STUDIES IN THE GENUS HYPERICUM L.

by

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Ever since Linnaeus drew attention to the presence of groups of stamens in the flowers of certain species by establishing his Class XVIII Polyadelphia, this condition has been the subject of recurrent investigations and speculation. Interest has centred largely in species of the genus Hypericum which is the only member of the class Polyadelphia to be found in Europe. Botanists have approached the problem from several angles but, although much information has been obtained, there appears to have been no attempt to synthesise it. The following work has therefore been done with the aim of throwing more light on the morphological variation in the flowers of Hypericum and related genera, and in the hope that the knowledge gained in this way will help to suggest a method of reclassifying this group in a more natural manner. No attempt has been made to treat Hypericum monographically; but this morphological, anatomical, cytological and geographical survey may be of use in a future revision of the genus.
CHAPTER I.

INTRODUCTION.

(1) The Taxonomic Relationships of Hypericum.

Most authorities agree that the series of genera to which *Hypericum* belongs is closely related to the *Theaceae* and the *Dilleniaceae*; but, while Bentham and Hooker (1862) and Hutchinson (1926) give it the rank of a family, *Hypericaceae*, other authors, e.g. Engler (1895, 1925), Bessey (1915) and Wettstein (1924), include it in the *Guttiferae* (or *Guttiferaceae*, as Bessey calls it). The two points of view may be summarised by quoting the respective classifications of Bentham and Hooker, and Engler:

**Bentham and Hooker**

- *Ternstroemiaceae*
  - Tribe VI *Bonnetieae* *(Kielmeyera etc.)*

**Hypericaceae**

- Tribe I *Hypericeae*
  - II *Cratoxyleae*
  - III *Vismieae*

**Guttiferae**

- Tribe I *Clusieae*
  - II *Moronobeae*
  - III *Garcinieae*
  - IV *Calophylloideae*
  - V *Quiineae*

**Engler**

- *Guttiferae*
  - Sub-fam. I *Kielmeyeroideae*
    - Tribe 1. *Kielmeyereae*
    - 2. *Carapiaceae*
  - Sub-fam. II *Hypericoideae*
    - Tribe 1. *Hypericeae*
    - 2. *Cratoxyleae*
    - 3. *Vismieae*
  - Sub-fam. III *Calophylloideae*
    - Tribe 1. *Calophylleae*
    - 2. *Endodesmiaceae*
  - Sub-fam. IV *Clusioideae*
    - Tribe 1. *Clusieae*
    - 2. *Garcinieae*
  - Sub-fam. V *Moronoboidae*
There is also general agreement that the Guttiferae s.l. are most closely allied to the Bonnetiaceae among the tribes of the Theaceae, an idea which has received support from the anatomical investigations of Muller (1882) and Vestal (1937). Vestal concluded that the Quiineae differ morphologically and anatomically from the other Guttiferaeous tribes of Bentham and Hooker, and considered that it has been derived from the Theaceae in a line parallel with the one along which the Guttiferae have evolved. He also pointed out that there are no fundamental differences between the Hypericaceae and the rest of the Guttiferae, and that the one is a 'logical outgrowth' from the other, so that the question of separating them as two families or not is one of personal preference. On the basis of the available evidence he, himself, regarded them as parts of the same family.

In the latest edition of the 'International Rules for Botanical Nomenclature' (1952), 'Guttiferae' is listed as a 'nomen conservandum' and 'Hypericaceae' as an alternative name ending in '-aceae', i.e. the two names are treated as synonymous. However, since the name Hypericaceae has not been in general use in the broad sense, it might cause more confusion to adopt this usage than it would if Guttiferae were made to include both groups, as Engler and others have done. It is therefore suggested that the name Guttiferae be applied in the Englerian sense, with the possible exclusion of the Kielmeyeroideae. This tribe is undoubtedly closely related to the Bonnetiaceae, probably more so than to the Guttiferae.
Guttiferae. Indeed, Metcalfe and Chalk (1950) separate the Bonnetiaceae as a family, Bonnetiaceae, which they place between the Theaceae and the Guttiferae, at the same time pointing out its resemblances to the Kielmeyceroidaceae.


Before discussing Hypericum it will be helpful to give a brief description of the variation in floral morphology to be found in theHypericoideae as a whole. The three tribes of this subfamily, according to Engler, are (a) Vismiae, characterised by e.g. a baccate or drupaceous fruit; (b) Cratoxyleae, where the fruit is capsular and the seeds winged; and (c) Hypericeae, in which the fruit is usually also capsular. These tribes contain the following genera:

Vismiae - Vismia (Velloz. ex) Vand., Psorospermum, Spach, Harungana Lam.
Cratoxyleae - Cratoxylon Blume, Eliaea Cambess.
Hypericeae - Hypericum L., Ascyrum L.

The genera of the first two tribes have flowers in which groups of stamens (fascicles) alternate with structures whose morphological significance has been much discussed. These structures, which are reminiscent of staminodes, are absent from most species of Hypericeae.

The perianth in the Hypericoideae, unlike that of many species in the rest of the Guttiferae, is nearly always pentamericous, although tetramermy occurs as an
an aberration in Hypericum and as the typical condition in Ascyrum. However, in Psorospermum chevalieri Hochr. all the floral whorls vary between pentamery and hexamery (Hochreutiner, 1919). When the calyx is pentamericous the sepals are quincunxially imbricate, but the tetramericous forms have two opposite and decussate pairs of sepals which continue the foliar phyllotaxis. On the other hand, the petals always arise at the same level, i.e. in a single whorl, the aestivation of which is usually contorted. In some species each petal bears a basal appendage analogous to those which occur in Ranunculus. Such appendages are constantly present in Hypericum elodes L., H. aegypticum L. and H. russegeri Fenzl, sometimes absent in Eliaea (Perrier de la Bathie 1948, 1951), and present in only some species of Cratoxylon. In Psorospermum they are usually present but may be very small (Perrier de la Bathie, l.c.), while they do not occur at all in Vismia (Hochreutiner, 1918). It is not known whether or not they are found in Harungana.

The androecium of the Vismiaceae, Cratoxyleae, and most of the species of Hypericeae consists of fascicles of stamens (usually five or three, more rarely four), which are antepetalous when they are isomerous with the perianth members; but Ascyrum and most American species of Hypericum have an androecium in which the stamens are not arranged in fascicles. If staminode-like structures are present they alternate with /
The ovary may consist of from five to two carpels, five and three being the most usual numbers. All the **Vismieae** have five carpels (except in some flowers of *Psorospermum chevalieri* mentioned above) and the **Cratoxyleae** have three, but in *Hypericum* and *Ascyrum* the number varies from five to two and four to two respectively. The styles are equal in number to the carpels, except in some 5-carpellary flowers of *H. habbeense* A.C. Smith which have six styles (Smith, 1941). They are free, except in some species of *Hypericum* and *Ascyrum*. The placentation is usually axile, but all transitions between axile and parietal occur in *Hypericum* and it is completely parietal in *Ascyrum*.

The fruit in *Vismia* is a many-seeded berry, in *Psorospermum* a few-seeded berry, while *Harungana* has a few-seeded drupe. In the other two tribes it is usually capsular but, while the capsule in the *Hypericineae* is always septicidal, the mode of dehiscence varies in the **Cratoxyleae**. In *Cratoxylon* it appears to be always loculicidal, but authorities differ with regard to the capsule of *Eliaea*. Spach (1836) describes it as septicidal, Engler (1925) calls it loculicidal, while Perrier de la Bathie (l.c.) states that it dehisces septicidally first and then loculicidally. Certain species of *Hypericum* have evolved more or less succulent fruits (e.g. *H. androsaemum* L., *H. peplidifolium* A. Rich.), while in *H. olivieri* (Spach) Boiss. the deeply tri-
sulcate /
sulcate capsule splits into one-seeded mericarps.

The seeds are non-endospermic in all three tribes, as in the rest of the Guttiferae. Those of the Cratoxyleae have cartilaginous wings. In a few species of Hypericum the seeds are also winged, but the wings in this genus are membranous.

The floral formulae of the three tribes are as follows:

Vismieae - K₅ C₅ A₅s+5f G(5) (s = staminode-like structure, f = fascicle)

Cratoxyleae - K₅ C₅ A₅s+5f, or 3s+3f G(5)

Hypericeae - K₅-4 C₅-4 A₀s+3-5f, or 3s+3f, or 0s+00f G(5)-(2)

It may be seen that, while the first two tribes show little variation in numbers of floral parts, the numbers in the Hypericeae vary more widely, and this morphological variability has led to several conflicting methods of classifying the tribe.

(3) The Classification of Hypericum.

Authors have differed widely in their interpretation of the generic limits of Hypericum, and so it will be necessary to consider all the plants included in Engler's Hypericeae. He divides this tribe into two genera /

* Excluding some flowers of Ps. chevalieri.
genera, _Hypericum_ (with a pentamerous perianth) and _Ascyrum_ (with a tetramerous perianth), but remarks that _Ascyrum_ may be polyphyletic. It consists of a number of related species in N. America and the Antilles, and also a single species from the Himalayas (_A. filicaule_ [Hook. f. et Th.] Dyer) which, he states, is probably more closely related to some Old World species of _Hypericum_ than to the other species of _Ascyrum_. It will be shown later that this idea is correct.

The most recent revision of _Hypericum_ as a whole was made by Keller (1925) who, like all the previous authors, based his subdivisions mainly on differences in floral structure. The following is a summary of his classification:

A. Flowers with hypogynous glands (_staminodes ?)._  
   (Carpels 3).  
   a. 3 fascicles, each with 9-13 stamens. Glands (_staminodes ?) fleshy.  
      Sect. I _Triadenia_ (Spach) Keller.  
      Sect. II _Adenotrias_ (Jaub. et Spach) Keller.  
   b. 3 fascicles, each with 3-5 stamens. Glands (_staminodes ?) scale-like.  
      Sect. III _Elodes_ (Adans.) Keller.  
      Sect. IV _Elodea_ Juss.

B. Flowers without glands (_staminodes ?)._  
   a. Stamens in fascicles.  
      I. Stamens in 5 fascicles. (Carpels 5).  
         Sect. /
Sect. V Thasium Boiss.

Sect. VI Eremanthe (Spach) Endl.

Sect. VII Campylosporus (Spach) Endl.

Sect. VIII Norysea (Spach) Endl.

Sect. IX Roseynia (Spach) Endl.

II. Stamens in 5 fascicles (carpels 5), or often 4 fascicles and 4 carpels.

Sect. X Psorophytum (Spach) Endl.

III. Stamens in 5 fascicles, carpels 3.

Sect. XI Androsaemum (Adans.) Gren. et Godr.

IV. Stamens in 3 fascicles, carpels 5.

Sect. XII Humifusoidesm Keller.

V. Stamens in 3 fascicles, carpels 3.

Sect. XIII Webbia (Spach) Endl.

Sect. XIV Euthypericum Boiss.

b. (b) All stamens very shortly fused together, or almost free.

Sect. XV Campylocus (Spach) Endl.

Sect. XVI Myriandra (Spach) Endl.

Sect. XVII Brathydium (Spach) Endl.

Sect. XVIII Brathys ([Mutis ex] L.f.) Choisy.

It will be seen that Keller lays most emphasis on the presence or absence of what he refers to as 'hypogyne Drusen (Staminod.?)'. These structures have been called nectaries, hypogynous glands, disc (axial) structures and staminodes by different authors. However, Hochreutiner (1918) has pointed out that they do /
do not secrete nectar and are not glandular, and so the first two terms are inappropriate. Since similar structures occur constantly in the other tribes of the Hypericoideae, the inference has been drawn that the species in the first four sections of Hypericum are relicts which still retain some of the ancestral characters of the genus. Indeed, they have been placed in separate genera by some authors. Adanson (1763) proposed the genus Elodea for H. aegypticum (Sect. Triadenia) and, apparently, for H. elodes (Sect. Elodes). (Although he does not mention this species by name, one of his citations refers to it.) Spach (1836, 1842) made all four sections into separate genera, but Endlicher (1840, 1850) reunited them as Elodea, and Bentham and Hooker (1862) included them all in Hypericum. Recently, however, several authors have separated Sect. Elodea again as Triadenum Raf.; while Kimura (1935, 1951) has united Sects. Triadenia and Adenotrias as the genus Elodes (Clusius ex) Adans. and placed H. elodes in a new genus, Spachelodes Kimura. He even transferred these genera from his Hypericoideae to the Vismioideae, implying that they are more closely related to the tropical genera than to Hypericum.

The question therefore arises whether the staminode-like structures in this group are homologous with those of Vismia, Cratoxylon etc. or have arisen 'de novo'. If they are homologous, Kimura's classification may be correct; but if they are 'new' floral structures, then a reclassification of Hypericum would be indicated, since there would be no justification for deeming /
deeming their presence to be of primary importance, as Keller does.

This problem has already been investigated by one or two authors, but their results are conflicting. Hirmer (1917) considered the structures to be nectaries, and stated that they appeared later in the ontogeny of the flower than the other parts. On this evidence he asserted that they were not staminodia but a completely sterile part of the floral axis, a conclusion which he supported by the observation that they contained numerous rudimentary vascular strands.

Saunders (1936) agreed that they had "the usual form of disc (axial) outgrowths", but maintained that they were not vasculated. Both these authors examined *H. elodes* and *H. aegypticum*. The only species of Sect. *Adenotrias* (*H. russeggeri* Fenzl) differs from *H. aegypticum* in one or two technical characters, but appears to be closely related to it. These three species all have yellow petals with appendages and occur in the Mediterranean region or W. Europe. On the other hand, Sect. *Elodea* occurs in E. Asia and E. North America, and its species have pinkish-purple or white petals with appendages. Hence it would seem that Keller's subdivision of this group of four sections according to the number of stamens per fascicle and the nature of the 'hypogynous glands' is artificial, and that the first three sections have much more in common with each other than with Sect. *Elodea*.

The problems posed by the present classifications of these four sections (the *Elodes* group) are:

(i) /
(i) whether these staminode-like structures are, in fact, staminodes or merely axial outgrowths;

(ii) whether they are homologous with those in other species of Hypericoideae, and

(iii) how the members of the Elodes group are related to one another and to the rest of Hypericum.

The remaining sections of Hypericum are divided into two series depending on whether the androecium consists of fascicles of stamens or an indefinite number of almost free stamens; and it is this division that has been the subject of so much speculation by morphologists. The various interpretations of the stamen fascicles may be classified under three general theories:

(a) Goebel (1905) and Hirmer (a pupil of Goebel) among others have supported what may be termed the Aggregation Theory, according to which the occurrence of fascicles is thought to be a result of the restriction of stamen formation to certain sectors of the torus. In Goebel's view this restriction is due to sterilisation of the antesepalous toral sectors, while Corner (1946) related it to a "prominent humping, or radial lobing of the floral disc in its early stages [which] seems very clearly to be connected with the diminution in size of the floral bud." He attributes the humping to "the pressure of the perianth segments on the floral disc as they develop", and to "their very close proximity with the incipient androecium." The adherents of the Aggregation Theory therefore regard the afascicular androecium as the primitive type from which the fascicular condition has been derived.
(b) The Dédoublement Theory of Moquin-Tandon (1826) has been invoked to interpret the floral structure of Hypericum by many workers e.g. Dunal (1829), Moquin-Tandon and Barker-Webb (1848), Payer (1857), Hofmeister (1868), Pfeffer (1872), Molly (1875), Eichler (1875, 1878), Celakovsky (1894), Velenovsky (1910), Warming (1872, 1873, 1909) and Saunders (1936, 1939). All these authors refer to a splitting or multiplication of an originally single primordium with the result that "in place of one stamen, which ordinarily exists in organic symmetry, one finds many stamens" (Moquin-Tandon's definition of dédoublement). On the basis of this theory, then, one would have to postulate an ancestral type of flower with five single antepetalous stamens, from which has evolved the typical Hypericum flower with five fascicles.

