence of secretory glands on either side, ovary now with only a placental column.

7.3 Near base, ovary completely septate, sepals, petals and stamens now very close together with base of 'stamens' expanding in front of petals - part of 'flaps' of secretory tissue.

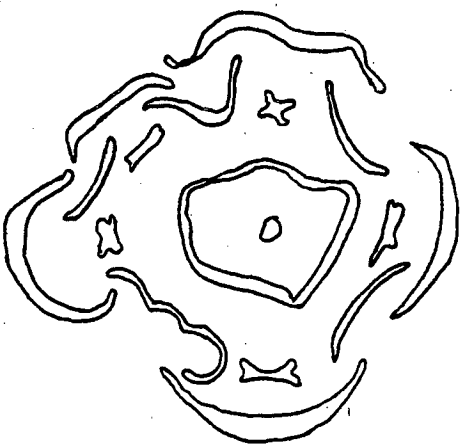
7.4 Base of ovary now solid, sepals touching, petals very small, stamens fused into a stamen tube, the stamens 'united' by a 'flap' of secretory tissue in front of petal.

7.5 Petals and stamens now fused, sepals still free.

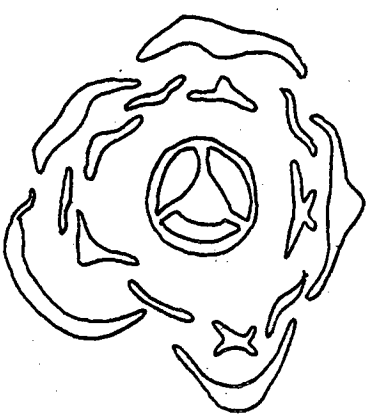
FIGURE 7



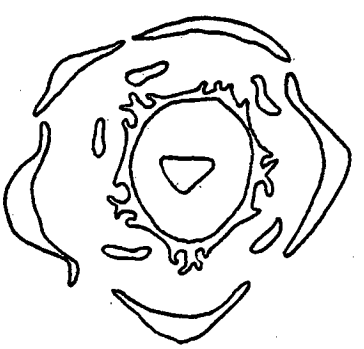
7.1



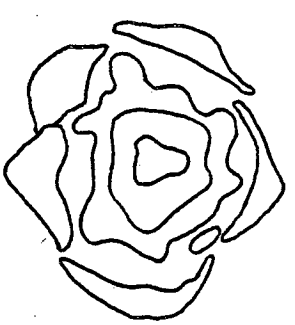
7.2



7.3



7.4



7.5

Scale 1 mm

by examining transverse sections of the flowers that the staminodes were either fused to the perigynous zone in front of, inner to, the antisepalous stamens (Gymnocarpos, Lochia) or that the stamens and staminodes fused at the same level (Scleranthus sp., Herniaria, Illecebrum, Paronychia). It was also observed that no membranous flap or structure was ever evident in front of these staminode structures; Corrigiola alone has staminodes which appear petaloid, all the other staminodes are filiform. Thus in this subfamily there are genera which possess petals and others where petals are absent and staminodes are found (Table 42). The loss of petals and the retention of the second or inner stamen whorl in the form of staminodes is found in the tribes Paronychieae and Scleranthea. The retention of petals, but the loss of the second whorl of stamens is found in the tribes Habrosieae, Pollichieae, Pterantheae and Polycarpeae. It seems likely that these 2 groups have separately evolved from primitive Caryophyllaceous species which were probably similar to present Alsinoideae species.

A number of authors have felt that the structures which alternate with the sepals (apart from those structures which are clearly fertile stamens) have either all to be staminodes or all to be petals. Chaudhri (1968) considered all the structures to be petals in the tribe Paronychieae subtribe Paronychiinae in which he included Paronychia, Herniaria, Lochia, Gymnocarpos, Corrigiola and Sphaerocoma, a view also followed in Flora Iranica (1980). The earlier work of Pax and Hoffm. (1934) followed the view of Lüders (1907) and concluded that the structures were staminodes. This, surprisingly, included Spergula and Spergularia in which most of the species also have fertile antipetalous stamens. But there have been a few earlier works, Spach (1836) and Pouchet (1836), which considered it possible to have both petals and staminodes in this subfamily, even although they differed in which genera they considered to have petals and which to have staminodes.

Pollen grains are either porate or furrowed, the genus Corrigiola having both types of pollen grain (Nowicke 1975). Nowicke (1975) and Erdtman (1952) disagree on the condition found in Drymaria sp., D. cordata is described by Erdtman as having furrowed grains but by Nowicke as having porate grains, and D. letophylla (D. tenella) is/ ....

TABLE 42

List of genera showing those which possess petals and those which possess staminodes.

Character / Genus	Fertile antipetalous stamens	2nd whorl of stamens reduced to staminodes	Petals Present
Achyronychia	-	-	+
Cardionema	-	-	+
Cerdia	-	-	-
Cometes	-	-	+
Chaetonychia	-	-	-
Corrigiola	-	+	-
Dicheranthus	-	-	-
Drymaria	-	-	+
Gymnocarpos	-	+	-
Habrosia	-	-	+
Haya	-	-	+
Herniaria	-	+	-
Illecebrum	-	+	-
Krauseola	-	-	+
Lochia	-	+	-
Loeflingia	-	-	+
Microphyes	-	-	+
Ortegia	-	-	-
Paronychia	-	+	-
Pollichia	-	-	+
Polycarpaea	-	- or +	+
Polycarpon	-	-	+

(continued on following page)

TABLE 42 (contd.)

Genus \ Character	Fertile antipetalous stamens	2nd whorl of stamens reduced to staminodes	Petals Present
Pteranthus	-	-	-
Scleranthus	- or +	- or +	-
Sclerocephalus	-	+	-
Scopulophila	-	-	+
Spergula	+ or -	-	+
Spergularia	+ or -	-	+
Sphaerocoma	-	-	+
Stipulicida	-	-	+
Telephium	-	-	+

is described by Erdtman as having porate grains but by Norwicke as being furrowed. Drymaria arenariodes, the type species, also has furrowed pollen grains, but with more than 3 furrows. This may also be the case in some Spergula, and Spergularia species. Corrigiola species either have 3 pores or 3 furrows, most of the other porate pollen grains having more than 3 pores. Porate grains tend to be found in those genera which lack petals, whereas furrowed pollen grains tend to be present in those with petals.

Carpels. The ovary is usually sessile but occasionally is on a short stipe. In a few of the genera the ovary is fused to the wall of the extended perigynous zone. Projections are often present on the apex of the ovary and hairs may be present at the base. On the whole, the genera with more than one ovule have dehiscent fruits, and those with only a single ovule have indehiscent fruits. The capsules open by the number of carpels forming the fused ovary, either 2, 3 or 5 valves.

The styles are fused in almost all of the genera. However, Habrosia and Scleranthus always have free styles and Telephium, Corrigiola and Herniaria have species with either fused or free styles. Spergula and Spergularia usually have free styles although in some plants in some of the species the styles are fused. In a quarter of the genera the styles are fused for more than half their length: Lochia, Gymnocarpos, Achyronychia, Microphyes, Polycarpon, Cometes, Krauseola, but in the other genera fusion is less complete and occasionally the 2 styles of some species of Paronychia are just fused at the base and no more. Only 3 genera have a single style with a stigmatic knob at the apex: Ortegia, Polycarpon, Haya, caused by the total fusion of 3 styles. As already stated there are either 2, 3, or 5 styles found in species in this subfamily (Table 43).

Of the 3 types of fused style described by Hanf (1935): open, solid, half-closed, the fused styles in this subfamily can be said to be solid. However, in some of the fused styles holes often appear to form in the centre, between the vascular strands. Of 14 genera examined only about half had fused styles with no evidence of holes: Pternathus, Paronychia sp., Herniaria sp., Corrigiola sp., Chaetonychia, Pollichia, Sphaerocoma. Of the remaining genera, Cometes/ ....

TABLE 43

The number of styles in genera in the subfamily Paronychioideae.

2 styles		3 styles		5 styles	
Free	Fused	Free	Fused	Free	Fused
Habrosia	Achyronychia	Corrigiola	Achyronychia	Spergula	Krauseola
Herniaria	Cardionema	Spergularia	Pteranthus		Spergula
Scleranthus	Cerdia	Telephium	Cardionema		
	Chaetonychia		Chaetonychia		
	Herniaria		Cometes		
	Illecebrum		Corrigiola		
	Paronychia		Dicheranthus		
	Pollichia		Drymaria		
	Pteranthus		Gymnocarpos		
	Sclerocephalus		Haya		
	Sphaerocoma		Illecebrum		
			Lochia		
			Loeflingia		
			Microphyes		
			Ortegia		
			Polycarpaea		
			Polycarpon		
			Sclerocephalus		
			Scopulophila		
			Spergularia		
			Stipulicida		
			Telephium		

Cometes, Dicheranthus, Drymaria, Gymnocarpos, Lochia, Haya, Polycarpon, Achyronychia, there is evidence of holes. In Haya and Drymaria sp. there is also a small continuous hole appearing towards the base of the fused style extending into the apex of ovary. In Haya the rest of the fused style remains solid but in Drymaria even in styles taken from flowers at anthesis small holes are evident along the entire length, but not a continuous hole. In the rest of the genera the fused styles are solid at the base, but with small holes along the rest of the fused style. In some, Lochia, Gymnocarpos, Dicheranthus, Achyronychia, the margins of the styles are fused but the centre remains hollow for a short distance at the apex. It is probable that the holes that are found occasionally in the centre, along the length of the fused style are due to either the tissue of the style disintegrating after the pollen tubes have grown through the transmitting tissue of the styles, or due to disintegration brought about by the preparation of the material for sectioning. It is unlikely that this represents a true open or half-closed style type.

The ovary is originally septate and multi-ovulate in most of the genera in the tribes Polycarpeae and Habrosieae, becoming unilocular with the disintegration of the septa at/before anthesis except for the strands of transmitting tissue/septal attachments. In Haya and Sphaerocoma included in the former tribe here, there is evidence of the strands of transmitting tissue and in the case of Sphaerocoma of septal ridges on the placental column, but it is not clear if either genus has completely septate ovaries at any point in its development. In the tribes Pollichieae and Sclerantheae, the former with 2 - 4 ovules, the latter with only 1 ovule, there is evidence of a strand of transmitting tissue/ septal attachment, but only scant evidence of septal ridges on the ovary wall. In the tribes Paronychieae and Pterantheae, both with genera with only a single ovule, there is no evidence of a strand of transmitting tissue/ septal attachments. In some genera there is evidence of septal ridges or similar structures on the ovary wall. However, there is no evidence to suggest that at any time these ovaries are totally septate, but the base of the ovaries may be.

4.3 Classification.

Historical Perspective. The family (order) Caryophyllaceae of B. Jussieu (1759) included 4 of the then known genera of the subfamily Paronychioideae: Ortegia, Loeflingia, Polycarpon, Spergula, the remaining known genera: Corrigiola, Telephium, Herniaria, Illecebrum, Scleranthus, being placed in the family (order) Polygonaceae. A. L. Jussieu (1789) divided the family Caryophyllaceae into 6 groups on calyx characters, stamen and style number. He placed the first 3 genera above, in the first group along with Minuartia, Mollugo and Queria, placing Spergula in a separate group with Cerastium and other genera now included in the subfamily Alsinoideae. The remaining genera were divided between 2 families, Amaranthi (sic) and Portulaceae (sic). In the former family were placed Illecebrum in one group and in another group Paronychia and Herniaria and in the latter family, in a single group, Telephium, Corrigiola, Scleranthus and Gymnocarpos.

In 1815 A. Saint-Hilaire recognised the similarity between some of these genera which had been placed in 3 separate families (orders) by A. L. Jussieu and recognised the family (order) Paronychieae with 2 divisions or groups which he considered could be separate. The first, Scleranthea, consisted of 5 genera placed in 2 sections, the first section consisting of Minuartia and Loeflingia and the second section of Scleranthus, Herniarum and Queria. The second division, Paronychieae, also consisted of 2 sections, the first section of Polycarpon and Hagea (Polycarpaea) and the second section of Paronychia, Herniaria and Gymnocarpos. The genera in the family (order) being separated from those of Amaranthaceae and Caryophyllaceae by their stipulate leaves. In 1816 A. L. Jussieu recognised the family Paronychieae of A. Saint-Hilaire, adding to the second division Pollichia, Illecebrum and Anychia and recognising Corrigiola, and Telephium as having affinities with this new family.

When the first volume of A. P. De Candolle's Prodr. Syst. Nat. was published in 1824 the family Caryophyllaceae consisted of only 2 tribes, Sileneae and Alsineae. In the latter of these tribes were included Spergula and Drymaria, still not considered to be part of the new family. In the third volume in 1828 the family of A. St. - Hilaire/ ....

Hilaire was recognised, but with a number of added genera. The 4 subdivisions of A. St.-Hilaire were recognised as tribes with the addition of a further 3 tribes. Telephium and Corrigiola were recognised as belonging to this family and placed in the tribe Telephiae, Queria was separated from Scleranthus and Moniarum and placed in the monotypic tribe Queriaceae. The genus Pollichia described in 1789 was also recognised as belonging to this family and placed in the monotypic tribe Pollichieae. Illecebrum, not included by A. St.-Hilaire but included by A. L. Jussieu, was placed with Herniaria, Paronychia and Gymnocarpos and along with Anychia described in 1803 and Cardionema described for the first time in this book in the tribe Illecebrae, a name proposed a few years earlier in 1810 by R. Brown as a tribe in the family Amaranthaceae whose genera had distinct perigynous flowers and stipulate leaves. Along with Polycarpon and Polycarpaea were placed Stipulicida described in 1803 and Cerdia described for the first time in this book. These 4 genera, along with Ortegia which had been in the family Caryophyllaceae of A. L. Jussieu and had been placed, with some uncertainty in the tribe Alisineae in the first volume of A. P. De Candolle's Prodromus, formed the tribe Polycarpaeae. Guilleminea was also included in this family for the first time and placed in the tribe Sclerantheae along with Moniarum and Scleranthus. Two years later in 1830, Bartling recognised both the tribes Alsineae and Sileneae to be separate families (orders) and separated the tribe Sclerantheae from the family Paronychieae, which he also recognised to form a fourth separate family. In Paronychieae he recognised 4 divisions. The first, Illecebrea, equivalent to the tribe Illecebreae and Pollichieae of De Candolle, the third, Molluginea, consisted of 3 genera, now no longer considered to be in this family, Mollugo, Pharnaceum and Adenogramer; the fourth, Telephiea of De Candolle and in the second division, Spergulea, along with the tribes Polycarpaeae and part of Minuartieae of De Candolle, Spergula, Spergularia and Drymaria, here for the first time included in the family Paronychieae.

In 1839, Endlicher's Genera Plantarum was published. In this work, Fenzl included as subfamilies (suborders), the families Paronychieae and Sclerantheae of Bartling in the family Caryophyllaceae. In the former subfamily he recognised five tribes. The first/ ....

first tribe, Illecebreae was the same as that of De Candolle but with the addition of Corrigiola placed in a separate subtribe from the other genera. Two genera, Pteranthus and Cometes, were included in the subfamily for the first time in the tribe Pterantheae. The third tribe, Pollichieae, was as described by De Candolle with the fourth tribe, Telephieae, of De Candolle being reduced to a monotypic group containing only Telephium. Queria and Minuartia were rightfully excluded and the tribe Minuartieae, now called Loeflinieae was included in the tribe Polycarpeae as a monotypic subtribe containing Loeflingia. Fenzl followed the view of Bartling and included Spergula, Spergularia and Drymaria in the second subtribe Sperguleae of the tribe Polycarpeae, along with the other genera placed in that tribe by De Candolle. The subfamily Scleranthea continued to include Guilleminea, Mniarum and Scleranthus. Walpers' Repertorum Botanices Systematicae I published in 1842, followed the work of Fenzl, uniting Paronychieae and Scleranthea with the family Caryophylloceae. However, a year earlier, in 1841, C. F. Ledebour had published Fl. Rossica 1 and 3 in which he reverted to the views of Bartling, recognising separate families but modified the tribes and subtribes to those of Fenzl.

A new family name was proposed by Lindley in 1846, the Illecebraceae, to include all the genera of Fenzl's subfamily Paronychieae and, with the addition of Spergula, Spergularia and Drymaria and exclusion of Mniarum, Scleranthus and Guillemina, the family Paronychieae of De Candolle. This name was adopted by Bentham and Hooker in 1880 but the contents of the family were greatly altered. The tribe Polycarpeae of De Candolle, with the additional genera of Fenzl's tribe was placed in the family Caryophyllaceae as one of the 3 tribes they recognised in this family. Pycnophyllum, Lyallia, Microphyes and Sphacerocoma described after Fenzl's work were also included in this tribe. However, Spergula and Spergularia were placed in the tribe Alsinoideae, in the family Caryophyllaceae. The family Illecebraceae contained only 4 tribes. Scleranthus was included along with Habrosia, described in 1843 in the tribe Scleranthea, originally excluded from the family by Lindley. A new tribe Paronychieae was formed which contained the same genera as Illecebreae of De Candolle with the addition of the genus Sclerocephalus described in 1843 but excluding Illecebrum and Pentacaena/ ....

Pentacaena (Cardionema). These 2 genera and Dysphania were placed in a sub-group of the tribe Pollichieae which also included, as well as Pollichia the genus Achyronychia described in 1868 in the other sub-group. Dicheranthus described in 1846 was placed in the fourth tribe, Pterantheae, along with Cometes and Pteranthus.

Pax in Engler and Prantl's Natürl. Pflanzenfam. Ed. 1. recognised only 2 subfamilies in the Caryophyllaceae, Silenoideae and Alsinoideae. Included in Alsinoideae were 5 groups with genera considered at some time to be in the subfamily Paronychioideae. The first group Sperguleae contained Spergula, Tissa (Spergularia) and Telephium combined together for the first time. The second group Polycarpeae contained the same genera as that of Bentham and Hooker's tribe and the name Paronychieae was again used, but the tribe contained a few additions from that of Bentham and Hooker's. Sphaerocoma, originally placed in the Polycarpeae, the 4 genera of the tribe Pollichieae of Bentham and Hooker (excluding Dysphania), and 2 new genera, Lochia and Haya both described in 1884, were added to the group Paronychieae. The tribes Scleranthea and Pterantheae remained unchanged and a new group, Dysphanieae, was created for the genus Dysphania. Dysphania is now placed in a monotypic family Dysphaniaceae. Ascherson and Groebner in 1919 chose to follow Pax, recognising only 2 subfamilies in the Caryophyllaceae, recognising the same tribes for the genera described.

Two works appeared in 1907. Vierhapper re-established the subfamily Paronychiadeae of Fenzl, recognising 4 tribes, Sperguleae, Polycarpeae, Paronychieae and Pterantheae. The tribe Scleranthea was placed in the subfamily Alsinoideae. However, Lüders chose to recognise the tribes at the subfamily level, Scleranthoideae, Polycarpoideae, Paronychioideae, Pteranthoideae. The subfamilies Scleranthoideae and Pteranthoideae contained the same genera as the respective tribes of Bentham and Hooker. The second subfamily contained the same genera as the tribe Polycarpeae of Pax except for the addition of Sphaerocoma and the exclusion of Lyallia, now placed in a separate family Hectorellaceae. The only subfamily to contain tribes being Paronychioideae in which 3 tribes were recognised. The first tribe, Pollichieae, contained Pollichia and Achyronychia, recognised by Bentham and Hooker as having clear similariies. Illecebrum/ ....

Illecebrum and Dysphania were placed in a new tribe, Dysphanieae, having previously often been included in the same tribe as Pollichia. The third tribe Paronychieae contained the same genera as that of Bentham and Hooker's with the addition of Haya.

Thus by 1934, when Pax and Hoffman came to write their account of the subfamily in Engler and Prantl's Natürl Pflanzenfam., several groupings had been tried. As early as 1815 with A. St.-Hilaire, the striking similarities between the genera had led to the formation of a separate family, the Paronychieae, a view which was a few years later followed by de Candolle in his work of 1828 and of Bartling in 1830, although with the addition of a number of newly described genera and now with a number of tribes. However, by 1839 Fenzl had recognised the similarities between this family and the Caryophyllaceae, in which a number of genera had originally been placed by A. L. Jussieu, and recognised the family as a subfamily of the Caryophyllaceae. This view was followed by Walpers in 1842 but not by Ledebour in 1841 who recognised separate families. Lindley in 1846 again recognised the genera as forming a separate family and for some reason gave it the new name of Illecebraceae. Bentham and Hooker took up this new family name in their work of 1880 but greatly altered the family by removing the tribe Polycarpeae and including it in the family Caryophyllaceae. Pax in 1889 took a much wider view and again placed the genera in the Caryophyllaceae but in the subfamily Alsinoideae not as a separate group. However, in 1907 Vierhapper recognised the subfamily Paronychioideae again, but in the same year Lüders recognised each tribe in this subfamily as separate subfamilies of the Caryophyllaceae.

Pax and Hoffmann in Engler and Prantl's Nat. Pflanzenfam. Ed. 2, choose to recognise the subfamily Paronychioideae, containing 5 tribes. The tribe Scleranthеae was placed in the subfamily Alsinoideae as was the new tribe Habrosieae which contained only Habrosia. The first tribe Paronychieae corresponded to the subfamily Paronychioideae of Lüders, with 3 subtribes being recognised: Paronychiinae, Pollichiinae, Illecebrinae. The first subtribe corresponded to the tribe Paronychieae of Bentham and Hooker's except for the addition of the genus Lochia. Pollichiinae was the same as the tribe Pollichieae of Lüders with the addition of the genus/ ....

genus Scopulophila which had been described in 1908 having originally been part of the genus Achyronychia. The third subtribe consisted of Illecebrum, Haya, Cardionema and Chaetonychia; Illecebrum and Cardionema (Pentacaena) had been placed in the same group by Bentham and Hooker but Haya had usually been placed in the tribe Paronycheae with genera placed in this work in the subtribe Paronychiinae. Chaetonychia had also been closely linked with this group of genera, having originally been part of the genus Paronychia. The tribe Pterantheae contained 4 genera, 3 of which had always been included in this tribe; the fourth Hafunia, a synonym for Sphaerocoma, was mistakenly placed in this tribe because of the presence of sterile lateral flowers, Sphaerocoma having been placed in the subtribe Paronychiinae of the tribe Paronychieae. The tribe Polycarpeae contained the same genera as that of Bentham and Hooker, except for the exclusion of Sphaerocoma and with the addition of Krauseola first described in 1931 under an illegitimate name only being corrected in this work of Pax and Hoffmann. A new monotypic tribe Xerotieae was recognised containing Xerotia, an unknown genus. The last tribe Sperguleae contained the same 3 genera recognised in this tribe by Pax in 1889.

Flora Europaea, published in 1964, recognised the subfamily Paronychioideae, but following Pax and Hoffman's view placed Scleranthus in the subfamily Alsinoideae. The Flora of Turkey followed Bentham and Hooker, recognising the family Illecebraceae to include the genera Corrigiola, Scleranthus, Paronychia and Herniaria but placing Spergula, Spergularia, Polycarpon, Loeflingia and Telephium in the subfamily Paronychioideae in the family Caryophyllaceae equivalent to the tribe Polycarpeae but with the addition of Spergula, Spergularia and Telephium.

Classification Adopted. In this present work the subfamily Paronychioideae is recognised and is divided into 6 tribes and a number of subtribes on floral characters including type of pollen grain.

Key to Tribes and Subtribes

1. Fruit dehiscent ..... Tribe IV Polycarpeae

a)/ ....

a) leaves alternate; stipules adnate to leaves .... subtribe Telephiinae

a) Leaves opposite; stipules rarely adnate to leaves

b) Sepals 5 - 8 arranged in a spiral, styles 5 fused .. subtribe Krauseolinae

b) Sepals 5 (- 4) arranged in a single whorl; styles 2 or 3 fused, rarely 5

c) Styles 3 or 5 usually free or occasionally fused; fertile antipetalous stamens often present; leaves in a whorl at node ..... subtribe Spergulinae

c) Styles 2 or 3 fused; antipetalous stamens usually absent or present as staminodes; leaves opposite or in fasicles at nodes subtribe Polycarpinae

1. Fruit indehiscent
   2. Distinct lateral sterile branched structures in each group of flowers ..... Tribe III Pterantheae
   2. No distinct lateral sterile branched structures
      3. Petals usually present, where absent flap of tissue present alternating with sepals; 1 - 4 ovules
         4. Stipules distinct, free; greatly elongated perigynous zone; no distinct glands at base of antisepalous stamens ..... Tribe II Pollichieae
         4. Stipules in distinct, totally adnate to leaf margins; short perigynous zone present; distinct glands at base of antisepalous stamens ..Tribe VI Habrosieae

3./ ....

3. Petals or petaloid staminodes rarely present, where present only a short perigynous zone; 1 ovule

5. Stamens 1 - 10, sterile filaments present in the form of staminodes; stipules not distinct; styles free ..... Tribe V Sclerantheae

5. Stamens 1 - 5; usually with 5 staminodes occasionally with 5 petals or petaloid staminodes; stipules distinct; styles usually fused .... Tribe I Paronychieae

a) Petals or petalloid staminodes absent

b) Alternisepalous staminodes usually present; pollen grains porate ..... . subtribe Paronychiinae

b) Alternisepalous staminodes always absent; pollen grains furrowed ..... subtribe Chaetonychiinae

a) Petals or petaloid staminodes present

c) Leaves opposite ..... . subtribe Cardioneminae

c) Leaves alternate ..... subtribe Corrigiolinae

TRIBE I PARONYCHIEAE Pax in Engler & Prantl, Natürl Pflanzenfam. 3 Teil 1b: 88 (1889)

Syn: Illecebraceae - Paronychieae Bentham & Hooker f., Gen. Plant 3: 13 (1880);

Paronychioideae Lüders in Engler Bot. Jahrb. 40 Beibl. 91: 22 (1907).

Pollen grains porate, occasionally furrowed; petals or petaloid staminodes rarely present; 1 ovule; fruit indehiscent; staminodes usually present; no evidence of strand of transmitting tissue from apex of ovary to apex of funicle; style fused or free.

Subtribe Paronychiinae Pax & Hoffmann in Engler & Prantl, Natürl Pflanzenfam. Band 16c: 298 (1934).

Syn/ ....

Syn: Telephiae Bartl., Beitr. 2: 157 (1830);

Paronychioideae - Paronychieae Lüders in Engler Bot. Jahrb. 40 Beible. 91: 28 (1907).

Pollen grains porate; petals absent; staminodes usually present (absent in some species of Paronychia and Herniaria); styles fused or free.

Paronychia, Herniaria, Lochia, Gymnocarpos, Sclerocephalus, Illecebrum.

Subtribe Chaetonychiinae. Pollen grains furrowed; staminodes always absent; petals absent; styles fused.

Chaetonychia.

Subtribe Cardioneminae. Pollen grains porate; distinct petals present; no staminodes present; styles fused.

Cardionema.

Subtribe Corrigiolinae Fenzle in Endl., Gen. Plant.: 956 (1839).

Syn: Corrigiolacea Reichb. in Mössl., Handb. Ed. 2 I, 51 (1826)

Caryophyllaceae - Corrigiolinae Graebn. in Ascher. & Graebn., Syn. Mitteleur. Fl 5 (1): 866 (1919).

Pollen grains 3 - porate or 3 - furrowed; petals or petaloid staminodes present; leaves alterante; styles fused or free.

Corrigiola.

TRIBE II POLLICHIEAE DC., Prodr. 3: 377 (1828).

Syn: Illecebraceae - Pollichieae - ** Bentham & Hooker f., Gen. Plant. 3: 12 (1880);

Paronychieae - Pollichiinae Pax & Hoffm. in Engler & Prantl, Natürl Pflanzenfam. Band 16c: 302 (1934).

Pollen grains porate; 1 - 4 ovules; fruit indehiscent; petals or modified petals usually present; staminodes usually absent; evidence of strand of transmitting tissue from apex of ovary to apex of placental column; styles fused.

Pollichia, Achyronychia, Scopulophila.

TRIBE III PTERANTHEAE Fenzl in Endl., Gen. Plant.: 959 (1839).

Syn: Illecebraceae - Pterantheae Bentham & Hooker f., Gen. Plant. 3: 13 (1880);

Caryophyllaceae - Pteranthoideae Lüders in Engler Bot. Jahrb. 40 Beibl. 91: 29 (1907).

Pollen/ ....