(c) Wilson (1937 et seq.) has recently opened up a new line of thought by applying the Telome Theory to this problem. To him, "an explanation of the stamen fascicle may be obtained by postulating as the ancestor of the stamen a primitive dichotomous branch system, similar to those known to have existed in ancient and now extinct plants." According to this theory, then, the flowers with fascicles of stamens would be regarded as nearest the ancestral type of Hypericum, the afascicular androecium having evolved by a merging of the fascicles to form a continuous whorl of stamens.

It will be noted that the Aggregation and Telome Theories lead to opposite interpretations of the evolutionary /
evolutionary trends in the Hypericum androecium, i.e. from free stamens to fascicles and the reverse, respectively. In a sense the Dédoublément and Telome Theories also lead to opposite conclusions, i.e. that there has been an elaboration or reduction respectively in the androecium. The problem is therefore resolved into finding out which, if either, of the two groups of Hypericum proper approaches most nearly the ancestral condition for the genus, i.e. whether the species with stamen fascicles have a more, or a less, specialised androecium than those with afasciculur androecia, or if both conditions are derived from five single stamens by dedoublement.

(4) The Floral Ontogeny of Hypericum.

The two main problems outlined above, i.e. (1) the nature of the staminode-like structures in the Elodes group and (2) the relative evolutionary position of fascicular and afasciculur androecia in Hypericum as a whole, can be approached from several directions, three of which seem to hold promise of affording a solution, namely gross morphology, floral ontogeny and floral anatomy. Since most of the previous work on these problems has been concerned with floral ontogeny, it was thought that a systematic investigation of the floral anatomy of Hypericum, in conjunction with a study of the gross morphology of the genus, might yield some useful results, especially since the few existing papers on this subject deal only with species which have stamen fascicles. However, it is necessary to discuss briefly the /
the general results which have been produced by the study of the ontogeny of *Hypericum* flowers.

Payer (1857) showed that the individual floral whorls of a *Hypericum* flower were initiated in acropetal succession. The calyx develops quincuncially and the corolla as a single whorl. If the stamens are in fascicles, the fascicle primordia appear first, and on them the individual stamens arise in centrifugal succession. In *H. prolificum* L. (Sect. *Myriandra*) he described five antepetalous primordia as in the other species examined. The stamens arose on these centrifugally, but the primordia later merged to produce an even zone bearing an indefinite number of stamens.

Hofmeister (1868) claimed that the petal primordia developed after the staminal ones in *H. calycinum* L. and *H. hircinum* L., but Molly (1875) and Sachs (1875) agreed with Payer that the order of appearance of the floral whorls was regularly acropetal. Molly explained that, although the petal primordia appear before the fascicle primordia, they are soon concealed by the latter which develop more quickly and soon overtop the small, retarded petals. These fascicle primordia become two-lobed, and the second (outer) lobe was what Hofmeister mistook for a petal primordium.

Hirmer (1917) confirmed Molly's findings regarding the development of the flower with stamen fascicles, but was not able to see Payer's "five primordia which are separate at first and later fuse" in *H. prolificum*. He alleged that five antepetalous groups of three /
three stamens appeared first, followed by the other stamens in an irregular, centrifugal progression. (It will be recalled that Payer favoured the Dédoublement Theory, while Hirmer was a proponent of the Aggregation Theory). However, in *H. drummondii* (Grev. et Hook.) Torr. et Gr. (Sect. Brathys), another species of the afascicular group, he described the appearance of five original antepetalous stamen primordia, after which one or two more stamens arose below each of the first five.

More recently, Breindl (1934) showed that the sepals in *Hypericum* do not arise in a regular, quincuncial manner. The first two sepals tend to develop almost simultaneously at an angle of divergence wider than the theoretical one of 72°. This tendency is also noticeable to a lesser extent in the next pair of sepals. Breindl explained that these aberrations are a result of the change from the opposite and decussate phyllotaxis of the leaves to the spiral phyllotaxis of the calyx.

From a study of the foregoing and other information on the floral ontogeny of *Hypericum* the following salient points emerge:

1. The floral whorls are initiated in acropetal succession, but the androecium and gynaeceum may develop almost simultaneously.

2. The calyx tends to develop in 2/5 spiral succession, but the time and position of origin of the sepals is modified by the change from foliar to calycine phyllotaxis.

(3) /
(3) In normal flowers the petals arise simultaneously, but their growth is retarded and the androecial members may obscure them for a time.

(4) The individual stamens arise centrifugally, either on fascicule primordia or from the torus.

(5) In *H. elodes* and *H. aegypticum* the primordia of the staminode-like structures arise long after the initiation of the androecium (Hirmer). (The floral ontogeny of *Hypericum Sect. Elodea* and of the other tribes of the *Hypericoideae* has not been investigated.)

(6) Apart from the androecium, the development of flowers with afascicular stamens is similar to that described for flowers with stamen fascicles. Payer claimed that the stamens in *H. prolificum* appear originally on five antepetalous primordia, but Hirmer denied this.
CHAPTER II.

THE FLORAL ANATOMY OF THE HYPERICOIDEAE.

(1) Introduction.

From the above account of the floral ontogeny of Hypericum it will be seen that the researches in this subject have not shed much light on the two basic problems in the genus. Since it is difficult to study the arrangement of the stamens in the mature flowers of many species, it was thought that the floral anatomy might give a clue to the fundamental structure of the flower. Some writers have questioned the value of floral anatomy in helping to solve morphological and evolutionary problems, on the grounds that a vascular strand develops in relation to the nutritional requirements of the organ. If this were so, the presence or absence of vascular tissue would not necessarily be of evolutionary or systematic significance. However, Puri (1951) has collated a large amount of evidence which shows that floral anatomy, when properly interpreted, can be of the greatest assistance in such problems, an opinion which is shared by the author.

Several other workers have investigated the floral anatomy of Hypericum species, notably Saunders (1936, 1939), but all their work has been done on the species with fascicular androecia. Saunders studied H. elodes L. and H. aegypticum L. but, as we have seen, her findings contradicted those of Hirmer (l.c.) in some respects. The only reference to other species of Hypericoideae /
Hypericoideae is made by Wilson (1937), who describes part of the floral vasculature of *Vismia dealbata* HBK.

(2) *Methods and Materials.*

The method usually adopted in studies of floral anatomy has involved a mental reconstruction of the whole flower (or at least the torus and the ovary base) from an examination of serial sections. By this method one is able to make detailed investigations into the orientation of the xylem, phloem and other tissues, but the process of reconstruction is laborious and the danger of misinterpretation considerable. In view of these objections, it was decided to bleach and clear entire flowers, so that the vasculature could be studied as a whole.

Fresh, preserved and dried flowers and buds were used. Herbarium material regained its former shape (more or less) after the treatment described by Tillson and Bamford (1938), i.e. it was soaked in hot water (below 100°C.) for one to two hours and then placed in 5 per cent ammonia at 50°C. for twelve to twenty-four hours. After rinsing in running water the material was bleached and cleared in the same way as fresh or preserved flowers. Fresh material was depigmented in 1:1 alcohol-acetone, but this treatment was not necessary for the preserved or dried buds.

Three bleaching methods were tried. Sporne (1948) advocates the use of alkaline hydrogen peroxide, but this was found to be too weak to bleach any but the smallest flowers, and numerous bubbles were produced in the /
the tissues. A second method (Vautier, 1949) proved to be more satisfactory. A specimen tube with a tightly-fitting cork is half filled with absolute alcohol and the material placed in it. A smaller tube containing a little $\text{KClO}_3$ is then inserted into the larger one, so that the introduction of several drops of concentrated $\text{HCl}$ into the smaller tube results in the evolution of chlorine. (Care must be taken to prevent the alcohol from entering the small tube.) When the cork is fitted the chlorine will dissolve in the alcohol, the solution acting as the bleaching agent. The process is accelerated by putting the tube in the sun, or even in front of a strong artificial light. By this means some small flowers (e.g. those of *H. elodes*) were completely bleached over-night, but in others some colour remained even after two months of repeated immersions in fresh bleaching solutions.

Most of the flowers were bleached by this second method. Towards the end of the work, however, it was found that 'Parazone' would act very much more rapidly without rendering the material any more fragile than Vautier's method did. The largest flowers, e.g. those of *H. cernuum* Roxb., required about two days in concentrated 'Parazone', but most others could be completely bleached in a shorter time using a 25 per cent solution.

The rapid clearing technique suggested by Sporne (l.c.) was found to be quite satisfactory, provided that the material had previously been completely decolorised. This technique "consists of heating the material /
material for a few minutes in pure lactic acid (B.P.) kept at 100°C in a boiling water-bath. The preparation can then be examined in a watch-glass under a binocular microscope and any dissection which may be required can then be carried out."

It was difficult to bleach all but the smallest flowers when entire, while thick hand sections (Sporne, l.c.) tended to disintegrate, and so the ovary was usually removed and bleached separately. The bleaching of both parts was accelerated thereby, and it was usually quite easy to discover how the traces in the ovary base connected with those in the torus. It was necessary to trim off all the floral organs of some of the larger flowers (e.g. those of *H. calycinum* L.), leaving only the torus. As a result of the bleaching and clearing technique the tissues tended to become rather delicate, but examination and storage in lactic acid involved a minimum of disturbance. It was possible to study the cleared flowers without staining the vascular tissues.

In general, *Hypericum* and *Ascyrum* flowers were more easily bleached than those of *Vismia*, *Cratoxylon* or *Ploiarium* Korth. (*Bonnetieae*). Hypericin, the red pigment in the dark glands and the ovary of species of *Hypericum* (and of *Vismia* ?), is partly soluble in alcohol, but it seemed to be impossible to remove the secretions completely from some flowers (especially those of *Vismia* species).

The /
The following is a list of the material examined:

Hypericum, Section:-

Triadenia - H. aegypticum L. (Lampedusa; Ross, Hb. Sic. 117).

Elodes - H. elodes L. (Dartmoor, Devon; Robson).


Eremanthe - H. calycinum L. (from seed ex Oxford Botanic Gdn.).

Campylosporus - H. lanceolatum Lam. (Transvaal, nr. Lydenburg; Wilms. 138).


" - H. cernuum Roxb. (Mussoorie, India; Capt. A. Anderson).


" - H. natalense Wood et Evans. (Mooi R., Natal; Johnston 204).
Humifuscoideum — H. sonderi Bredell. (Natal; Rudatis 246).

Webbia — H. floribundum (Dryand. in) Ait. (Teneriffe; J. Ball, It. Can. 1888).

Euhypericum — H. thymifolium Banks et Soland. (Acre, Palestine; Davis 3636).


" — H. concinnum Benth. (Mt. Tamalpais, California; Brandegee).

" — H. erectum Thunbg. (Tokyo; H. Sakurai).

" — H. scouleri Hook. (Jonesville, California; Copeland 426).

" — H. punctatum Lam. (Knoxville, Tennessee; Ruth 64).

" — H. pulchrum L. (Bucksburn, nr. Aberdeen; Robson).

" — H. humifusum L. (Whiting Bay, Arran; Robson).


Myriandra — H. prolificum L. (Solon, New York; Wiegand 6812).

" — H. prolificum L. (Newport, Penn.; Adams and Adams 3631).

" — H. kalmianum L. (Pontiac, Quebec; Marie Victorin et al. 43,419).

Brathydium — H. ellipticum Hook. (Brookside, Conn.; Eames 412).

Brathys /
23.

Brathys
- H. goyanesii Cuatr. (Cundinamarca, Colombia; Balls B. 5764).
- H. brasiliense Choisy. (Brazil; Luiz 20,037).
- H. canadense L. (Newfoundland; Mackenzie and Triscom 10,344).
- H. gentianoides (L.,) BSP. (Houston, Texas; G.L. Fischer).

Ascryrum
- A. stans Michx. (Sonnerton Creek, Virginia; Fernald and Long 9099).
- A. hypericoides L. (Bellevue, Jamaica; Robertson).

Vismia
- V. magnoliasfolium Cham. et Schl. (Minas Geraes, Brazil; Mexia 418).
- (V.) Caopia crassa Rusby. (Yungas, Bolivia; Bang 683).
- V. guianensis (Aubl.) Choisy. (Para, Brazil; Schultes 8071).
- V. micrantha Mart. (Minas Geraes, Brazil; Regnell III 298).

Cratoxylon
- C. polyanthum Korth. (Royal Botanic Gdn., Edinburgh).

Ploiarium
- P. alternifolium (Vahl) Melch. (Sarawak; C.D. 162).

('z' indicates species which have been listed under sections other than those in which they were placed by Keller).
More than one flower of each species was examined.

The drawings have all been made as accurately as possible by freehand, because a stereoscopic binocular was necessary to study the cleared flowers. A camera lucida could therefore not be used.

(3) The Floral Anatomy of Hypericum (excluding the Elodes Group) and Ascyrum.

Previous work on the floral anatomy of the above genera has been practically confined to the species with fascicular androecia, of which the following have been investigated:

van Tieghem (1875) – H. calycinum L. (Eremanthus), H. humifusum L. (Hpericium).
Henslow (1890) – H. androsaemum (Androsaemum).

In addition, Saunders includes a drawing of a vascular trunk of H. rhodopseum Friv. (Campylous), but does not comment upon it in connection with the arrangement of the stamens. Since all the findings of these authors have been confirmed and elaborated in the present work, they will not be discussed here.

It was found that the various arrangements of the vascular tissues in the flowers of Hypericum and Ascyrum /
Fig. 1. Plan of the basic floral vasculature of *Hypericum*.

The following symbols are used throughout this work:

- **SL-5** = sepal traces 1-5.
- **SM** = sepal midrib trace.
- **SL** = lateral sepal trace.
- **CSL** = commissural lateral sepal traces.
- **P** = petal trace.
- **St** = stamen fascicle trace.
- **Std** = staminode trace.
- **OC** = outline of carpel.
- **C** = carpel trace.
- **CD** = dorsal carpel trace.
- **CV** = ventral carpel trace(s).
- **CL** = lateral carpel trace.
- **OT(T)** = ovule trace(s).
Fig. 2. Toral vasculature of a flower of *H. hookerianum*, lateral view. Only the front part has been drawn in this and similar figures. (x 20)

Fig. 3. Carpel vasculature of *H. hookerianum*. In this and similar figures the joint ventral carpel traces (CV) have been drawn outside the line of the carpel (OC) for the sake of clarity. In fact, of course, they proceed up the centre of the ovary. (See text for the use of the word 'trace' in this sense). (ca x 12)
Ascyrum could be regarded as modifications of a single, basic type which is shown diagrammatically in Fig. 1. The sepal traces (s 1-5) emerge at different levels owing to the quinuncial development of the sepals, the 'genetic spiral' being either clockwise or anti-clockwise in different individuals. The other floral organs develop in whorls and, correspondingly, the traces for the members of each whorl emerge at roughly the same level. The sepal and petal (p) traces are unilacunar (i.e. each of them emerges from one place in the stele, and so only one parenchymatous 'gap' is formed) and each trace divides to form three main branches. The trace to each fascicle of stamens (st) arises in two parts, one on each side of the petal trace, and both parts dichotomise. If the inner branches fuse, as they often do, the fascicle trace will have three main branches like the petal and sepal traces. The carpel traces, too, have three main branches, a midrib (cd) and two ventrals (cv). Ventral traces from adjacent carpels usually fuse.

The species whose vascular pattern was found to most closely resemble Fig. 1 were H. hookerianum and H. cernuum (Norysea). One flower of the former species was anatomically exactly like the basic type, but in the others which were examined the carpel traces were irregular in some respects. Fig. 4 shows such a flower from which the ovary has been removed, and Fig. 5 is the plan of the whole toral trace system of the same flower. The sepal and petal traces are similar to those in Fig. 1, but the inner branches of the two parts of /
Fig. 4. Tornal vasculature of H. hookerianum, from above — not the same flower as in Fig. 2. (C1-5 = carpel traces 1-5.) (x 35)

Fig. 5. H. hookerianum. Plan of Fig. 4.
of the fascicle traces fail to fuse except those of st 1/3 (i.e. the fascicle trace on the radius between sepals 1 and 3). The ramifications of the fascicle traces become very fine, and it is not always possible to follow their course from the first branchings until each ultimate ramification enters a filament. Nevertheless, the first branchings of the other four fascicle traces are similar to that of st 1/3 (Fig. 5). It will be seen that the trace to the carpel opposite s_1 (i.e. c_1) also arises in two parts which unite for a short distance before the trace divides into three to form the dorsal and ventral traces. From each ventral trace two lateral traces (c_1) arise, one of which is larger than the other. The other carpel traces are less regular, and will be discussed later.

Fig. 2 shows one side of another flower from which the ovary has not been removed. The carpel traces are also irregular. Note the long distance between the uppermost sepal trace (s_5) and the petal and fascicle traces, and also the general outline of the vascular skeleton which is widest at the level of the petal and fascicle traces and then contracts at the base of the ovary. The placentation is axile in *H. hookeri-janum* and other members of Sect. *Norysca*.

Fig. 3 gives a diagrammatic representation of the vasculature of one carpel. The dorsal trace always extends almost up to the stigma, but the height of the two lateral traces varies. The stylar traces are all unbranched. (The term 'trace' is not strictly applicable to /
Fig. 6. Toral vasculature of a flower of *H. ascyron*, lateral view. (x 20)

Fig. 7. *H. ascyron*. Plan of Fig. 6. (x = commissural parts of adjacent lateral sepal traces. The dotted line encloses the three parts of trace S4.)

Fig. 8. Carpel vasculature of *H. ascyron*. (In this and later figures the ovule traces from the carpel ventral traces have been omitted.) (ca x 12)
to vascular strands after they leave the torus (see Puri, 1952); but since the point of transition between torus and organ is not usually discernible, it was thought advisable to use the same term for a vascular strand throughout its length.)

The floral vasculature of *H. cernuum* was essentially similar to that of *H. hookerianum*.

The remaining species have been placed in five series, in each of which the modification of the basic vascular pattern takes a different course. For the most part these series do not transgress Keller's sectional boundaries, but they have suggested some interrelationships which have not been proposed before. These series will now be considered in turn.

**Series I:**

The species in this series all have androecia which consist of fascicles of stamens, and the placentation is nearly always axile.

In the flower of *H. ascyron v. americanum* (Sect. Roscyna) there are five fascicles and five carpels and so its vascular pattern is essentially similar to that of *H. hookerianum* (see Fig. 7). However, the skeleton is more robust, and there is a greater degree of adnation among the fascicle and carpel traces, and among the parts of the carpel and fascicle traces themselves (Figs. 6, 7). The carpel traces are all regular, but the sepal traces differ from those of *H. hookerianum*. They are trilacunar, not unilacunar, i.e. each emerges from /
from three different places in the stele. This change from unilacunar to trilacunar traces is an example of what Eames (1931) has called 'working back of the branching tendency to the stele', i.e. it is as if the original trifurcation took place before the trace leaves the stele, so that each part of the trace produces a separate, parenchymatous 'gap'. It will be seen that each sepal trace occupies a larger proportion of the stelar circumference than would a corresponding unilacunar trace, i.e. the relative width of insertion of the trilacunar trace is greater. A further stage in this trend is seen between s 5/2 and s 1/3 respectively, where the adjacent laterals (or part of them) emerge as a joint trace from below the petal trace (x, Fig. 7). Such joint traces are termed 'commissural laterals'.

In contrast to those of *H. hookerianum*, the stylar traces of *H. ascyron* are branched (Fig. 8). The dorsal trace dichotomises to produce eventually twelve branches below the stigma, while the lateral traces each dichotomise once. The styles, which are broader at the apex than below, are fused together at the base in this species, but not in all members of Sect. Rosacnia.

*H. rhodopeum*, the sole member of Sect. Campy-
lopus, also belongs to this series. It has been placed in a section by itself partly because all the stamens are said to be fused together at the base, i.e. they are said to be monadelphous, not in fascicles (polyadelphous). On the other hand, Stefanoff (1932-4) describes the stamens as "triadelpha vel tetradelpha, filamentis basi brevissime connatis". At a first glance the flowers examined /
Fig. 9. Toral vasculature of *H. rhodopeum*, from above. (x = vestigial left 'leg' of C₄.)

Fig. 10. *H. rhodopeum*. Plan of Fig. 9.
examined seemed to have an indefinite number of ungrouped stamens, but on dissection they were all found to have five separate fascicles of stamens, each of which could be removed as a whole. Four- or five-carpellary flowers have been reported in this species, but all those examined had three carpels. Thus *H. rhodopeum* is a species which usually shows a reduction in the number of carpels in comparison with *H. ascyrion*. From Stefanoff's description it would appear that there is sometimes also a reduction in the number of fascicles; but there is no doubt that the androecium of this species is truly fascicular. Any cohesion of the fascicles at the base is secondary.

Figs. 9 and 10 show that all five pairs of lateral sepal traces are commissural. There are still five separate fascicle traces visible, one of which (st 4/1, i.e. the trace between sepals 4 and 1) arises wholly on one side of a petal trace instead of on both sides of it. For descriptive purposes such departures from the basic pattern will be termed 'displacements', but no actual displacement during development is necessarily implied. This particular displacement seems to be connected with the presence of only three carpels. Trace C5 is completely absent but C4 is still to be seen. It is fused with C1 so that C4 + C1 together innervate one carpel. However, only a small part of the left 'leg' of C4 remains (x). The change from pentamery to trimery seems to have caused some stresses to develop during the differentiation of the vascular tissue, and these are probably responsible for the splits in the carpel.
Fig. 11. Carpel vasculature of *H. rhodopeum*. Note how the joint ventral trace splits and a cross-branch (*y*) is formed between two ventral traces. In some other flowers the joint ventral trace did not split except at the apex. The placentation in such flowers was wholly axile (c.f. Fig. 12). (x 20)

Fig. 12. Cleared ovary of *H. rhodopeum* showing the course of two of the three joint ventral carpel traces (*CV*) and a cross-branch (*y*). The depicted ovary is unilocular in its upper half (*x*). (x 12.5)

Fig. 13. Double fascicle trace of *H. olympicum* which simulates a three-branched single trace. (x 40)

Fig. 14. Carpel vasculature of *H. olympicum*. (ca x 14)
carpel traces and the irregular ventral traces of carpels 2/4 and 1/3. The simultaneous development of androecium and gynaeceum in Hypericum may account for the fact that stresses due to the change from a pentamerous to a trimerous gynaeceum have apparently had an influence on the vasculature of the androecium (st 4/1).

The carpel vasculature of H. rhodopeum (Fig. 11) is rather different from that of the other species of Hypericum which have been studied. Some ovaries, including the one illustrated in Fig. 12, are unilocular in the upper part (a fact not mentioned by previous authors); but others appear to be completely trilocular. The adjacent ventral carpel traces fuse normally, but just below the unilocular part of this ovary they separate again and a cross branch fuses with a corresponding one from the other ventral trace of the same carpel (y, Figs. 11, 12). Only the dorsal trace dichotomises in the style (Fig. 11).

Keller's sections Euhypericum and Webbia both contain species with '3 stamen fascicles and 3 carpels'; but while Webbia consists of two closely related species from the Canary Islands and Madeira, Euhypericum is a large heterogeneous section whose species are united because they possess this number of fascicles and carpels. Most of the species with this type of flower were found to belong to the present series (Series I), but H. floribundum (Webbia) and H. thymifolium (Euhypericum) have the narrow toral cylinder of Series III (see below).

H. olympicum is a large-flowered species of Euhypericum /
Fig. 15. Toral vasculature of H. olympicum, from above. (x 20)

Fig. 16. H. olympicum. Plan of Fig. 15. Note the double fascicle traces opposite S4 and S5 respectively, and the single fascicle trace on the radius 1/3.
Euhypericum whose floral anatomy shows how the '5-fascicled' androecium has evolved. There are no signs of any traces to the absent fourth and fifth carpels, but the other carpel traces are very irregular. Although there appear to be only three stamen fascicles, all five fascicle traces are still present (Figs. 15, 16). There is a tendency for the traces on either side of the radii of s4 and s5 to be drawn together, which suggests that a force of contraction operated along these radii during the development of the traces to the petals, stamens and carpels. This force must have been strongest along radii 5/3 and 4/2 respectively, because the traces in these regions have been displaced further than in other parts of the flower. These contractions along the s4 and s5 radii have produced corresponding tensions in the regions of s2 and s3/s1, particularly in the carpel traces. A glance at Fig. 16 will suffice to show that the two antesepalous fascicles are double structures, while the antepetalous one is still single. It was not possible to follow the further branchings of the double fascicle traces in the flower illustrated, but in other flowers the adjacent branches from each part fused so that the double trace resembled a single trace in this respect (Fig. 13). The stylar traces are unbranched and the laterals short (Fig. 14).

In the smaller flowers of H. pulchrum (Euhypericum) the trimery (and pseudotrimery) of the inner whorls is reflected in the almost triangular outline of the toral vasculation (Fig. 17). There are fewer irregular and displaced traces than there were in H. olympicum.
Fig. 17. Toral vasculature of *H. pulchrum*, from above. (x 40)

Fig. 18. *H. pulchrum*. Plan of Fig. 17.
olympicum, but signs of contraction along the radii of the double fascicles are still apparent (Fig. 18). The lateral carpel traces extend further into the style than they do in H. olympicum, and they arise from the dorsal trace, not the ventral ones (Figs. 18, 19).

Other species in Sect. Euhypericum which were found to have a floral vasculature similar to that of H. olympicum and H. pulchrum are H. erectum, H. scouleri, H. punctatum and H. humifusum. H. sonderi (H. aesthiopicum Thunbg. p.p.) is also classified in this section by Keller, but it will be discussed later. In addition, H. concinnum comes within Series I. It is a Californian species which Bentham (1848) described as having three fascicles and three carpels, but which Keller and others have classified in Sect. Androsaemum, a section with which it has no apparent affinity. The species of Sect. Androsaemum are broad-leaved shrubs whose flowers have five fascicles, while H. concinnum is herbaceous and has small, narrow leaves. All the flowers examined had two double fascicle traces and a single one, and Jepson (1936) includes it among the species with 'three' fascicles. However, the flowers are relatively large (about the size of those of H. olympicum) and it is possible that five separate fascicles may sometimes occur.

Several authors have previously pointed out that the anteseptalous fascicles in flowers of the Euhypericum type were double structures; Saunders (1936, 1939) came to this conclusion from anatomical studies, but /
Fig. 19. Carpel vasculature of *H. pulchrum*. (x 20)

Fig. 20. Toral vasculature of *H. calycinum*, lateral view. (x 20)
but Payer (l.c.) has surmised it seventy-nine years earlier as a result of his ontogenetical work. He found that the anteseopalaeous fascicle primordia were larger than the antepetalous one, although stamen formation followed a similar course in all three. His findings have been confirmed by Sachs (1875), Hirmer (1918) and Breindl (1934), despite the opinion of Eichler (1875) that 'double fascicles' were an unnecessary fiction. Saunders and Hirmer both point out that the double fascicles nearly always comprise a larger number of stamens than the single fascicle does, and that the fascicle opposite s₅ is usually smaller than the one opposite s₄. The following list gives averages for the numbers of stamens in each fascicle, calculated from Saunders' figures (Saunders, 1936):

<table>
<thead>
<tr>
<th>Species</th>
<th>St 1/3</th>
<th>St 4</th>
<th>St 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. orientale L.</td>
<td>12</td>
<td>16.56</td>
<td>15.44</td>
</tr>
<tr>
<td>H. reflexum L.</td>
<td>8.93</td>
<td>13</td>
<td>11.04</td>
</tr>
<tr>
<td>H. coris L.</td>
<td>8.53</td>
<td>11.22</td>
<td>9.59</td>
</tr>
<tr>
<td>H. humifusum L.</td>
<td>4.05</td>
<td>5.62</td>
<td>4.62</td>
</tr>
</tbody>
</table>

Both Hirmer and Saunders also noticed that in occasional flowers which had four carpels there were four fascicles, three of which were antepetalous and single while the fourth one (double) was opposite sepal 5.

It should be noted that isomery or pseudo-isomery in the androecium and gynaeceum is biologically advantageous,
advantageous, because the styles then protrude between the fascicles and so favour cross-pollination.

Another example of a pseudo-trimerous androecium occurs in species of Cucurbitaceae as a result of the fusion of two pairs of adjacent stamens, not fascicles (see Chakravarty, 1955). The bithecal stamens so formed have pairs of traces, each of which originates separately, while the monothecal stamen has a single trace.

Thus from this first series of Hypericum species the following conclusions can be drawn:

(a) Meiomery affects the gynaeceum before the androecium.

(b) Carpel 5, and then carpell 4, is 'omitted'.

(c) The androecium does not undergo true meiomery, but the fascicles on each side of the radii of the missing carpels merge.

(d) The vascular pattern indicates that a force of contraction operates along these radii during development of the flower.

Series II:-

Two of the species with stamen fascicles were found to differ from those in Series I in having a relatively broader and shallower toral vascular cylinder.

_H. calycinum_ (Sect. Eremanthe) has five fascicles and five carpels like _H. hookerianum_ and _H. ascyron_; but, as a result of the relatively broad and shallow toral cylinder, the carpel traces emerge at the level of the sepal traces and are not fused to the petal-stamen /
**Fig. 21.** *H. calycinum.* The same specimen as in Fig. 20, from above.  (ca × 15)

**Fig. 22.** *H. calycinum.* Plan of Figs. 20 and 21. Note that the carpel traces are free from the petal-stamen trunk traces.
stamen trunk traces at all (Figs. 20-22). The carpel traces are irregular, as in some flowers of *H. hookeri-ianum* and *H. cernuum*, but it will be seen that this irregularity is due to a tendency towards contraction along or near the radii of sepals 4 and 5. These opposite contractions have exerted a stress on trace C1, producing splits in the vascular tissue.

Figs. 20 and 21 also show a feature of the vascular system which was noticeable in most of the large flowers, namely a tendency for the larger traces to curve inwards at the edges, or even to form a cylinder for a short distance (Fig. 20, s3). Arber (1950, p. 104) interprets this tendency as a 'striving' of subsidiary members of the vascular system (dorsiventral traces) towards the radial organisation of the stele, i.e. a tendency for the partial shoot to approach the structure of a whole shoot. Wardlaw (1952, p. 433), on the other hand, suggests that it may be a tendency towards a state of equilibrium, if dorsiventral symmetry is assumed to be a less stable condition than radial symmetry.

We may now return to consider the carpel traces of *H. hookeri-anum*. In Figs. 4 and 5 all the petal-stamen trunk traces curve in at the margins. Moreover, the upper parts of the carpel traces in Fig. 5 show a slight tendency towards contraction along the radii of s4 and s5, so that the meiomerie tendencies which are apparent in smaller, more reduced flowers may even have an influence on the development of these larger ones. Breindl (l.c.) describes a flower of *H*.
Fig. 23. Toral vasculature of *H. elatum* from above. (x 20)

Fig. 24. *H. elatum*. Plan of Fig. 23.
H. patulum (a close relative of H. hookerianum) in which the fifth carpel is smaller than the others, another example of the effect of this tendency.

The other species which has been included in Series II is H. elatum (Sect. Androsaemum), which usually has five fascicles and three carpels; but Lowe (1868) states that flowers with four or five carpels are sometimes found. All the flowers examined had three carpels, but in each one all five carpel traces were present (Figs. 23, 24). Carpel 1 always had a single trace, but the other two carpels were innervated by two traces each (i.e. C4 and C2 supply one and C5 with C3 the other).

The carpel vasulation of H. calycinum is exactly the same as that of H. hookerianum (Fig. 3), but in H. elatum the stylar traces dichotomise (Fig. 25). In both species (as in the other members of Sect. Androsaemum) the ovary is unilocular in the upper part.

Thus the species in Series II show a tendency towards meiomyry in the gynaecoom and contraction along the radii of sepals 4 and 5; but no species was found in which the wide, shallow torus was correlated with the formation of double stamen fascicles.