Pollen grains furrowed; 1 ovule; fruit indehiscent; petals present or absent; staminodes absent; no evidence of strand of transmitting tissue from apex of ovary to apex of funicle; styles fused; distinct lateral sterile floral branches in each group of flowers. Pteranthus, Dicheranthus, Cometes.

TRIBE IV POLYCARPEAE DC., Prodr. 3: 373 (1828)

Syn: Paronychieae Reichb., Consp.: 161 (1828);

Caryophyllaceae - Polycarpeae Bentham and Hooker f., Gen. Plant. 1 : 144 (1867);

Polycarpoideae Lüders in Engler Bot. Jahrb. 40 Beibl. 91: 20 (1907).

Pollen grains furrowed; ovules 2 - ∞, occasionally reduced to 1 ovule; fruit dehiscent; petals absent or present; staminodes rarely present; evidence of strand of transmitting tissue from apex of ovary to apex of placental column; styles fused or free.

Subtribe Polycarpinae. Petals present or absent; leaves opposite; styles fused.

Polycarpaea, Drymaria, Loeflingia, Microphyes, Polycarpon, Stipulicida, Ortegia, Cerdia, Sphaerocoma, Haya.

Subtribe Spergulinae Pax & Hoffm. in Engler and Prantl, Natürl Pflanzenfam. Band 16c: 311 (1934).

Petals present; leaves in a whorl at node; styles fused or free.

Spergula, Spergularia.

Subtribe Telephiinae Ascher & Graebn., Syn. Mitteleur. Fl. Synopsis 5 (1): 854 (1919).

Syn: Telephieae Bartl., Beitr. 2: 157 (1828).

Petals present; leaves alternate.

Telephium

Subtribe Krauseolinae. Petals present; sepals arranged in a spiral; leaves opposite; styles 5, fused.

Krauseola

TRIBE V SCLERANTHEAE A. St. - Hil. in Bull. Soc. Philom.: 38 (1815).

Syn: Apetalae - Scleranthea Link, Enum. Hort. Berol. Alt 1: 417 (1821);

Caryophyllaceae - Scleranthea Fenzl in Endl. Gen. Plant. 962 (1840);

Scleranthoideae/ ....

Scleranthoideae Lüders in Engler Bot. Jahrb. 40 Beibl. 91: 4 (1907);

Alsinoideae - Scleranthеae Vierh in Österr. Bot. Zeitschr. 57: 96 (1907).

Pollen grains porate; 1 ovule; fruit indehiscent; petals absent; stamens 1 - 10 or reduced to 1 - 5 fertile stamens with 5 staminodes alternating with the sepals; evidence of strand of transmitting tissue from apex of ovary to apex of funicle; 2 free styles; stipules present as a narrow membranous margin at base of leaves. Scleranthus.

TRIBE VI HABROSIEAE Pax & Hoffmann in Engler & Prantl, Natürl Pflanzenfam. Band 16c: 335 (1934).

Pollen grains porate; 2 ovules; fruit indehiscent; petals present; staminodes absent; evidence of strand of transmitting tissue from apex of ovary to apex of placental column; 2 free styles; stipules present, totally adnate to margin of leaves at base but clearly evident. Habrosia

TRIBE I PARONYCHIEAE

This tribe contains four subtribes, 3 of which are monotypic and which may be separate tribes but have similarities with the genera in the main subtribe, Paronychiinae. The subtribe Paronychiinae, containing 6 genera, may itself be divided into smaller groups. Lochia, Gymnocarpos and Sclerocephalus are all similar, in being woody and having a distinctly elongated perigynous zone. Indeed with further specimens from a wider geographic distribution, it may be possible to combine Lochia and Gymnocarpos into a single genus.

Paronychia and Herniaria share many similarities in the arrangement of floral parts and in the usually short perigynous zone. The species in the subgenus Siphonychia of Paronychia, with their strongly perigynous flowers, links this pair of genera with the former 3 genera. The other genus included in this subtribe Illecebrum is least like the other genera but has been included here because of its general similarity to Paronychia and Herniaria.

The 3 remaining genera in this tribe have each been place in a separate subtribe because of important floral differences between them/ ....

them, and between them and the genera of the main subtribe. Chaetonychia and species of Corrigiola have furrowed pollen grains, with the porate species of Corrigiola usually having only 3 pores. This character is usually found in species in which petals are found and which are closely linked to the subfamily Alsinoideae. Most genera with petals, however, also have ovaries with strands of transmitting tissue from the apex of the ovary to the apex of the placental column or funicle. In neither of these genera are there strands evident. In Chaetonychia petals are not found but in Corrigiola petaloid structures are found, alternating with the sepals but there would appear to be derived from sterile stamens as there are no flaps of tissue in front of the base. The presence of these petaloid structures and of the 2 types of pollen grain in Corrigiola may well indicate that this genus is an intermediate between the tribes Paronychieae and Polycarpeae.

The genus Cardionema, while having multi-porate pollen grains aslo has petals, but is otherwise similar to genera in the subtribe Paronychiinae.

TRIBE II POLLICHIEAE

This tribe contains only 3 genera which are all closely linked. All the genera have flowers with a greatly elongated perigynous zone, the outer surface of which, in the fruiting stage, develops 5 prominent projections below each of the sepal lobes in the fused area in 2 of the genera. Pollichia is unusual in this subfamily in that the pedicels and peduncles become fleshy and enclose the flower in the fruiting stage.

TRIBE III PTERANTHEAE

The 3 genera in this tribe are separated from the other genera in this subfamily by the presence of elaborate sterile structures formed in each group of flowers. These structures have been interpreted as bracts, but on closer observation of the flower and bract sequence in the 3 - 7 flowered groups, it is clear that these structures do not represent elaborate bracts but are more likely to be sterile/ ....

sterile floral branches. This is most clearly demonstrated in the genus Dicheranthus, where these structures do not take the form of branches with elaborate spines, as in the other 2 genera, but a short branched structure consisting of only a few sepal-like organs.

The genera are linked to the tribe Polycarpeae by the presence of furrowed pollen grains and in some of petals and in others no structures alternating with the sepals to the last 3 subtribes of the tribe Paronychieae.

TRIBE IV POLYCARPEAE

This tribe contains those genera most closely linked to the Alsinoideae: Spergula, Spergularia, Drymaria, Telephium. Four subtribes are recognised because of the inclusion in this tribe of genera with distinct characters, which in past has resulted in these genera being placed in separate tribes. The first and largest subtribe, the Polycarpinae, contains all the genera usually included in this group but with the addition of Haya and Sphaerocoma which have previously been placed in this tribe or the Paronychieae, occasionally in the Pterantheae. In this subtribe, styles are always fused, but petals, although usually present, are totally absent in Cerdia and Ortegia.

Spergula and Spergularia are placed in a separate subtribe, Spergulinae, as the styles are usually free, the nectaries are in a different position and because of the distinct whorl of leaves at each node. Species in Drymaria, in the subtribe Polycarpinae, however, closely resemble Spergula and Spergularia. Drymaria itself being closely linked to the Alsinoideae, as although pollen grains are furrowed there are more than 3 colpi. Telephium has been placed in a monotypic subtribe , Telephiinae, as this genus has alternate leaves and fused or free styles, but in a number of respects it resembles Spergula, Spergularia and Drymaria, i.e. position of nectaries.

The last subtribe Krauseolinae contains the very distinct genus Krauseola. This genus has sepals arranged in a spiral with petals in a separate whorl and also has 5 styles which are always fused. The arrangement of petals and sepals makes this genus a very unusual member/ ....

member of the Caryophyllacae, if it indeed belongs to this family.

TRIBE V SCLERANTHEAE

Scleranthus has been placed in both this subfamily and the subfamily Alsinoideae. It has been included in the subfamily Paronychioideae here, because of its stipulate leaves, the presence of a greatly elongated perigynous zone and the one-seeded indehiscent fruit. In many ways it resembles genera in the tribe Pollichieae: porate pollen grains, presence of transmitting tissue from apex of ovary to apex of placental column/funicle, but it is separated from this group on the presence of 2 free styles rather than fused styles and the presence in some species of 10 fertile stamens. Where the stamen number is reduced to 5, the stamens between the sepals are reduced to staminodes and in this respect Scleranthus also has links with the tribe Paronychieae, especially the genera Lochia and Gymnocarpos.

TRIBE VI HABROSIEAE

As with Scleranthus, Habrosia has also been placed in the subfamily Alsinoideae, especially as in general appearance it resembles species in the genera Minuartia and Arenaria. However, stipules are present, the fruit is indehiscent and the sepals are extended by a long awn which is not found in genera in the Alsinoideae. The presence of porate pollen grains and petals links it to the subtribe Cardioneminae in the tribe Paronychieae except that the styles are free and there is no evidence in Cardionema of a strand of transmitting tissue from the apex of the ovary to the apex of placental column/funicle.

Key to Genera in the Paronychioideae

1. Leaves alternate
   2. Ovules 1; fruit indehiscent ..... Corrigiola 9.
   2. More than 1 ovule; fruit dehiscent ..... Telephium 28.
1. Leaves opposite

3./ ....

3. Ovule 1

4. Distinct free petals, or petals and stamens fused into a distinct ring

5. Petals and stamen filaments fused into a distinct ring; flowers in distinct groups of 3 with lateral spiny structures ..... Cometes 15.

5. Petals and stamen filaments free; no lateral spiny structures.

6. Styles elongated with stigmatic knob at apex; sterile lateral flowers usually present; fruit dehiscent ..... Haya 25.

6. Styles short 2- or 3-fid at apex; no sterile lateral flowers present; fruit indehiscent .. .. Cardionema 8.

4. Staminodes present, alternating with sepals

7. Sepals always 4; 2 distinct larger outer sepals and 2 smaller inner sepals; peduncle greatly elongated in fruit, flat, compressed, triangular to spathulate in shape ..... Pteranthus 13.

7. Sepals usually 5 (except in Herniaria subgenus Heterochiton); peduncle not as described above

8. Stipules reduced to a narrow membranous margin at base of leaves; 1 - 10 stamens .... Scleranthus 30.

8. Stipules always distinct, free or partially adnate to base of leaves; 1 - 5 stamens

9. Undershrub; stems woody

10. Flowers in groups of 3, central flower fertile, 2 lateral flowers ♀ sterile; often 2 pairs of sterile lateral structures ..... Dicheranthus 14.

10. Not as described; all flowers hermaphrodite; no sterile lateral branched structures

11. Bracts conspicous, brown, scarious ovate, almost concealing the flowers; staminodes reddish brown in colour ..... Lochia 3.

11./ ....

11. Bracts foliar, rarely upper bracts completely scarious, usually shorter than flowers; staminodes white in colour, resembling stamen filaments..Gymnocarpos 4.

9. Prostrate or erect herbs

12. At maturity, flowers fused into a globular head with the spiny foliar bracts; ovary adnate to wall of extended perigynous zone ..... Sclerocephalus 5.

12. Flowers not in a spiny globular head at maturity; ovary free, sessile

13. Staminodes absent; apex of sepals distinct white sac .... Chaetonychia 7.

13. Staminodes present; apex of septals not as described

14. Sepals spongy white; styles 2 - 3 sessile or fused, very small....Illecebrum 6.

14. Sepals with green or brown strip in centre not spongy; styles 2, elongated, free or fused

15. Sepals 4 - 5, hood, mucro or spine absent at apex; style usually with apical stigmatic knob (occasionally style completely covered in stigmatic papillae); stipules not conspicuous .... Herniaria 2.

15. Sepals 5, with or without apical spine, mucro or hood; 2 styles usually fused, without stigmatic knobs at apex; stipules/ ....

stipules usually conspicuous..*Paronychia* 1.

3. Ovules, 2 or more

16. Sepals totally fused into a distinct elongated perigynous zone at least 0.5 mm in length

17. Pedicels/peduncles becoming fleshy in fruiting stage; style exceeding the sepals at anthesis ..... *Pollichia* 10.

17. Pedicels/peduncles not becoming fleshy; style shorter than sepals

18. Prostrate herb; perigynous zone greater than 0.5 mm in length at anthesis; small membranous flap stretched in front of base of petals .... *Achyronychia* 11.

18. Erect herb; perigynous zone only 0.5 mm in length at anthesis; distinct free red flap of tissue in front of base of petal ..... *Scopulophila* 12.

16. Sepals fused at base only into a short perigynous zone

19. Petals absent

20. Style, single, apex bi-lobed; 1 - 2 stamens ..... *Cerdia* 23.

20. Style, single, apex swollen, slightly tri-fid; 3 stamens ..... *Ortegia* 22.

19. Petals present

21. Styles 5, free or fused

22. Sepals, about 8, arranged in a spiral; petals, 5 - 8, triangular in shape; styles 5, fused.....*Krauseola* 29.

22. Sepals and petals 5, arranged in 2 alternating whorls, not spirally arranged; petals ovate to oblanceolate; styles 5, free, rarely fused ..... *Spergula* 26.

21. Styles 2 - 3, free or fused

23./ ....

23. Styles 2, free; stipules totally adnate to leaves Habrosia 31.

23. Styles 2 - 3, fused, or styles 3, free; stipules usually free, if adnate to leaves then not totally so

24. Woody undershrub; 2 fused styles ..... Sphaerocoma 24.

24. Herbs; usually 3 fused style or 3 free styles

25. Some or all of sepals with lateral membrous awns .... Loeflingia 18.

25. Sepals without lateral awns

26. Petals deeply bilobed, often with elabroate lateral structures ..... Drymaria 17.

26. Petals entire or emarginate

27. Sepals hooded

28. Apex of sepals with short spine; styles 3, fused; antipetalous stamens absent ..... Polycarpon 20.

28. Apex of sepals without spine; styles 3, usually free; antipetalous stamens usually present .... Spergularia 27.

27. Sepals not hooded.

29. Base of petals with serrated margins; petals, stamens and ovary raised above level of insertion of sepals on a solid, fleshy androgynophore..... ..... Stipulicidia 21.

29. Not as above

30. Apex of style with a stigmatic knob; stipules always present ..... Polycarpaea 16.

30. Apex of single fused style trifid; stipules present or absent ..... Microphyes 19.

4.4 Description of Genera/ ....

4.4 Description of Genera

The genera are arranged according to the tribes and subtribes described above. For each genus a general description is given with the synonyms. In most cases the type species (but not usually the type specimen) has been described and where the genus is larger more species have been described. If the genus has been separated into subgenera and sections, keys to the subgenera are given and a species belonging to each subgenus and sometimes each section has also been described. For each species the synonyms and the distribution has been indicated and the specimen on which the floral morphology is based has been cited.

TRIBE I PARONYCHIOIDEAE
Subtribe Paronychiinae

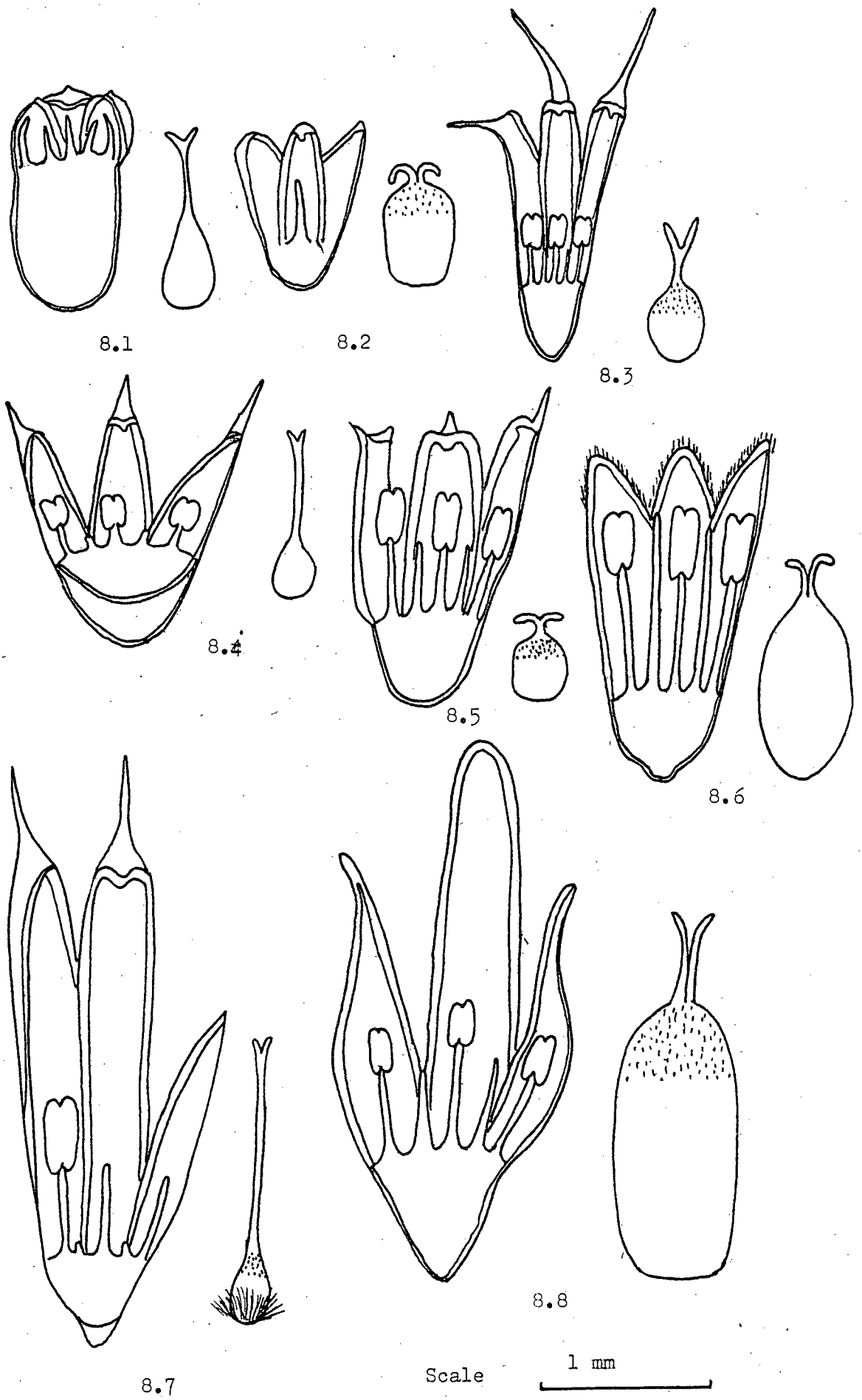
1. PARONYCHIA [Tournef.] Miller, Gardn. Dict. Ed. 4 vol. 3 (1754). Syn: Anychia Michx., Fl. Bor. Am. 1: 112 (1803); Buinalis Rafin., New Fl. Am. 4: 40 (1838); Plottzia Rn. in Lindl., Introd. Nat. Syst. Ed. 2: 441 (1836); Argyrocoma Rafin, New Fl. Am. 41: 41 (1838); Plagidia Rafin., New Fl. Am. 4: 42 (1838); Siphonychia Torrey & Gray, Fl. N. Am. 1: 173 (1838); Forcipella Small in Bull. Torrey. Club 25: 150 (1898); Gibbesia Small in Bull. Torrey. Club 25: 621 (1898); Anychiastrum Small, Fl. S.E. US: 400 (1903); Odontonychia Small, Fl. S.E. US: 401 (1903); Nyachia Small in Torreya 25: 11 (1925); Gastronychia Small, Fl. S.E. U.S.: 480 (1933). (Fig. 8)
Type Species. P, argentea Lam.
Other Species c. 106 species.

Perennial or occasionally annual herbs, erect or prostrate, up to 60 cm. Stems glabrous or pubescent, usually much branched, often becoming woody at base. Leaves opposite, linear to lanceolate, ovate, oblong or spathulate, mucronate or obtuse, glabrous or pubescent, sessile, subsessile or with distinct petiole. Stipules usually conspicuous, occasionally much shorter than leaves, membranous ovate or triangular. Inflorescence of terminal or axillary clusters, occasionally lax terminal cymes. Bracts conspicuous, membranous or foliar. Flowers sessile to subsessile. Sepals 5, membranous margins, hooded, mucronate with short spine or obtuse. Petals/ ....

FIGURE 8

8.1 L.S. of flower of Paronychia americana (Nutt.) Fenzl
8.2 L.S. of flower of P. canadensis (L.) Wood
8.3 L.S. of flower of P. setacea Torr. & Gray
8.4 L.S. of flower of P. herniarioides (Michx.) Nutt.
8.5 L.S. of flower of P. argentea Lam.
8.6 L.S. of flower of P. kapela (Hacq.) Kermer
8.7 L.S. of flower of P. argyocoma (Michx.) Nutt.
8.8 L.S. of flower of P. capitata (L.) Lam.

FIGURE 8



Petals lacking. Stamens 5, antisepalous; staminodes 5 alternisepalous. Ovary ovate often with small projections at apex; 1 ovule; no evidence of strand of transmitting tissue from apex of ovary to apex of funicle; styles 2, usually fused at base, occasionally single elongated style with bi-fid apex. Fruit indehiscent.
Distribution: W. & S. Europe, N. Africa, Caucasia, Iran, Turkey, Syria, Jordan, Palestine, Cyprus, Sardinia, N. & S. America.

Species examined. This work follows the subgenera, sections and subsections of Chaudhri (1968).

Key to Subgenera

1. Greatly elongated perigynous zone; style elongated, apex bi-fid ..... 1. Subgenus Siphonychia.
1. Short perigynous zone; styles free or almost so, or styles fused but usually for not greater than half length
   2. Sepals with distinct mucro or spine, hooded .... 2. Subgenus Paronychia.
   2. Sepals without distinct mucro or spine, not hooded .... 3. Subgenus Anoplonychia.

1. Subgenus Siphonychia Chaudhri, A Revision of the Paronychiinae: 82 (1968).

Syn: Siphonychia Torrey & Gray, Fl. N. A,. 1: 173 (1838); Buinalis Rafin., New Fl. Am. 4: (1838); Forcipella Small in Bull, Torrey Club 25: 150 (1898); Gibbesia Small in Bull. Torrey Club 26: 621 (1898); Odontonychia Small, Fl. S. E. U. S.: 40 (1903)
Type Species: P. americana (Nutt.) Fenzl ex Walp.
Other Species: P. patula Shinners, P. erecta (Chapman) Shinners, P. rugeli Shuttleworth ex Chapman

First combined with Paronychia by L. H. Shinners (1962), it is still often considered a separate genus. Apart from the lack of conspicuous bracts, the species in this subgenus have a distinct elongated perigynous zone and petaloid sepal lobes. The elongated style with bi-fid apex is also unusual in the genus Paronychia, and apart from species in this subgenus is found only in the monotypic series Longistylae and Argyrocomae in the subsection Paronychia, section Paronychia subgenus Paronychia.

Paronychia americana (Nutt.) Fenzl ex Walp., Repert. Bot. Syst.: 262 (1842)

Syn: Herniaria americana Nutt. in Am. J. Sci. 5: 291 (1822); Siphonychia americana (Nutt.) Torrey & Gray, Fl. N. Am. 1: 173 (1838); S. urceolata Shuttl. in Litt. ined.; Paronychia uroceolata Shuttl. ex Chapman, Fl. S. U. S.: 47 (1860); Buinalis americana (Nutt.) Kuntze, Rev. Gen. 2: 534 (1891); Siphonychia pauciflora Small, Fl. S. E. U.S.: 402: (1903).

Annual herb, erect, up to 40 cm. Stem filiform, much branched, often purple in colour, often covered in short hairs. Leaves opposite, linear, 7 - 10 mm, subsessile, slightly fleshy, pubescent. Stipules 1 pair each leaf, ovate to lanceolate, c. 5 mm. Flowers forming distinct glomerula at end of small lateral branches. Bracts foliar, but reduced to membranous structures (stipules) only in dense glomerules, not inequal lobes, outer surface of perigynous zone covered in hooked spines, lobes with narrow membranous margins, wider at apex, slightly hooded, small mucro at apex. Stamens, 5 antisepalous; 5 staminodes alternating with sepals, shorter than fertile stamens; both fused to perigynous zone at some level. Ovary ovate; 1 ovule; style longated, extending beyond level of sepals, apex bifid. (Fig.81)

Distribution: Georgia, Florida.

A. H. Curtis 5546, Florida.

2. Subgenus Paronychia

Syn: Anychia Michx., Fl. Bor. Am. 1: 112 (1803); Plagidia Rafin., New Fl. Am. 4: 49 (1838); Anychiastrum Small, Fl. S. E. U. S.: 400 (1903); Nyachia Small in Torreya 25: 11 (1925).

Type Species: P. argentea Lam.

Other Species: 56 species

Section Nyachia (Small) Pax & Hoffmann in Engler & Prantl, Natürl Pflanzenfam. 16c: 300 (1934).

P.pulvinata Small

Section Paronychia

1. Subsection Fasciculatae Chaudhri, l.c.: 85 (1968).

P. fasciculata Chaudhri, P. camphorosmoides Camb.

2./ ....

2. Subsection Polygonoideae (D.C.) Chaudhri, l.c.: 85 (1968).
P. suffruticosa (L.) D.C.

3. Subsection Anychia (Michx.) Chaudhri, l.c.: 85 (1968).
Syn: Anychia Michx., Fl. Bor. Am. 1: 112 (1803); Argyrocoma Rafin., New Fl. Am. 14: 41 (1838); Plagidia (Rafin., l.c.: 42 (1838); Anychiastrum Small, Fl. S. E. U. S.:400 (1903).
P. canadensis (L.) Wood, P. fastigata (Raf.) Fernald, P. montana (Smoll) Pax & Hoffmann, P. beldwinii Fenzl

Paronychia canadensis (L.) Wood, Class Book 262 (1861).
Syn: Queria canadensis L., Sp. Pl. Ed. 1: 90 (1753); Q. dichotoma Moench, Meth.: 351 (1794); Anychia dichotoma Michx., Fl. Bor. Am. 1: 113 (1803); Anychia canadensis (L.) Ell., A Sketch Bot. S. Carolina & Georgia 1: 307 (1817); Queria capillacea Nuttl., Gen. N. Am. 1: 159 (1818); Anychia capillacea (Nutt.) DC., Prodr. 3: 369 (1828); A. filiformis Rafin ex Briton in Bull. Torrey Club 13: 187 (1886).

Annual herb, prostrate to erect up to 30 cm. Stems glabrous filiform, much branched above. Leaves opposite, ovate to oblong, up to 2 cm, obtuse, glabrous, distinctly petiolate. Stipules triangular, membranous, c. 5 mm, 1 pair each leaf. Inflorescence lax, terminal cymes. Flowers subsessile. Bracts membranous similar to the stipules, shorter than flowers. Sepals 5, with narrow membranous margins, slightly hooded, small apical mucro, glabrous. Stamens reduced in number, usually 2 antisepalous fertile stamens; staminodes absent. Ovary sessile, apex covered in a number of small projections; 1 ovule; 2 styles hardly fused at base. (Fig.8.2)
Distribution: N. America.

A. E. Radford 45030 N. Carolina, A. A. Heller & E. G. Halback Oct. 1892 S. Pennsylvania.

4. Subsection Chartaceifolia Chaudhri, l.c.: 86 (1968).
P. setacea Torrey & Gray, P. lindheimeri Engelm., P. ehorizanthoides Small, P. monticola Cory, P. jamesii Torrey & Gray, P. depressa Nutt., P. virginica Sprengel, P. sessiliflora Nutt., P. wilkinsonii S. Watson, P. albomarginata Core.

Paronychia setacea Torr. & Gray, Fl. N. Am. 1: 170 (1838).

Small annual herb, erect, up to 8 cm. Stems dichotomously branching above, purple, covered in small adpressed hairs, leaves opposite, linear, c. 1 cm, usually covered in short hairs, apex with a short mucro. Stipules much shorter than leaves, c. 4 mm, 1 pair each leaf, lanceolate. Inflorescence dense or lax terminal cymes. Bracts foliar with a distinct mucro, shorter than flowers. Flowers subsessile. Sepals 5, outer surface pubescent, long hairs at base, fleshy, distinct membranous margins, hooded, with long spine at apex. Stamens 5, antisepalous; 5 staminodes alternating with sepals, about equal in length to fertile stamens; stamens and staminodes adnate at base to form a membranous ring, ring attached to sepals, fused to apex of fleshy perigynous zone. Ovary ovoid, covered in small projections at apex; 1 ovule; styles fused for less than $\frac{1}{2}$ length. (Fig. 8.3)

Distribution: Texas.

Drummond 33 Texas.

5. Subsection Paronychia

Series I Longistylae Chaudhri, l.c.: 88 (1968).