Series III:

In contrast to all the previous species, those in Series III have a narrow toral vascular cylinder and a narrow torus. They also possess in common certain morphological features which will be discussed later.
Fig. 25. Vasculature of a carpel of *H. elatum* at an early fruiting stage. (ca x 9)

Fig. 26. Carpel vasculature of *H. lanceolatum*. All five styles are connate up to the point where they widen out (x). (x 20)
H. lanceolatum (Sect. Campylosporus) occupies an early stage in this series. In the flowers of this species, which have five fascicles and five carpels, the vascular cylinder does not widen out in the torus so far as it does in previous examples (Fig. 27), and the fascicle traces are relatively closer together than in H. ascyron (c.f. Fig. 6). Otherwise the vascular plan (Fig. 28) is essentially similar to that of the latter species. Each stylar trace dichotomises once, and the styles themselves are appressed or fused together up to the point where they broaden out (Fig. 26). The placentation is axile, as in all the species of Sect. Campylosporus.

H. floribundum (Sect. Webbia) also has a toral cylinder which is narrow in comparison with the 'Euphyllophyllum' (3+3) type of flower in Series I (Fig. 29). Again it may be seen that two of the three fascicles are served by double traces, while the third (at 3/1) is single (Fig. 30). The carpel laterals arise from the dorsal trace as is usual in this series. An example of another feature which is commonly found in species of Series III is the 'dissection' of the carpel trace opposite s1, i.e. the two parts do not fuse but enter the base of the ovary separately. The dorsal carpel trace dichotomises in the style, but the laterals do not (Fig. 31). H. thymifolium (Euhypericum) has the narrow /
Fig. 27. Toral vasculature of H. lanceolatum, lateral view. The outline of this figure is narrow in comparison to that of Fig. 6, (H. ascyron). (x 20)

Fig. 28. H. lanceolatum. Plan of Fig. 27.
narrow toral cylinder of Series III, and the lateral carpel traces are branches of the dorsal trace as in *H. floribundum*.

In *H. prolificum* and *H. kalmianum* (Sect. *Myriandra*) the toral cylinder is still narrower. This section is one of those in which the stamens are apparently afascicular, but from Figs. 32 and 33 it will be seen that the vascular plan of *H. prolificum* is essentially similar to that of *H. floribundum*. There are five fascicle traces each of which arises from the sides of a petal trace and branches profusely in all directions. The ultimate branches from adjacent traces may or may not fuse. (Note that the only fusion in Fig. 33 occurs on the radius of s5). *H. kalmianum* usually has five carpels, as is shown in Fig. 35, but the carpel traces tend to be irregular, especially those to carpels 3, 4 and 5. This irregularity has resulted in the division of fascicle trace 4/1 in Fig. 35 into two parts but otherwise the fascicle traces are essentially similar to those of *H. prolificum*, i.e. the afascicular gynaeceum is supplied by five separate fascicle traces.

To return to *H. prolificum*, the flower whose vasculature is shown in Fig. 33 has three carpels which are innervated by the traces opposite s1, s2 and s3 respectively. But parts of the traces for the missing carpels are still present. The right-hand part of C5 acts as a ventral trace for C2, while the right-hand part of C4 fuses with C1.

In both these species the placentation is completely /
Fig. 29. Toral vasculature of *H. floribundum*, lateral view. (x 30)

Fig. 30. *H. floribundum*. Plan of Fig. 29.

Fig. 31. Carpel vasculature of *H. floribundum*. (x 12.5)
completely axile, or almost so; but in nearly all the other species of Sect. Myriandra and all those of the closely related Sect. Brathydium the ovary is incompletely trilocular or unilocular. In both these sections the styles are completely appressed together and the stigmas are minute (x, Fig. 34). H. ellipticum, a member of Sect. Brathydium, had a vascular plan similar to that of H. prolificum but on a smaller scale. It also resembled the vascular plans of the American species of Ascyrum which were investigated, except in the pentamery of the outer whorls.

The above-mentioned species of Ascyrum, which also have parietal placentation, small stigmas, more or less appressed styles and an afascicular androecium, were found to possess a narrow toral cylinder-like that of the previous species (Fig. 37). The calyx and corolla are tetramerous, and Fig. 36 shows that, here again, the uniform arrangement of the stamens is not reflected in that of the androecial traces. On the contrary, the prevailing tetramery is continued in the androecium, i.e. there are four fascicle traces present. In A. hypericoides (Fig. 38) they are fused with the carpel traces for some distance. The gynaeceum may consist of four or three carpels in A. stans. Flowers of A. hypericoides have only two carpels (Fig. 38), but traces for the other two are still present. The dorsal traces for the two missing ones serve the first four ovules (Figs. 38, 39). In A. stans there are three stylar traces, but in A. hypericoides only one lateral carpel trace develops at each side of the ovary and /
Fig. 32. Toral vasculature of *H. prolificum*, lateral view. (x 40)

Fig. 34. Carpel vasculature of *H. kalmianum*. In some flowers the lateral traces do not enter the style. (x = minute stigma). (ca x 12)

Fig. 35. Plan of the toral vasculature of *H. prolificum*, but not of the same flower as in Fig. 32. There are five fascicle traces, two of which have fused in the radius of S5.
and does not enter the style (Fig. 39). The dorsal trace dichotomises once.

In all species of *Ascyrum* except *A. microsepalum* Torr. et Gr. the outer pair of sepals is much larger than the inner pair, and correspondingly the outer traces are trilacunar whereas the inner ones are unilacunar (Figs. 36, 38).

The floral morphology and vasculature of the species in Series III can be related to the relatively narrow torus which they possess. In the later species the stamen fascicles all merge together in a ring instead of four of them fusing in pairs, although the tendency towards contraction along the radii of sepals 4 and 5 is still present. This tendency is indicated by the melomery in the gynaeceum and by the alterations in the carpel traces. It is significant that the species which have a constantly tetramerous perianth should also have a narrow torus. Tetramery never becomes constant in the outer floral whorls of species in the other series, except possibly in 'Ascyrum' *filicaule* from Sikkim which will be considered later.

**Series IV:**

This comprises Sect. *Brathys*, which Keller (1925) divided into two subsections: *Eubrathys* contains shrubs with crowded leaves and, usually, few-flowered inflorescences, while the species of *Spachium* are herbaceous and have longer stem internodes and much-branched inflorescences. The whole section is characterised by e.g. parietal placentation, an afascicular or irregular androecium, and diverging styles which usually /
Fig. 35. Plan of the toral vasculature of *H. kalmianum*. Fascicle trace 4/1 is divided into two parts by the right 'leg' of C4.

Fig. 36. Plan of the toral vasculature of *Ascyrum stans*. The dotted line encloses the three parts of an outer sepal trace (S1).
usually terminate in broad or capitate stigmas. The carpels vary in number from five to two.

In H. brasiliense, a species of Spachium with five carpels, the stamens are all fused together in a narrow ring, but separate fascicle traces are still present (Figs. 40, 41). However, in contrast to Series III, the torus is not narrow but widens considerably up to the level of the petal traces. The fascicle traces extend laterally so that they form an almost continuous line round the ovary, the trace branches being all in roughly the same plane. (It will be recalled that the ring of stamens in H. prolificum and H. kalmianum is wide, and the fascicle traces branch in all directions. However, the smaller flowers of Sect. Brathydium and of Aescrum have only a narrow ring of stamens.) Even in this isomerous flower one of the carpel traces (C₄) is 'dissected' (x, Fig. 41) and others are somewhat irregular. This condition is characteristic of the series, as is the absence of lateral carpel traces (Fig. 42).

H. goyanesii (Eubrathyd) has only three carpels, but it is clear from Fig. 43 that traces C₃ and C₅ fuse to innervate one carpel, C₂ and C₄ together innervate a second, while the third has a single trace (C₁). The androecium and its traces are similar to those of H. brasiliense.

H. saruwagedicum, a species from the mountains of New Guinea, was found to have a floral vasculature essentially similar to that of H. goyanesii. H. saruwagedicum is a shrub with crowded leaves, few-flowered inflorescences /
Fig. 37. Toral vasculature of *Ascyrum hypericoides*, lateral view. (x 40)

Fig. 38. Plan of the toral vasculature of *A. hypericoides*, but not of the same flower as in Fig. 37. One of the outer sepal traces is enclosed by the dotted line. There are four carpel traces, as in Fig. 36, but they innervate only two carpels; the alternate dorsal carpel traces each serve two ovules.

Fig. 39. Vasculation of an ovary of *A. hypericoides* at an early fruiting stage. (a) Dorsal view, (b) lateral view. (x 12.5)
inflorescences and afascicular stamens like the species in *Eubrathys*, but unlike the other *Brathys* species the placentation is sometimes semi-parietal, the placentae projecting some distance in from the ovary wall. Until Diels (1922) described *H. saruwagedicum*, Subsect. *Eubrathys* was thought to be confined to the Andes and the mountains of Guiana, Costa Rica and Guatemala; but Diels suggested that his species was related to the shrubby ones from the Andes, a theory which is supported by the similarity in floral anatomy between *H. goyannisii* and *H. saruwagedicum*.

In the more reduced species of Subsect. *Spachium* the stamens are fewer in number and do not form a continuous ring round the ovary. They are usually described as irregular, but in the flowers of *H. canadense* which were studied, the five fascicle traces remain separate (Figs. 44, 45). The stamens themselves are not always irregularly arranged. Fig. 46 shows a T. S. of an androecium and gynaeceum in which five groups of stamens are discernible. Some species of *Spachium* have only five stamens, i.e. each fascicle is reduced to a single stamen. Indeed Linnaeus placed *H. gentianoides* in a separate genus, *Sarothra*, which he included in *Pentandria Trigynia*. Two flowers of this species were cleared and dissected, and both were found to have seven stamens in five groups (1, 1, 1, 2, 2).

The stamens of *Spachium* species are sometimes said to be in three irregular groups. This may be due in part to the shape of the tricarpellary ovary, because the stamens in these species often remain close to the ovary; /
Fig. 40. Toral vasculature of H. brasiliense, from above. (x 100)

Fig. 41. H. brasiliense. Plan of Fig. 40. (x = a 'dissected' trace)
ovary; but in Fig. 45 the fascicle trace 3/5 is displaced towards s5 and st 1/4 is likewise displaced towards s4, so that there are signs of a tendency to contract along these radii, which might lead to a vague grouping of the stamens.

The carpel traces in Fig. 45 are so much 'dissected' that there is hardly any correspondence between their positions and those of the sepal traces.

Series V:—

This series comprises Sect. Humifusoidesmum, whose floral anatomy resembles that of Series IV in several respects, e.g. the lateral carpel traces are absent, the dorsal trace does not branch in the style, the fascicle and carpel traces are often irregular, and the stamens are usually all shortly fused together at the base. On the other hand, the placentation is axile in the species at present included in Sect. Humifusoideum.

Keller (1925) recognised two species in this section, H. peplidifolium A. Rich. (from tropical Africa) and H. natalense Wood et Evans (from Natal and Transvaal), which he separated from all the other species of Hypericum because their flowers were said to have three stamen fascicles and five carpels. Keller's view of the section must have been based solely on H. peplidifolium. He cannot have seen an authentically named specimen of H. natalense because he described H. woodii from an isotype of that species (Medley Wood 4034) — see Bredell (1939). Keller regarded his own H. woodii as an atypical member of Sect. Ruhypericum because the number /
Fig. 42. Carpel vasculature of *H. brasiliense*. Note the absence of lateral carpel traces. (x 33)

Fig. 43. Plan of the toral vasculature of *H. goyanesii*, showing how five carpel traces serve three carpels: $C_3 + C_5$, $C_2 + C_4$, $C_1$. 
number of carpels varied (Keller, 1923).

Saunders became interested in *H. peplidifolium* because of the reported occurrence in this species of five carpels and only three fascicles, an arrangement which seemed to differ from that of the other species in the genus in which the number of fascicles is either greater than, or equal to, the number of carpels. She therefore examined seven flowers of this species and reported that they all had five fascicles and five carpels, so that they did not constitute an exception to the general rule (Saunders, 1937). However, Milne-Redhead (1953) describes the stamens of *H. peplidifolium* as "usually in 3 often rather indefinite groups of 7-10, but sometimes totalling as many as 60"; while Bredell (l.c.) states that the filaments in *H. natalense* are "free or connate at the base into 3 or 4 irregular groups".

A clue which has helped to reconcile these conflicting statements is provided by Wood and Evans (1897) who point out that *H. natalense* has much the appearance of *H. aethiopicum* Thunbg., "for which species it has no doubt been mistaken". Bredell, too, seems to think that these two species are rather similar, stating that his *H. sonderi* v. *transvaalense* links *H. sonderi* (= *H. aethiopicum* p.p.) and *H. natalense*. Keller, on the other hand, places *H. aethiopicum* s.l. in *Euhypericum*, a section which has no other native representatives in South Africa. To be sure, *H. aethiopicum* sometimes has flowers with three fascicles and a trilocular ovary as in *Euhypericum*; but the stamens may also be rather irregular /
Fig. 44. Toral vasculature of *H. canadense*. Note how it widens out and compare with e.g. Figs. 32 and 37. (x 100)

Fig. 46. *H. canadense*. T. S. of ovary and stamens to show the five stamen fascicles. (x 20)

Fig. 45. *H. canadense*. Plan of Fig. 44. Note the extreme 'dissection' of the carpel traces (see text).
irregular and the carpels vary from three to four. Also, the glands in the leaves and sepals are yellowish and resinous like those of *H. natalense*, while the resinous vittae in the carpel walls are often swollen in a manner unlike that of any in *Euhypericum* species, but resembling those on the capsule walls of some specimens of *H. natalense*. The capsule valves of *H. aethiopicum* may be covered with numerous, very narrow, longitudinal vittae interspersed with a few small, oval glands, or the vittae may be more or less interrupted. In the extreme condition very numerous, small, oval glands cover the whole valve. In *Euhypericum* species the vittae may also be narrow and entire or swollen and interrupted, but they are never interspersed with small, oval glands and, if they are interrupted, the glands are never so numerous as in some specimens of *H. aethiopicum*. The black-dotted petals of *H. aethiopicum* are reminiscent of those of some species of *Euhypericum*; but *H. natalense* and *H. peplidifolium* may have some dark dots round the petal margin, and so their presence in *H. aethiopicum* is not inconsistent with a relationship between it and the present members of Sect. *Humifusoidaeum*.

Once it was realised that *H. aethiopicum* s.s. and *H. sonderi* belong to Sect. *Humifusoidaeum*, it became possible to interpret the vascular systems of *H. peplidifolium* and *H. natalense*, whose course had seemed rather obscure till then. *H. peplidifolium* usually has five carpels, but four out of the seventeen flowers examined had one less; in *H. natalense* the number of carpels varies from three to five, but four is the most usual number;
Figs. 47, 48, 49. Carpel vasculature of *H. sonderi*, *H. natalense* and *H. peplidifolium* respectively. (All x 12.5)
number; while *H. aethiopicum* usually has three carpels but may have four. Thus there would appear to be a reduction trend in carpel number from *H. peplidifolium* (usually five) to *H. aethiopicum* (usually three). On the other hand, there are several characters in which a trend occurs in the opposite direction. Thus (a) *H. aethiopicum* and *H. natalense* are semi-shrubby, while *H. peplidifolium* is a procumbent herb. (b) *H. aethiopicum* has terminal, cymose inflorescences; in *H. natalense* the flowers are terminal but single (and smaller); while *H. peplidifolium* has single flowers which are usually smaller still, and which sometimes appear to be axillary owing to the development of only one axillary bud at each node. (c) *H. aethiopicum* and *H. natalense* have capsular fruits, while those of *H. peplidifolium* are succulent. (d) A reduction trend in the size of the ovary and the relative length of the style runs parallel to the trend in flower size (Figs. 47-49).

If the above trends are borne in mind, i.e. that the size of the flower and its parts decreases in the order: *H. aethiopicum* (and *H. sonderi*) → *H. natalense* → *H. peplidifolium*, while the usual number of carpels increases in the same order, the correct interpretation of the floral vasculature becomes clearer. In *H. sonderi* (Fig. 50) only three carpel traces are present; and these arise on the radii of sepals 1, 2 and 3 respectively, as in e.g. *H. pulchrum*, the third trace leaning towards sepal 5 so that the three traces are symmetrical at the base of the ovary. There are five separate /
Fig. 50. Plan of the toral vasculation of *H. sonderi*. Carpel trace 1 shaded; \(x\) = dorsal carpel trace (c.f. Fig. 51); (i)-(vi) = the six half traces which serve three carpels (c.f. Figs. 51-55).

Fig. 51. Plan of the toral vasculation of *H. natalense*. The shaded traces (C4 and C1) correspond to trace C1 in Fig. 50. \(x\) = joint ventral trace, which corresponds to a dorsal carpel trace in Fig. 50. (i)-(vi), see text.
separate fascicle traces, unlike those of comparable species in Series I, in which the pairs of traces to the double fascicles tend to fuse together. When Fig. 50 is compared with Fig. 43 it will be seen that the vasculature of *H. sonderi* is similar to that of *H. goyanesii*, apart from the complete absence of any traces to carpels 4 and 5, and the presence of 'trunks' to all the remaining carpel traces. The lack of lateral carpel traces in both species is typical of their respective series.

The many splits in the vasculature of *H. natalense* (Fig. 51) may be interpreted as an indication that stresses are set up when a larger number of carpels than the three of *H. sonderi* occurs in a smaller flower. If allowance is made for these split vascular strands, it will be apparent that six half carpel traces leave the stele, as in *H. sonderi* (i-vi, Figs. 50, 51), but that these supply four carpels. Inspection reveals that carpel trace 1 is modified so that it supplies both carpel 1 and carpel 4. The joint ventral trace of these two carpels is narrower than the other three joint ventral traces, and corresponds in position to the dorsal trace of carpel 1 in Fig. 50.

The tendency towards contraction along the radii of sepals 4 and 5, which was noticeable in previous series, is very marked here, as also is a corresponding tendency towards expansion along the radii 1/3 and 2/4. This is reflected in the positions of the fascicle traces. As in Fig. 50, traces 3/5 and 5/2 in Fig. 51 are both single, not in two parts, and they are close together.
Figs. 52, 53 (and 54, 55). Plans of the toral vasculature of specimens of $H$. peplidifolium, showing how five carpel traces are derived from three. (i)-(x) = half carpel traces, which have been numbered from left to right of each figure, so that the numbers in different figures do not necessarily correspond.
together opposite sepal 5. The expansions along radii 1/3 and 2/4 have led to separation of the halves of the fascicle traces on these radii. Fascicle traces 3/5 and 5/2 form a double trace and so does trace 4/1 and half of trace 2/4; but the other half of trace 2/4 and both halves of trace 1/3 remain separate, so that there are five unequal fascicle traces, two large and three small ones.

The modification of one carpel trace to serve two carpels is shown more clearly in the flowers of *H. peplidifolium*. In Fig. 52 it is carpel trace 2 which has been modified in this way in a 4-carpelled flower. A further stage in this trend is shown in Fig. 53, in which the flower has five carpels but still only six half carpel traces leave the stele. Carpel trace 3 serves carpels 3 and 5 (c.f. carpel trace 2 in Fig. 52), and carpel trace 2 serves carpels 2 and 4. Fig. 54 shows a flower in which there are eight half carpel traces, carpels 5 and 2 being served by one pair while carpel 4 has its own trace; whereas in Fig. 55 the carpel traces are almost regular (five pairs of half traces), except those of carpels 5 and 3 which are not quite separate.

A comparison between the carpel traces in Series I (where the trends in flower size and carpel number are parallel) and in Series V (where these trends proceed in opposite directions) reveals fundamental differences in arrangement. Tricarpellary flowers in the other series show no sign of 'compound carpel traces' such as have just been described in *H. natalense* /
Figs. 54, 55. *H. peplidifolium*. For legend see Figs. 52, 53.
natalense and H. peplidifolium. Indeed we have the opposite phenomenon of two carpel traces supplying one carpel (c.f. H. rhodopeum, Fig. 10 and H. elatum, Fig. 24). Thus it is unlikely that the trends in the vas-culation of the species of Sect. Humifusoides have been interpreted in the wrong direction, i.e. that the vas-culation of the trimerous gynaeceum of H. sonderi is derived from that of the pentamerous type of H. peplidi-folium by fusion of adjacent pairs of carpel traces. We may therefore deduce that the pentamerous condition in the gynaeceum of H. peplidifolium is secondary, be-cause it seems to have been derived from the trimerous condition.

Floral anatomy also throws some light on the varied reports of the arrangement of stamens in H. peplidifolium. All the fifteen flowers of that species which were examined had five fascicle traces, but these were arranged similarly to those of H. natalense. The displacements and contractions towards the radii of sepals 5 and 4 and away from the radii 1/3 and 2/4 are visible in all four examples (Figs. 52-55). Usually fascicle traces 1/3 and 2/4 are not displaced but traces 1/4, 2/5 and 5/3 are, so that in Figs. 52-54 there are two pairs of (separate) traces opposite sepals 4 and 5 and a single trace between sepals 1 and 3. In Fig. 55 the presence of five carpel traces results in the fascicle traces being relatively far apart, but the contraction towards sepal 5 has affected the position of fascicle trace 5/1.

The writer was unable to compare the arrangement /
arrangement of fascicle traces with the arrangement of the stamens in the same flower, but flowers of each of the species were soaked out and dissected in order to investigate their gross morphology. The only specimen in which the stamens were obviously in three fascicles was one of *H. sonderi* (Wilms 137). In a specimen of *H. aethiopicum* (Cooper 238), the specimens of *H. natalense* (Medley Wood 11055 and Johnston 204) and those of *H. peplifolium* (Volkens 1157 and G. Adamson 302) it was more difficult to discern a regular arrangement. *H. aethiopicum* had three irregular fascicles, and Medley Wood's flower of *H. natalense* had what appeared to be one double fascicle and three single ones, while the other flower and those of *H. peplidifolium* seemed to have five rather obscure fascicles. In none of these flowers was the arrangement clearly fascicular.

To summarise the above discussion: we have in Series V a group of plants in which the number of carpels and the size of the flower bear an inverse relationship. The morphology and vasculation of the smaller flowers of *H. natalense* and *H. peplidifolium* can be interpreted in terms of the larger flower of *H. aethiopicum* s.l., which has 'three' stamen fascicles, three carpels and a relatively simple vascular skeleton. The traces for the extra carpels are provided by division of the existing traces so that the midrib becomes a joint ventral trace. The tendency towards contraction along radii 4 and 5 with consequent expansion along radii 1/3 and 2 or 2/4 is noticeable in this series as in /
in the previous ones. A result of this tendency is that the fascicle traces usually form three groups (two pairs and a single), although the halves of fascicle trace 1/3 may be separated so that two larger and two smaller groups are formed (Fig. 51). When five more or less separate carpel traces are present (Fig. 55), the fascicle traces are farther apart, although the contractions are still evident. These groupings of fascicle traces are reflected to a greater or lesser extent in those of the fascicles themselves, which explains why five, four and three irregular traces have been reported in this group.

Discussion.

(a) The Afascicular Species and Ascyrum.

Several general tendencies have been mentioned, one in particular being found in practically all the species which were examined — a tendency towards contraction along the radii of sepals 4 and 5. Saunders (1936) and Breindl (l.c.) also noticed this tendency, and the latter suggested that there should be a corresponding tendency towards expansion between sepals 1 and 3. This also has been detected in most species (e.g. in H. pulchrum and H. natalense). Saunders postulated that the reduction in the number of carpels and the fusion of pairs of fascicles were both results of the quincuncial development of the calyx. — "Now, it is obvious that, as the sepals arise successively with a divergence of \( \frac{\pi}{5} \), the available 'ground' space will decrease /
decrease with the development of each successive member, and that the congestion or crowding will be most marked in the region of the last two sepals (4 and 5) and will be greater in the neighbourhood of sepal 5 than of sepal 4." (Saunders, 1936).

However, this argument will not explain why the fascicles merge in a ring in other species of Hypericum, and such causal explanations involving spatial relations are rarely completely convincing by themselves. As Goebel has said — "If we can see in a flower that the primordia appear in greater number where there is more room at the vegetative point of the flower, this does not necessarily mean that we can say that the relationships of space are those conditioning the numerical relationships; just as well can we assume that there is more space provided where the vegetative point of the flower is disposed most to the building of primordia of organs. All 'mechanical' explanations are excluded in these relationships." (Goebel, 1905, p. 534, footnote). On the other hand, Goebel's own suggestion (l.c.) that nutritional differences may be involved in the reduction to three carpels and 'three' fascicles is equally unconvincing. The expression of a genotype can be very much modified by variations in nutrition; but one cannot validly attribute differences between plants with different genotypes to such variations alone, although the genotypes probably influence the nutritional requirements of the respective plants.
Fig. 56. Outlines of toral vasculature in Hypericum. Basic Form and Series I. (a) *H.* hookerianum (basic form), (b) *H.* ascyron, (c) *H.* olympicum, (d) *H.* rhodopeum, (e) *H.* pulchrum, (f) *H.* elodes. For explanation see text. (All x 35)
Now, it has also been observed that there is considerable variation in the shape, as well as in the size, of the floral receptacle, and this variation seems to be the other fact (complementary to the tangential condensation) which is required in order to interpret the differences in floral morphology among the various species of Hypericum and Ascyrum. The variations in toral shape are accompanied by parallel variations in the shape of the vascular cylinder which are depicted in Figs. 56-60. (These figures have been produced by sketching the outline of the toral vasculature, drawing the outline of a longitudinal section through the radius of a petal trace, and then repeating this outline in reverse on the other side of the sketch.)

If H. hookerianum (Fig. 56a) is taken as having the basic form of toral vascular cylinder, that of H. (b) ascyron can be derived from it by contractions in the regions of the stamens and the carpels, as indicated by the dotted arrows. H. olympicum (c) can be similarly derived from H. ascyron, while H. pulchrum (e) is relatively narrower than H. olympicum in the region of the petal and sepal lateral traces. H. rhodopeum (d) differs from H. olympicum in that the contractions have affected only the carpel traces, the stamen ones remaining almost erect. This can be related to the fact that H. rhodopeum sometimes has five fascicles and three carpels, whereas the fascicles in H. olympicum have been reduced to 'three'. Thus when the torus at the level of the androecial /
Fig. 57. Outlines of toral vasculature in Hypericum. Series III.
(a) H. lanceolatum, (b) H. floribundum, (c) H. prolificum,
(d) H. ellipticum (Ascyrum stans similar but larger), (e) Ascyrum
hypericoides, (f) H. aegypticum, (g) H. thymifolium. (All x 35)
androccial traces becomes narrower than it is at the level of the corolla traces, the 'double fascicles' are produced; while, if the contractions affect the carpel trace region only, the five fascicles tend to remain separate. *H. elodes* (f), which will be shown to belong to this series, can be derived from *H. pulchrum* by a slight vertical contraction. Therefore, the occurrence of 'three' fascicles throughout the later stages of Series I may be correlated with a tendency towards contraction in the regions of the fascicle and carpel traces which, in conjunction with the general tendency towards tangential contraction, results in the formation of two double fascicles. Vertical and horizontal contractions occur only in the more reduced species in the series.

The situation in Series III (Fig. 57) is rather different. Here the main emphasis is placed on horizontal contraction. The vascular cylinder of *H. lanceolatum* (a) is more elongate than those of Series I or of *H. hookerianum*, especially between the levels of the petal and fascicle traces. A contrast is afforded in this series by *H. floribundum* (b) and *H. prolificum* (c), both of which show a horizontal contraction (in the region of the petal traces) when compared with *H. lanceolatum*; for, while the fascicular *H. floribundum* ("3' + 3") is also contracted in the fascicle and carpel trace regions, the afascicular *H. prolificum* is contracted only in the carpel trace region, the fascicle traces remaining erect and free. In *H. ellipticum* (d) and the species of *Ascyrum* (e) the fascicle traces are more /
Fig. 58. Outlines of toral vasculature in Hypericum. Series IV.
(a) H. saruwagedicum, (b) H. goynesii, (c) H. brasiliense,
(d) H. canadense (H. gentianoides similar but smaller). (All x 35)

Fig. 59. Outlines of toral vasculature in Hypericum. Series V.
(a) H. sonderi, (b) H. natalense, (c) H. peplidifolium. (All x 35)
more adnate to the carpel traces again. This, however, is a result not of a contraction at the level of the fascicles but of the wider distance between the carpel traces owing to the parietal placentation in these species. *H. thymifolium* (g) and *H. aegypticum* (f) will be shown to belong to an early offshoot in this series, where the flowers are of the Euhypericum type. From Fig. 57 it will be seen that in comparison with *H. floribundum* they show a slight vertical contraction, but that they both have a relatively narrow toral cylinder. Thus, in Series III as in Series I, where the fascicle region is affected by tangential contraction double fascicles are produced; but, owing to the general tendency towards reduction in width in this series, where the fascicle region is not so affected (as in *H. prolificum*) all the fascicles merge to form a uniform whorl of stamens. It is also understandable that the group whose torus is relatively narrow in the petal region should be the one in which there is a reduction to constant tetramery in the perianth (*Ascyrum*).

Turning to Series IV (Fig. 58), *H. Saruwagedicum* (a) is derived from *H. hockerianum* by a vertical contraction so that fascicle, petal and lateral sepal traces emerge at about the same level. This species has semi-parietal placentation; but in the other species in the series the placentation is completely parietal, so that the ventral carpel traces are relatively far apart at the base of the ovary. The fascicle traces are erect or they may even lean outwards (*H. canadense*, *H. gentianoides*). As in other species with erect fascicle /
fascicle traces (e.g. H. prolificum), the androeclium is afascicular; but in this series the fascicles merge to form a narrow line of stamens (see Figs. 40, 41). It will be seen that this difference in the width of the whorl of stamens in the two groups is correlated with a difference in the form of the toral vasculature. Thus, while the main contractive tendency in Series III is horizontal and results in a crowding-together of the fascicles to form a wide ring of stamens in the species with larger flowers, the main tendency in Series IV seems to be towards vertical contraction, which leads to a widening of the vascular cylinder in the region of the petal traces (see H. goyanesii, Fig. 58 (b)). The widening of the torus would have the effect of 'squeezing out' the stamens in each fascicle laterally so that a narrow, continuous line is produced. This idea is supported by the fact that in the species of Series IV the stamens always lie closely appressed to the ovary. In the smaller flowers of H. brasiliense (c) and H. canadense (d) the mid-part of the torus is relatively narrower than in H. goyanesii (b), but the stamens either form a continuous ring (H. brasiliense) or appear irregularly arranged (H. canadense, where the stamens may be so few in number that a continuous ring cannot be produced).

In Series V (Fig. 59), whose species have axile placentation, the form of the toral vascular cylinder of H. sonderi (a) resembles that of H. saruwagedicum except for the position of the lateral sepal traces. However, the retention of axile placentation in /
Fig. 60. Outlines of toral vasculation in Hypericum. Series II.
(a) H. calycinum, (b) H. elatum. (Both x 12.5)

Fig. 61. Leaf trace (LT) and axillary bud trace (BT) in Hypericum.

Fig. 62. Petal trace (e.g. H. hookerianum) and fascicle trace.

Fig. 63. The splitting of one trace by superposition on another (e.g. H. prolificum).

Fig. 64. A fascicle trace arising wholly on one side of a petal trace (St 4/1 in H. rhodopeum, Fig. 10).
in this series is correlated with a contraction in the region of the fascicle traces which is especially noticeable in *H. natalense* (b) and *H. peplidifolium* (c). Hence the form of the vascular cylinders of these species bears a general resemblance to that of the smaller species in Series I.