P. herniarioides (Michx.) Nutt.

Paronychia herniarioides (Michx.) Nutt., Gen. Am. 1: 159 (1818). Syn: Anychia herniarioides Michx., F. Bor. Am. 1: 113 (1803); Anychiastrum herniarioides (Michx.) Small, Fl. S. E. U. S.:401 (1903); Plagidia herniarioides (Michx.) Niewl, in Amer. Mid. Nat. 3: 154 (1913); Gastronychia herniarioides (Michx.) Small, Man. S. E. Fl.: 480 (1933).

Annual herb, erect to prostrate, often mat forming, up to 13 cm. Stems much branched at base, covered in small, white adpressed hairs. Leaves opposite, oblanceolate to oblong up to 7 mm, the lower leaves longer than the upper up to 1.5 cm, mucronate. Stipules ovate to lanceolate, membranous, c. 2mm, 1 pair each leaf. Flowers in lax terminal cymes. Bracts foliar, "stipules" not enlarging. Flowers sessile. Sepals 5, linear, very narrow membranous margin, slightly hooded, long spine at apex. Stamens 5, antisepalous; 5 staminodes alternating with sepals, c. $\frac{1}{4}$ length of fertile stamens. Stamens and/ ....

and staminodes attached to fleshy perigynous zone at same level. Ovary ovate, styles 2, fused for more than ½ length, extending beyond or to level of sepals. (Fig8.4)
Distribution: Georgia, Florida.

J. Bozeman 9501, Georgia, U.S.A.

Series II Corriculatae Chaudhri, l.c.: 88 (1968).
P. drummondii Torrey & Gray, P. jonesii M. C. Johnston.
Series III Paniculatae Chaudhri, l.c.: 89 (1968)
P. Canariensis (L.f.) Juss.
Series IV Villosae Chaudhri, l.c.: 89 (1968).
P. microphylla Philippi.
Series V Plantorae Chaudhri, l.c.: 89 (1968).
P. brasiliana D C., P. franciscana Eastwood.
Series VI Echinatae Chaudhri, l.c.: 90 (1968).
P. echinulata Chater, P. rouyana Coincy.
Series VII Argyrocomae Chaudhri, l.c.: 90 (1968).
P. argyrocoma (Michx.) Nutt.

Paronychia argyrocoma (Michx.) Nutt., Gen. Am. 1: 160 (1818). Syn: Anychia argyrocoma Michx., Fl. Bor. Am. 1: 114 (1803); Argyrocoma imbricata Rafin., New Fl. Am. 4: 41 (1838).

Perennial herb, prostrate to erect, often forming dense mat, up to 16 cm. Stems much branched, covered in short, silky hairs. Leaves opposite lanceolate to linear, up to 2 cm, mucronate, covered in short, white adpressed hairs. Stipules membranous, c. 1 cm, 1 pair each node, ovate to lanceolate, acute. Flowers in dense terminal cymes. Bracts foliar with large membranous ovate to lanceolate stipules completely obscuring the flowers. Sepals 5, lobes equal or unequal in length, fleshy with narrow membranous margin, hooded, apex with long spine, outer surface covered in white adpressed hairs. Stamens 5, antisepalous; 5 staminodes alternating with sepals very small, c. 0.2 mm. Stamens and staminodes attached to perigynous zone at about the same level as sepals. Ovary ovoid, base covered in long white hairs, apex with short projections; styles 2, fused for more than ½ length, shorter than sepals. (Fig. 8.7)
Distribution: S. Appalachian, Tenesse, Carolina, New England, Virginia.

A. Gray, Tenessee, U.S.A.

Series VIII Paronychia

29 species.

Paronychia argentea Lam., Fl. Fr. 3: 230 (1778).

Syn: Illecebrum paronychia L., Sp. Pl. Ed. 1: 206 (1753); Illecebrum argenteum Pour. in Memb. Acad. Toul. 3: 321 (1788); Paronychia nitida Gartn., Fruct. Sem. Pl. 2: 218 t. 128 (1791); P. glomerata Moench, Meth.: 315 (1794); Illecebrum italicum Vill. in Schrader, J. für die Bot. 1801: 411 (1801); Paronychia hispanica DC. in Pour., Encycl. 5: 24 (1804); Illecebrum mauritaricum Willd. ex Schult. in Roem. & Schult., Syst. Veg. 5: 516 (1819); Paronychia italica (Vill.) Schult. in Roem. & Schult. Syst. Veg. 5: 518 (1819); Chaetonychia paronychia Samp., Lista Herb. Portug.: 78 (1913); Plottizia paronychia Samp., App. Lista Herb. Portug.8 (1914); Paronychia paronychia (L.) Graebn. in Ascher. & Graebn., Mittleur Fl. Syn. 5 (1): 896 (1919); P. mauritanica (Willd. ex Schult.) Rothm. & Silva in Agron. Lusit. 1 (1): 382 (1939).

Perennial or occasionally biennial herb, erect to prostrate, up to 60 cm. Stem much branched at base, sometimes woody, covered in short, white hairs. Leaves opposite, subsessile, oblong to oblanceolate, 4 - 15 mm, short mucro, margins ciliate otherwise glabrous or covered in short hairs. Stipules membranous 1 pair each node, usually shorter than the leaves but occasionally equal in length to lower leaves. Flowers sessile, in dense terminal or axillary cymes, glomerules distinct c. 7 - flowered. Bracts foliar; stipules much enlarged, ovate up to 6 mm, completely concealing the flowers. Sepals 5, fleshy with narrow membranous margin, hooded, short spine at apex, outer surface pubescent, occasionally glabrous. Stamens 5, antisepalous; 5 staminodes alternating with sepals, brown tips, about equal in length to fertile stamens. Ovary sessile, apex covered in short projections; styles 2, fused for less than $\frac{1}{2}$ length, lobes bivarcate. (Fig. 8.5)

Distribution: Europe, N. Africa, Turkey, Syria, Jordan, Palestine, Cyprus.

Bianco 168, Spain.

3. Subgenus Anoplonychia (Fenzl) Chaudhri, l.c.: 91 (1968).

Type Species: P. Kapela (Hacq.) Kemer.

Other Species: 48 species.

Section Anoplonychia.

Subsection Anoplonychia.

33 species.

Paronychia kapela (Hacq.) Kemer in Ost. Bot. Zeit. 19: 367 (1869). Syn: Illecebrum Kapela Hacq., Pl. Alp. Cam.: 8, t. 2, f. 1 (1782); I. lugdunense Vill, in Schrader, J. für die Bot. 1801: 412 t. 4 (1801); Paronychia capitata DC. in Poir., Encycl. 5: 25 (1804); P. serpullifdia senus Mert ex Koch in Röhl. Deut. Fl. Ed. 3: 280 (1826); Illecebrum serpyllifolium sensu Host., Fl. Austr. 1: 311 (1827); Paronychia imbricata Reich., Fl. Germ. Excurs. 564 (1832); P. Kochiana Boiss., Diagn. Ser. 1 (10): 13 (1849) Pro pate.

Perennial herb, small, forming dense mat up to 25 cm. Stems much branched at base usually woody at base, younger stems covered in short hairs. Leaves opposite, oblong to elliptical - obovate, 4 mm, glabrous except for hairs on margins, sessile to subsessile. Stipules membranous, lanceolate, equal to or just shorter than leaves, 1 pair each leaf, usually connate at base to give the appearance of 1 pair each node with a deeply bifid apex. Flowers in dense glomerules, terminal on lateral branches. Bracts ovate to ovoid, membranous, completely concealing the flowers, up to 5 mm. Sepals 5, equal length, fleshy with narrow membranous margins, hooded, no awn or mucro, outer surface covered in short hairs, especially towards the apex. Stamens 5, antipetalous; 5 staminodes alternating with sepals, longer than fertile stamens. Stamens and staminodes connate at base to form membranous area attached to base of sepals. Small perigynous zone, sepals attached by centre, but more or less distinct, receptacle involved in lower part of perigynous zone. Ovary sessile, glabrous; styles 2, more or less free. (Fig.8.6)

Distribution: Mediterranean, Morocco.

E. Reverchon & A. Derbez 257, France.

Subsection Quadristipulatae Chaudhri, l.c.: 94 (1968).

P. Boissiei Rouy, P. caespitosa Stapf, P. mesopotamica Chaudhri.

These 2 subsections in the section Anoplonychia probably should be combined. They have been separated because it was thought that the subsection Anoplonychia had only 2 stipules at each node and that subsection/ ....

subsection Quadristipulatae had 4 stipules per node. It would appear that in the former subsection there are 4 stipules, but because they are usually connate at the base, appear as 2. Also in the other 2 subgenera there are a number of sections in which there appear to be both 2 stipules and 4 stipules each node.

Section Heterosepalae Chaudhri, l.c.: 94 (1968).
Subsection Heterosepalae
11 species

Paronychia capitata (L.) Lam., Fl. Fr. 3: 229 (1778).
Syn: Illecebrum capitatum L., Sp. Pl. Ed. 1: 207 (1753); I. herniarioides Pour. in Mem. Acad. Toul. 3: 321 (1788); Paronychia rigida Moench, Meth.: 315 (1794); P. nivea DC. in Pour. Encycl. 5: 25 (1804); Illecebrum niveum (DC.) Pers., Syn: Pl.1: 261 (1805).

Perennial herb, prostrate to sub-erect, up to 10 cm, often mat forming. Stems covered in short hairs. Leaves opposite, lanceolate to oblinear, acute, sessile, c. 4 mm, usually pubescent on both surfaces, margins ciliate. Stipules 1 pair each leaf, membranous, lanceolate, equal to or just shorter than glomerules of about 7 flowers, terminal. Bracts entire membranous ovate to orbiculate, totally concealing the flowers. Sepals 5, unequal, 2 outer larger than 2 inner, fleshy with narrow membranous margins, outer surface densely covered in short hairs. Stamens 5, antisepalous; 5 staminodes alternating with sepals; stamens and staminodes fused at same level to fleshy perigynous zone. Ovary sessile, apex covered in short projections; 2 styles free or occasionally slightly fused at base. (Fig. 8.9)
Distribution: Mediterranean.

E. Reverchon 1163, Spain.

Subsection Rectisepalae Chaudhri, l,c,: 95 (1968).
P. somaliensis Baker.

There again seems to be little reason to separate these 2 subsections; the leaf and sepal characters do not hold in all species.

2. HERNIARIA (Bauh.) L., Gen. Pl. Ed. 1: 34 (1737), Spec. Pl. Ed. 1: 218 (1753).

Syn:/ ....

Syn: Heterochiton Graebn. & Mattf. in Ascher & Graeb., Syn. Mittleur. Fl. 5 (1): 870 (1919).

Type Species: H. glabra L.

Other Species: 47 species

Perennial or annual herbs, up to 25 cm. Stems erect to prostrate, much branched, becoming woody at base, usually densely covered in short hairs, occasionally almost glabrous. Leaves opposite, or in fascicules, due to condensing of lateral branches, ovate to oblanceolate, often fleshy, glabrous or covered in short hairs, margins occasionally ciliate, sessile to shortly petiolate, leaves 2 - 7 mm. Stipules membranous, triangular with ciliate margins, occasionally purple/brown in colour (Subgenus Heterochiton), shorter than leaves, c. 1 mm, 1 pair each leaf. Flowers in dense glomerules in axils of leaves. Bracts membranous, triangular to ovate with ciliate margins, short than or equal in length to flowers. Flowers subsessile. Usually 5 sepals, rarely 4 (Subgenus Heterochiton and Subgenus Herniaria section Paronychiella), central green area with membranous margins, occasionally slightly hooded, apex usually with short apine, pubescent or glabrous on outer surface. Petals absent. Stamens 5 or 4 rarely 2 antisepalous, much shorter than sepals; 5 or 4 staminodes alternating with sepals, rarely becoming petaloid. Ovary ovoid, sessile, apex often covered in short projections; 1 ovule with no evidence of strand of transmitting tissue from apex of ovary to apex of placental column/funicle, some evidence of remains of 2 septal ridges on ovary wall; styles 2, fused or free, usually with a distinct knob of stigmatic tissue at apex. Fruit indehiscent, calyx persistent.

Distribution: Europe, N. Africa, Canary and Madeira Islands, Russia, Iran, Iraq, Turkey, Syria, Jordan, Lebanon, Arabia, Afghanistan, India, Pakistan, S. Africa.

Species examined. Two subgenera recognised in this genus, following the treatment of the genus by Chaudhri (1968).

Key to Subgenera

1. Sepals 5, rarely 4; bracts membranous never purple/brown in colour, staminodes filiform ..... 1 Subgenus Herniaria.

1./ ....

1. Sepals always 4; bracts membranous usually always purple/brown in colour; staminodes usually petaloid .... 2 Subgenus Heterochiton.

1. Subgenus Herniaria

Section Herniaria

37 species

Herniaria glabra L., Sp. Pl. Ed. 1: 218 (1753)

Syn: Herniaria vulgaris Hill, Veg. Syst. 26: 9 (1775); H. vulgaris Sprenglel, Syst. Veg. 1: 929 (1825) pro parte; H. rotundifolia Vis. in Flora 12, Erganzungsbl. 1: 9 (1829); H. germanica Döll var. glabra (L.) Döll Rhein. Fl.: 619 (1843); H. arenaria O. Kuntze var. glabra (L.) O. Kuntze, Taschenfl. Lepzig: 224 (1867); H. ceretanica Sennen in Bol. Soc. Arag. 15: 263 (1916); H. ceretana Sennen in Bol. Soc. Iber. 27: 68 (1928); H. graebheri Hermann in Fedde's Repert. 42: 215 (1937).

Perennial, occasionally annual herb up to 15 cm. Stem erect to prostrate, much branched, becoming woody at base; sparsely covered in short hairs to glabrous. Leaves opposite ovate to elliptical, subsessile to distinctly petiolate, fleshy, glabrous, 2 - 6 mm. Stipules membranous, triangular with ciliate margins, much shorter than leaves, c. 1 mm, 1 pair each leaf. Flowers ciliate margins, c. 1 mm, triangular to ovate. Flowers subsessile, up to 0. 5 mm. Sepals 5, more or less equal in length, central green area with large membranous margins, pubescent on outer surface in region of perigynous zone. Stamens 5, antisepalous; 5 staminodes alternating with sepals, filiform.. Ovary ovate, sessile, apex covered in short projections; styles 2, free with a stigmatic knob at apex distinctly red/brown in colour. (Fig. 9.1)

Distribution: Europe, N. Africa, Russia, Iran, Iraq, Turkey, Syria.

P. Auquier 3158.

Section Paronychiella (Williams) emend. F. Hermann in Fedde's Repert. 42: 205 (1937)

H. polyama J. Gay, H. nigrimontium F. Hermann, H. degenii (Herm.) Chaudhri.

Herniaria polygama J. Gay in Duch., Rev. Bot. 2: 371 (1847).
Syn: H. odorata Andrz in Hohenack., Pl. Exs. (1839).

Small annual herb, up to 20 cm. Stems suberect to prostrate, sparsely covered in short hairs, internodes distinct up to 8 mm. Leaves opposite, ovate, narrowed at base, 4 - 7 mm, glabrous, margins occasionally ciliate. Stipules membranous, triangular, margins ciliate, shorter than leaves c. 0.7 mm, 1 pair each leaf. Flowers in dense glomerules in axils of leaves of lateral branches. Bracts membranous with ciliate margins, triangular. Flowers subsessile. Sepals 4, central green area with narrow membranous margin, apex with short spine. Stamens 4, antisepalous; 4 staminodes, filiform alternating with sepals. Ovary sessile, ovate; styles 2, fused for more than $\frac{1}{2}$ length, apex with distinct stigmatic knob, papillae red/brown in colour. (Fig. 9.2)
Distribution: S. Russia.

N. Zinger 3638, Ukraine.

Subgenus Heterochiton (Graebn. & Mattf.) F. Hermann in Fedde's Repert. 42: 205 (1937).
Syn: Heterochiton Graebn. & Mattf. in Ascher. & Graebn., Syn Mittleur. Fl. 5 (1): 870 (1919).
H. Fontanesii J. Gay, H. mauritanica Murb., H. hemistenon J. Gay, H. arabica Hand.-Mazz., H. ericifolia Tourns, H. fruticosa L., H. canariensis Chaudhri, H. pujosii Sauv. & Vindt.

Herniaria fontanesii J. Gay in Duch. Rev. Bot. 2: 371 (1847).
Syn: Heterochiton fontanesii (J. Gay) Graebn. & Mattf. in Asch. & Graebn. Syn. Mittleur. Fl. 5 (1): 870 (1919); Herniaria teknensis Sauv. in Bull. Soc. Sci. Nat. Maroc. 25 - 27: 367 (1949).

Perennial herb, prostrate to suberect, up to 10 cm. Stem becoming woody towards base, densely covered in short hairs to almost glabrous. Leaves opposite, often in fascicules, ovate to oblanceolate, 2 - 5 mm, fleshy covered in short hairs, densely or sparsely. Stipules, 1 pair each node, distinctly purple/brown in colour up to 1.5 mm with a narrow membranous ciliate margins, triangular in shape. Flowers in dense glomerules in axils of leaves. Bracts similar to stipules but smaller c. 0.5 mm. Sepals distinctly in 2 pairs, 2 inner sepals much shorter than the 2 outer sepals, all sepals covered/ ....

covered in short hairs, sometime papillate, apex slightly hooded. Outer surface of perigynous zone covered in hairs, often hooked hairs. Stamens 4, antisepalous; 4 staminodes, alternating with the sepals, triangular, petaloid with distinct, red tips. Stamens and staminodes fused at base to give a membranous ring which is then fused to perigynous zone, ring sometimes breaking down so that there appears to be flaps of tissue in front of staminodes. Ovary ovate, sessile; styles 2, distinctly brown/red in colour covered with stigmatic papillae. (Fig.903)

Distribution: Spain, Sicily, Canary Is., N. Africa.

B. Balansa 874, Algeria

3. LOCHIA Balf. f. in Proc. Roy. Soc. Edinb. 12: 409 (1884).

Type species: L. bracteata Balf. f.

Monotypic Genus.

Perennial woody undershrub, erect, up to 40 cm. Stems with distinct swollen nodes, glabrous or sparsely covered in short hairs. Leaves opposite, or occasionally in fascicles due to condensation of lateral branches, sessile to shortly petiolate, linear to lanceolate or ovate to oblanceolate, up to 1 cm, fleshy, glabrous, with short spine at apex. Stipules triangular, membranous, brown in colour up to 2 mm. Flowers in compact, terminal, dichasial cymes, shortly pedunculate. Bracts brown membranous, ovate, c. 3 mm. Flowers subsessile to sessile. Sepals 5, equal in length with narrow membranous margins, apex hooded with short spine. Petals 0. Stamens 5, antisepalous; 5 staminodes alternating with sepals, red/brown in colour., c. $\frac{3}{4}$ length of stamen filaments. Stamens and staminodes fused at base to form a membranous ring which is fused to sepals at the apex of the greatly elongated perigynous zone, below membranous ring, fleshy area extends to base of zone, the apex of which often breaks up into brown flaps. Ovary slightly fused to perigynous zone at base, 1 ovule; greatly elongated style with trifid apex; usually twisted; no evidence of strand of transmitting tissue from apex of ovary to apex of funicle/placental column. Calyx persistent in fruit.

Distribution: Socotra, Abd al Kuri Is.

Species/ ....

Species examined. Lochia bracteata Balf. f. subsp. abdulkusiana Chaudhri (Fig. 10 I).

Ogilvie-Grant - Forbes 1898 - 99, Socotra.

4. GYMNOCARPOS Forskal, Fl. Aegypt.: 65 (1775).

Syn: Gymnocarpus Juss., Gen. Pl.: 314 (1789); Gymnocarpum DC., Prod. 3: 369 (1828); Gymnocarpon Pers., Syn. Pl. 1: 262 (1805).

Type Species: G. decander (decandrum) Forskel.

Other Species: G. przewalskii Bunge ex Maxim.

Perennial woody undershrub up to 50 cm. Stems often white to grey in colour, young stems may be furrowed, often powdery, nodes swollen. Leaves opposite or in fascicles due to condensed lateral branches, linear, 0.4 - 1.6 mm, fleshy, sessile to subsessile, with short spine at apex. Stipules small, inconspicuous, 1 pair each leaf, triangular to ovate, membranous, up to 1.5 mm. Flowers in terminal or axillary glomerules shortly pedunculate. Bracts either membranous ovate equal to, or exceeding the flowers or foliar with stipules fused to base of leaf short than flowers, may be reddish. Flowers sessile. Sepals 5, equal with membranous margins, apex hooded with short spine. Petals 0. Stamens 5, antisepalous; 5 staminodes alternating with sepals. Stamens and staminodes fused at base into a short membranous ring fused to sepals of apex of the greatly elongated perigynous zone, below membranous ring of fleshy area extending to base of perigynous zone, the apex of which often breaks to form brown flaps. Five antisepalous stamen filaments adnate to centre of sepal just above the fusion of stamens to staminodes. Ovary sessile, slightly adnate at base to walls of perigynous zone; 1 ovule; greatly elongated style, twisted, trifid apex; no evidence of strand of transmitting tissue from apex of ovary to apex of funicle / placental column. Calyx persistent in fruit.

Distribution: N. Africa, Canary Is., Iran, Syria, Jordan, Palestine, Arabia, Afghanistan, W. Pakistan, N. W. China, Mongolia.

Gymnocarpos decander (decandrum) Forsk., Fl. Aegypt. Arab.: 65 (1775).

Syn: Trianthema fruticosa Vahl., Symb. 1: 32 (1790); Gymnocarpon fruticosum (Vahl.) Pers., Syn. 1: 262 (1805); Gymnocarpos salsoides Webb ex Christ in Bot. Jb. 9: 104 (1888); Paronychia decandra (Forskal) Rohur. & K. Urmi in Bot. Jahrb. 96: 407 (1975).

As/ ....

FIGURE 9

9.1 L.S. of flower of Herniaria glabra L.
9.2 L.S. of flower of H. polygama J. Gay
9.3 L.S. of flower of H. fontanesii J. Gay

FIGURE 10

10.1 L.S. of flower of Lochia bracteata Balf. f.
10.2 L.S. of flower of Gymnocarpos decander Forsk.

FIGURE 9

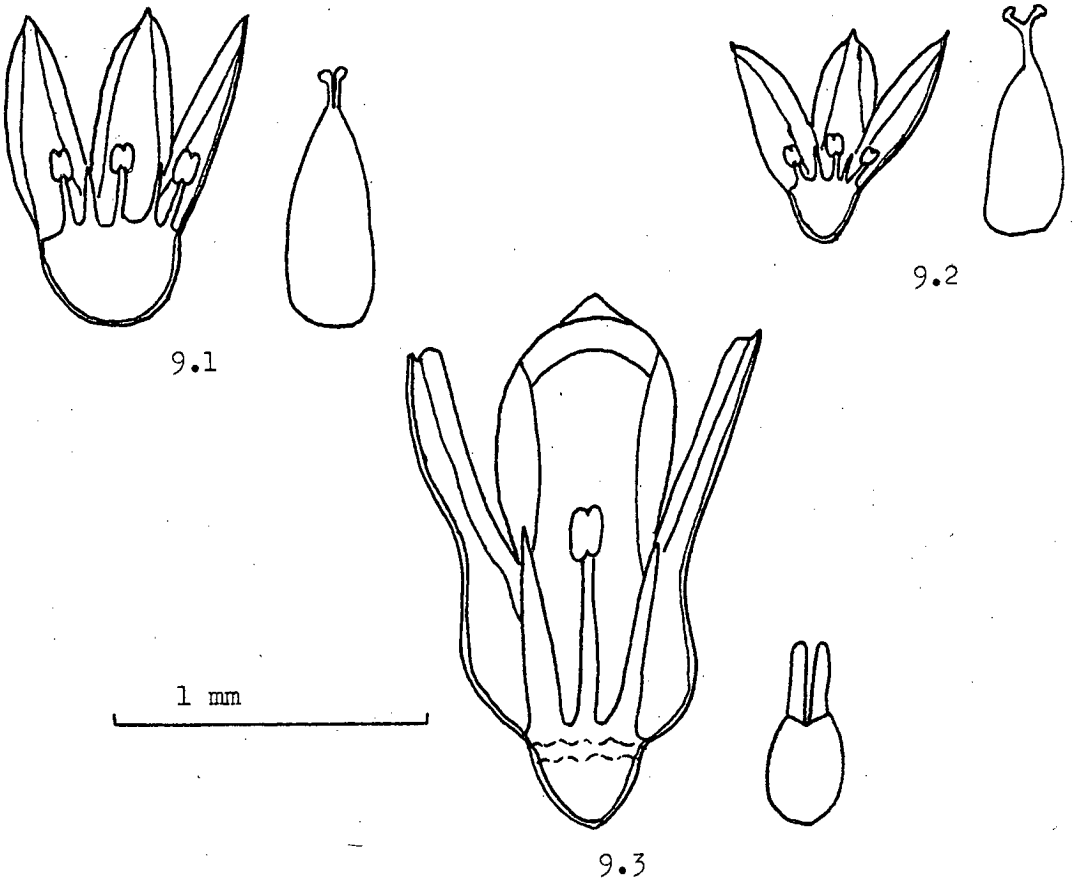
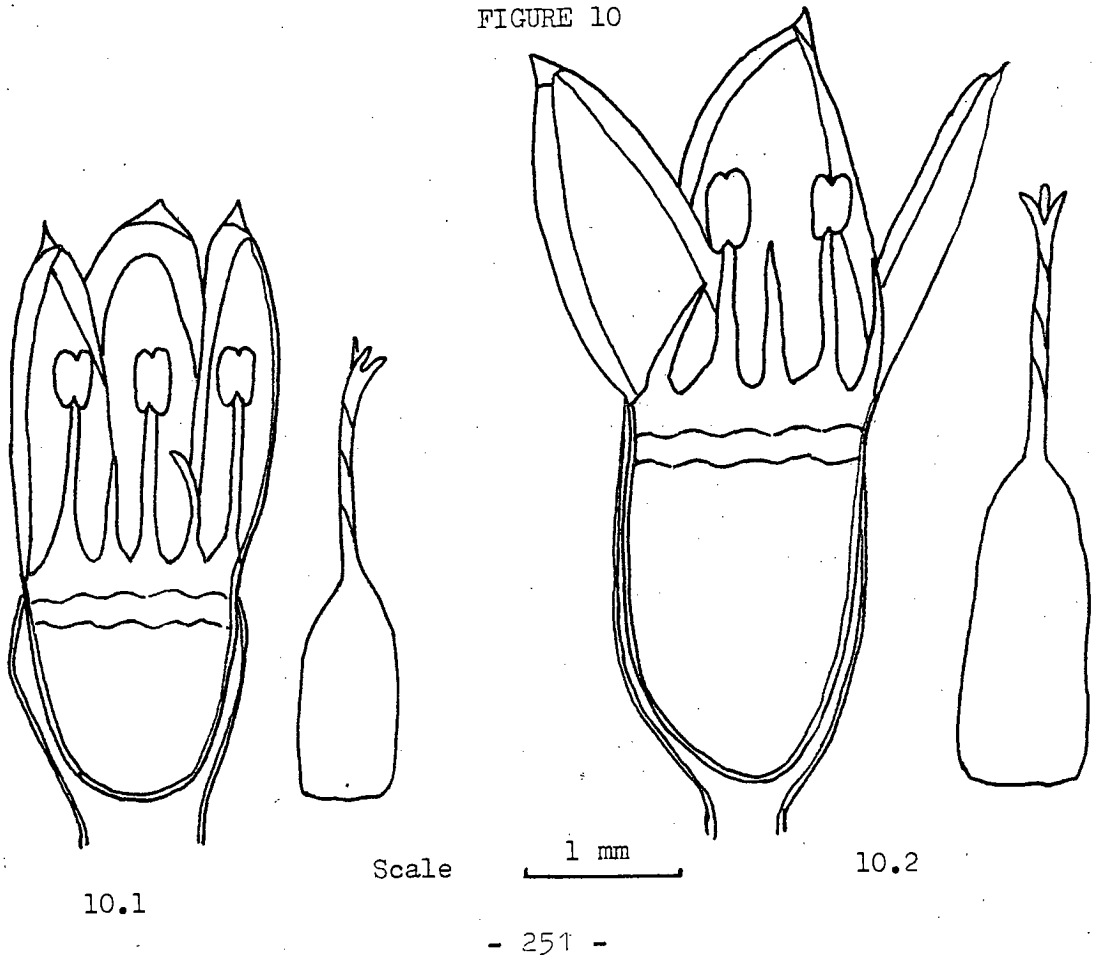


FIGURE 10



As described for genus except bracts foliar. (Fig.10.2)

Distribution: N. Africa, Canary Is., Iran, Syria, Jordan, Palestine, Arabia, Afghanistan, W. Pakistan.

Davis 49090, Morocco.

5. SCLEROCEPHALUS Boiss., Diagn. Ser. 1 (3): 12 (1843).

Type Species: S. arabicus Boiss.

Monotypic Genus.

Annual herbs, suberect to prostrate, up to 20 cm. Stem glabrous, occasionally furrowed, much branched. Leaves opposite or occasionally in fascicles due to condensed lateral branches, sessile, linear, up to 1.5 cm, slightly fleshy apex with short apine. Stipules membranous, triangular, up to 5 mm, margins entire, apex occasionally bilobed, 1 pair each node. Flowers in compact glomerules, terminal and in axils of leaves on peduncles. Bracts foliar, c. 7 mm with long spines at apex. Flowers sessile. Sepals 5, membranous margins, apex hooded with stout spine. Petals 0. Stamens 5, antisepalous; 5 staminodes alternating with sepals. Stamens and staminodes fused at base to form a membranous ring which is fused to sepals of apex of fleshy perigynous zone. Outer surface of greatly extended perigynous zone usually covered in long hairs. Ovary connate at base to walls of perigynouse zone; 1 style, apex bilobed occasionally trilobed, lobes covered in stigmatic papillae on all surfaces; no evidence of strand of transmitting tissue from apex of ovary to apex of funicle/placental column. At the fruiting stage, calyx and perigynous zone become very hard, flowers and bracts fusing to give a spiny spherical structure composed of several flowers and bracts which is dispersed as a single unit.

Distribution: N. Africa, Iran, Iraq, Syria, Arabia, Sudan.

Sclerocephalus arabicus Boiss., Diagn. Ser. 1 (3): 12 (1843).

Syn: Paronychia sclerocephala Decne. in Ann. Sci. Nat. Ser. 2 (3): 262 (1835). (Fig. 11.1)

J. R. Edmondson 3168, Oman; Ptard 3/4/1909, Tunisia.

6. ILLECEBRUM L., Sp. Pl. Ed. 1: 206 (1753).

Syn: Corrigiola Moeh. Hort. priv.: 31,106 (1756); Bergertia Bubani, Fl. Pyren. 3: 10 (1901).

Type/ ....

Type species: I. verticillatum L.
Monotypic Genus.

Annual or biennial herbs, prostrate, mat forming, 5 - 60 cm. Stems glabrous, brown to red in colour, much branched, rooting at nodes. Leaves opposite, oblong to ovate, occasionally spathulate, c. 4mm, subsessile, glabrous, stipules membranous, lanceolate to ovate, c. 1 mm in length. Flowers in glomerules in axils of leaves, from base of plant to apex, 1 - 6 flowers each cluster. Bracts membranous lanceolate c. 0.8 mm. Flowers subsessile, pedicels up to 0.2 mm. Sepals 5, white spongy, keeled, margins membranous, apex hooded with long awn, occasionally apex tinged pink. Stamens 5, antisepalous, often reduced in number; 5 staminodes alternating with the sepals, red. Stamens and staminodes fusing to perigynous zone at same level. Ovary sessile; 1 ovule; no evidence of transmitting tissue strands from apex of ovary to apex of funicle/placental column; 2 or 3 styles sessile or fused, all surfaces apparently covered in stigmatic papillae. Calyx persistent, becoming hard.
Distribution: Europe, Tunisia, Morocco, Canary Is., Russia.

Illecebrum verticillatum L., Sp. Pl. Ed. 1: 206 (1753).
Syn: Corrigiola verticillata Moehr., Hort. Priv.: 106 (1736); Paronychia verticillata Lam., Fl. Fr. 3: 23 (1778); Bergertia uliginosa Bubani, Fl. Pyren 3: 10 (1901). (Fig.112)
Davis & Lammond, D. 57866, Tunisia.

Subtribe Chaetonychiinae

7. CHAETONYCHIA Sweet, Hort. Brit. Ed. 2: 220 (1830).
Type Species: C. cymosa (L.) Sweet
Monotypic Genus.

Small annual erect herbs, up to 7 cm. Stems branched, covered in short hairs. Leaves opposite, occasionally in fascicles due to condensing of lateral branches, linear, 2 - 7 mm, slightly fleshy, covered in short hairs, basal leaves usually much smaller than upper ones. Stipules, 1 pair each leaf, linear to lanceolate, c. 1.5 mm, membranous, pubescent. Flowers in terminal or axillary dense glomerules on long peduncles or flowers forming very distinct inflorescence, original dichasial cyme becoming monochasial forming branches with a row/ ....

row of flowers on the same side up to 1.5 cm. Bracts membranous about ½ length of flowers, brown in centre with white margins, ovate, acute. Flowers sessile or on short pedicels; pedicels and peduncles pubescent. Sepal 5, 3 outer, 2 inner, margins membranous increasing in width at base, apex hooded with white spongy sac, and short spine, spine reduced in length in inner sepals. Petals 0. Stamens 5, antisepalous, fused to apex of short fleshy perigynous zone. Ovary sessile; 1 ovule; no evidence of strand of transmitting tissue from apex of ovary to apex of funicle/ placental column; short style, apex bifid, occasionally trifid. Calyx persistent in fruit.
Distribution: Portugal, Spain.

Chaetonychia cymosa (L.) Sweet, Hort. Brit. Ed. 2: 220 (1830).
Syn: Illecebrum cymosum L., Sp. Pl. Ed. 1: 206 (1753); Paronychia cymosa (L.) DC. in Poir., Encycl. 5: 26 (1804). (Fig.11.3)
Murray 1889, Portugal.

Subtribe Cardioneminae

8. CARDIONEMA DC., Prodr. 3: 372 (1828).
Syn: Bivonaea Moc. & Sesse, ex DC. Prodr. 3: 372 (1828); Pentacaena Bartl. in Presl., Rel. Haenk. 2: 5 (1830); Acanthonychia Rohrb. in Mart., Fl. Bras. 14, 2: 249 t. 56 (1872).
Type Species: C. ramosissima (Weinm.) Nelson & Macbride.
Other Species: C. rosetta (Walp.) Nelson & Macbride, ? C. congesta (Benth.) Nelson & Macbride.

Perennial, prostrate to suberect herbs, up to 30 cm. Stems woody, branched, glabrous or pubescent. Leaves opposite, linear, 0.6 - 1.2 cm, grooved, glabrous, short spine at apex up to 1 mm. Stipules membranous, c. 6 mm, apex with short spine, adnate to margins of leaves at base. Flowers in axils of leaves in clusters of 2 - 4 flowers. Bracts similar to stipules, membranous short or equal in length to flowers. Flowers subsessile. Sepals 5, 3 outer, larger than the 2 inner, margins membranous, apex hooded, margins with long hairs, especially dense towards the apex, apex also with long awn becoming brown and hard at tip. Petals 5, triangular, membranous, with small flap in front of base of petals extending above level of insertion of stamens on perigynous zone. Stamens 5, antisepalous, staminodes/ ....

staminodes absent. Inner sepals totally fused to perigynous zone, outer 3 sepals centre area only fused to zone. Ovary sessile; 1 ovule; no evidence of a strand of transmitting tissue from apex of ovary to apex of funicle/placental column; styles short, bifid or occasionally trifid. Calyx persistent in fruit.
Distribution: N. & S. America.

Cardionema ramosissima (Weinm) Nelson & Macbride, Bot. Gaz. 56: 473 (1913). Syn: Loeflingia ramosissima Weinm, in Flora 3: 608 (1820); Paronychia ramosissima (Weinm) DC., Prodr. 31: 372 (1828); Cardionema multicaule DC. Prodr. 3: 372 (1828); Bivonaea multicaulis Moc. & Sesse ex DC., Prodr. 3: 372 (1828); Pentacaena polycnemoides Bartl. in Presl., Rel. Haenk., 2: 5 (1830); Pentacaena ramosissima Hook & Am. in Hook., Bot. Misc. 3: 338 (1833); Paronychia polycnemoides (Bartl.) Schlecht. in linnaea 13: 407 (1839); Pentacaena tenuior Steud., Nom, Ed. 2, 2: 298 (1840); P. polycnemoides Walps,Repert. Bot. Syst. 1: 261 (1842); Acanthonychia ramosissima (Weinm) Rohrb. in Mart., Fl. Bras. 14, 2: 249 (1872); A. polycnemoides (Bartl.) Rohrb. in Mart. Fl. Bras. 14, 2: 250 (1872).

C. congesta (Berth.) Nels. & Macbride, may also be included in this species. (Fig. 11.4)
Reino Alava 2305, California.

Subtribe Corrigiolinae.

9. CORRIGIOLA L., Gen. Ed. 1: 340 (1737), Sp. Pl. Ed. 1: 271 (1753), non, Moehr., Hort. Priv. 31 & 106 (1736), non sensu O. Kuntze, Rev. Gen. Pl. 2: 535 (1891).

Syn: Polygonaria Heist., Syst.: 6 (1748); Polygonifolia Vaill. ex Adams., Fam. 2: 272 (1763); Furera Bubani, Fl. Pyren. 3: 16 (1901).
Type Species: C. litoralis L.
Other Species: C. madagascariensis (Baker) H. Perrier, C. squamosa Hook & Am., C propinque Cl. Gay, C. andina Triana. & Plach., C. capensis Willd., C. drymarioides Bak. f., C. telephiifolia Pour., C. palaestina Chaudhri, C. crassifolia Chaudhri, C. paniculata Peter.
Perennial/ ....

Perennial, biennial or annual herbs, prostrate, erect or occasionally climbers, up to 55 cm. Stems glabrous. Leaves alternate to spirally arranged, oblanceolate to linear up to 3 cm, sessile or shortly petiolate, obtuse, glabrous. Stipules membranous, c. 1 mm, triangular to ovate, 1 or 2 pairs each node. Flowers in terminal and lateral lax or dense cymes or in lax cymes in axils of leaves. Bracts membranous, triangular to ovate, short than or equal to the flowers, c. 0.7 mm. Flowers sessile or with short pedicels of c. 1 mm. Sepals 5, margins membranous, apex hooded. Short perigynous zone, outer surface glabrous. Stamens 5, antisepalous; 5 staminodes, petaloid, white, ovate about equal in length to sepals. Stamens and staminodes fused to perigynous zone at the same level. Ovary sessile, strongly 3-sided; 1 ovule, no evidence of septal ridges or of strand of transmitting tissue from apex of ovary to apex of placental column/funicle; 3 styles free or fused. Calyx persistent in fruit.

Distribution: France, Germany, Spain, Portugal, Greece, Morocco, Algeria, Somalia, Rhodesia, S. Africa, Natal, Palestine, Chile, Colombia, Mexico, Australia, Turkey.

Corrigiola litoralis L., Sp. Pl. Ed. 1: 271 (1753).

Syn: Corrigiola psammatrophoides Baker in J. Linn. Soc. 20: 238 (1883); Polygonifolia utoralis (L.) O. Kuntze, Rev. Gen. Pl. 1: 535 (1891); Paronychia litoralis (L.) Krause in Strum., Fl. Deut. Ed. 2, 5: 25 (1901); Corrigiola nusselliana Chav. in Bull. Mus. Hist. Nat. Paris Ser. 2, 4: 316 (1938).

Perennial, biennial or annual herb, suberect to erect, up to 30 cm. Stems much branched from base, glabrous. Leaves alternate, sessile oblanceolate, up to 10 mm, glabrous. Stipules membranous, inconspicuous, c. 1 mm, ovate to triangular, 1 pair each leaf. Flowers in terminal or lateral clusters or in axils of leaves. Bracts small, triangular, about equal in length to pedicels. Flowers sessile to subsessile; pedicels c. 0.7 mm. Sepals 5, green/brown central area with membranous margins, slightly hooded. Stamens 5, antisepalous; 5 staminodes, petaloid, alternating with sepals. Stamens, staminodes and sepals attached to fleshy perigynous zone at about the same level. Ovary distinctly 3-sided; styles 3, free with knob at apex. (Fig.115)

Distribution/ ....

FIGURE 11

11.1 L.S. of flower of Sclerocephalus arabicus Boiss. x 20 .

11.2 L.S. of flower of Illecebrum verticillatum L. x 20 .

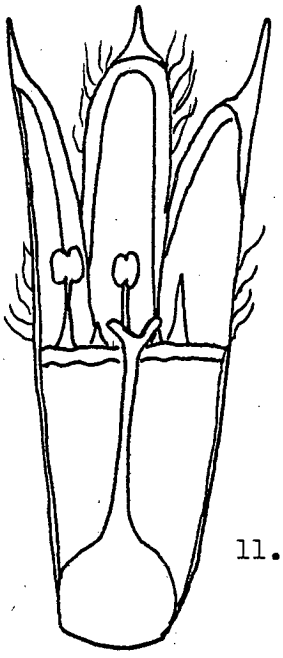
11.3 L.S. of flower of Chaetonychia cymosa (L.) Sweet x 20 .

11.4 L.S. of flower of Cardionema congesta (Berth.) Nels. & Macbride x 10 .

11.5 L.S. of flower of Corrigiola litoralis L. x 50 .

11.6 L.S. of flower of C. propinqua Cl. Gay x 50 .

FIGURE 11



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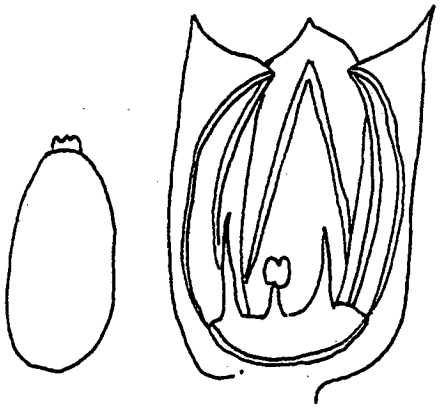

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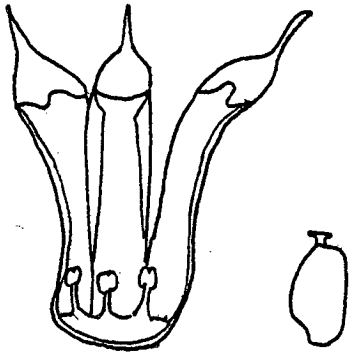

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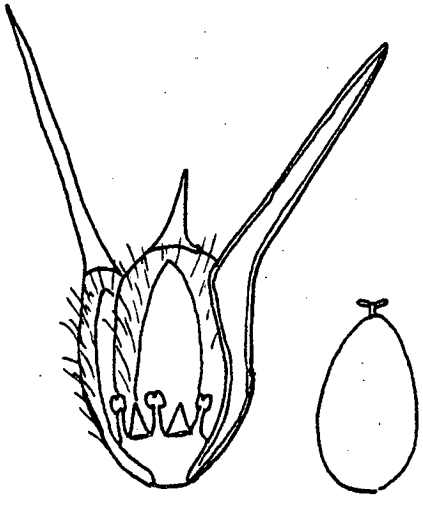
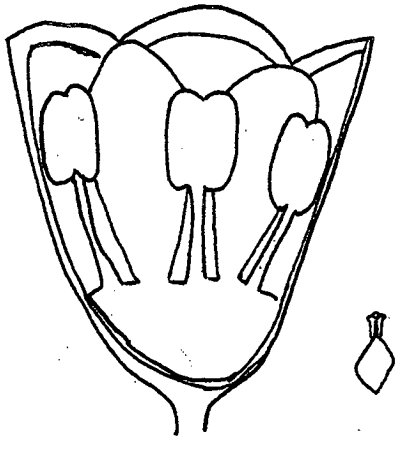


11.4



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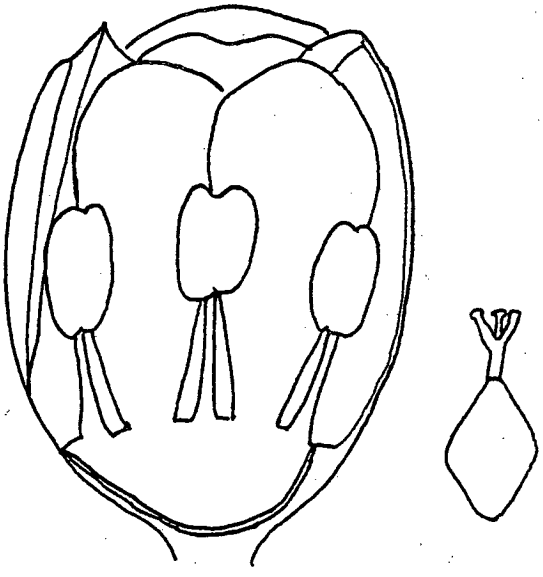


11.6

Distribution: Germany, Spain, France, Algeria, Rhodesia, S. Africa, Natal, Australia, Turkey.

B. Fal des 3/73, Spain.

Corrigiola propinqua Cl. Gay, Fl. Chil. 2: 519 (1846).

Perennial herb, prostrate, up to 50 cm. Stems glabrous, internodes up to 6 cm in length. Leaves alternate, sessile, oblong to oblanceolate up to 3 cm. Stipules membranous, white or brown, c. 1 mm, 1 pair each node. Flowers in dense terminal clusters and on leafless lateral branches in dense clusters. Bracts small, membranous, white to brown, much smaller than flowers. Flowers subsessile. Sepals 5, with central green area with membranous margins, apex slightly hooded. Stamens 5, antisepalous; 5 petaloid staminodes alternating with sepals, about equal in length to sepals. Stamens, staminodes and sepals attached to perigynous zone at about the same level. Ovary distinctly 3-sided; 3 fused styles, fused for $\frac{1}{2}$ length or less. (Fig 11.6)

Distribution: Chile.

Werdermann 22, Chile.

TRIBE II POLLICHIEAE

10. POLLICHIA Solander in Ait., Hort. Kew Ed. 1: 5 (1789).

Syn: Meerburgia Moench, Meth. Suppl.: 116 (1794); Neckeria J. F. Gmelin, L. Syst. Nat. Ed. 13: 16 (1796).

Type Species: P. campestris Solander

Monotypic Genus.

Perennial undershrubs, up to 50 cm. Stems much branched, woody, pubescent often densely so. Leaves, 4 - 6 per node, linear to lanceolate 3.5 - 15 mm, glabrous above, often woolly beneath, apex with short spine. Stipules membranous triangular c. 5mm. Flowers in axils of leaves in 2 condensed cymes, up to 30 flowers per cyme. Flowers subsessile. Bracts membranous, triangular, larger than flowers, 3 - 4 mm. Sepals 5, margins membranous, apex not hooded, short spine. Petals 5, or absent, ovate, white, c. 0.3 mm. Stamens 1 - 2 antisepalous, c. 0.4 mm, stamens fused to a membranous ring at the apex of the greatly elongated perigynous zone; secretory glands evident as membranous flaps of tissue alternating with the sepals/ ....

sepals (when petals present, flaps in front of petals), flaps c. 0.1 mm. Perigynous zone greatly elongated, often pubescent on outer surface. Ovary subsessile; 2 ovules, 1 seed; evidence of a strand of transmitting tissue from apex of ovary to apex of placental column; style 1, apex bi-fid, extending beyond the sepals at anthesis. In the fruiting stage, calyx persistent, tightly enclosing the ovary, small protusions being formed below each sepal on the outer surface of the perigynous zone; peduncles becoming brown in colour and fleshy, completely enclosing the fruit.
Distribution: Ethiopia, S. Africa, Arabia.

Pollichia campestris Solander in Ait., Hort. Kew Ed. 1: 5 (1789).
Syn: Meerburgia glomerata Moench, Meth. Suppl.: 116 (1794); Neckeria campestris (Solander) Gmelin, L. Syst. Nat. Ed. 13: 16 (1796). (Fig.12.1 & 122)
Pooley 295 Natal, Chaudhary Feb 1977, Yemen.

11. ACHYRONYCHIA Torrey & Gray in Proc. Am. Acad. 7: 330 (1868).
Type Species: A. cooperi Torrey & Gray
Other Species: A. parryi Hemsl.

The 2 species in this genus appear to be very different and are placed in separate subgenera by Pax and Hoffmann in Engl. & Prantl, Natürl Pflanzenfam. 2 Band 16c: 302 (1934), and may indeed represent 2 separate genera. Each species is thus described.

Achyronychia cooperi Torrey & Gray in Proc. Am. Acad. 7: 331 (1868)

Annual herb, small, prostrate, mat forming. Stems glabrous much branched. Leaves opposite, spathulate, obtuse, slightly fleshy, sessile. Stipules membranous, 1 pair each node, ovate c. 0.2. Flowers in axils of leaves, in dense cymose clusters, or terminal. Bracts small, membranous, ovate c. 0.1 mm shorter than flowers. Sepals 5, about equal in length, central green area with large membranous margins giving appearance of petals. Stamens 1 - 2 antisepalous; 2 - 3 filiform structures alternating with sepals which may be equal to staminodes or may be dissected petals, no evidence of flap of tissue in front of these structures. Distinct elongated perigynous zone, outer surface glabrous. Ovary sessile; 1 - 2 ovules, 1 seed, no clear evidence of transmitting tissue strands from apex of ovary to apex of placental column; style 1 with 2 lobes.
Calyx/ ....

Calyx persistent in fruit becoming larger and hard. (Fig.123)
Distribution; California.

E. K. Balls 11177, California.

Achyronychia parryi Hemsl., Diag. Pl. Mexico Pars Altera: 36 (1879)

Perennial, prostrate herb, up to 20 cm. Stems much branched, covered in short hairs, especially the younger branches. Leaves ovate, c. 1.5 mm, with short spine at apex, sessile. Stipules conspicuous, membranous, ovate, 1 pair each node, c. 0.3 mm. Flowers in clusters in axils of leaves. Bracts similar to stipules c. 0.8 mm, shorter than or equal in length to the flowers. Flowers subsessile. Sepals 5, more or less of equal length, fleshy central green area with membranous margins. Petals 5, alternating with sepals, distinct brown membranous flaps at base, not extending above level of insertion of stamens to perigynous zone. Stamens 5, antisepalous, about the same length as petals. Greatly elongated perigynous zone. Ovary sessile; 2 - 4 ovules, 1 seed; slight evidence of strands of transmitting tissue from apex of ovary to apex of placental column; elongated style, apex trifid, becoming red in mature flowers. Calyx persistent in fruit, with small protuberances appearing on outer surface of perigynous zone, beneath each calyx lobe. (Fig.124)
Distribution: Mexico.

C. G. Pringle 1890, Mexico. (Type seen.)

Of the 2 species A. parryi resembles more closely the other species placed in this tribe. The position of A. cooperi is unclear.

12. SCOPULOPHILA M. E. Jones, Contr. West. Bot. 12: 5 (1908).
Syn: Eremolithia Jepson, Fl. of Calif. 1: 499 f. 100 (1914).
Type Species: S. rixfordii (Brand.) Munz & Johnston
Monotypic Genus.

Perennial herbs, erect, up to 9 cm. Stems much branched, filiform, glabrous, internodes up to 2 cm. Leaves opposite, occasionally 4 at each node, linear to ovate, c. 1 cm, often with short spine at apex; basal leaves breaking down. Stipules membranous triangular, c. 2 mm, 1 pair each node. Flowers in axils of leaves in clusters. Bracts membranous about $\frac{1}{2}$ length of flowers, lanceolate, c. 1 mm. Sepals 5, more or less equal in length, central area, green, with/ ....

FIGURE 12

12.1 L.S. of flower Pollichia campestris Solander

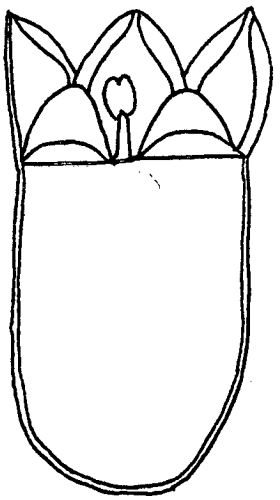
12.2 Fruit of Pollichia campestris Solander

12.3 L.S. of flower Achyronychia cooperi Hemsl.

12.4 L.S. of flower of Achyronychia parryi Torrey & Gray

12.5 L.S. of flower of Scopulophila rixfordii (Brand.) Munz & Johnston

FIGURE 12



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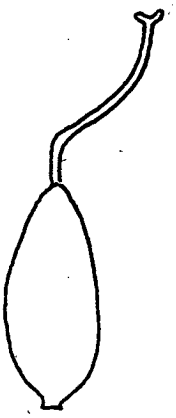

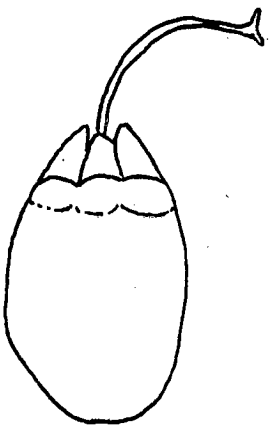

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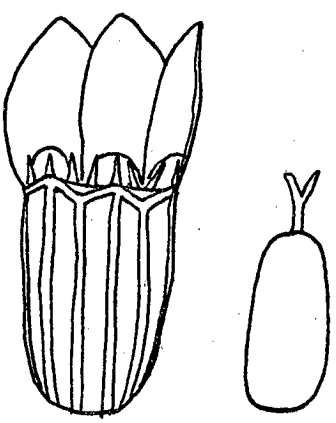

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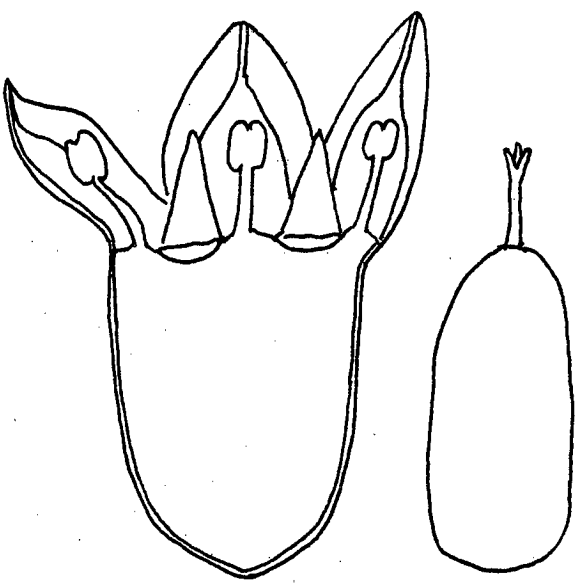
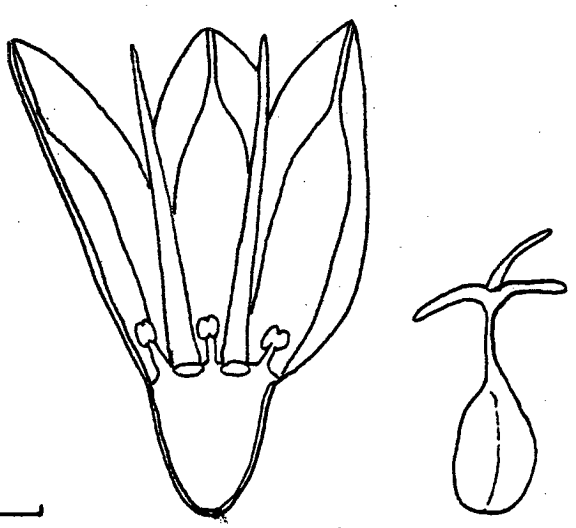


12.4



12.5

Scale 1 mm

with wide membranous margins, apex with short spine. Petals 5, linear, about equal length of sepals. Stamens 5, antisepalous; 5 distinct brown/red membranous flaps inserted slightly below stamens on perigynous zone opposite base of petals. Stamens and petals attached to apex of greatly elongated perigynous zone. Ovary distinctly 3-sided; 2 - 4 ovules; no evidence of septal ridges on ovary wall but some evidence of strands of transmitting tissue from apex of ovary to apex of placental column; styles fused, apex of fused style distinctly tri-lobed. Fruit indehiscent.
Distribution: California.

Scopulophila rixfordii (Brand.) Munz & Johnston in Bull. Torrey Club 49: 351 (1922)

Syn: Achyronychia rixfordii Brand. in Zoe 1: 230 (1890); Scopulophila nitrophiloides M. E. Jones, Contr. West. Bot. 12: 5 (1908); Eremolithia rixfordii Jepson, Fl. Calif. 1: 499 f. 100 (1914).
(Fig.125)

C. A. Purpus May - Oct. 1898, California.

TRIBE III PTERANTHEAE

13. PTERANTHUS Forskal, Fl. Aegypt.: 36 (1775).
Syn: Louichea L'Heritier, Strip. Nov.: 135 (1789).
Type Species: P. dichotomus Forskal
Monotypic Genus.