Finally, in Series II (Fig. 60) the shape of the torus of *H. calycinum* (a) can be regarded as the result of a vertical condensation of the *H. hookerianum* type. Note that the fascicle traces are completely free from the carpel ones in both species. In *H. elatum* (b) the carpels are reduced to three, but there are five separate fascicles. The tangential contraction which affects the carpel whorl has no influence on the fascicles, and the traces to the two whorls remain separate also. It is significant that this series, which corresponds to Sections *Eremanthex*, *Psorophytum* and *Androsaemum*, contains no species in which four of the fascicles are fused in pairs, although one pair is sometimes fused in *H. balearicum* (*Psorophytum*). This is probably related to the fact that the vasculature of the stamen and carpel whorls remains separate in these species.

As Goebel has said (v.s.), it is not possible to speculate validly on the reasons for these various contractions and reduction trends, but it is possible to correlate them with trends in floral morphology in order to elucidate the ways in which they take place. Thus we have seen that all the variations in floral morphology are accompanied by parallel variations in the /
the shape of the vascular cylinder in the torus. These variations, in turn, can be analysed into (a) a general trend towards contraction along the radii of sepals 4 and 5 (i.e., a tangential contraction), and (b) various lateral (radial) or vertical contractions which combine with the first one in different ways in each series.

(b) The Stamen Fascicle.

It has been shown that the stamen fascicle is innervated by a trace that usually arises in two parts, one on either side of the petal trace. The apparent doubleness of these traces has been noted by several previous authors, one of whom (Henslow, 1890) suggested that the fascicles themselves are double in origin. However, when the fascicle trace is displaced to one side of the petal trace it is a single structure (e.g., Fig. 64 or st 4/1 in Fig. 54), so that the origin in two parts would seem to be connected with the superposition of the fascicle trace on the petal trace and its 'gap'. The petal trace itself may arise in two parts when commissural lateral sepal traces emerge just below it (Fig. 63). Arber has come to a similar conclusion with regard to the 'double' traces in the stamens of Hypericum, i.e., "that this double character is merely a direct result of a particular mode of branching associated with the superposition of a stamen to a petal" (Arber, 1932). Hence the fascicle trace in Hypericum arises in a way exactly analogous to the method of origin of the stamen trace in Hypericum. Arber also notes that the relation between petal trace and stamen trace in Hypericum /
Hypeccum is similar to that of many axillary buds and their subtending leaves. The leaf traces in the Guttiferae are all unilacunar (Metcalfe and Chalk, l.c.), and the axillary bud trace arises in two parts from the sides of the petal gap (Fig. 61), just as the fascicle trace does from the petal gap (Fig. 62) or the carpel traces from the sepal gap.

The fascicle trace also resembles traces to the other floral organs in being fundamentally tripartite, i.e. it branches first into three. This is seen most clearly where the trace is not split (Fig. 64). The sepal traces are usually trilacunar so that the first three 'branches' depart separately from the stele; but if the insertion of the sepal is narrow in relation to the length of the circumference the trace is unilacunar (c.f. H. hookerianum and the inner sepals of Ascyrum hypericoides). The insertion of the petals is always narrow, and so their traces are always unilacunar although they may branch into three very soon after emerging. The carpel traces, too, divide originally into three, one branch being the dorsal trace and the others the ventral traces. They are usually unilacunar (e.g. in the whole of Series I), but they may become 'dissected' so that two or three parts of the trace arise separately from the stele (e.g. in H. canadense).

Thus /

* The tripartite trace can be derived theoretically by fusion of the adjacent branches of two secondary dichotomies (see Wilson, 1942, fig. 18).
Thus the fascicle trace shows points of resemblance to (a) an axillary bud trace and (b) the traces to other floral organs. There is no evidence whatsoever to suggest that it is a composite structure consisting of the aggregated traces to a cluster of stamens. On the contrary all the indications are that the fascicle trace is a single structure which remains evident even when the individuality of the organ it serves is obscured (e.g. in *H. prolificum*). The use of the word 'organ' here to describe the fascicle of stamens seems justifiable on the grounds that, if the trace to the fascicle is not compound, it is difficult to see how the fascicle itself can be a composite structure. Therefore we can dismiss the Aggregation Theory as not being in accordance with the facts.

The two remaining theories both regard the fascicle as a single organ, but they differ as to how it has been derived. To adherents of the 'Dedoublement' Theory the fascicle is an elaborated stamen, while to those who favour the Telome Theory the stamen is a simplified fascicle. We have seen that some species of *Hypericum* Sect. *Brathyrs* Subsect. *Spachium* can have an androecium of five, single, antepetalous stamens. But these are annual herbs with reduced leaves and small flowers, in which the floral vasculature is reduced and modified by displacements and the placentation is parietal. It is most unlikely that the tall, shrubby and semi-arborescent species in Sects. *Norysea* and *Campylosporus* could have evolved from such small herbs, or even that an ancestral shrubby species with five-stamened flowers /
flowers could have given rise to both types.

On the other hand, if the stamen fascicle is taken as the ancestral condition, all the main morphological and anatomical trends fall into place. A flower with five stamens and parietal placentation then appears as the ultimate stage in a reduction series originating in the shrubby species with five fascicles and axile placentation. Thus a reduction in the number of stamens in a fascicle can be compared to a reduction in the degree of branching of an axis or of the venation of a leaf. In contrast, the reduction in number of carpels in each series and also of the other floral members in Ascyrum, results in the omission of whole organs.

To summarise the main conclusions from this section: the afascicular androecium is a derivative condition which has arisen in two separate parts of the genus in different ways. Sect. Campylopus (H. rhodopeum) is not truly afascicular. In Sects. Myriandra and Brathydium and in Ascyrum the afascicular androecium has arisen as a result of a radial contraction of the torus, while in Sect. Brathys it has been produced by vertical condensation and radial expansion of the torus so that the fascicles are 'squeezed out' below the ovary to form a narrow, continuous ring of stamens. The tetrmerous perianth and androecium of Ascyrum can be attributed to the effect of the same contractive tendency as that which produced the afascicular androecium in Series III. A reduction to 'three' fascicles is brought about by the merging of two adjacent pairs of fascicles, and results from differential tangential contraction /
Fig. 65. Toral vasculation of *Vismia guianensis*, from above.  (x 40)

Fig. 66. *V. guianensis*. Plan of Fig. 65. The dotted lines enclose the five staminode traces.
contraction (i.e. contraction along two radii) as opposed to the overall radial contraction which produces the afascicular type of androecium in *H. prolificum*.

(4) The Floral Anatomy of *Vismia*, *Cratoxylon* and the **Elodes Group of Hypericum**.

The conclusion that the fascicular androecium is primitive in *Hypericum* is supported by the fact that this type of androecium is the only one which occurs in the flowers of the other tribes of the *Hypericoidae* (*Vismieae* and *Cratoxyleae*). Their flowers differ from all those considered up till now in having a whorl of sterile staminode-like structures which alternate with the stamen fascicles and equal them in number. In the *Vismieae* the floral whorls are pentamerous throughout, while in the *Cratoxyleae* and the *Elodes* group of *Hypericum* (Sects. I-IV) the gynaecium is trimerous and the androecium pseudo-trimerous.

The floral anatomy of species of *Vismia* and *Cratoxylon* was found to differ in several respects from that of the *Hypericum* species described above. In particular, it was more complex. The flower of *Vismia guianensis* whose vasculature is illustrated in Figs. 65 and 66 has rather irregular sepal traces. They are basically trilacunar with commissural laterals, but 'extra' traces occur for sepals 1 and 4. The fascicle traces occupy the same position relative to the petal traces as they do in *Hypericum*, but the organisation of the traces themselves is different. Whereas in *Hypericum* the parts adjacent to the petal trace come together (Fig. /
Fig. 67. Basic plan of petal and fascicle traces in Hypericum.

Fig. 68. Basic plan of petal and fascicle traces in Vismia.

Fig. 69. Part of the ovary vasculatation of V. guianensis, lateral view. (x 20)

Fig. 70. Carpel vasculatation of V. guianensis. (x 20)

Fig. 71. T. S. of a flower of Vismia dealbata, showing the outer androecial whorl of vasculated staminodes. (Enlarged from Wilson, 1937).
(Fig. 67), in V. guianensis the outer parts curve round and join so that the halves of the trace are, in effect, inverted (Fig. 68). The carpel traces (Fig. 66) resemble those of H. brasiliense (Fig. 41), except that one or both ventral traces are split into two parts.

However, the carpel vasculature has quite a different appearance from that of any species of Hypericum that has been studied (Figs. 69, 70). True lateral traces are absent; but, on the other hand, the dorsal trace is more strongly developed and branches before it enters the style.

Returning to Figs. 65 and 66, it will be seen that the sterile, staminode-like structures are provided with traces (Std) which arch over those of the sepals. They are more irregular than the fascicle traces, possibly because the sepal traces are not unilacunar like the petal ones. If allowances are made for this irregularity, the traces to these structures can be seen to form an outer antesepalous whorl corresponding to the whorl of stamen fascicle traces on the petal radii. Now, discs and other structures of axial origin are usually innervated by branches from traces to one of the floral organs, not by independent traces, a fact which suggests that the organs served by these traces are staminodial, i.e. that the antesepalous bodies constitute an outer, sterile, androecial whorl. Wilson (1937) came to the same conclusion from a study of Vismia dealbata H.K. Each staminode (Fig. 71) is comparable in width to a stamen fascicle, and so they may be regarded as sterile fascicles rather than as sterile /
Fig. 72. *Vismia micrantha*. Plan of the toral vasculature.

Fig. 73. Carpel vasculature of *V. micrantha*. (x 35)

Fig. 74. Petal and fascicle traces in *Plomarium alternifolium*. (x 20)

Fig. 75. Outline of the toral vasculature of *Vismia guianensis*. (x 35)

Fig. 76. Outline of the toral vasculature of *Cratoxylon polyanthum*. (x 35)
sterile single stamens. The irregularity of the staminode traces may also be related to the sterility of the organs which they serve. They branch profusely within each staminode but do not reach the apex of the organ.

Most of the features of the floral vasculat-ion of *V. guianensis* (i.e. inverted fascicle traces, irregular sepal traces and branching carpel midribs) also occur in the other species of *Vismia* that were examined. The one with the smallest flowers (*V. micrograntha*) had the least complex vascula-tion (Figs. 72, 73). In this species, which has only three to five stamens per fascicle, the similarity between the fascicle traces and the staminode traces is striking. The fascicle traces are not 'inverted', probably as a consequence of a reduction in the total amount of vascular tissue. The carpel traces are more 'dissected' than in *V. guianensis*. Only one branch develops from each dorsal trace below the level of the style, and the ventral traces remain free throughout their length. The sepal traces are regularly trilacunar, but not even in this small flower are the laterals commissural in the radius 3/1.

In *V. magnoliaefolia* the sepal traces are even more irregular than in *V. guianensis*, so much so that it was not possible to make an intelligible drawing of the vascula-tion of a flower of this species. The floral vascula-tion of *V. crassa* is essentially similar to that of /
Fig. 77. Cratoxylon polyanthum. Plan of the toral vasulation. (VStd = vestigial staminode trace, x = 'blind' traces.)

Fig. 78. Carpel vasulation of C. polyanthum. (x 12.5)

Fig. 79. Carpel vasulation of H. petiolatum pp. (Triadenum waiteri). (x 12.5)
of *V. guianensis*.

The basic features of the floral anatomy of the *Vismia* species were also found in *Ploiarium alternifolium* (*Theaceae, Bonnetieae*), whose flower is also essentially similar, i.e. pentamerous throughout with a whorl of staminodes alternating with the stamen fascicles. In particular, the fascicle traces are inverted (Fig. 74), and true lateral carpel traces are absent, the carpel being innervated by numerous branches from the dorsal trace as in *V. guianensis*.

*Cratoxylon polyanthum* has a flower which is comparable in some ways with the 'Euhypericum' type, i.e. it has two double fascicles and a single one, and three carpels; but it also has three staminodes. In contrast to *Vismia*, where the toral vascular cylinder is vertically condensed (Fig. 75), in *Cratoxylon* the vascular cylinder is conical with tangential condensation in the upper part (Fig. 76). This difference in toral shape may be correlated with the isomery of the inner whorls in *Vismia* (vertical condensation) and the meiomericy of these whorls in *Cratoxylon* (tangential condensation along the radii of sepals 4 and 5). The tangential condensation results in fusion of the upper toral vascular tissue, and not 'splitting' of the carpel traces as in *Vismia* (Fig. 77).

The floral vasculature of *Cratoxylon*, like that of *Vismia*, is rather irregular. Several groups of traces seem to be blind, i.e. they do not enter any floral organ ('x' in Fig. 77). The sepal traces are again basically trilacunar without commissural laterals, and /
Fig. 80. *H. petiolatum* pp. (*Triadenum walteri*). Plan of the toral vascul-ation. The traces marked 'x' serve staminodes, not stamen fascicles.

Fig. 81. *H. virginicum* pp. (*Triadenum fraseri*). Plan of the toral vascula-tion.
and the petal traces are unilacunar. In this species the two parts of each fascicle trace (st) leave separate gaps, except for st 3/5 and st 5/3, parts of which share one gap. The staminode traces (Std) are even more irregular than in Vismia, but again they obviously serve an outer whorl of the androecium. In contrast to the fascicles, two of which are double, the three staminodes must be single, because vestigial traces for the two missing staminodes (vstd) are visible below the double fascicle traces. Thus the staminodial whorl undergoes true meiometry like the carpels. The carpel vasculature (Fig. 78) is rather different from that of Vismia since two of the laterals enter the base of the style, and the way in which the dorsal trace branches in the style does not resemble that of any other species which has been examined. The majority of the vascular tissue remaining after the departure of the dorsal carpel traces forms traces to individual ovules (OTT, Figs. 77, 78), since the ovules in this genus arise at the base of the ovary. Only three small strands proceed up the centre of the ovary as joint ventral traces of pairs of adjacent carpels (cv).

Hypericum Sect. Elodea (= Triadenum).

In H. petiolatum the three structures which alternate with the stamen fascicles have traces similar to those in Cratoxylon but more regular (Fig. 80). At first glance their traces appear to form an inner whorl, since the branches marked 'x' belong to them and not to the fascicle traces. But closer inspection reveals that they arise below the fascicle traces, although they /
Fig. 82. *H. aegypticum*. Plan of the toral vasculation. Note the absence of any staminode traces.

Fig. 85. Staminode viewed from below. (VT = vestigial traces)  (x 35)

Fig. 83. Carpel vasculation of *H. aegypticum*. (x 12.5)

Fig. 84. *H. aegypticum*. Profile view of the petal and stamen fascicle of a long-styled flower (anthers omitted). (A = petal appendage, PT = petal trace, FT = fascicle trace.) (x 12.5)
they are secondarily fused with the carpel traces at a higher level. Therefore the order of whorls is the same in this species as in Cratoxylon, and so the sterile structures must be homologous with those of Vismia and Cratoxylon, i.e. they must be staminodes also. Unlike Cratoxylon, however, there are no vestigial traces to the missing staminodes. The sepal traces also resemble those of Cratoxylon in the absence of commissural laterals; but the carpel vasculature is simpler since none of the traces branch (Fig. 79). However, the laterals emerge at the same position as they do in Cratoxylon.

In H. virginicum (Fig. 81) the vasculature is more reduced than that of H. petiolatum, especially the staminode traces, but there are still no commissural lateral sepal traces. The carpel vasculature is also similar to that of H. petiolatum.

Hypericum Sect. Triadenia.