Annual herbs, up to 15 cm. Stems glabrous or pubescent, often grooved and glaucous, much branched. Leaves sessile, linear to spathulate, opposite, up to 2 cm, slightly fleshy. Stipules connate to base of leaves, free above, membranous, ovate, entire, obtuse. Flowers terminal or in axils of leaves in groups of 3 on distinct peduncles; peduncles ovate to spathulate, compressed, up to 1 cm, glabrous or glandular. Bracts membranous, c. 0.2 mm, with green or brown strip in centre, margins serrated, hairy. Each group of flowers consisting of a central flower, occasionally female sterile, at right angles to first flower, with 2 much branched lateral structure, each of these lateral structures consisting of spirally arranged sepal like structures with green central strip and membranous margins the apex with a short spine. Lateral structures here interpreted as sterile/ ....

sterile floral structures, 3 pairs of bracts found in each group of flowers. Flowers sessile to subsessile. Sepals 4, 2 outer larger than 2 inner, membranous margin often hairy, outer surface pubescent, glabrous or glandular, apex with short spine. Petals absent. Stamens 4, antisepalous, connate at base to form a membranous ring around the base of ovary. Ovary with 1 ovule; no evidence of strands of transmitting tissue from apex of ovary to apex of placental column; fused style bifid, occasionally trifid at apex, ovary slightly adnate to perigynous zone at base. Calyx persistant in fruit becoming hard, group of 3 flowers dispersed as a unit with the compressed peduncle.

Distribution: N. Africa, Iran, Iraq, Jordan, Palestine, Cyprus.

Pteranthus dichotomus Forskal, Fl. Aegypt.: 36 (1775). Syn: Camphorosma pteranthus L., Mant. Pl. 1: 41 (1767); Louichea pteranthus L'Herit., Strip. Nov.: 135 (1789); Pteranthus echinatus Desf., Fl. Atlantica 1 : 144 (1798); P. trigynous Cab. in Biol. Soc. Esp. Hist. Nat. 13: 88 (1913). (Fig.13.1 & 13.2)

L. Boulos & W. Jallad 7970, Jordan.

14. DICHERANTHUS Webb, in Ann. Sc. Nat. Ser 3, 5: 27 (1846).

Type Species: D. plocamoides Webb

Monotypic Genus

Perennial, woody undershrub up to 35 cm. Stems with distinct swollen nodes, much branched. Leaves opposite, sessile, linear up to 1.5 cm, fleshy, glabrous with very short spine at apex. Stipules small, c. 0.4 mm, acute, those of basal leaves tending to be hairy, 1 pair each leaf fused at base to leaves, but not totally. Inflorescence compact cymes, terminal, many or few flowered, pedunculate. Flowers subsessile. Bracts foliar, becoming membranous with central strip of green. Within inflorescence, flowers in groups of 3, 1 main flower and 2 lateral side branches, each of side branches with central flower and either 2 sterile flowers or 2 branched sterile floral structures. Main flower hermaphrodite; sepals 5, 2 outer, 3 inner, green central strip with membranous margins apex hooded with short spine; inner sepals longer than 2 outer sepals; 3 inner sepals fused around base of ovary with perigynous zone, 2 outer sepals fusing behind the 3 inner sepals to perigynous zone/ ....

zone; 1 - 3 stamens, opposite each of the 3 inner sepals, connate at base to form a small ring around the ovary; ovary distinctly 3-sided subsessile, 1 ovule, no evidence of strands of transmitting tissue from apex of ovary to apex of funicle/placental column, single elongated style, twisted, just shorter than sepals or extending above, apex trifid. Lateral flowers, female sterile; sepals 5, 2 outer, 3 inner, green central area with membranous margins, hooded with short mucro at apex, outer 2 with wider membranous margins than inner 2, both inner and outer sepals covered in stout hairs; 1 - 3 stamens fused at base into a short stamen ring; ovary present, hollow, sometimes with a single very short style, or with 2 very long styles emerging from side of style. Sterile floral structures composed of sepal-like structures similar to those of central flowers in a single whorl or arranged on an elongated structure. Calyx persistent in fruit.

Distribution: Canary Is.

Dicheranthus plocamoides Webb in Ann. Sc, Nat, Ser 3, 5: 27 (1846). (Fig.13.3 & 13.4)

Bramwell 2031, Canary Is.

15. COMETES L., Mant. Pl. 1: 4 (1767).

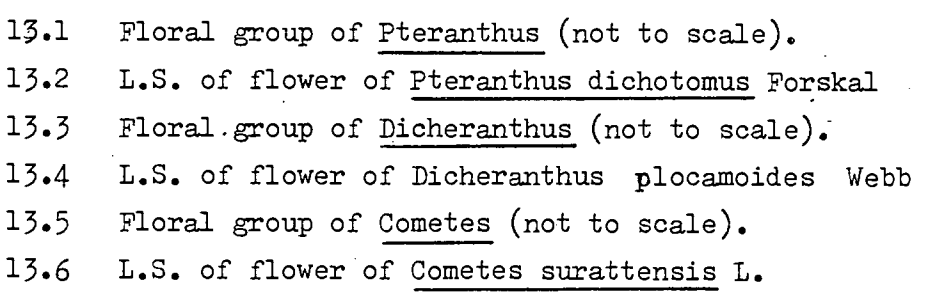
Syn: Cometes Burman, Fl. Ind.: 39 t. 15 f. 5 (1768); Saltia R. Br. in Salt, Abyss. App.: 64 (1814); Ceratonychia Edgew. in J. As. Soc. Beng. 16: 1215 (1847).

Type Species: C. surattensis L.

Other Species: C. abyssinica R. Br.

Annual herbs, erect up to 20 cm. Stems much branched, occasionally woody at base, often hairy. Leaves opposite, linear to lanceolate, sessile in C. abyssinica; orbiculate, ovate, subsessile to petiolate in C. surattensis, apex in both with a short mucro often hairy. Stipules membranous, triangular c. 1 mm, adnate to base of leaves, free above, inconspicuous. Flowers terminal and in axils of leaves on long peduncles c. 1 cm, in clusters of 3 flowers c. 1.5 mm. Each group of flowers consisting of a central flower and 2 lateral branches, each lateral branch consisting of central flower (sometimes absent) and 2 lateral sterile structures, each sterile, lateral structure consisting of branch with short branches with long spines, spines becoming/ ....

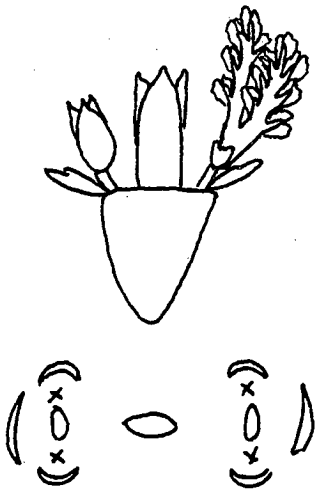
FIGURE 13



13.1 Floral group of Pteranthus (not to scale).
13.2 L.S. of flower of Pteranthus dichotomus Forskal
13.3 Floral group of Dicheranthus (not to scale).
13.4 L.S. of flower of Dicheranthus plocamoides Webb
13.5 Floral group of Cometes (not to scale).
13.6 L.S. of flower of Cometes surattensis L.

o - flower
(- bract
x - branches sterile floral structure

FIGURE 13



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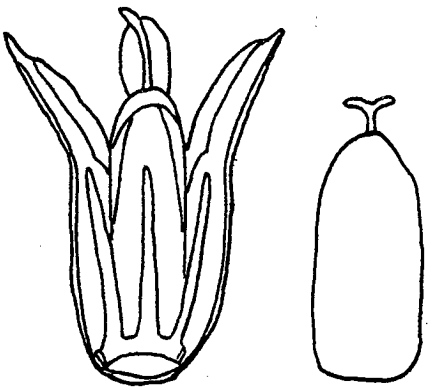
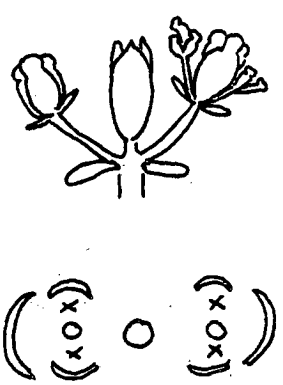
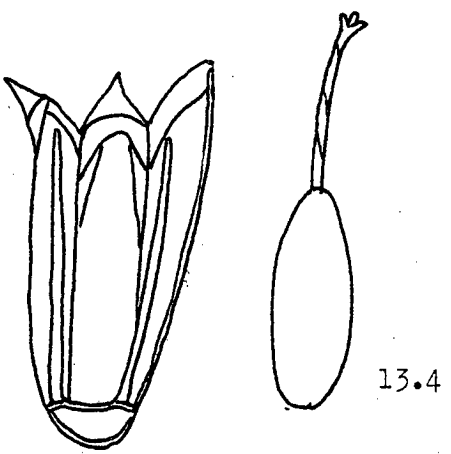


13.2

Scale 1 mm

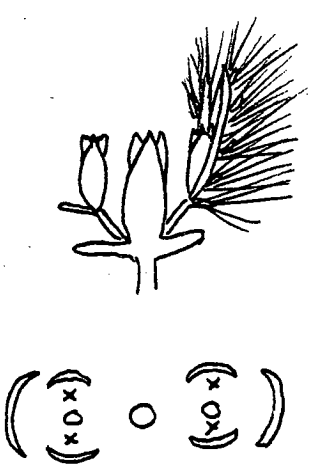


13.3

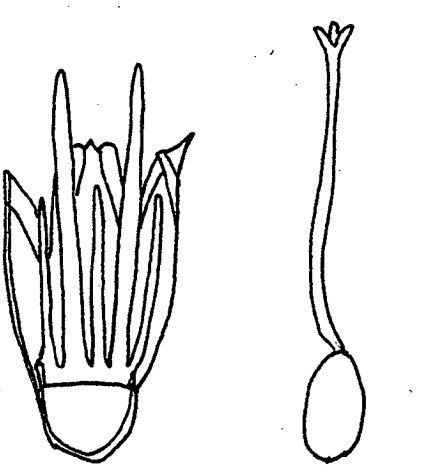


13.4

Scale 1 mm



13.5



13.6

Scale 1 mm

becoming more prominent in fruit, 3 pairs of bracts each group of flowers. Flowers sessile to subsessile. Sepals 5, 3 outer, 2 inner, outer surface covered in small projections, margins membranous, apex hooded with mucro. Petals 5, linear, white, longer than sepals. Stamens 5, antisepalous, slightly shorter than petals. Petals and stamens fused into a short membranous ring at base, petals fusing behind stamens, ring situated at apex of fleshy perigynous zone to which sepals also attached. Ovary sessile, fused at base to perigynous zone; 1 ovule; styles fused, apex of fused style trifid, extending beyond the sepals at anthesis. Calyx persistent in fruit.
Distribution: Somalia, Iran, Arabia, Socotra, W. Pakistan.

Cometes surrattensis L., Mant. Pl. 1: 4 (1767).
Syn: Cometes surrattensis Burm., Fl. Ind.: 39, + 15, f. 5 (1768); Ceratonychia nidus Edgew. in J. As. Soc. Beng. 16: 1215 (1847).
(Fig.13.5 & 13.6)

Edmondson E 3446, Oman.

TRIBE IV POLYCARPEAE
Subtribe Polycarpinae

16. POLYCARPAEA Lam. in J. Hist. Nat. Paris 2: 8 (1792) non. cons.
Syn: Polia Lour., Fl. Cochinch. 97: 164 (1790); Policarpaea Lam. in J. Hist. Nat. Paris 2: 25 (1792); Hagaea Vent. Tab. 3: 240 (1799); Hagea Pers., Syn. Pl. 1: 262 (1805); Mollia Willd., Hort. Berol. 1: 11, t. 11 (1806); Lahayea Roem. & Schutt., Syst 5: 402 (1819); Aylmeria Mart. in Nov. Act. Nat. Cur. 13: 276 (1826); Hyala L'Herit ex DC., Prodr. 3: 373 (1828); Polycarpia Webb ex Berth., Hist. Nat. Isles Canary 3^{e}: 156 (1836 - 1850); Alymeria D. Dietr., Syn. 1. Ind: 13 (1839); Planchonia J. Gay in Herb. Book ex Benth. & Hook. f., Gen. Pl. 1: 154 (1862); Polycarpea Pomel, Nouv. Nat. Fl. Atl.: 202 (1874); Polycarpa sensu O. Kuntze, Rev. Gen. 1: 50 (1891) pro parte; Polycarpus O. Kuntze in Post & O. Kuntze, Lexicon: 452 (1903) pro parte.
Type Species: P. teneriffae Lam., type cons.
Other Species: 32 - 36 species

Perennial, biennial or annual herbs, prostrate to erect, up to 35 cm. Stems glabrous or pubescent, sometimes woody at base, often with distinct swollen nodes. Leaves opposite, sometimes in fascicles due/ ....

due to condensed lateral branches, linear to lanceolate, to ovate to spathulate to elleptical, up to 3 cm, glabrous or pubescent, apex usually with short spine, usually sessile but sometimes with short petiole. Stipules membranous, triangular to lanceolate, shorter than leaves, up to 5 mm. Inflorescence terminal cymes, lax or dense, sometimes forming distinct glomerules, occasionally flowers in dense symes in axils of leaves. Bracts membranous, triangular, about the same length as flower. Flowers sessile to subsessile. Sepals 5, usually membranous, sometimes with central green or brown strip, occasionally brightly coloured red or brown/pink, glabrous or pubescent, free or nearly so, perigynous zone formed but usually small. Petals 5, triangular to lanceolate, usually entire, apex occasionally emarginate, usually shortly fused to stamens to give a short membranous ring, occasionally totally fused to stamen filaments to form a distinct petal/stamen tube. Stamens 5, antisepalous; 5 staminodes, antipetalous usually absent, but present in some species; membranous flaps evident in front of petal base, except in those species with antipetalous staminodes and those with petals and antisepalous stamens fused into a distinct tube, flaps usually bifid, here interpreted as nectaries but have been interpreted as staminodes (Bakker 1957). Ovary subsessile or with a distinct stipe; ovules numerous, arranged on a short basal placental column; evidence that ovary at same stage in development completely septate with evidence of strands of transmitting tissue from apex of ovary to apex of placental column, single elongated style, apex usually a knob covered in stigmatic papillae, rarely trifid. Capsule dehiscing by 3 valves, calyx persistent in fruit.

Distribution: N. Africa, Ehtiopia, Nyassaland, S. Rhodesia, S. Africa, Kenya, Madagascar, Sinai, Jordan, India, China, Thailand, Paraguay, Brazil, Br. Guana, Australia Socotra.

This genus has been divided into 3 sections; Benth., Fl. Austr. 1: 163 (1863), Bakker in Acta Bot. Neerl. 6: 48 - 53 (1957) or into 4 sections by Pax & Hoffmann in Engler & Prantl, Natürl Plfanzenfam.: 309 (1934) in which they included the genus Robbairea Boiss. as a section of this genus. In this work, 3 sections are recognised.

1. Petals and fertile stamens united into a distinct tube; antipetalous staminodes absent; no evidence of flap of tissue at base of/ ....

of petal ..... Section I Planchania.

1. Petals and fertile stamens more or less free or slightly united at base before attachment to perigynous zone; antipetalous staminodes present or flap present at base of petals

2. Antipetalous staminodes present ..... Section II Aylineria.

2. Antipetalous staminodes absent, membranous flap at base of petals ..... Section III Polycarpia.

I Section Planchania (J. Gay) Benth, Fl. Austr. 1: 164 (1863).
P. longiflora Muell., P. spirostyles Muell., P. synandra Muell., P. glabra C. T. White & Francis.

Polycarpaea longiflora F. Muell., Rep. Babb.: 8 (1858).

Large annual herb, erect, up to 30 cm. Stems densely covered in short hairs. Leaves opposite, but usually in fascicles up to 2.5 cm, sparsely covered in short hairs, apex with short spine. Stipules membranous, much shorter than leaves, c. 0.4 mm. Inflorescence terminal dichasial cyme, compact. Bracts membranous, ovate, entire, up to 6 mm. Flowers on short pedicels, sometimes longer than flowers, pedicels up to 1.3 cm. Sepals 5, more or less equal in length, glabrous on outer surface, membranous, yellow, brown, often pink towards apex, more or less free to base. Petals 5 membranous, apex bifid. Stamens 5, antisepalous, filaments fused with petals for about half length of filaments, petals fused behind stamens; staminodes absent; no evidence of flaps in front of petal base. Ovary on short stipe, ovate to elliptical; c. 14 ovules arranged on basal placental column; evidence of septal ridges on ovary wall and placental column, and evidence of strands of transmitting tissue from apex of ovary to apex of placental column; long single style with swollen apex covered in stigmatic papillae. Capsule opening by 3 valves. (Fig. 14.1)

Distribution: Australia

J. Staer Aug. 1905, Australia.

II Section Aylmeria (Mart.) Benth., Fl. Austr. 1: 164 (1863).
P. violacea (Mart.) Benth., P. staminodina Muell.

Polycarpaea staminodina F. Muell., Rep. Babb. Exped.: 8 (1858).

Annual herb, erect up to 22 cm. Stems covered in short hairs. Leaves opposite, often in fascicules, linear, 5 - 12 mm, covered in short hairs, apex with short spine. Stipules membranous, 1 pair each leaf, triangular to ovate, entire, shorter than leaves, c. 4 mm. Inflorescence terminal dichasial cyme, compact. Bracts membranous, ovate, entire, equal in length to flowers. Flowers on short pedicels; pedicels up to 8 mm, more or less equal in length to flowers, covered in short hairs. Sepals 5, glabrous on outer surface, totally membranous, slightly adnate to perigynous zone. Petals 5, lanceolate, apex slightly emarginate. Stamens 5, antisepalous, shorter than petals; 5 staminodes, antipetalous, distinct red tips. Petals, stamens and staminodes more or less free at base, attached to apex of fleshy perigynous zone. No evidence of flap at base of petal. Ovary with short stipe, ovate; c. 7 ovules arranged on basal placental column; evidence of septal ridges on ovary wall and of strands of transmitting tissue; style elongated, with knob of stigmatic tissue at apex; capsule dehiscing by 3 valves. (Fig.142)
Distribution: Australia.

J. Staer Aug. 1905, Australis.

III Section Polycarpia

P. somalensis Engl., P. aristata C. Sm. ex DC., P. aurea W. & Am., P. brasiliensis Camb., P. breviflora F. Muell., P. caespitosa Balf. f., P. carnosa C. Sm., P. corymbosa Lam., P. involucrata F. Muell., P. linearifolia DC., P. microphylla Cav., P. mozambica Kunth & Bouche, P. smittii Link, P. spicata W. & Am., P. stellata DC., P. teneriffae Lam., P. tenuifolia DC., P. gomerensis Burch., P. repens (Forskal) Ascher. & Schwenf., P. grahamis Turrill, P. tenuistyla Turrill, P. sumbana Bakker, P. tumorensis Bakker, P. zollvingeri (Fenzl) Bakker, ? P. euspidata Schlecht, ? P. pobeguini Berhaut, ? P. rhodesica Suess., ? P. billei Leb.

Polycarpaea teneriffae Lam. in J. Hist. Nat. Paris 2: 3 - 5 (1792).
Syn: Illecebrum divaricatum Solander in Ait., Hort. Kew Ed.1, 1: 291 (1789); Hagaea teneriffae Pers., Syn. Pl. 1: 262 (1805); Mollia diffusa Willd., Hort. Berol. 1: 11, + 11 (1806); Mollia latifolia Willd., Enum, Hort. Berol.: 269 (1809); Polycarpaea latifolia (Willd.)/ ....

(Willd.) Pour., Encycl. Suppl. 4: 473 (1816); Hagaea diffusa (Willd.) Sweet, Hort. Brit. Ed. 1 : 176 (1818); Polycarpaea divaricata (Solander) Poir. ex Steud, nom. Ed. 2: 369 (1840); Polycarpon teneriffae (Lam.) Steud. Nom. Ed. 2: 718 (1840); Polycarpaea lancifolia Christ in Bot. Jahrb. 9: 103 (1888); Polycarpa lancifolia (Christ) O. Kuntze, Gen. Pl: 50 (1891)

Perennial herbs, erect to suberect, up to 30 cm. Stems woody at base, much branched above, densely covered in short hairs. Leaves opposite, usually in fasicicles, due to condensing lateral branches elliptical to ovate, 4 - 14 (- 20) mm, glabrous or covered in short hairs, margins usually with long hairs, distinct petioles covered in dense short hairs. Stipules, 1 pair each leaf, membranous with narrow brown central strip, lanceolate to triangular, shorter than leaves, c. 2 mm, apex with short spine. Inflorescence much branched dichasial cyme, often forming dense glomerules, terminal, occasionally in axils of leaves. Bracts membranous, shorter than flowers, c. 3 mm with central brown strip, apex pungent, margins often serrated. Flowers sessile. Sepals 5, outer surface sparsely covered in short hairs, 2 outer sepals slightly smaller than 3 inner sepals, broad green central area with wide membranous margins, margins slightly serrated, not hooded. Petals 5, lanceolate. Stamens 5, antisepalous; 5 bilobed flaps in front of base of petals. Stamens and petals free to base. Ovary distinctly 3 sided; c. 100 ovules arranged on basal placental column; style elongated apex with knob of stigmatic papillae Capsule dehiscing by 3 valves. (Fig.14.3)

Distribution: Canary Is.

D. G. Long 5545, Tenerife.

Polycarpaea repens (Forskal) Ascher & Schwenf. ex Ascher. and the above species, differ from the rest of the species in the genus in having sepals with a distinct central green fleshy area. The other species having completely membranous sepals. Polycarpaea repens also differs in having a slightly trifid style, the other species usually having a stigmatic knob at the apex. This makes this species very close to the genus Polycarpon from which it differs in not having hooded sepals and in having ovules arranged on a basal placental column not an elongated one.

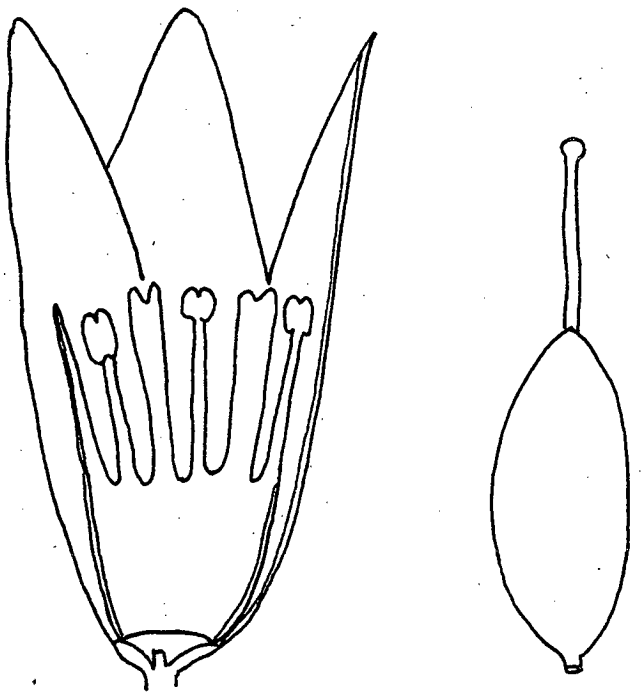
FIGURE 14

14.1 L.S. of flower of Polycarpaea longiflora F. Muell.

14.2 L.S. of flower of P. staminodina F. Muell.

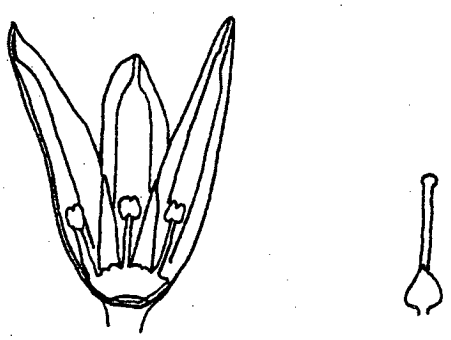
14.3 L.S. of flower of P. teneriffae Lam.

FIGURE 14



14.1

14.2



14.3

Scale 1 mm

17. DRYMARIA Willd. ex Roem. & Schult., Syst. Veg. 5: 406 (1819).
Syn: Pinosa Urb. in Arkiv. Bot. 24: 70 (1930); Mollugophytum M. E. Jones in Extr. Contr. West. Bot. 18: 35 (1933).
Type Species: D. arenarioides Humb. & Bonpl. ex Roem. & Schult.
Other Species: 48 species.

Annual or occasionally perennial herbs, up to 45 cm. Stems erect or prostrate, occasionally mat forming, glabrous or pubescent, occasionally covered in stout sharp hairs. Leaves opposite, sometimes forming fascicles, lanceolate to ovate, occasionally elliptical, glabrous or pubescent, usually distinctly petiolate but sometimes sessile. Stipules usually present but absent in D. holosteoides and D. pachyphylla, membranous, lanceolate to ovate, entire or deeply bifid, 1 pair each leaf, much shorter than leaves. Inflorescence a lax terminal or lateral dichasial cyme or in compact axillary cymes, rarely solitary flowers in axils of leaves. Bracts membranous or foliar, shorter than flowers. Flowers on distinct pedicels, sessile or subsessile. Sepals 5, green with membranous margins, ovate to laneolate, glabrous occasionally pubescent or glandular. Petals 5, but may be reduced in number or totally absent, deeply bilobed, the lobes often splitting into a number of lateral lobes, usually white in colour. Stamens 1 - 5, antisepalous, antipetalous stamens absent except in D. stipitata, base of stamens connate to form a short or elongated stamen ring, free from petals and sepals, stamen ring occasionally forming a bilobed flap in front of base of petal, here interpreted as nectary glands. Ovary sessile, occasionally shortly stipulate; large number of ovules, seeds arranged on central placental column; septal ridges present on ovary wall and evidence of strands of transmitting tissue from apex of ovary to apex of placental column; 3 styles, occasionally 2 or 4, fused, sometimes only shortly. Capsule dehiscing by valves equal in number to styles; calyx persistent in fruit.
Distribution: S. Africa, Ethiopia, India, Malaya, Japan, China, Thailand, New Guinea, N. & S. America.

J. A. Duke (1961), separated species in this genus into 17 informal series. On the whole the species can be separated into 2 large groups: Group A, those that bear a resemblance to Spergula and Spergularia, with the sepals clearly adnate to perigynous zone; and those, Group B, which do not resemble Spergula and Spergularia, with/ ....

with sepals more or less free and with a very distinct stamen filament tube.

GROUP A

A. Holosteoides J. A. Duke.

D. holosteoides Benth., D. pachyphylla Wooton & Standl.

Drymaria pachyphylla Wooton & Standl. in Contr. U.S. Nat. Herb. 16: 121 (1913)

Annual herbs with slender top roots, suberect to prostrate, up to 9 cm. Stems glabrous, much branched at base; internodes very long up to 6 cm; each node producing a number of lateral branches. Leaves opposite, slightly fleshy, orbiculate to ovate 5 - 8 mm in length, distinctly petiolate; petioles up to 6 mm. Stipules absent. Inflorescence terminal or of lateral compact cymes, glomerules. Bracts membranous, with a central green/brown strip. Flowers on pedicels up to 6 mm. Sepals 5, ovate, glabrous, slightly fleshy, with central green area with narrow membranous margins, fused to perigynous zone at base. Petals 5, deeply bilobed, with 2 smaller lobes between the main lobes, petals shorter than sepals. Stamens 5, antisepalous. Ovary on short stipe; 3 styles fused for less than $\frac{1}{2}$ length. Fruit dehiscing by 3 valves. (Fig.15.1)

Distribution: N. Mexico, W. U.S.A.

E. O. Wooton 405, holotype, Mexico.

D. Arenoides J. A. Duke

D. mulluginea (Lag.) Didr., D. axillaris Brand., D. barkleyi J. Duke & Steyer., D. polycarpoides A. Gray, D. arenarioides Humb. & Bonpl. ex Roem & Schult.

Drymaria arenarioides Humb. & Bonpl. ex Roem. & Schult., Syst. Veg. 5: 406 (1819).

Syn: D. frankenioides Humb., Bonpl. & Kunth, Nov. Gen. Sp. 6: 21 pl. 515 (1823); D. peninsularis S. F. Blake in J. Wash. Acad. 14: 285 (1924); D. johnstonii Wiggins in Proc. Col. Acad. 4^{25}: 203 (1944).