It will be recalled that Sect. Elodea differs morphologically in several respects from the first three sections of Hypericum. Differences are also noticeable in the floral anatomy of species in these two respective groups. Thus in H. aegypticum (Fig. 82) the adjacent laterals of sepals 3 and 5 are commissural, and the carpel laterals arise from the dorsal trace. However, as in the species of Sect. Elodea, they do not enter the style and the dorsal trace remains unbranched (Fig. 83). Nevertheless, the most important difference in the floral vasculature of this species is the complete absence of any traces to the staminodes (Figs. 82, 86). Likewise,
Fig. 86. *H. aegypticum*. Ovary base of a cleared flower, showing (i) that the staminodes form an outer whorl of the androecium, (ii) that they have no vascular connection with the stele, and (iii) that the stamen traces in the fascicle remain separate although the filaments are united. (*Std* = staminode, *St* = stamen fascicle.) (x 35)

Fig. 88. Carpel vascul-ation of *H. elodes*. (x 20)

Fig. 87. *H. elodes*. Plan of the toral vascula-tion. Note the absence of staminode traces.
Likewise, the petal appendages are non-vascular, in contrast to those of Ranunculus (A, Fig. 84). The staminodes are almost flush with the stamen fascicles, but they can still be seen to form an outer whorl of the androecium (Fig. 86). Although they have no traces connecting them with the stele, the staminodes are not without vascular tissue. A close inspection reveals that there are several very fine strands running up the centre of each one. These are hardly visible from the side, but they can be detected when a staminode is viewed from below (Fig. 85). Similar very faint vascular strands were found to occur in the staminodes of Viannia, Cratoxylon and Hypericum Sect. Elodea, but in these species they were continuous with the main staminode traces.

Hypericum Sect. Elodes.

In H. elodes all the lateral sepal traces are commissural (Fig. 87). As in H. aegypticum, there is no vascular connection between the staminodes and the stele, but faint longitudinal vascular strands are visible within them. The staminodes are almost flush with the fascicles or slightly outside them. The petal appendages are also non-vascular. In H. elodes the ovary is unilocular except at the base, which means that the lateral and ventral carpel traces remain very close together (Fig. 86). The dorsal trace dichotomises once in the style.

Discussion.
Discussion.

(a) The Staminodes.

It has been shown that the vasculature of these structures is comparable with that of the stamen fascicles in *Vismia*, *Cratoxylon* and *Hypericum* Sect. *Elodea*. In the other *Hypericum* species there are what appear to be vestigial vascular strands within the staminodes, and therefore Hirmer (1917) was correct in claiming that they were vascular. On the other hand, the anatomical and morphological evidence indicates that both Hirmer and Saunders were wrong to call them 'sterile outgrowths' from the receptacle' and 'disc (axial) outgrowths' respectively, and that in fact they form an outer androecial whorl, each staminode being a sterile fascicle.

The essential similarity between the staminode traces and the fascicle traces is strong evidence in favour of the interpretation of the fascicle as a single structure and not an aggregation, since otherwise the staminodes would also have to be regarded as aggregated structures. The androecium of *Vismia* would then have to be interpreted as ten clusters of originally separate stamens, the outer five of which have become sterile. It seems much more in accord with the anatomical and morphological facts discussed above to consider the structures as ten condensed, branching stamens, five fertile (antepetalous) and five sterile (antesepalous). From this point of view the flower of *Vismia* is isomericous, pentamerosus, pentacyclic and diplostemonous; while in *Hypericum*, where the outer androecial whorl is normally /
normally absent, the flowers of e.g. Sect. Norysca are isomerous, pentamerous and tetracyclic.

(b) The Species of Hypericum.

The floral anatomy of the species of Hypericum Sect. Elodea bears a definite resemblance to that of Cratoxylon. Thus (i) the lateral sepal traces never become commissural, (ii) lateral carpel traces are present and emerge in a similar position in both groups, and (iii) the whorl of staminodes is innervated by antesepalous traces which emerge from the stele. In fact, if allowance is made for the different positions of the ovules in Sect. Elodea and Cratoxylon, Fig. 80 can be seen to represent a reduced condition of Fig. 77.

H. aegypticum and H. elodes differ from these species in that functional traces to the staminodes are completely absent, though vestigial vascular tissue is visible in the centre of these structures. They also differ in the possession of (non-vascular) petal appendages. The staminodes of H. aegypticum definitely form an outer androecial whorl, but in H. elodes they are almost at the same level as the fascicles. The dorsal carpel traces of H. aegypticum are unbranched, like those of the Sect. Elodea species, but in H. elodes they dichotomise once. Finally, some at least of the lateral sepal traces of H. aegypticum and H. elodes are commissural. Thus these two species differ anatomically from those of Sect. Elodea. On the other hand their floral anatomy is essentially similar to that of species of the 'Euhypericum' type which have neither staminodes nor petal appendages.
CHAPTER III.

THE RELATIONSHIPS OF THE EOLES GROUP OF HYPERICUM.

(1) Triadenum and Hypericum.

The floral anatomy of Hypericum Sect. Elodea leads one to suspect that this section is more closely related to Cratoxylon than to the other Hypericum species—a conclusion which is borne out by a morphological comparison of these groups (see below). Hence it seems justifiable to follow Holm (1903) and Gleason (1947), who separate it from Hypericum as the genus Triadenum Rafinesque.

(a) The most obvious difference between Triadenum and Hypericum is in the colour of the petals, which is yellow in Hypericum (often tinged with red, rarely wholly red [H. laeve Boiss. et Hausskn. v. rubrum Boiss] or white [H. aviculariaefolium Jaub. et Sp. v. albilorum Huber-Morath, H. locheri Merrill]), but white or pinkish purple, never yellow in Triadenum. Among the rest of the Hypericoideae, the Vismieae (Vismia, Psorospermum and Harungana) have yellow or white flowers, while in the Cratoxyleae they are white (Eliacea) or purplish (Cratoxylon). It seems possible that the pinkish-purple colour is produced by an anthocyanin and a white flavone, while the red tinges in Hypericum are due to the same anthocyanin with a yellow flavone.

(b) The corolla in Hypericum always has convolute (i.e. contorted) aestivation, but Gleason (l.c.) mentions that /
Fig. 89. Two forms of aestivation in Triadenum fraseri, intermediate between imbricate and valvate.

Fig. 90. Inflorescence plans of (a) and (b) H. aegypticum, (c) H. pallens, (d) H. russeggeri and (e) H. ternatum.
that in *Triadenum* it is imbricate. Two buds of *Pr. fraseri* (H. St. John 2797) were dissected and were found to have an intermediate type of aestivation (Fig. 89). An examination of species of *Cratoxyleae* for comparison revealed that the aestivation of one flower of *Eliaea articulata* Spach was wholly imbricate, and that of seven flowers in four species of *Cratoxylon* two were imbricate, two were convolute and the rest were intermediate like the *Triadenum* flowers. The corollas of *H. elodes* and *H. aegypticum* are always convolute like the rest of *Hypericum*.

(c) Petal appendages are present in *H. aegypticum*, *H. russeggeri* and *H. elodes*, in *Psorospermum* species (*Vismieae*), and sometimes in *Eliaea* and *Cratoxylon* (*Cratoxyleae*). However, in most species of *Cratoxylon* they are absent, as they are in *Triadenum*. In *H. elodes* at least, they seem to act as nectaries, since the tissue at their base is succulent and might easily be punctured by an insect. Knuth (1908), Vol. II, p. 206, says that they "perhaps secrete nectar"; but no nectar secretions were found in the flowers of *H. elodes* which the author examined.

(d) There are only three stamens in each fascicle in all species of *Triadenum*; whereas in *Hypericum* all three fascicles rarely, if ever, consist of an equal number of stamens.

(e) Some species of *Triadenum* (*e.g.* *T. walteri*) have indeterminate inflorescences comprising axillary clusters of flowers, and some species of *Cratoxylon* (*e.g.* /
(e.g. *C. polyanthum*) have a similar inflorescence, but this type is unknown in *Hypericum*. The species of *Hypericum* which Kimura separated as *Takasogoya* have axillary flowers, but the inflorescence is not indeterminate.

(f) Metcalfe and Chalk (l.c.) record that the stomata in the *Cratoxyleae* and the *Vismieae* are rubiaceous, i.e. they are surrounded by only two subsidiary cells, while in *Hypericum* they are surrounded by three or more cells, i.e. ranunculaceous. Of the species examined *Cratoxylon polyanthum* and *Triadenum walteri* had the rubiaceous type, whereas *Hypericum calycinum*, *H. maculatum* Cr., *H. aegypticum* and *H. elodes* had stomata of the ranunculaceous type.

(g) The known basic chromosome numbers in *Hypericum* are 10, 9, 8, 7 and possibly 6, but *Triadenum virginicum* has $n = 19$ (see later).

From the above information it will be apparent that, whereas *H. aegypticum* and *H. elodes* resemble other *Hypericum* species in all respects but for the possession of staminodes, nectaries and filaments which are connate for most of their length, the species of *Triadenum* differ from *Hypericum* in several rather fundamental ways. *Triadenum*, in turn, shows many points of resemblance to the *Cratoxyleae* and to *Cratoxylon* itself in particular. Nevertheless it differs in some respects from that genus, e.g. the species of *Triadenum* are marsh herbs, not tall shrubs or small trees; their seeds do not have the cartilaginous wings which occur in the seeds of *Cratoxylon*.
ylon; and the capsule of Triadenum dehiscences septicidally, not loculicidally. (It may be noted, however, that the capsules of Eliaea dehisce in both ways.)

The geographical distribution of Triadenum also suggests a relationship with Cratoxylon. The Vismieae are found in Tropical Africa and Madagascar, and Vismia itself also occurs in Central and South America. In the Cratoxyleae, Eliaea is a monotypic genus from Madagascar, while Cratoxylon occurs in S.E. Asia. Now Triadenum is found in Khasia (H. [Triadenum] breviflorum Wall., the only species with white flowers), Manchuria, Korea, Japan and S.E. Siberia, and also in Eastern North America in the area bounded by Florida, Labrador, Manitoba and Texas (Fernald, 1950). Thus it seems very probable that Triadenum has evolved in S.E. Asia from Cratoxylon, and has migrated into the temperate region of E. Asia and across to America. Its present distribution is similar to that of many genera and species which had a panboreal distribution in the pre-glacial era, but there is no evidence to show that Triadenum ever occurred in the western part of the Old World.


These three monotypic sections are geographically quite separate from Triadenum. H. russeggeri (Adenotrias) grows in only three localities, one in the Amanus and two in W. Asia Minor; and H. aegypticum s.l. (Triadenia) comprises several populations scattered over the Mediterranean area (Ionian Islands, Crete, Cyrenaica, Malta, /
Malta, S. Algeria (?) and Morocco). Both these species are low shrubs with small, coriaceous leaves. Their flowers differ in several ways, however. Those of *H. aegypticum* show dimorphic heterostyly; the petals and stamen fascicles persist after flowering; and each capsule loculus contains several seeds arranged in two rows. In *H. russeggeri* the flowers are homostyled; the petals and stamen fascicles are deciduous after flowering; and each capsule loculus contains only two seeds. These floral differences have been thought sufficient to warrant putting the species into two separate, monotypic sections, or even different genera (Spach, 1842); but outwardly they are rather similar.

On the other hand, *H. elodes* grows in N.W. Europe and the Azores; it is a sub-aquatic herb with a shaggy tomentum on the stem and leaves; and its flowers differ in several respects from those of *H. aegypticum* and *H. russeggeri*. The petal appendage is fringed, not rounded (although those of *H. aegypticum* which were examined had more or less eroded margins); the sepals are bordered by stalked glands; and the staminodes are flattened in the upper part and emarginate at the apex, not roughly cubical. The pattern on the seed-coat is also quite different (see later), and *H. elodes* does not have the fleshy appendage to the seeds which occurs in the others. Therefore, in spite of having flowers with staminodes and nectaries, *H. elodes* does not seem to be closely related to the other two species.

The flowers of all three species are specialised for insect pollination. Thus they are pseudo-gamopetalous.
ous like those of the Silenoideae, since the gamosepalous calyx of *H. elodes* and the erect, coriaceous sepals of the other species make the corolla effectively tubular. The petal appendage lies against the stamen fascicle (Fig. 84) in such a way as to guide the probing tongue of an insect to the succulent (? nectariferous) tissue at its base, while at the same time the insect's back will brush against the anthers so that some pollen will be deposited on it.

The fascicles in the above species differ from those of other species of *Hypericum* in that the filaments cohere for most of their length, a condition which seems to bear some relation to the pseudo-gamo-petalous corolla. The fusion of the filaments must be a secondary development from the evolutionary viewpoint, because the fascicle traces branch in exactly the same way as they do in other species of *Hypericum* where the filaments are free from near the base (Fig. 86). Wilson (1937) has come to the same conclusion with regard to the fascicles in *Vismia*.

We have seen that the staminodes in the above species of *Hypericum* are probably homologous with those of the *Vismieae* and *Cratoxyleae*. Hochreutiner (1918) discovered that the young flowers of *Psorospermum* have small staminodes which later become very thick. In *Hypericum elodes* they widen at the base and then lean out against the sepals. He claimed that this helps to expand the sepals and petals from the bud, just as lodicules help the expansion of the glumes in grasses. In *Elaeae*, /
Liliaea, too, the little conical staminodes were seen to aid anthesis. Now, all these plants (Psorospermum, Liliaea and H. elodes) have nectaries. In the species of Vismia, which have no nectaries, the staminodes do not expand radially nearly so much. Hochreutiner suggested that the large staminodes in Cratoxylon might combine the functions of nectary and lodicule, but it has not been possible to verify this suggestion. The enlargement of the staminodes just before anthesis may account for the report by Hirmar (i.e.) that the staminodes ('nectarien') develop long after the fascicles.

The dimorphic heterostyly in H. aegypticum is another evolutionary development which indicates specialisation for insect pollination. This condition has been reported elsewhere in the Hypericoideae only in Cratoxylon formosum (Dyer, 1872; Darwin, 1880), but a perusal of figures of some other species of Cratoxylon suggests that Cr. formosum is not the only member of the genus with dimorphic flowers.

Apart from the staminodes, then, there is no evidence to show that Sects. Triadenia, Adenotrias and Elodes are derived directly from pre-Hypericum ancestors in which the outer androecial whorl was still present. On the contrary, these sections seem to represent two independent evolutionary tendencies within Hypericum towards specialised entomophily, as opposed to the unspecialised 'pollen' flowers of the rest of the genus. If this theory is correct, how can one account for the presence /
presence of staminodes in these species? It seems possible that the ancestral staminodes have reappeared atavistically (?) in two different parts of the genus, and have been retained since they perform a special function, i.e. they act as lodicules. The absence of any vascular connection between the staminodes and the stele is a point in favour of this suggestion, while the presence of vestigial traces in the centre of the staminodes speaks for the homology between these structures and the staminodes in Vismia etc. Genetical studies might throw light on this question. The occurrence of staminodes (? and nectaries) may be governed by a recessive gene, or a gene whose activity is usually suppressed in Hypericum. It would then follow that similar adaptations towards specialised entomophily in different parts of this genus were correlated with the removal of the inhibiting factor.

It may be noted that, at least in Britain, the entomophilous specialisation in H. elodes does not result in a high reproductive capacity (Salisbury, 1942). Seed production in this species is not very great, and propagation appears to be mainly vegetative.


If the species which comprise these three sections do indeed belong to Hypericum, it should be possible to discover their nearest relatives among the rest of the species in the genus, whose flowers have remained /
remained unspecialised for insect pollination. When the staminodes, nectaries and connate stamens are discounted, the Elodes type of flower is no different from that of 'Euhypericum'; and so it is in that large and variable section that we should look for these relatives.