Perennial herb with slender woody top roots, suberect, up to 15 cm. Stems much branched, woody towards base, covered in short stout hairs. Leaves opposite, slightly fleshy, glabrous or sparsely pubescent/ ...

pubescent, occasionally in fascicles, 4 - 7 mm, lanceolate, subsessile. Stipules much shorter than leaves, 1 pair each leaf, entire linear, covered in short stout hairs, membranous. Inflorescence of lax terminal or lateral dichasial cymes. Bracts foliar. Flowers on long pedicels; pedicels up to 7 mm covered in hairs. Sepals 5, green with narrow membranous margins, outer surface covered in glandular hairs, fused at base to perigynous zone. Petals 5, deeply bilobed with 2 bilobed structures between the lobes of petal, white in colour. Stamens 5, antisepalous, connate at base to form short stamen filament ring, with bilobed nectary glands evident in front of petal base. Ovary sessile, ovate; 1 style with trilobed apex, extending beyond sepals at anthesis; c. 30 ovules arranged on central placental column. (Fig.15.3)

Distribution: C. America.

C. G. Pringle 715, Chihuahua, Mexico.

GROUP B

E. Viscosae J. A. Duke

D. viscosa S. Watson ex Orcutt

H. Leptophylla J. A. Duke

D. effusa A. Gray, D. leptophylla (Cham. & Schlecht.) Fenzl ex Rohrb.

Drymaria leptophylla (Cham. & Schlecht.) Fenzl ex Rohrb in Linnaea 37: 195 (1871).

Syn: Arenaria leptophylla Cham. & Schlecht. in Linnaea 5: 233 (1830); Drymaria tenella '. Gray, Pl. Fendl.: 12 (1849); D. nodosa Englem, in A. Gray, Pl. Fendl.: 12 (1849); D. nodosa var. gracillima Hemsl., Diagn. Pl. Nov. 2: 22 (1879); D. gracillima (Hemsl.) J. N. Rose in Contri. U.S. Nat. Herb. 5: 132 (1897); D. cognata S. F. Blake in J. Wash. Acad. 14: 285 (1924); D. tenella var. nodosa (Engelm.) Wiggins in Proc. Cal. Acad. 425: 205 (1944); D. gentryi Fosberg in Proc. Biol. Soc. Wash. 62: 147 (1949).

Annual herb, erect, up to 25 cm. Stems much branched, covered in minute stout hairs. Leaves opposite, linear 4 - 17 mm, glabrous or sparsely covered in stout hairs. Stipules membranous, 1 pair each leaf, linear, much smaller than leaves, c. 1 mm in length. Inflorescence terminal, much branched, dichasal cyme. Bracts small, membranous/ ....

membranous with central green strip, ovate, c. 1.5 mm in length. Flowers on short pedicels; pedicels c. $\frac{1}{3}$ length of flower, glabrous or sparsely covered in glandular hairs. Sepals 5, 2 outer slightly larger than 3 inner sepals, green with short spine, ovate, free to base. Petals 5, bilobed for $\frac{1}{3}$ length, white. Stamens 5, antisepalous, slightly longer thanpetals, connate at base into a membranous stamen ring around the ovary, with petals fused to base of ring on aboxial surface. Ovary subsessile to sessile; 3 styles fused for about $\frac{1}{2}$ length, styles not exceeding petals at anthesis; c. 13 ovules arranged on central placental column. (Fig.5.2)

Distribution: C. America.

C. G. Pringle 6482, Mexico.

I. Tenues J. A. Duke

D. anomala S. Watson, D. tenuis S. Watson

M. Laxiflores J. A. Duke

D. laxiflora Benth.

Q. Cordatae J. A. Duke

D. gracilis Cham & Schlecht., D. glandulosa Presl., D. xerophylla A. Gray, D. ladewii Rusby, D. cordata (L.) Willd. ex Roem, & Schult.

Drymaria cordata (L.) Willd. ex Roem. & Schult., Syst. Veg. 5: 406 (1819).

Syn: Holosteum cordatum L. Sp. Pl. Ed. 1: 88 (1753); H. diandrum Siv. Prodr.: 27 (1788); Loeflingia renifolia Lag., Gen. et Sp. Nov.: 2 (1816); Drymaria diandra Blume, Bidjr. F. Nederl. Ind.: 62 (1825); D. retusa Wallich ex Wight & Arnott, Prodr. Fl. Ind. Or.: 359 (1834); D. diandra MacFadyen, Fl. Jam. 1: 52 (1837); D. cordata β diandra Tr. & Pl. in Ann. Sci. Nat. 4: 148 (1862); D. extensa Wallich ex Edgw. & Hook. f. in Hook. f., Fl. Brit. Ind. 1^2: 244 (1874); D. gerontogea F. Miller, Descr. Papuan Pl. 1: 87 (1877); D. procumbens J. N. Rose in Contri. U.S. Nat. Herb. 1: 304 (1895); D. adenophora Urb. in Fedde Repert. Sp. Nov. 21: 213 (1925); Stellaria adenophora (Urb.) Leon in Leon & Alain, Fl. de Cuba 2: 154 (1950).

Annual herb, prostrate to erect, spreading, up to 40 cm. Stems often grooved, covered in short stout hairs, sometimes glabrous, or covered/ ....

covered in glandular hairs, much branched. Leaves opposite, cordate to orbiculate, 0.4 - 20 mm in width x 4 - 22 mm, distinctly petiolate; petioles 1 - 8 mm. Stipules linear, lacerate, membranous, c. 1 mm, usually glabrous or sparsely covered in short hairs. Inflorescence, lax, much branched, terminal dichasial cyme. Bracts small, membranous, ovate, up to 1.5 mm, with central green strip. Flowers on short pedicels; pedicels about ½ length of flower covered in glandular hairs. Sepals 5, laneolate, green central strip with narrow membranous margins, outer surface covered in glandular hairs, and/or stout short hairs. Petals 5, bilobed for more than ½ length, white. Stamens 5, antisepalous, about equal in length to petals, connate at base into a short membranous stamen ring around the base of ovary, petals fused to base of ring on abaxial surface, sepals more or less free to base. Ovary ovate, with stipe; 3 styles fused for about ½ length, occasionally 2 fused styles. Fruit dehiscing by (2-) 3 (-4) valves. (Fig. 15.4)

Distribution: S. Africa, India, China, Philippines, New Guinea, N. & S. America, Australia.

The taxonomic position of the following series of J. A. Duke is unknown;

B. Lyropetala

D. elata J. M. Johnston, D. subumbellata I. M. Johnston, D. suffruitcosa A. Gray, D. lyropetalas I. M. Johnston.

C. Stipitatae

D. stipitata Fosberg

F. Ortegioides

D. ortegioides Griseb.

G. Excisae

D. hyericifolia Briq., D. exicisa Standl., D. longepedunculata S. Watson

J. Frutescentes

D. stellarioides Humbl. & Bonpl., D. stereophylla Mattf. D. auriculipetala Mattf., D. frutescens Mattf.

FIGURE 15

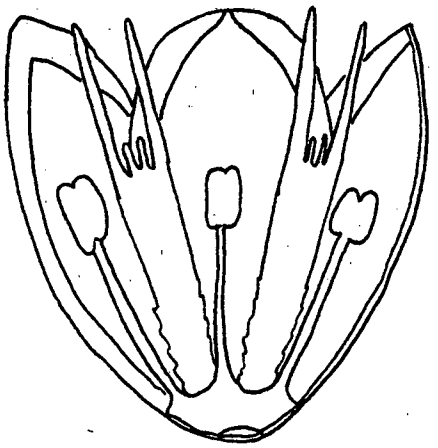
15.1 L.S. of flower of Drymaria pachyphylla Wooton & Standl.

15.2 L.S. of flower of D. leptophylla (Cham. & Schlecht) Fenzl

15.3 L.S. of flower of D. arenarioides Humb. & Bonpl. ex Roem. & Schult.

15.4 L.S. of flower of D. cordata (L.) Willd. ex Roem. & Schult.

FIGURE 15



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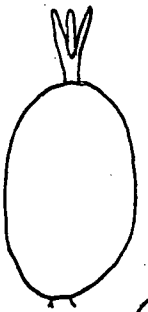
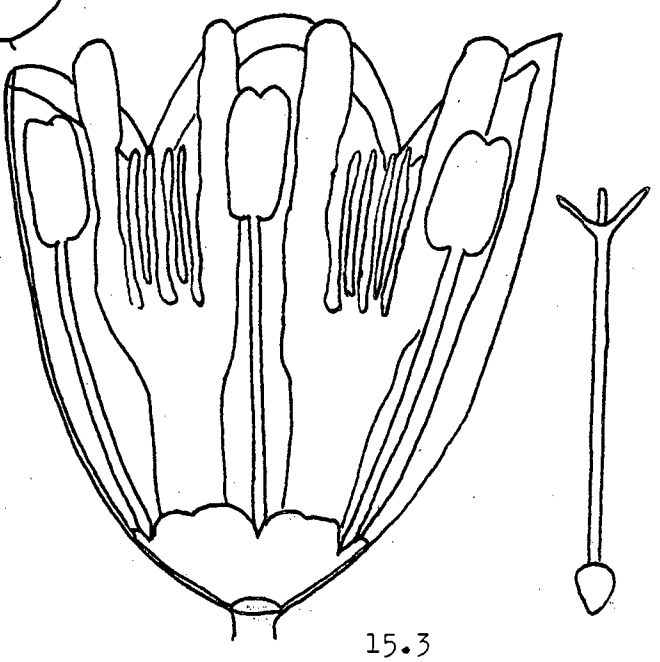
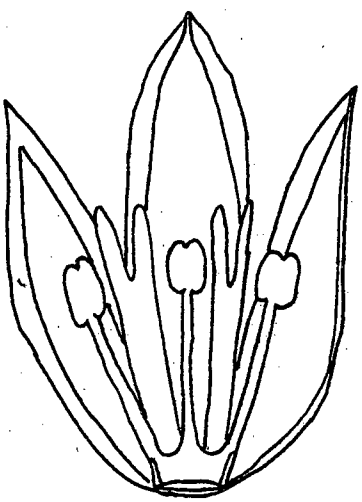
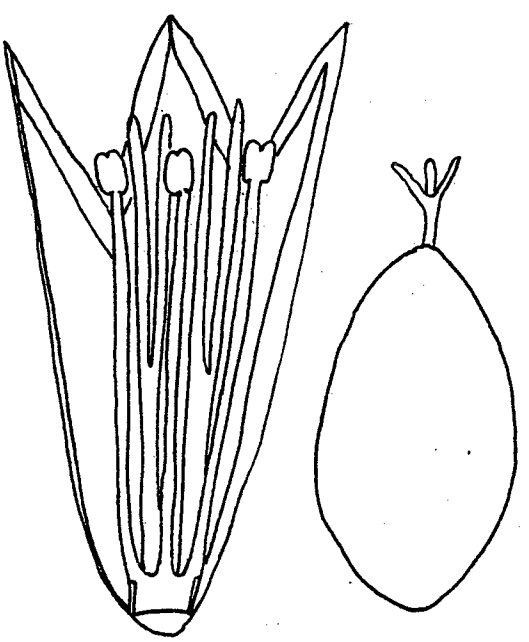




15.3



15.2



15.4

Scale 1 mm

K. Fasciculatae

D. fasciculata A. Gray, D. engleriana Muschler, D. praecox Baehri & Macbride.

L. Debiles

D. debiles Brand.

N. Villosae

D. multiflora Brand., D. conzattii J. A. Duke, D. malachioides Briq., D. villosa Cham. & Schlecht.

O. Grandiflores

D. firmula Stey., D. ovata Humbl. & Bonpl., Dapetala Bantl., D. glaberrima Bartl., C. monticola Howell, D. grandiflora Bantl., D. paposana Phil., D. rotundiflora A. Gray

P. Divaricatae

D. divaricata Humbl., Banpl., & Kunth.

18. LOEFLINGIA L., Sp., Pl. Ed. 1: 35 (1753)

Syn: Loeflingia Neck., Elem 2: 153 (1790); Loeflingia Hedw. f., Gen: 30 (1806).

Type Species: L. hispanica L.

Other Species: ?L. micrantha Boiss. & Reut., L. squarrosa Nutt. ex T. & Gray, L. traveresiana Samp., ? L. baetica Lag.

Annual herbs, small, erect to prostrate, occasionally forming dense mats, up to 25 cm. Stems much branched, often woody at base, covered in short hairs, occasionally almost glabrous, internodes may be up to 2 cm, but often shorter, 0.5 cm. Leaves opposite, rarely in fascicles due to condensed lateral branches, linear to lanceolate, 4 - 19 mm, fleshy, margins often ciliate, apex with a short spine, glabrous or nearly so. Stipules membranous, lanceolate, c. 2mm, 1 pair each leaf, adnate to margins of leaf base for about $\frac{1}{2}$ length. Inflorescence, dense glomerules 1 - 4 flowered in axils of leaves and terminal. Bracts foliar, shorter than leaves, c. 4 mm. Flowers sessile to subsessile. Sepals 5, usually 2 outer and 3 inner, with distinct lateral lanceolate membranous awns present on most sepals but sometimes confined to inner 3 sepals, awns extending up to 3 mm, outer/ ....

outer surface of sepals pubescent. Petals 5, white, triangular, shorter than sepals. Stamens 5, antisepalous; no staminodes; flaps evident in front of petal base; petals, stamens and sepals adnate to fleshy perigynous zone. Ovary sessile; c. 10 ovules arranged on a short basal placental solumn; evidence of ovary being completely septate at an early stage in development; short fused style, apex distinctly trilobed.

Distribution: W. Europe, N. Africa, Iran, Jordan, Israel, N. America.

Loeflingia hispanica L., Sp. Pl. Ed. 1: 35 (1753).

Syn: Loeflingia pentandra Cav., Icon 2: 39 (1792); L. prostrata Moench, Meth.: 266 (1794); L. gladitana Boiss & Reut., Pugill. Pl. Nov.: 23c (1852); L. vaucheri Briq. in Conc. & Jard. Bot. Geneve 17: 356 (1914).

Annual herb, small, erect to prostrate, up to 15 cm. Stems pubescent, occasionally glabrous, much branched. Leaves linear to lanceolate. Inflorescence a dense glomerule, few to many flowered in axils of leaves and terminal. Bracts foliar, larger than flowers. Flowers sessile. Sepals 5, fleshy green central area, membranous ciliate margins, apex with short spine, extended by 2 membranous lateral awns. Petals 5, linear to triangular, longer than stamens, about $\frac{1}{3}$ length of sepals with small, often bifid flap in front of petal base. Stamens 5 antisepalous. Ovary sessile, elliptical, distinctly 3 sided; c. 6 ovules; fused style distinctly trilobed. (Fig.16 .1)

Distribution: W. Europe, N. Africa, Iraq, Jordan.

Davis 58570, Algeria.

19. MICROPHYES Phil, Fl. Atacama: 20, 119 + , 1 f. F. (1860).

Type Species: M. litoralis Phil.

Other Species: M. lanuginosus Phil.

Annual herbs, small, up to 6 cm. Stems slender, covered in short hairs, velutinous. Leaves in basal rosette, linear to spathulate, up to 7 mm; stem leaves opposite, spathulate to linear, 4 - 7 mm, occasionally in fascicles, both types of leaf covered in short hairs sometimes sparsely covered. Stipules present in M. litoralis but absent in M. lanuginosus; stipules ovate to rotundus, membranous, margins ciliate, 1 pair each node, c. 1.5 mm, much shorter than leaves/ ....

leaves. Inflorescence a compact terminal dichasial cyme, few to many flowered. Flowers on short pedicels; pedicels 0.5 - 1.8 mm covered in short hairs. Bracts foliar and densely pubescent in M. lanuginosus or membranous ovate c. 2 mm in M. litoralis. Sepals 5, sub-equal with wide membranous margins, outer surface densely pubescent in M. lanuginosus but only sparsely so in M. litoralis, more or less free to base. Petals 5, linear, white, shorter than sepals. Stamens 5, antisepalous; nectaries evident in front of petal base. Ovary with short stipe, ovate; c. 14 ovules arranged on basal placental column; evidence that ovary "completely" septate at early stage in development; fused style short, apex trifid. Fruit dehiscent capsule, 3 valves.

Distribution: Chile.

Microphyes litoralis Phil., Fl. Atacama: 20, 119 t. 1 f. F.: (1860). (Fig. 16.2)

Morong 1160, Chile.

20. POLYCARPON Loefl. ex L., Syst. Ed. 10: 881 (1759)

Syn: Trichlis Hall, Hort. Gatting: 26 (1743); Polycarpa Loefl., Iter. Hisp.: 7 (1758); Anthyllis Adams., Fam. 2: 271 (1763); Arversia Camb. in A. St. Hil., Fl. Bras. Mer. 2: 184, + 112 (1829); Hapalosia W. & Arn., Prodr.: 358 (1834); Robbairea Boiss., Fl. Or. 1: 755 (1867); Polycarpa O. Kuntze., Rev. Gen. 1: 50 (1891) pro parte; Polycarpus Post & O. Kuntze., Lexic. Gen. Phaner.: 452 (1903).

Type Species: P. tetraphyllum (L.) L.

Other Species: P. depressum Nutt ex Torrey & Gray, ? P. peploides DC., P. colomense Porta, P. prostratum (Forskal) Asch. & Schweinf, P. suffruticosum Graeb., P. anamolum Hassl., P. robbairea O. Kuntze.

Perennial, biennial or annual herbs, prostrate to erect , up to 20 cm. Stems usually covered in short hairs, occasionally glabrous much branched. Leaves opposite, often in fascicles due to condensed lateral branches, linear to lanceolate, ovate to almost orbiculate usually covered in short hairs, but may be glabrous, apex pungent, sometimes with short spine, sessile to shortly petiolate, leaves 2.5 - 12 mm. Stipules membranous, triangular, c. 2 mm, 1 pair each leaf. Inflorescence much branched, terminal, dichasial cymes, lax rarely in cymes in axils of leaves. Bracts membranous, triangular, c. 1.5 mm, apex pungent. Flowers on short pedicels, up to 3.5 mm. Sepals 5/ ....

Sepals 5, more or less equal in length, usually keeled, hooded, apex with short spine or mucro, central green fleshy area with membranous margins. Petals 5, apex usually emarginate, shorter than sepals, sometimes separated into a short claw and limb. Stamens 5, antisepalous; small nectary glands/flaps, in front of petal base. Ovary subsessile, usually on short stipe, ovate to elliptical; numerous ovules arranged on central placental column; fused style short or elongated, apex trifid, occasionally bifid; evidence that ovary at early stage in development completely septate. Capsule opening by 3 valves, occasionally 2.

Distribution: Europe, N. Africa, Egypt, Nigeria, Natal, S. Africa, Canary Is., Iraq, Turkey, Lebanon, Syria, Israel, India, Thailand, West Indies, California, Australia.

Robbairea Boiss. has usually been either considered a separate genus or been placed as a section of Polycarpaea. It is considered in this work to be in this genus, close to P. colomense Porta.

Polycarpon tetraphyllum (L.) L., Syst. Ed. 10: 881 (1759). Syn: Mollugo tetraphylla L., Sp. Pl. Ed. 1: 89 (1753); Polycarpa tetraphylla (L.) Loefl., Iter. Hisp.: 7 (1758); Loeflingia caspica S. Gmel in Reise Russl. 3: 130 t.35, f. 1 (1774); Polycarpon diphyllum Cav., Icon. 2: 40 t.151 f. 1 (1793); Holosteum tetraphyllum (L.) Thunb., Pl. Cap.: 24 (1794 - 1800); Paronychia striata DC. in Poir., Encycl. 5: 25 (1804); Polycarpon alsinefolium DC., Prodr. 3: 376 (1828); P. succulentum Webb. & Berth., Phyto. Canar. 1: 155 (1836 - 40); P. floribundum Wilk. in Bot. Zeit 5: 430 (1847).

Perennial or annual herb, small, prostrate to suberect, up to 20 cm. Stems slender, covered in short hairs, grooved. Leaves opposite or in fascicles, ovate to lanceolate, 2.5 - 12 mm, sometimes with distinct petiole, apex pungent, occasionally with a short spine, glabrous or occasionally pubescent. Stipules triangular, c. 2 mm, margins occasionally serrated, 1 pair each leaf. Inflorescence, lax, much branched, dichasial cyme, terminal. Bracts membranous, shorter than flowers. Flowers on pedicels; pedicels c. 3 mm. Sepals 5, keeled, hooded, central green area with membranous margins, apex pungent, occasionally a short spine, 3 inner sepals larger than 2 outer. Petals 5, small, triangular, white, apex emarginate. Stamens/ ....

Stamens 5, antisepalous; slightly bilobed flaps in front of petal bases. Ovary ovate, subsessile, short stipe; numerous ovules arranged on central placental column; short fused style, apex trifid. (Fig.16.3)
Distribution: Europe, N. Africa, Iraq, Turkey, Palestine, Lebanon, India, West Indies, N. America, Australia.

Davis 41508, Turkey.

This species may also include Polycarpon peploides DC., Prodr. 3: 376 (1828).

Polycarpon colomense Porta, Nuov. Giorn. Bot. Ital. 19: 305 (1887).

Perennial herb, prostrate to suberect, up to 10 cm. Stem becoming woody at base, much branched, covered in short hairs. Leaves opposite or in fascicles, ovate to lanceolate, glabrous, shortly petiolate. Stipules small triangular, c. 0.5 mm. Inflorescence much branched, dichasial, terminal cyme. Bracts small, membranous, c. 1.5 mm, with central green strip. Flowers on pedicels; pedicels c. 3 mm. Sepals 5, with green central area with membranous margins, keeled, slightly hooded, apex pungent. Petals 5, ovate, with a distinct claw and limb, apex emarginate, slightly tinged pink. Stamens 5, antisepalous; nectaries in front of petal bases. Ovary ovate, subsessile, short stipe; numerous ovules arranged on central placental column; fused style elongated, apex trilobed. (Fig.16.4)
Distribution: Balearic Islands.

Porta April 11 1885 Balearum insual type.

Polycarpon robbairea O. Kuntze., Rev. Gen. 1: 5 (1891) as Polycarpa robbairea.

Syn: Alsine prostrata sensu Delile, Fl. D'Egypte Expl. Pl.: 68 pl. 24, f. 4 (1813) non Forskal; Arenaria prostrata Ser. in DC., Prodr. 1: 400 (1842) pro parte, quoad descr., excl. non et synom. Fork.; Polycarpaea prostrata Decne. in Ann. Sci. Nat. Ser. 2, Bot. 3: 263 (1835) pro parte quoad descr. excl. nom et synom et spec. Forskal; Robbairea prostrata Boiss., Fl. Or. 1: 755 (1867) pro parte, quoad descr., excl. nom et synom Forskal; ?Spergularia akkensis Cass. in Bull. Soc. Bot. Fr. 22:55 (1875); ?Robbairea akkensis (Cass.) Ascher. in Ost. Bot. Ztschr. 39: 326 (1889); ? Polycarpaea akkensis (Cass.) Pax in Bot. Jahrb. 22: 592 (1893); Robbairea delileana Milne-Rehead in Kew Bull.: 452 (1948).

Perennial/ ....

FIGURE 16

16.1 L.S. of flower of Loeflingia hispanica L.

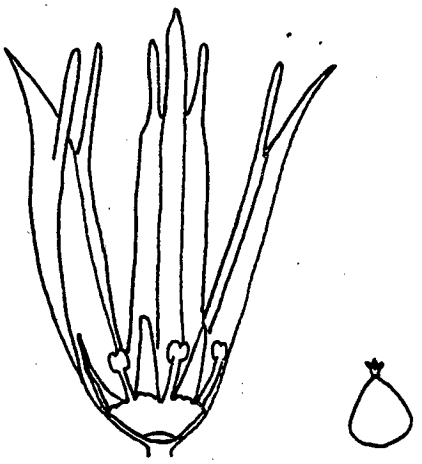
16.2 L.S. of flower of Microphyes litoralis Phil.

16.3 L.S. of flower of Polycarpon tetraphyllum (L.) L

16.4 L.S. of flower of P. colomense Porta

16.5 L.S. of flower of P. robbairea O. Kuntze

FIGURE 16



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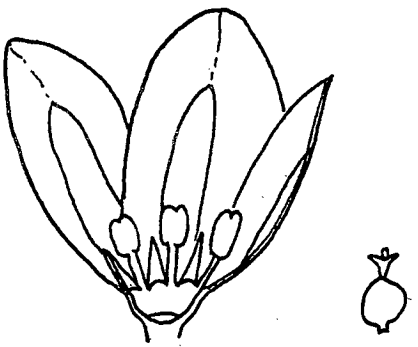
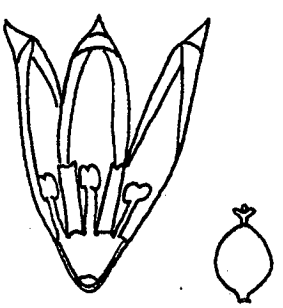


16.2



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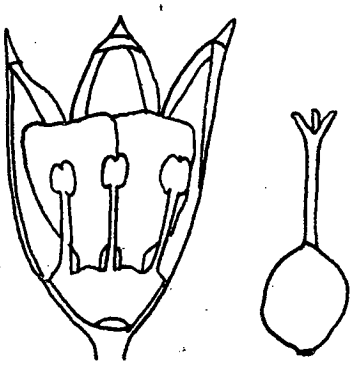

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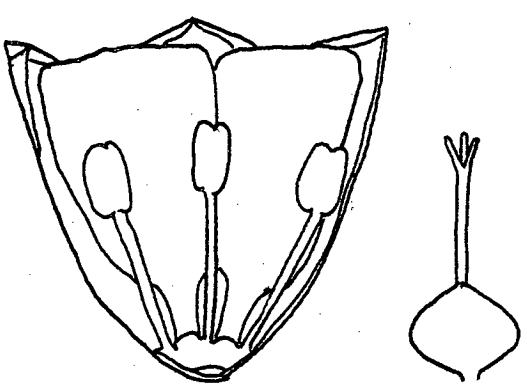


16.5

Scale 1 mm

Perennial herb, small prostrate to suberect, up to 20 cm. Stems filiform, glabrous, much branched. Leaves opposite, sometimes in fascicles, linear to lancolate, occasionally oblanceolate, 3 - 14 mm, glabrous, sessile to subsessile. Stipules membranous, triangular, c. 1 mm, serrated margins, 1 pair each leaf. Inflorescence much branched lax terminal dichasial cyme. Bracts membranous, ovate, c. 1.5 mm, with central green strip. Flowers on pedicels; pedicels up to 7 mm, longer than flowers. Sepals 5, linear to ovate, central green area with membranous margins, slightly hooded, glabrous on outer surface. Petals 5, pink to white, with distinct claw and limb, apex emarginate. Stamens 5, antisepalous; 5 small nectary glands in front of petal bases. Sepals more or less free to base. Ovary ovate, subsessile; c. 42 ovules arranged on a central placental column; style elongated, fused, apex trilobed, occasionally bilobed. (Fig.16.5)
Distribution: Morocco, Libya, Egypt, Yemen, Israel, Jordan, Syria, Iraq.

Davis 6307B, Egypt.

21. STIPULICIDA Michx., Fl. Bor. Am. 1: 26 (1803).

Type Species: S. setacea Michx.

Monotypic Genus

Perennial herbs, erect, up to 15 cm. Stems filiform, covered in short hairs, much branched, often woody at base, internodes up to 3 cm. Leaves forming a rosette at base, spathulate to lanceolate c. 1.2 cm, petiolate, covered in short hairs, apex with or without a short mucro, leaves persistent at base but disintegrating; stem leaves smaller, opposite, linear, c. 2 mm, glabrous or sparsely pubescent, apex acute. Stipules small, membranous, 1 pair each leaf, totally adnate to margins of leaf base, often disintegrating into a number of linear strands, c. 1 mm. Inflorescence, terminal compact glomerules, 3 - 12 flowered. Bracts foliar, membranous margins (stipules) serrated, linear, more or less equal in length to flower, up to 2 mm. Flowers sessile to subsessile. Sepals 5, central brown to green area with wide membranous margins, apex sometimes with short spine, outer surface usually glabrous. Petals 5, white, extending beyond the sepals, apex emarginate, slightly constricted in centre, margins serrated towards base. Stamens 5, or reduced in number to

3/ ....

3, antisepalous, attached to fleshy projections on perigynous zone, projections extending in front of petal bases but not forming flaps. Petals, stamens and ovary situated on a raised fleshy structure, sepals fused to base of structure. Ovary subsessile, often with short stipe, distinctly 3 sided; c. 24 ovules arranged on a placental column; evidence that ovary at some stage completely septate; 3 styles fused for less than $\frac{1}{2}$ length, short. Calyx persistent in fruit; capsule opening by 3 valves.

Distribution: Florida, N. Carolina, Georgia.

Stipulicida setacea Michx., Fl. Bor. Am. 1: 26 (1803).

Syn: Polycarpon stipulifiolum Pers., Syn. Pl. 1: 111 (1805); Stipulicida filiformis Nash in Bull. Torrey. Club 22: 148 (1895). (Fig.17.1)

R. A. Howard 12959, Florida.

22. ORTEGIA Loefl. ex L., Sp. Pl. Ed. 1: 560 (1753) corr. Gen. Pl. Ed. 5: 21 (1754).

Syn: Ortega L., Sp. Pl. Ed. 1: 560 (1753); Ortegia Loefl., Iter. Hisp.: 112 (1758); Mosina Adans., Fam. 2: 272 (1763); Juncaria (Clus. ex) DC., Prodr. 3: 375 (1828); Terogia Rafin., Fl. Tellur. 3: 56 (1836); Ortegaea O. Kuntze in Post & O. Kuntze, Lexion. Gen. Phaner.: 405 (1903).

Type Species: O. hispanica L.

Monotypic Genus

Perennial herbs, erect, up to 20 cm. Stems filiform, much branched, long internodes, woody at base, grooved, sometimes covered in short spines. Leaves opposite, sometimes in fascicles, linear to lanceolate 7 - 18 mm, glabrous, with a short spine at apex, sessile. Stipules lanceolate, membranous, c. 1 mm, 1 pair each leaf, distinct black swollen area at base. Inflorescence compact, terminal, dichasial, cymes, occasionally flowers in compact cymes in axils of leaves on long peduncles. Flowers sessile or subsessile. Bracts foliar, stipules adnate to leaves with black swollen areas at base, larger than flowers, c. 3 mm. Peduncles covered in short spines. Sepals 5, 3 inner and 2 outer, unequal, central green area with membranous margins, margins serrated, apex with short spine, 3 inner sepals adnate to perigynous zone, 2 outer sepals more or less free to/ ....

to base. Stamens 3, antisepalous, attached to fleshy perigynous zone, opposite the 3 inner sepals. Ovary subsessile, ovate to elliptical; c. 25 ovules arranged on placental column; evidence that ovary at some stage completely septate; styles fused, elongated, apex swollen, slightly trifid, all surfaces of swollen area stigmatic. Calyx persistent in fruit, capsule opening by 3 valves.
Distribution: Italy, Spain, Portugal.

Ortegia hispanica L., Sp. Pl. Ed. 1: 560 (1753).
Syn: O. dichotoma L., Mant. 12: 174 (1771); Terogia dichotoma Rafin., Fl. Tellur. 3: 56 (1836). (Fig.17.2)
E. Schmutz 823, Portugal.

23. CERDIA Moc. & Sesse ex DC., Prodr. 3: 377 (1828).
Syn: Cardia Reichb., Consp.: 161 (1828); Cordia Reichb., Handb.: 235 (1836).
Type Species: C. virescens Moc. & Sesse
Other Species: C. purpurescens Moc. & Sess ex DC., L congestiflora Hemsl., C. glauca Hemsl.
(The 2 species of Moc. & Sesse unknown to me may be the same as those of Hemsley.)

Perennial, small herbs, prostrate, mat forming, up to 10 cm. Stems much branched, glabrous, becoming woody at base. Leaves opposite, occasionally in fascicles, linear, 7 - 12 mm, slightly fleshy with distinct spine at apex, sessile. Stipules totally adnate to margins of leaf base, membranous, appearing absent, or stipules linear to ovate, c. 1 mm adnate to base of leaves, but not totally, in both cases adjacent stipules connate at base to give membranous band between leaves, 1 pair each leaf. Flowers in axils of leaves on short peduncles/pedicels; peduncles/pedicels c. 0.5 mm; flowers usually solitary occasionally in compact cymes. Bracts foliar (Stipules totally adnate), membranous margins serrated, about equal in length to flowers or slightly longer, 1.5 - 2 mm, distinct spine at apex. Flowers subsessile. Sepals 5, membranous margins, slightly serrated or entire, apex with short spine, glabrous on outer surface, 2 outer larger than 3 inner, slightly adnate at base to perigynous zone. Stamens greatly reduced, 1 or occasionally 2, attached/ ....

attached to fleshy perigynous zone, antisepalous. Ovary ovate, sessile; c. 14 ovules arranged on short placental column; evidence ovary completely septate at some stage; 2 styles fused for less than ½ length.

Distribution: Mexico.

Cerdia congestiflora Hemsl., Diagn. Pl. Nov.: 23 (1878). Stipules linear to ovate, c. 1 mm, bracts c. 1.5 mm. (Fig.18.1)

Pringle 6965, Mexico.

24. SPHAEROCOMA T. Anderson in J. Linn. Soc. 5: 15, t.3 (1860).

Syn: Psyllothamnus Oliver in Hooker's Icon. Pl. 15: 77, t. 1499 (1885); Hafunia Chiov., Fl. Somalis 1: 90, t. 3, f. 1 (1929).

Type Species: S. hookeri T. Anderson

Other Species: S. aucheri Boiss.

Perennial undershrubs, woody, up to 35 cm. Stems woody, much branched, glabrous at base, densely hairy in younger stems, nodes swollen. Leaves opposite or in fascicles, linear to spathulate, up to 2 cm, often fleshy, glabrous. Stipules small, triangular, c. 1.4 mm, membranous, brown coloured in centre. Flowers in dense glomerules on long peduncles; peduncles up to 2 cm; flowers in axils of leaves or more often terminal on the condensed lateral branches. Flowers subsessile. Bracts brown, membranous, apex with short spine. Sterile flowers often found in flower clusters, flowers in group of 3. Sepals 5, with central brown area with membranous serrated margins, also brown in colour, similar to bracts, apex with short spine, spine becoming more prominent in fruit. Petals 5, oblong, white, brown tinged at apex. Stamens 5, antisepalous; 5 fleshy nectary glands, slightly bilobed, in front of petal base, sometimes slightly fused to petal. Petals glands and stamens fused at base to form a membranous ring, fused to perigynous zone, almost closing apex of zone. Sterile flowers much reduced, sterile stamens and ovary smaller than fertile flowers, about ⅓ size of fertile flowers, spines at apex of sepals in sterile flowers reduced in S. aucheri. Ovary subsessile; short fused style, apex bilobed, lobes spreading, occasionally trilobed; 2 - 3 ovules, only 1 seed, arranged on basal placental column; evidence of 2 (or 3) separate strands of transmitting tissue from apex of ovary to apex of placental column/ ....

column with 2 (or 3) septal ridges. Calyx persistent in fruit.
Distribution: Egypt, Somalia, Iran, Arabia, Pakistan.

Sphaerocoma hookeri T. Anderson in J. Linn. Soc. 5: 16, t. 3 (1860). Syn: Psyllothamus beevori Oliv. in Hooker's Icon. Pl. 15: 77, t. 1499 (1885); Hafunia globifera Chiov., Fl. Somalia : 90, t. 3, f.1 (1929). (Fig.17.3)

A. Deflers 520, Arabia.

25. HAYA Balf. f. in Proc. Roy. Soc. Edin. 12: 408 (1884).
Type Species: H. obovata Balf. f.
Monotypic Genus

Perennial herbs, prostrate, up to 20 cm. Stems glabrous, often woody at base. Leaves opposite or often 4 at each node, oblong, c. 1 cm, margins serrated, often with long hairs, otherwise glabrous, apex with short spine. Stipules triangular, 1 pair each leaf, brown, membranous, pungent. Flowers in clusters in axils of leaves, clusters consisting of flowers in groups of 3, central flower fertile, lateral flowers sterile, lacking stamens and carpels or much reduced. Bracts membranous, similar to stipules, brown. Sepals 5, occasionally 4, similar to bracts, membranous, brown, margins serrated, apex with short spine, 2 outer, 3 inner sepals slightly longer. Petals 5, or occasionally 4, fleshy, with a distinct brown fleshy base which appears slightly bifid in T. S. Stamens 5, antisepalous, fusing at base to give very short stamen ring, extending in front of petal base. Stamens, petals and sepals fused to form short fleshy perigynous zone. Ovary subsessile, occasionally with a distinct short stipe; 1 ovule; evidence of strand of transmitting tissue from apex of ovary to apex of placental column/funicle; single fused style, with knob of stigmatic papillae at apex; strongly 3 sided ovary. Calyx persistent in fruit.
Distribution: Socotra.

Haya obovata Balf. f. in Proc. Roy. Soc. Edin. 12: 408 (1884) (Fig.18 .2)

Ogilvie-Grant-Forbes 193, Socotra.

Subtribe Spergulinae/ ....

FIGURE 17

17.1 L.S. of flower of Stipulicida setacea Michx.

17.2 L.S. of flower of Ortegia hispanica L.

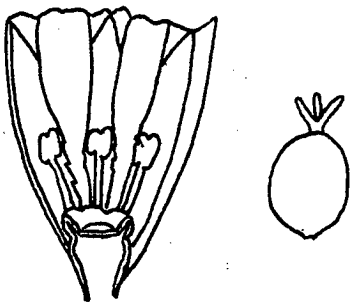
17.3 L.S. of flower of Sphaerocoma hookeri T. Anderson

FIGURE 18

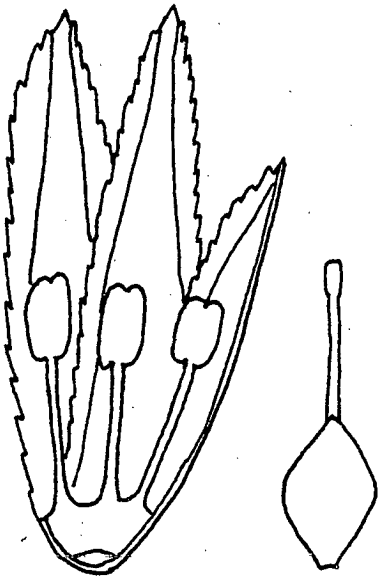
18.1 L.S. of flower of Cerdia congestiflora

18.2 L.S. of flower of Haya obovata Balf. f.

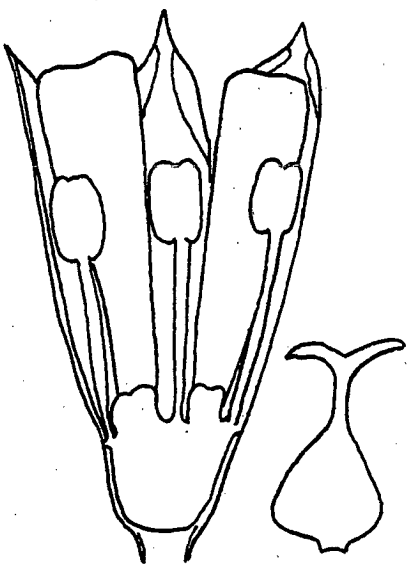
FIGURE 17



17.1



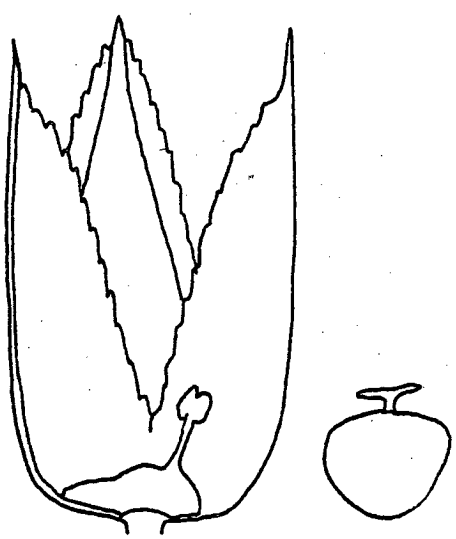
17.2



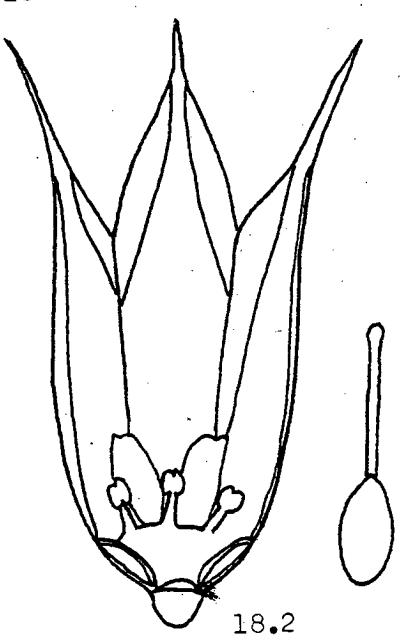
17.3

Scale 1 mm

FIGURE 18



18.1



18.2

Scale 1 mm

Subtribe Spergulinae

26. SPERGULA L., Sp. Ed. 1: 440 (1753).

Syn: Arenaria sensu Adans. Fam. 2: 256 (1763).

Type Species: S. arvensis L.

Other Species: S. pentandra L., S. viscosa Lag., S. fallax (Lowe) E. H. L. Krause, S. morisonii Boreau.

Annual or occasionally perennial herbs, erect, up to 30 cm. Stems much branched, often grooved, usually covered in hairs which may be glandular. Leaves linear, in whorls at nodes, 8 - 20 "leaves" per node in 2 equal groups, 8 - 20 mm, often covered in hairs. Stipules, 2 pairs each node, membranous, triangular, shorter than the leaves, c. 1 mm in length, positioned on either side of each group of "leaves". Inflorescence, terminal, dichasial cyme, much branched, very lax, central flower of cyme often male - sterile. Bracts membranous, triangular c. 1.5 mm with central green stripe. Flowers on pedicels which elongate at fruiting stage; pedicels up to 9 mm at anthesis, elongating to up to 2.5 cm at fruiting stage, often covered in glandular hairs, occasionally tinged pink. Petals 5, ovate, white, or slightly tinged pink, with distinct green fleshy cushion at base which is totally adnate to perigynous zone. Stamens 5 - 10, antisepalous and antipetalous, antipetalous stamens when present with base of filaments totally adnate to green cushion at base of petal. Glandular tissue on adaxial surface of stamen filament base or where antipetalous stamen absent, for a short distance stretched in front of petal base, adnate to green fleshy cushion. Ovary ovate, subsessile; numerous ovules arranged on central placental column; evidence that ovary completely septate at some stage. Capsule dehiscing by 5 valves.

Distribution: N. Africa, Ehtiopia, Somalia, S. Africa, Europe, Palestine, Lebanon, Turkey, Iraq, Oman, Nad, India, Pakistan, Ceylon, Japan, New Guinea, Australia, S. America.

Spergula arvensis L., Sp. Pl. Ed. 1: 440 (1753).

Syn: S. decandra Gilib., Fl. Lut. 2: 156 (1782); S. geniculata Pers., Syn. Pl. 1: 522 (1805); S. sativa Boen., Prod. Fl. Monast.: 135 (1824); S. vulgaris Boen., Prod. Fl. Monast.: 135 (1824); S. maxima Weihe in Boen. L. c.: 135 (1824); S. refracta Deth. ex Reichb., Fl. Gem./ ....

Gem. Excur.: 567 (1830 - 32); Spergularia maxima (Weihe) G. Don in Sweet, Hort. Brit. Ed. 3: 69 (1839); Spergula chieusseana Pamel, Nouv. Nat. Fl. Atl.: 206 (1874); S. pseudomorisonii Iverus in Bot. Nat.: 8 (1875); S. linicola Bor. ex Nym., Consp. 1: 122 (1875). (Fig.191)

Davis 50902 B, Portugal.

27. SPERGULARIA (Pers.) J. & C. Prsel, Fl. Cech.: 94 (1819). Syn: Corium Mitt. in Act. Nat. Cur. 8: 208 (1748); Buda Adans., Fam. 2: 507 (1763); Tissa Adans., l.c.: 507 (1763); Stipularia Haw., Syn. Pl. Succ.: 103 (1812); Lepigonum Wahlb., Fl. Gothola: 45 (1820); Alsinella Hornem., Nom. Fl. Dan.: 33 (1827); Delia Dum., Fl. Belg.: 110 (1827); Balardia Camb. in A. St. Hil., Fl. Bras. Mer. 2: 180 t. 111 (1829); Melagyra Ref., F. Thellur. 3: 81 (1836); Fasciculus Dulac, Fl. Hautes- Pyren.: 245 (1867); Hymenogonium Rich. ex Lebel in Mem. Soc. Sc. Cherbourg 14: 30 (1868).

Type Species: S. rubra (L.) J. & C. Presl.

Other Species: 40 species.

Perennial or annual herbs, erect to prostrate, up to 40 cm. Stems glabrous or pubescent, or with glandular hairs, occasionally woody. Leaves linear in whorls at nodes, 2 - 25 mm, occasionally fleshy, sometimes with short spine at apex. Stipules triangular to ovate, usually much smaller than leaves, 2 - 7 mm, apex emarginate, 1 or 2 pairs of stipules each node. Inflorescence, much branched terminal dichasial cyme. Bracts foliar, but shorter than leaves. Flowers on long pedicels, extending in fruiting stage, up to 3 cm. Central flower often male sterile. Sepals 5, pubescent or glabrous or glandular, with membranous margins, slightly hooded. Petals 5, pink/red or white, equal in length to sepals or greater than sepals. Stamens 1 - 10, antipetalous and antisepalous, antipetalous stamens often reduced in number. Ovary sessile; numerous ovules arranged on central placental column; evidence that ovary completely septate at some stage; 3 styles, fused or free but degree of fusion not always uniform within species or individual plants. Capsules dehiscing by 3 valves; seed often winged.

Distribution: Europe, N. Africa, Egypt, S. Africa, Iran, Iraq, Turkey, Jordan, Palestine, India, N. America, Australia, New Zealand.

Spergularia rubra (L.) J. & C. Presl, Fl. Cech.: 94 (1819).
Syn: Arenaria rubra L., Sp. Pl. Ed. 1: 423 (1753); A. rubra & campestris L., Sp. Pl. Ed. 1: 423 (1753); Alsine rubra Crantz, Inst. 2: 407 (1766); Arenaria campestris All., Fl. Pedem, 2: 114 (1785); A. rubra Per., Syn. Pl. L: 504 (1805); Stipularia rubra (L.) Haw., Syn. Pl. Succ.: 103 (1812); Lepigonum rubrum (L.) Wahlb., Fl. Gothob.: 45 (1820); Buda rubra Dum., Fl. Belg.: 110 (1827) ; Melagyra rubra Rafin., Fl. Thellur. 3: 81 (1836); Spergula rubra (L.) Dietr., Syn. Pl. 2: 1598 (1840); Spergularia campestris (L.) Ascher., Fl. Prov. Brand. 2: 94 (1864); Fasciculus ruber (L.) Dulac, Fl. Hautes-Pyren. : 245 (1867); Tissa campestris (All.) Pax in Engler & Prantl, Natürl Pfanzenfam. 316: 45 (1889); Spergula campestris (All.) Murb. in Linds. Univ. Arsskrift 18: no. 3: 33 (1922).

Annual or shortly lived perennial herb, erect to subprostrate, sometimes woody at base. Stems glabrous or covered in hairs, often glandular, stems up to 30 cm. Leaves linear in whorls at nodes, 4 - 15 mm, with short mucro at apex. Stipules membranous, shorter than leaves, ovate to triangular, c. 4 mm, 1 pair each node. Inflorescence, terminal, much branched dichasial cyme. Bracts foliar. Flowers on long pedicels up to 1 cm. Sepals 5, glandular hairs on outer surface, sparse or dense, wide membranous margins, slightly hooded. Petals 5, ovate, pink, shorter than sepals. Stamens 10, antisepalous and antipetalous, all inserted at same level, antipetalous stamens not adnate to green cushion at base of petal. Ovary sessile; 3 free styles, occasionally fused; numerous ovules arranged on central placental column; ovary completely septate at some stage. (Fig.19.2)
Distribution: Europe, Morocco, Turkey, Iraq, Palestine, S. Africa, N. America, Australia.

Post May 1918, Turkey.

Subtribe Telephiinae

28. TELEPHIUM [Tourn.] L., Sp. Pl. Ed. 1: 271 (1753).
Syn: Merophragma Dulac, Fl. Hautes-Pyren.: 365 (1867); Raynaudetia Bubani, Fl. Pyren. 3: 17 (1901).
Type Species: T. imperati L.
Other/ ....

FIGURE 19

19.1 L.S. of flower Spergula arvensis L.

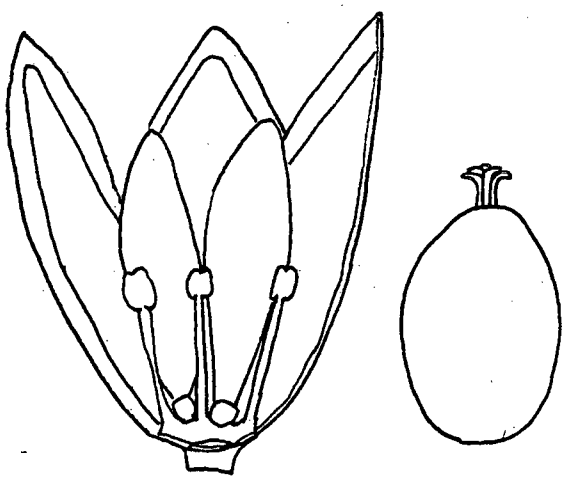
19.2 L.S. of flower of Spergularia rubra (L.) J. & C. Presl.

FIGURE 20

20.1 L.S. of flower of Telephium imperati L.

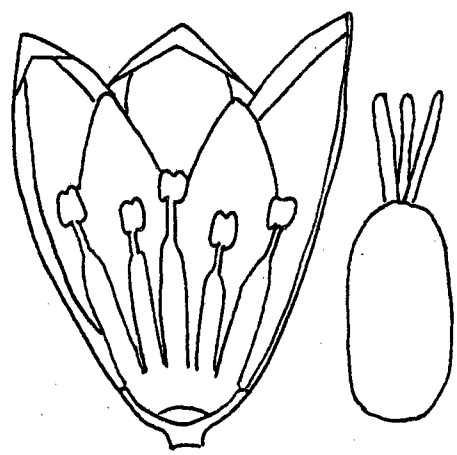
20.2 L.S. of flower of Krauseola mosambicina (Moss) Pax & Hoffm.

FIGURE 19



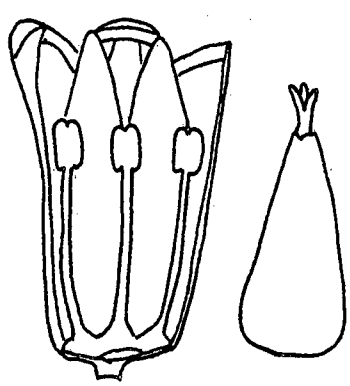
Scale 1 mm

19.1



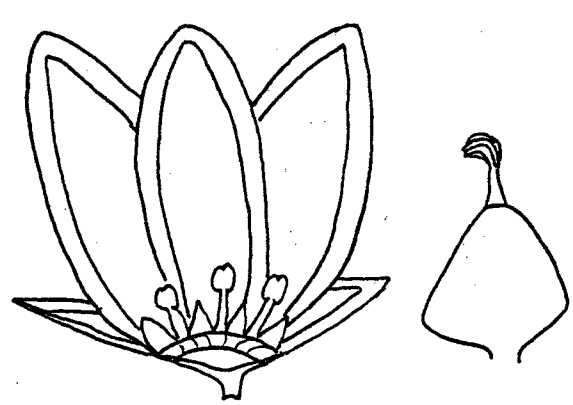
19.2

FIGURE 20



20.1

Scale 1 mm



20.2

Other Species: T. eriglaucum Williams, T. oligospermum Boiss., T. madagascariense Bok., T. sphaerosperum Boiss.

Perennial or occasionally annual or biennial herbs, erect to prostrate, up to 35 cm. Stems woody at base, usually glabrous. Leaves alternate, lanceolate to ovate, 4 - 22 mm, glabrous subsessile to shortly petiolate. Stipules membranous, ovate to triangular, shorter than leaves c. 1.5 mm, may be slightly adnate to leaf margins at base. Inflorescence terminal dichasial cyme, usually compact and many flowered occasionally few flowered. Bracts membranous, triangular to ovate, much shorter than flowers, c. 2 mm. Flowers on short pedicels; pedicels c. 1.2 mm, glabrous. Sepals 5, with membranous margins, hooded, free to base, very short perigynous zone. Petals 5, lanceolate, white, equal in length to sepals, or sometimes exceeding sepal length. Stamens 5, antisepalous, connate at base, forming small membranous flap in front of petal base. Ovary sessile, distinctly 3 sided; c. 14 ovules arranged at top of central placental column; evidence ovary completely septate at some stage; 3 styles, fused or free, with stigmatic papillae on the adaxial surface. Calyx persistent in fruit; capsule opening by 3 valves.
Distribution: Europe, N. Africa, Russia, Jordan, Lebanon, Turkey, Crete, Cyprus, Yemen.

Telephium imperati L., Sp. Pl. Ed. 1: 271 (1753).
Syn: T. alternifolium Moench, Meth.: 231 (1794); Merophragma terrestre Dulac, Fl. Hautes-Pyren.: 363 (1867); Reynaudetia mediterranea Bub., Fl. Pyren.: 17 (1901); Telephium oppositifolium L., Sp. Pl. Ed. 2: 388 (1762); T. repens Lam., Fl. Fr. 3: 71 (1778); ? T. album Guld. in Reis., Russl. Cac. Ed. Pallas 2: 209 (1791).

Perennial herb, suberect to prostrate, up to 20 cm. Stem woody at base, glabrous. Leaves alternate, ovate to elliptical, subsessile to distinctly petiolate, glabrous, 4 - 15 mm. Stipules membranous, triangular to ovate, c. 1.5 mm, 1 pair each leaf, slightly adnate to leaf base. Inflorescence terminal, compact, dichasial cyme, 20 - 30 flowered. Flowers on short pedicels; pedicels glabrous. Bracts membranous, much smaller than flowers. Sepals 5; petals 5, exceeding the sepals; stamens 5, antisepalous. Ovary sessile; 3 styles fused for about $\frac{1}{2}$ length, distinctly red/brown in colour; c. 12 ovules. Fruit/ ....

Fruit dehiscent capsule, opening by 3 valves, capsule extending beyond sepals, dark brown in colour. (Fig.201)

Distribution: Europe, N. Africa, Russia, Jordan, Lebanon, Turkey, Crete, Cyprus, Yemen.

Davis 44510, Turkey.

Subtribe Krauseolinae

29. KRAUSEOLA Pax & Hoffm. in Engler & Prantl, Natürl Pflanzenfam. Ed. 2, 16 c: 308 (1934).

Syn: Pleisepalum Moss in J. Bot. 69: 65 (1931) nom. rejic. (homonym; Pleisepalum Hand-Mazz. (1922))

Type Species: K. mosambicina (Moss) Pax & Hoffm.

Other Species: K. gillettii Turrill

Perennial or annual herbs, up to 40 cm. Stems much branched, glabrous below, pubescent above, internodes up to 2.5 cm. Leaves opposite, sometimes in fascicles, oblanceolate to spathulate, up to 3 cm, pubescent, shortly petiolate. Stipules small membranous, triangular, up to 3 mm. Inflorescence lax terminal dichasial cyme. Bracts membranous, green or brown central strip, triangular, much smaller than flowers, c. 2 mm. Flowers on short pedicels; pedicels c. 4 mm. Sepals, 8 - 11, spirally arranged, the inner larger than the outer; Turrill (1954), Moss (1931). (The sepals have also been considered to consist of 5 true sepals; the inner larger structures, with the outer sepals being considered to be an involucral of bracts as is found in Dianthus; Pax & Hoffm. (1934), the structures, however, appear to be arranged in a spiral from the outermost to the innermost, with no evidence that the outermost are arranged in opposite pairs as would be expected if these structures were bracts.) Petals, 5 - 8, white, triangular, arranged evenly around the apex of the fleshy perigynous zone, behind the stamens, but not necessarily alternating with the sepals. Stamens 5 - 8, arranged alternating with the petals, slightly longer than petals, fused to perigynous zone; no evidence of flap in front of petal base? Ovary ovate, subsessile to shortly petiolate; numerous ovules arranged on a long central placental column; 5 styles fused for about $\frac{1}{2}$ length. Capsule opening by 5 valves, calyx persistent.

Distribution: Kenya, Natal, S. Africa.

Krauseola mosambicina (Moss) Pax & Hoffm. in Engler & Prantl's Nat. Pflanzenfam Ed. 2, 16c: 308 (1934).

Syn: Pleisepalum mosambicina Moss in J. Bot. 69: 65 (1931). (Fig. 20.2)

Distribution: Natal, S. Africa.

Podey 2100, Natal.

TRIBE V SCLERANTHEA

30. SCLERANTHUS L., Sp. Pl. Ed. 1: 406 (1753).

Syn: Knawel Rupp., Fl. Jen. 3: 85 (1718); Knavel Adans., Fam. 2: 506 (1763); Mniarum Forst., Char. Gen. Pl.: 1 (1776); Ditoca Banks & Solander ex Gaertn., Fruct. 2: 196, t. 126 (1791); Gnaville Van Tieg., Traite de Bot.: 1560 (1891).

Type Species: S. annuus L.

Other Species: S. perennis L., S. biflorus (Forst.) Hook. f., S. pungens R. Br., S. diander R. Br., S. mniaroides F. Muell., ? S. minusculus F. Muell., ? S. alpestris Hay., ? S. hanatus Chiav., ? S. velebiticus Degen & Rossi.

Perennial or annual herbs, suberect to prostrate, mat forming up to 20 cm. Stems, glabrous or pubescent, sometimes purple in colour, much branched. Leaves opposite, linear to lanceolate, sometimes apex with short spine, sometimes very compact on stem, glabrous, 3 - 15 mm. Stipules reduced to a narrow membranous margin at base of leaves. Inflorescence a terminal, lax, dichasial cyme, or flowers in dense glomerules, or flowers in axils of leaves on peduncles/pedicels, elongating and becoming hard in fruiting stage, in pairs or solitary. Bracts either small, membranous, triangular, c. 1 mm, or foliar equal in length to flowers. Flowers subsessile to sessile. Sepals 5 or occasionally 4, fused with the greatly elongated perigynous zone, lobes equal, narrow or wide membranous margins, which may give the appearance of petals. Petals 0. Stamens 1 - 10, antipetalous and antisepalous, antipetalous stamens often sterile and reduced to small staminodes alternating with sepals. Apex of perigynous zone constricted so that only styles evident above perigynous zone. Ovary 1 ovule; 2 free styles; evidence of a strand of transmitting tissue from apex of ovary to apex of placental column/funicle, also evidence of septal ridges on ovary wall. Calyx persistent in fruit becoming hard; fruit indehiscent.

Distribution/ ....

Distribution: Europe, N. Africa, Turkey, S. Africa, N. Carolina, New Guinea, New Zealand, Australia.

Two subgenera are recognised in this genus.

1. Inflorescence a lax terminal dichasial cyme or flowers in compact glomerules; bracts foliar; usually 2 whorls of stamens 1 whorl often reduced to staminodes ..... Subgenus Scleranthus.
1. Flowers in axils of leaves on distinct peduncles/pedicels which become hard and elongated in fruiting stage; bracts membranous; stamens reduced to usually 1 whorl, staminodes usually absent. ..... Subgenus Mniarum.

Subgenus Scleranthus

Syn: Knawel Rupp., Fl. Jen. 3: 85 (1718); Knavel Adans., Fam. 2: 506 (1763).

S. annuus L., S. perennis L., S. pungens R. Br., S. diander R. Br., ? S. alpestris Hay., ? S. hanatus Chiov., ? S. velebiticus Degen & Rossi.

Scleranthus annuus L., Sp. Pl. Ed. 1: 406 (1753).

Syn: S. polycarpus L., Cent. Pl.: 216 (1755 - 56); S. collinus Horn. ex Opiz., Nat. 10: 232 (1825); S. comosus Dum., Fl. Belg.: 23 (1827); S. divaricatus Dum. l.c.: 23 (1827); S. verticillatus Tausch. in Flora 12: 50 (1829); S. uncinatus Schur in Verh Sieb. Ver. Nat. 1:107 (1850); S. beinnis Reut. in Compt. Rend. Soc. Hal.: 20 (1853 - 54); S. delorti Gren. in F. Schultz, Annot. Fl. Fr. & Allam. 205 (1855); S. martini Gren. l.c.: 206 (1855); S. pseudopolycarpos Lac. in Bul.. Bot. Fr. 6: 558 (1859); S. campestris Schur. Enum. Pl. Trans.: 224 (1866); S. praecox Wallr. ex Hoeme, in Ost. Bot. Zeit 24: 144 (1874); S. polycarpus DC. ex Nym., Consp.: 257 (1778 - 79); S. imbricatus G. Beck in Ann. Nat. Hof. Wein 2: 66 (1887); S. pumilus Gillot & Coste in Bull. Soc. Fr. 38: 127 (1891); S. ruscinonensis Gillot & Coste l.c.: 127 (1891); S. fasciculatus Gillot & Coste in Bull. Soc. Fr. 40: 123 (1893); S. microcarpus Schur in Verh. Nat. Ver. Brunn 33: 201 (1895); S. syraschicus Kleopov. in J. Bot. Acad. Sc. Ukrane (1839): 248 (1839); Reichenbach species in W. Rossler in Ann. Nat. Mus. Wien, Bd. 57: 97 - 129 (1949 - 50).

Small/ ....

Small annual or occasionally biennial herbs, suberect to prostrate. Stems covered in short hairs, up to 20 cm, much branched at base, occasionally purple in colour, often woody at base. Leaves opposite, sometimes in fascicles, linear, 4 - 15 mm, pungent, pubescent. Stipules totally adnate to leaf margins and connate at base to give small membranous structure between leaves. Inflorescence terminal dichasial cyme, much branched. Bracts foliar, larger than flowers, c. 5 mm. Sepals 5, lobes equal, narrow membranous margins. Stamens 5, antisepalous; 5 staminodes alternating with sepals c. 0.05 mm, both stamens and staminodes attached to apex of greatly elongated perigynous zone. Ovary 1 ovule; 2 styles; evidence of strand of transmitting tissue from apex of ovary to apex of placental column. (Fig.21.1)

Distribution: Europe, N. Africa, S. Africa, Turkey, N. America.

Brummitt 1966; Tobey 609, Turkey.

Subgenus Mniarum Pax in Engler & Prantl, Nat. Pflanzenfam. 3 Teil 16: 92 (1889).

Syn: Mniarum Forst., Char. Gen. Pl.: 1 (1776); Ditoca Banks & Solander ex Gaertn., Fruct. 2: 196 (1791).

S. biflorus (Forst.) Hook. f., S. mniaroides F. Muell., S. minusculus F. Muell.

Scleranthus biflorus (Forst.) Hook. f., Fl. New Zealand 1: 74 (1852).

Syn: Mniarum biflorum Forst. Char. Gen. Pl.: 1 (1776); Ditoca muscosa Banks & Solander ex Gaertn., Fruct 2: 196 (1791); Mniarum pedunculatum Labill., Fl. Nov. Holl.: 8, t.2 (1804); M. fasciculatum R. Br., Prod. Fl. Nov. Holl.: 412 (1810); Scleranthus fasciculatum (R. Br.) Hook. f., Fl. Tasman. 1: 42 (1855); S. brockiei P. A. Williams in Rec. Domin. Mus. N. Z. 3: 16c (1959); S. uniflorus P. A. Williams l.c.: 16 (1959).

Perennial herbs, small, occasionally suberect, usually prostrate, mat forming, often spreading over large area. Stems covered in short hairs, becoming woody at base, up to 15 cm. Leaves opposite, linear 3 - 6 mm, short spine at apex. Stipules reduced to membranous band joining the base of leaves together and as membranous margin of leaf. Flowers in axils of leaves on glabrous peduncles which elongate at maturity/ ....

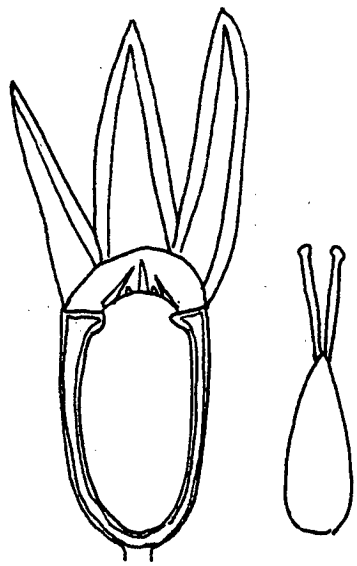
FIGURE 21

21.1 L.S. of flower of Scleranthus annuus L.

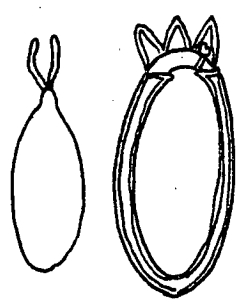
21.2 L.S. of flower of S. biflorous (Forst.) Hook. f.

21.3 L.S. of flower of Habrosia spinuliflora (Ser. ex D.C.) Fenzl

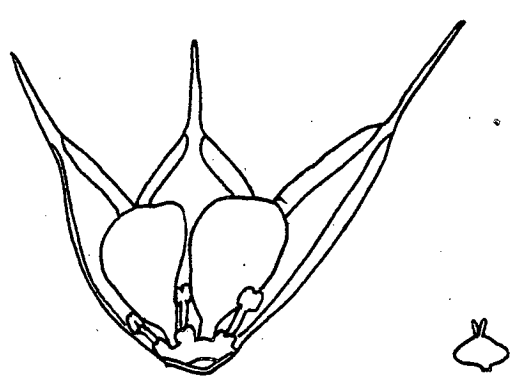
FIGURE 21



21.1



21.2



21.3

Scale 1 mm

maturity, very distinct, up to 15 mm. Flowers solitary or in pairs. Bracts membranous, triangular c. 0. 8 mm, shorter than flowers, usually 4 on each peduncle. Sepals 4 - 5, glabrous, hard, shiny, lobes equal with membranous margins. Stamens 1 - 2, antisepalous, no staminodes observed. Ovary ovate, sessile; 1 ovule; evidence of strand of transmitting tissue from apex of ovary to apex of placental column/ funicle; 2 styles, free. (Fig.21.2)

Distribution: Australia.

R. Brown 3040, Australia.

TRIBE VI HABROSIEAE

31. HABROSIA Fenzl in Bot. Zeit. 1: 322 (1843).

Syn: Habrozia Lindl., Veg. Kingd.: 528 (1847).

Type Species: H. spinuliflora (Ser. ex DC.) Fenzl.

Monotypic Genus.

Annual herbs, small, erect, up to 14 cm. Stems filiform much branched, slightly purple in colour, covered sparsely in very short hairs, sometimes glabrous. Leaves opposite, linear, obtuse, 0.7 - 2.5 cm, sparsely covered in short hairs or glabrous. Stipules totally adnate to margins at leaf base, with membranous band between the leaves at base. Inflorescence terminal, lax, cyme. Bracts foliar, shorter than leaves, c. 3mm. Flowers on pedicels; pedicels up to 6 mm in length. Sepals 5, glabrous, ovate, with wide membranous margins, apex with long spine. Petals 5, rotundus, narrowed at attachment to perigynous zone, white, shorter than sepals. Stamens 5, antisepalous, with distinct glands attached to adaxial surface extending in front of petal bases. Ovary very small, subsessile; 2 ovules, 1 seed, attached to short basal placental column; evidence ovary completely septate at some stage; 2 styles, free, very short. Fruit indehiscent.

Distribution: Turkey, Iraq, Syria.

Habrosia spinuliflora (Ser. ex DC.) Fenzl, in Bot. Zeit. 1: 322 (1843).

Syn: Arenaria spinuliflora Ser. ex Dc., Prodr.1: 406 (1824). (Fig.21.3)

Davis 42433, Turkey.

CHAPTER 5

CONCLUSIONS

The floral morphology of species examined in this work has revealed both new facts about the family Caryophyllaceae and has confirmed, with additional information, ideas already reached about the family by others. The 3 results chapters, while each standing on its own, are related, information from one chapter confirming conclusions reached in another.

The study of the reproductive biology of the family has shown that any adaptive significance in style number in this family is difficult to find. Style number, stigmatic area and pollen grain number appear not to be in any way positively related to ovule or seed number, even where comparisons are made between closely related species. This seems a very surprising result and I can only conclude that other factors not totally examined, such as stigmatic papillae density and number may be of importance. However, it has been shown that variation in style number, stigmatic papillae distribution and style fusion can be used to group the genera.

Further it is evident from the de-styling experiments of 5-styled species that the number of styles can be reduced to 3 or 2 without affecting the number of seeds formed per ovary. This suggests firstly that there is an upper limit to the number of ovules that can be fertilized and develop into seeds (as it is unlikely that the number of pollen tubes from 3 styles is as great as that from 5 styles and thus that the number of ovules fertilized is the same in 3-styled and 5-styled ovaries and, therefore, that a number of fertilized ovules must be aborted in 5-styled ovaries or that the number of pollen tubes from 3, 4 and 5 styles is greater than the number of ovules) and secondly because of the distribution of the seeds that crossing over of pollen tubes from 1 'carpel' to another readily occurs. It was also found that pollen tubes from 1 style could fertilize ovules in at least 3 locules or 'carpels'; the 'carpel' of the style and that on either side. In this family the stigmatic area of all the styles can be considered as a single unit because of the capability of the pollen tubes to cross so readily between 'carpels'.

The position of the transmitting tissue in those ovaries with more/ ....

more than 1 ovule described in the chapter on ovary morphology provided an answer to why pollen tubes should be able to move between 'carpels'. Of the 3 types of ovary found in this family;

1. multi-ovulate ovary completely septate at an early stage in development.

2. usually only 1 ovule, inner wall of ovary with septal ridges, and evidence at anthesis of septal attachments.

3. only 1 ovule, no evidence of septal attachments, but with some evidence of septal ridges.

in type 1 and partly in type 2 at the apex of the ovary the transmitting tissue of each style is found to separate into 2 parts which form part of adjacent septal attachments. Each septal attachment thus has transmitting tissue which is continuous with that of 2 styles. As the septa disintegrate, usually completely except for septal ridges on the ovary wall and the placental column and the septal attachments (disintegrating after anthesis) the transmitting tissue of each septal ridge/septal attachment has 'access' to ovules on either side, i.e. ovules from adjacent 'carpels'. Therefore because of the disintegration of the septa, giving free central placentation at anthesis in these 2 types of ovaries, pollen tubes from the transmitting tissue of 1 style has 'access' to the ovules of 3 locules or 'carpels'. Where the septa remain intact at the base of the ovary, thus preventing 'movement' of pollen tubes, this advantage is lost. This conclusion is supported by results from the de-styling experiments where in Silene coeli-rosa which remains septate at the base at maturity the number of seeds produced was less than in the other species examined.

However, in these 2 types of ovary crossing over of pollen tubes can also come about by a different method. At the apex of the ovary, before locules become evident, the transmitting tissue of all the styles fuse into a single tissue and there appears to be no barriers to prevent pollen tubes crossing from 1 area to the next. This explains why in Agrostemma githago, if even only 1 style is left on the ovary, seeds are found in all 5 locules.

In/ ....

In the third type of ovary, pollen tubes were found on the inner wall of the ovary sometimes on septal ridges on the ovary wall or in any position. Examination of these ovaries revealed different growth patterns of the septa. In some species no septa were evident, in others septal ridges were only evident on the ovary wall and often reduced in number to that expected, and in yet others, septal ridges were evident on the ovary wall and the base of the ovary appeared at some stage to be septate. Except in Corrigiola where no septal tissue was observed, pollen tubes were found in the transmitting tissue of the septa.

Observations of the ovary, particularly the growth of the septa and the vascular tissue, has led me to support the views of Melville, Meeuse, Moeliono and many others that in this family there is a fertile axial part to the ovary bearing the ovules, and a sterile part forming the ovary wall, the styles, and the septa and that each component of the ovary, usually termed a carpel, consists therefore of a sterile leaf-like component, the margins of which form the septa and a fertile branch system which bears the ovules. The nature of this fertile branch system is discussed in the chapter on ovary morphology but no firm conclusion could be reached as to the exact nature of the branching. Observations of the vascular system has also revealed that in Agrostemma githago the central vascular tissue (xylem vessels) extends into the septal tissue without supplying ovules and that this may well be the case in other species in this family.

Observations on the ovary have been of great value in helping to confirm the position of genera in the chapter on the taxonomy of the subfamily Paronychioideae, and the type of ovary found in each of the tribes is indicated. Examination of the floral morphology in this group has also identified which of the structures alternating with the sepals are sterile stamens and which are petals (assuming that in terms of describing the flower, there is a difference in these 2 structures) by observing the distribution of glandular tissue in this subfamily with that in the other subfamilies. This information and the information on ovary type has led me to transfer genera from one tribe to another and to create new subtribes. The descriptions of the genera and species include these new observations although no major changes have been made to the concept of the genera in this subfamily.

The/ ....

The study of floral morphology within the family Caryophyllaceae, has demonstrated how useful information gained from direct observation and from sections can be in revealing new factors: taxonomic, ecological, evolutionary and physiological. It also has demonstrated that information gained from one investigation, e.g. de-styling experiments, can be used to confirm conclusions reached in a different investigation. Further investigation of other species, especially of their vascular system, is required before any firm conclusion can be reached about the exact nature of the ovary in this family. It would also be of interest to study in the same detail other families with so-called free-central placentation such as the Primulaceae and Balsaminaceae to see if the position of the transmitting tissue within these ovaries is the same and to see if the same results would be found in de-styling experiments. A study of vascular tissue of Impatiens balsamina by L. Simon (1975) has found a similar internal and external vascular system and concluded that the ovary is composed of a sterile part forming the ovary wall and of a fertile axial part, the growth and disintegration of the septa being found to be the same.

Further work on several of the genera in the subfamily Paronychioideae (Lochia/Gymnocarpos and Polycarpon/Polycarpaea) would be helpful in separating these genera. Likewise within the other subfamilies much taxonomic work is still required especially around the Silene group of genera.

I hope this thesis has demonstrated the usefulness of investigations on floral morphology and that a great deal of information has still to be discovered.

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APPENDIX I

Subfamily Dianthioideae

Acanthophyllum korolkowii Rgl., R. Goodier 1216.

A. microcephalum Boiss., Davis 23/6 9.

Agrostemma githago L., Gahn (1899).

Allochrusa bungei Trautv., Davis 46862.

A. gypsophiloides Schischkin, F. Cusk 203.

Ankyropetalum gypsophiloides Fenzl, P. Sintenis 1157.

Bolanthus fraukenioides (Boiss.) Bark., J. Contandriopoulos et al. $22/6^{B}/2^{9}$.

B. graecus (Schneber) Bark., Dr. Heldreich (1885).

B. hirsuta (Labil.) Bark., Davis 9828.

Cucubalus baccifer L., Davis 13168

Dianthus furcatus Balb., Dr. E. D. Rostan (1880).

D. sequieri Vill., J. Kraenzle (1908).

Drypis spinosa L., Theodorus 185.

*Gypsophila elegans Bieb

*G. repens L., R. 7, 32 R. B. G.

Lychnis alpina (L.) D. Gunn., Henderseon & Wilson 474.

L. coronaria (L.) Desr., Davis 37780.

Petrocoptis glaucifolia (Lag.) Boiss., D. W. Dresser 1220.

*Petrorhagia saxifraga (L.) Link, Rock Gardens, R. B. G.

P. velutina (Guss.) Ball & Heywood, B. V. Burbidge 232.

Phryna ortegioides (Fisch. & Meyer) Pax & Hoffm., Schischkin 435.

Pleioneura griffithii (Boiss.) Rech. f., D. Podlech 12176.

*Saponaria officinalis L., Demonstration gardens, R. B. G.

S. glutinosa Bieb., Marsoran (1909).

+Silene alba (Mill.) Krause, Waste ground, Stirling Rd., Camelon.

S. alpestris Jacq., Dorfler (1886).

S. ampullata Boiss., J. Bornmüller 876.

*S. armeria L. R. 9 715 822 R. B. G.

S. coeli-rosa (L.) Gordon, P. E. Gibbs (1972).

S. conica L. T. Ekin 349.

S. conoidea L., Davis 43361.

*S. dioica (L.) Clairv., Demonstration Garden, R. B. G.

S. laeta (Ait.) A. Br., Lainz (1960).

S. macrantha (Panc.) Neu., F. Lempberg (1938).

S. thymifolia Sibth. & Sm., B. Kitanov (1954).

*Vaccaria pyramidata Medik., Annual border R. B. G.

Velezia fasciculata Boiss., Davis 4742.

V. hispida Boiss., Davis 18422.

V. quadridentata Sibth. & Sm., Herbarium Normale 4020.

V. rigida L., A. Fiori & R. Pampanini 259.

Viscaria viscosa Ascherson, S. A. Thumanian 47.

Subfamily Alsinoideae

Arenaria dianthoides Sm., J. Lamond 4657.

A. grandiflora L., Dominguez 203.

A. kotschyana Fenzl, Davis 31639.

A. orbiculata Royle ex Edgew. & Hooker f., Stainton, Sykes & Williams 374.

Brachystemma calycinum D. Don, L Martin 2978.

Bufonia calyculata Boiss., Davis 23, 878.

B. valentina Pall. Wilkomm 693.

*Cerastium arvense L., Nursery Garden Bed, R. B. G.

+C. fontanum Bourmg., Callendar Park, Falkirk.

+C. tomentosum L., Punscore Dumfriesshire.

Colobanthus quitensis (Kunth) Bartl., T. R. Dudley et al 1545B.

Holosteum marginatum C. A. Meyer, Tobey 523A.

Honckenya peploides (L.) Ehrh., C. Hansen 374.

Lepyrodicilis holosteoides (C. A. Meyer) Fenzl ex Fisch. & Meyer, R. W. Haines 608.

Minuartia geniculata (Poir.) Thell., P. E. Gibbs et al 828.69.

M. hamata (Hausskn.) Mattf., Davis 42790.

M. imbricata (M. B.) Woronow, Davis 32311.

M. juniperina (L.) Maire & Petitm., E. Parry 48.

Moehringia muscosa L., F. Kerner 559.

M. trinervia (L.) Clairv., P. Auquier 3118.

Moenchia graeca Boiss. & Heldr., O. Krebs (1895).

M. mantica (L.) Bartl., Demiriz 1586.

Myosoton aquaticum (L.) Moench, A. Roth (1889).

Pentastemonodiscus monochlamydeus Rechinger, Rechinger 17834, Typus.

Pseudostellaria europaea Schaeft., Deschmann 551.
Pychnophyllum convexum Gr., Flora Argentina 365.
Sagina apetala Ard., A. Perard 1384.
S. nodosa (L.) Fenzl, R. Alva 10136.
Schiedia spergulina A. Gray, A. A. Heller 2446.
+Stellaria alsine Grimm., Callendar Park, Falkirk
+S. graminea L., Callendar Park, Falkirk.
+S. media (L.) Vill, Callendar Park, Falkirk.
Thurya capitata Boiss. & Bal., Flora Orientalis 264.
Thylacospermum caespitosum (Camb.) Schischk., O. Polunin et al 1140.
Wilhemsia physodes (Ser.) McNeil, G. Halliday A 47/75.

Subfamily Paronychioideae

Achyronychia cooperi Torr. & Gray, Ball 11177.
Cardionema polychemoides Bartl., Abrams 2517.
Cerdia congestiflora Hemsl., Plantae Mexicanae 6 965.
Chaetonychia cymosa Sweet, R. V. Murray (1889).
Cometes surattensis L., H. Foroughi 10708.
Corrigiola litoralis L., B. Valdes 1111/73.
Dicheranthus placamoides Webb, D. Bramwell 2031.
Drymaria villosa Cham. & Schlecht., H. Kanoi et al 726404.
Gymnocarpos decander Forskal, H. Bobek 196.
Habrosia spinuliflora Fenzl, E. M. Rix 1894.
Haya obovata Balf, f., Oglive-Grant-Forbes 193.
Herniaria fontanesii J. Gay, Davis 57324.
H. glabra (Bauhn.) L., P. Auquier 3158.
Illecebrum verticillatum L., A. Matthies 4527.
Lochia bracteata Balf. f., Oglive-Grant-Forbes 84.
Loeflingia hispanica L., E. Boisser (1837).
Microphyes litoralis Phil., Dr. Werdemann 162.
Ortegia hispanica L. E. Jahandiez 5.
Paronychia arabica (L.) DC., Davis 8536.
P. argentea Lam., P. Gibbs et al 1626/69.
P. kapela (Hacq.) Kerner, S. Silvestre (1968).
P. mughlaei Chowdhuri, Davis 13393.
P. suffructicosa (L.) DC., Diminguez 121.
Pollichia campestris Ait., E. Meston 10.

Polycarpaea repens (Forskal) Ascher. & Schwenf. ex Ascher., Davis 9303.

P. teneriffae Lam., Dr. O. Burchard 117.

Polycarpon colomense Porta, Porta (1885) TYPE

P. robbairea O. Kuntze, Davis 49590.

P. tetraphyllum (L.) L., M. Coode et al 650.

Pteranthus dichotomus Forskal, R. Wheeler Haines (1955).

Scleranthus annuus L., Jacobsen et al (1969).

S. perennis L. Demiriz 356.

Sclerocephalus arabicus Boiss., Pitard (1909).

Scopulophila rixfordii (Brand.) Munz & Johnston, C. A. Purpus 6037.

Spergula arvenis L., S. Silvestre 1207/73.

Spergularia bocconii (Schede) Ascherson. & Graebn., R. K. Brummitt et al 942.

S. fimbriata Boiss. Smythies 161.

S. larranagae Phil., Dr. Werdemann 799.

Sphaerocoma hookeri T. And., A. Deflers 520.

Stipulicida setacea Michx., S. W. Leonard 4784.

Telephium oligospermum Steud., Davis 44992.

* Plants cultivated in the Royal Botanic Gardens, Edinburgh.

+ Plants collected from natural habitats.

All other plants observed from herbarium specimens, collector and number or date cited, held at the Royal Botanic Gardens, Edinburgh.

APPENDIX II

Variation of style length after drying and pressing

Myosoton aquaticum Acc. 82.

Character / Style No.	Fresh style length	Dry style length	Length after boiling dry style	Difference between boiled and fresh length
1	2.7 mm	1.9 mm	2.3 mm	- 0.4 mm
2	2.7 mm	2.2 mm	2.3 mm	- 0.4 mm
3	2.4 mm	2.1 mm	3.0 mm	+ 0. mm
4	2.5 mm	2.3 mm	2.0 mm	- 0.5 mm
5	2.7 mm	2.3 mm	2.3 mm	- 0.4 mm

One style from each flower, 5 flowers from same plant.

Lychnis coronaria Acc. 42.

Character / Style No.	Fresh style length	Dry style length	Length after boiling dry style	Difference between boiled and fresh length
1	11.5 mm	10.2 mm	13.0 mm	+ 1.5 mm
2	7.7 mm	6.6 mm	10.0 mm	+ 2.3 mm
3	10.8 mm	8.1 mm	12.0 mm	+ 1.2 mm
4	5.8 mm	5.8 mm	6.2 mm	+ 0.4 mm
5	13.0 mm	10.9 mm	11.7 mm	- 1.3 mm

One style from each flower, 5flowers from same plant.

Gypsophila/ ....

Gypsophila fastigiata Acc. 83

Character Style No.	Fresh style length	Dry style length	Length after boiling dry style	Difference between boiled and fresh length
1	6.3 mm	4.7 mm	5.2 mm	1.1 mm
2	5.3 mm	4.5 mm	4.5 mm	- 0.2 mm
3	5.5 mm	5.5 mm	5.0 mm	- 0.5 mm
4	6.0 mm	5.2 mm	4.8 mm	- 1.2 mm
5	3.5 mm	2.7 mm	3.2 mm	- 0.3 mm

Of the 3 species examined, in 2 style length decreased after drying and pressing followed by boiling and in the other, style length greatly increased after these procedures. It is likely that in the specimens examined that style length would be greater in some and in others less than the true style length where style length was determined from herbarium specimens by the styles (usually the whole flower) being gently boiled in water. The differences in values obtained from using these measurements rather than measurement of fresh material also has added error into the results obtained in the section on style length, style number, and ovule number in the family as a whole in Chapter 3.

Myosoton aquaticum Acc. 82, Gembloux, Belgium.
Lychnis coronaria Acc. 42, A. Baytop 38094, Turkey.
Gypsophila fastigata Acc. 83, Stockholm, Sweden.

INDEX TO SPECIES IN CHAPTERS 2, 3, & 4.

CHAPTER 2

CHAPTER 3

CHAPTER 4/ ....

CHAPTER 4

Only accepted names underlined.

Bivonaea/ ....

C./ ....

D./ ....

D./ ....

H./ ....

I./ ....

M./ ....

P./ ....

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S./ ....

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