**Hypericum aegypticum** and **H. russeggeri**.

Keller divided Euhypericum into nine subsections, three of which consist of sclerophyllous shrubs of the Mediterranean region (like *H. aegypticum* and *H. russeggeri*), while the members of the other two are nearly all herbaceous. In his revision of the Mediterranean and Oriental species, Stefanoff (l.c.) divided two of the three shrubby subsections into four and five sections respectively, and also added two more monotypic sections to the group:

<table>
<thead>
<tr>
<th>Keller (1925) - Subsections</th>
<th>Stefanoff (1932-4) - Sections</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coridium (Spach) Boiss.</td>
<td>Coridium Spach (1)</td>
<td>W. Alps.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Galilifolia Stef. (1)</td>
<td>E. Caucasus.</td>
</tr>
<tr>
<td>&quot;</td>
<td>Empetrifolia Stef. (2)</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Eriocides Stef. (2)</td>
<td>S. Spain,</td>
</tr>
<tr>
<td>Arthrophyllum (J. et S.) Boiss.</td>
<td>Arthrophyllum Jaub. et Spach (6)</td>
<td>Gilicia to</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Palestine,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Socotra.</td>
</tr>
</tbody>
</table>

Triadencidea /
<table>
<thead>
<tr>
<th>Keller (1925) - Subsections</th>
<th>Stefanoff (1938-4) - Sections</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Triadenioides</strong> (J. et S.) Boiss.</td>
<td><strong>Triadenioides Jaub. et Spach</strong> (1)</td>
<td><strong>Anatolia</strong>?</td>
</tr>
<tr>
<td>&quot;</td>
<td><strong>Serpyllifolium Stef.</strong> (1)</td>
<td><strong>W. Syria</strong> to <strong>Palestine</strong>.</td>
</tr>
<tr>
<td>&quot;</td>
<td><strong>Cuneatum Stef.</strong> (1)</td>
<td><strong>Cilicia</strong>, <strong>Lebanon</strong>.</td>
</tr>
<tr>
<td>&quot;</td>
<td><strong>Nummularia Nym.</strong> (3)</td>
<td><strong>Pyrenees</strong>, <strong>Alps</strong>, <strong>Cilicia</strong>, <strong>Amanus</strong>, <strong>W. Caucasus</strong>.</td>
</tr>
<tr>
<td>&quot;</td>
<td><strong>Fragilia Stef.</strong> (2)</td>
<td><strong>Aegean</strong>, <strong>Armenia</strong>.</td>
</tr>
<tr>
<td><strong>(Sect. Thasium Boiss. p.p.)</strong></td>
<td><strong>Haplophylloides Stef.</strong> (1)</td>
<td><strong>Albania</strong>.</td>
</tr>
<tr>
<td>&quot;</td>
<td><strong>Ovalifolium Stef.</strong> (1)</td>
<td><strong>N. Syria</strong>, <strong>Amanus</strong>.</td>
</tr>
</tbody>
</table>

The numbers after Stefanoff's sections indicate how many species each contains. Since his monograph was published, two more species which belong to this group have been described — **H. minutum** Davis et Poulter (Sect. **Fragilia**) from Anatolia, and **H. ternatum** Poulter (aff. Sect. **Cuneatum**) from Cilicia (Poulter, 1954). Stefanoff has carried 'splitting' to extreme lengths in this group. It might be more satisfactory to treat it as a single section, especially since the recently discovered **H. ternatum** combines the whorled phyllotaxis of Sect. **Coridium** with characters of some of the other species, e.g. **H. pallens** Banks et Soland. (Sect. **Cuneatum**).

Since certain of its members bear a definite resemblance to **H. aegypticum** and **H. russeggeri**, the above group was studied as a whole, whereupon certain morphological /
morphological and distributional relationships became apparent. (Herbarium specimens of all but one of the species have been examined, the exception being \textit{H. asperuloides} (Czern. ex) Turcz., the only member of Sect. \textit{Galilifolia}.) Morphological characters which are of taxonomical importance in these species include: (a) Leaf shape and phyllotaxis, (b) the sculpturing of the testa and the prominence of a keel or wing on the seeds, (c) the presence of a fringe of dark glands round the sepal margin, and (d) the habit of the plant. Correlated trends occur in these characters, the first three of which are indicated in Text Fig. 1. These trends are all more or less continuous, so that it is not strictly accurate to divide them into two or three hard and fast lines. Therefore, when one of the lines in this figure passes through the name of a section, it indicates that the character varies in that section, the predominant condition being shown by the position at which the line crosses the name. The interrelationships of the various species is certainly more complex than would appear from the diagram. The arrows merely indicate the directions of general morphological trends in the group, although they may have evolutionary significance as well.

The basic section appears to be \textit{Arthrophyllum}, which consists of broad-leaved, Vaccinioid shrubs. From this section there are two main trends, in one of which the leaves become orbicular-cordate (\textit{Califolium} etc.), while in the other they become linear and whorled (\textit{Cuneatum} /
Key to Seed Characters.
- Winged raphe  F - Foveolate testa  ( ) - Character slight
- Keeled  " R - Rugose  "  - - Character very marked
P - Papillose  "

Text fig. 1. Morphological Relationships of the Shrubby Species of Euhypericum, including Sects. Triadenia and Adenotrias.
Cuneatum etc.). In both these series there is a trend in habit which culminates in the semi-herbaceous species of Nummularia and Galiifolia respectively. The species of Arthropodium have sepals which are usually entire, but occasionally have sessile, dark glands on the margin. In the Ovalifolium series such a glandular fringe is constantly present, the glands becoming stipitate in the later sections; but this character is more variable in the Cuneatum series where, however, the least shrubby species also has gland-fringed sepals.

The seed characters, which Stefanoff (l.c.) regarded as very important, were also found to vary more or less continuously, but two generalisations can be made about them: (i) the raphe is keeled or winged only in the earlier sections, and (ii) the testa tends to become more papillose in the later sections. (Exceptions are found in Galiifolia, in which the testa is foveolate, and in Fragilia where it is very slightly foveolate-rugulose.)

H. heterophyllum Vent. (Triadenioidea) occupies a rather isolated position in this group, on account of its vegetative specialisation. Its lower leaves are obovate-spathulate like those of other species in the 'intermediate' group, but the upper ones are linear and acute. In the axils of the lower leaves there are very short shoots bearing small, broad, crowded leaves. On the other hand, this species has eglandular sepals and seeds which are foveolate and keeled, both of which are characteristic of the earlier species.
Now, *H. russeggeri* and *H. aegypticum* have many characters in common with these 'shrubby *Euhypericum*' species, and in particular with *H. pallens* (*Cuneatum*) and *H. ternatum*. Like the last two species they are low shrubs with small, coriaceous leaves which are often obovate-spathulate. With regard to the branching of the inflorescence, *H. pallens* and *H. aegypticum* both tend to produce flowers at the end of short shoots for some distance down the branch, whereas in *H. russeggeri* only the uppermost leaf axils bear flowering shoots. In *H. ternatum* the flowers are most often single and terminal, an arrangement which can also be found in some plants of the other species. (Fig. 90, between pp. 71-2).

While *H. aegypticum* and *H. russeggeri* always have entire, eglandular sepals, those of *H. pallens* often bear a few, small, marginal glands and the sepals of *H. ternatum* also very occasionally have one or two of these. The seeds of all four species are somewhat rugulose, nearly smooth in *H. ternatum* but almost papillose in *H. pallens*. The other two species are intermediate in this respect, but differ from all other members of the genus in having a fleshy appendage to their seeds. The morphological status of these appendages is not clear. Arils are not found in the *Hypericoideae*, but they do occur elsewhere in the *Guttiferae*, in the *Clusioidae*. Nevertheless, in the light of all the other evidence of specialisation in *H. aegypticum* and *H. russeggeri*, it is most unlikely that the presence of
of such appendages betokens a relationship to the tropical, woody Guttiferae. They may perform some function in seed dispersal (e.g. by ants), but no information on this point is available.

As we have seen, *H. russeggeri* was placed in a separate genus from *H. aegypticum* by Spach, because it differs from the latter in its deciduous petals and stamens, homostylic flowers and biovulate carpel loculi. Now, homostylic flowers are normal in *Hypericum*, and the remaining two characters are found in other sections of this Triadenioidae group, viz. deciduous petals and stamens in Sect. *Empetrifolia* and, to some extent, in Sect. *Coridium*, and biovulate carpel loculi in *H. heterophyllum* (*Triadenioidae*). Deciduous petals and stamens have considerable taxonomic value in some parts of *Hypericum*, but not in the part of the genus to which the *Triadenioidae* group belongs (see later, text fig. II).

Geographically, too, Sects. *Adenotrias* and *Triadenia* may be considered as typical members of the 'shrubby Euhypericum' group. From the distributions of the sections it will be seen that *Arthrophyllum*, *Triadenioidae* and *Cuneatum* (the earlier ones in the series in Text fig. I) are confined to the Middle East (Socotra, Persia, Lebanon), while the later sections are more widespread. Thus *Fragilia* extends from the Aegean region to the Caucasus and *Nummularia* from the Pyrenees to the Caucasus, while the species with narrow, whorled leaves (the *Coridium* group) occur disjunctly over the whole Mediterranean region and also in the Caucasus. The discovery in Cilicia of *H. ternatum*, the /
the other species with whorled leaves, helps to reduce the size of the disjunction from the Aegean region (Empetrifolia) to the Caucasus (Galiifolia).

_H. pallens_, _H. ternatum_ and _H. russeggeri_ all grow in the same region of the E. Mediterranean (Map 1). _H. russeggeri_ also occurs in the Aegean region, and so helps to bridge the gap in distribution between the Levant and the most eastern locality for _H. aegypticum_, in Crete. This latter species occurs in several isolated localities throughout the Mediterranean area (Map 1).

These four plants are also similar ecologically in that they all grow in saxatile habitats (cliffs or maritime rocks). Davis (1951) has shown that species which occupy such habitats frequently have discontinuous geographical distributions, and in this respect _H. aegypticum_ in particular is a typical saxatile species. Davis also shows that many chasmophytes have secondarily acquired a woody habit. Poulter (1952) suggested that the shrubbiness in this group of _Euhypericum_ was a derived condition, but this seems unlikely when its relationship to the tropical, woody _Norysca-Campylosporus_ group is considered (see Chap. V).

Taking into account the general westward trend from a centre in the Middle East which appears to have occurred in other parts of the Triadenicoida group, it seems reasonable to suggest that _H. russeggeri_, _H. aegypticum_, _H. pallens_ and _H. ternatum_ had a common ancestor, /
Map 1. The distribution of *H. aegypticum* and its allies, based on Stefanoff (1933) and Poulter (1954) with additional localities from Jahandiez & Maire — Cat. Pl. Maroc, II (1932) — and Pampini-Prodr. Fl. Cirenaica (1931).

- **H. aegypticum**. (The S. Algerian record has not been localised).
- **H. pallens**
- **H. russegeri**.
- **H. ternatum**.
ancestor, probably a chasmophyte, which grew in the E. Mediterranean region. Genetic drift in isolated colonies of this chasmophyte would result in the differentiation of the four species, three of which seem to have remained in the area of the parent species. The fourth (H. aegypticum) spread westwards through the Mediterranean, possibly because it grows mainly on maritime rocks rather than on cliffs. The area of each species will have been further dissected, resulting in their present 'relict' distributions; but this dissection must have taken place at a distant period of time because the various isolated communities of H. aegypticum differ markedly from one another. However, whether these differences warrant taxonomic segregation is another matter.

Hypericum elodes.

This species is a pubescent herb, so that its nearest relatives are likely to be found in the remaining part of Sect. Euhypericum, the members of which are all herbaceous. Keller divides this part into six subsections, but Stefanoff made sixteen sections from the European-Mediterranean species alone, five of these sections being practically the same as five of Keller's subsections. The sixth and largest subsection is Homotaeniurn, which contains herbs with opposite leaves, calyx segments which do not overlap, and capsules in which the carpel vittae are longitudinal, parallel and entire. Stefanoff divided it initially according to the sculpturing of the testa and the presence or absence
of short, axillary shoots as follows:

Semina foveolato-lineata vel leviscula

Axillis ramuligeris (excl. inferioris)nullis —
Sect. Montana Stef.

Axillis ramulos abbreviatos gerentibus —
Sect. Perforata Stef.

Semina papillosa vel tuberculata — Sects. Pulchra
Stef., Hyssopifolia Stef., Hirtella Stef.,
Spectabiles Stef. and Scabra Stef.

If the staminodes, nectaries and connate filaments of *H. elodes* are disregarded, its characters agree essentially with those of Sect. *Montana*. The species in this section are all more or less pubescent, apart from *H. linearifolium* Wahl, *H. australe* Ten. and *H. aucheri* Jaub. et Spach which, along with *H. humifusum* L., form an evolutionary side branch of *Montana* which shows a relationship to the adjacent Sect. *Origanifolia*. The pubescent species are distributed in the Mediterranean and N. African regions, apart from *H. montanum* itself, which extends into Central and Northern Europe, and two closely related species in the E. African mountains, one of which is also found in Sardinia. (Although *H. montanum* is mostly glabrous, the lower surface of the leaves is usually scabrid or slightly pubescent.)

*H. elodes* occurs in W. Europe and the Azores, with outlying stations in Germany, Austria, Liguria and Majorca (Map 2) — a typical 'Atlantic' distribution. Now, one of the species in Sect. *Montana* also inhabits regions bordering the Atlantic Ocean. This plant, *H.* /
Map 2. The distribution of H. elodes and its allies, based on Stefanoff (1933) with amendments in Britain and Austria.

- H. elodes.
- H. coadunatum.
- H. caprifolium.
- H. decaisneanum.
H. coadunatum Chr. Sm. is found in the Canary Islands, Morocco and Algeria, and differs from the closely related H. caprifolium Boiss. of S.E. Spain mainly in its smaller leaves and its sepals which are broader and not aristate.

A comparison of H. coadunatum and H. elodes has revealed many points of similarity between these species:

Habit - The N. African plants of H. coadunatum (which were described as a separate species, H. naudinianum Coss. et Dur.) appear to be less sturdy than the Canary Island ones (H. coadunatum s.s.). According to the original description (Cosson and Durieu, 1855), the caudex of H. naudinianum is semi-creeping and often emits sterile shoots, while the stems are diffuse and ascending or erect. (In other pubescent species of Sect. Montana the stems are nearly always erect.)

These stems and caudex may be compared with the long stolons of H. elodes which root at the nodes and emit sterile or fertile shoots.

Stems - In both species they are villous to sub-tomentose and terete, the latter character being found in all members of Sect. Montana. The presence of aer-enchymatous tissue in the rhizomes of H. elodes is attributable to its aquatic habitat. This tissue does not seem to occur in H. coadunatum, but the point was not studied thoroughly owing to lack of suitable material.

Leaves - In both species these are ovate to orbicular and obtuse (sometimes emarginate in H. elodes), with /
with a crisped pubescence which is denser on the lower surface. The upper leaves of *H. coadunatum* are perfoliate like all those of *H. caprifolium*, but the lower ones may be cordate-amplexicaul as in *H. elodes*. All the species of Sect. *Montana* have a row of intramarginal, dark glands, but these are smaller and fewer in number in *H. coadunatum* than in the other species. They are absent from the leaves of *H. elodes*.

**Inflorescence** — This is terminal in both species. Stefanoff and others lay stress on the 'lateral' inflorescence of *H. elodes* because such an arrangement is unknown elsewhere in *Hypericum*, but inspection reveals that it only appears to be lateral because one of each pair of axillary buds is retarded or fails to develop. When an erect inflorescence is formed at the end of a stem, one of the lower axillary buds develops into a shoot, i.e. growth is sympodial. The flowers are more numerous in *H. coadunatum* than in *H. elodes*, but they are about the same size. The pedicels of *H. coadunatum* are glabrous, like those of other species in Sect. *Montana*, and, although they are often sparsely pubescent in *H. elodes*, glabrous pedicels may be found in that species also.

**Sepals** — In *H. coadunatum* they are acute and subentire, with sessile or subsessile marginal dark glands and occasionally a few superficial ones; while *H. elodes* has obtuse to rounded sepals fringed with red glands, and never has any superficial ones. However, the red colour, which often diffuses into the surrounding tissue in dried specimens, indicates merely that the concentration /
Fig. 91. Seed-coat patterns in (a) H. caprifolium, (b) H. montanum (also in most of Sect. Montana and occasionally in H. elodes), and (c) H. elodes. (All ca. x 50)

Fig. 92. A stem node of H. pro- lificium showing the articulated leaf bases. (The axillary shoots have been omitted). (ca x 10)

Fig. 93. A stem node of H. perforatum, showing the unarticulated leaf bases. (ca x 10)
concentration of hypericin is lower in these glands than in the dark ones. (Hypericin in high concentrations appears almost black.)

Petals — In both species they are about three times as long as the sepals. The petals of *H. elodes* are always eglandular, but those of *H. coadunatum* sometimes have marginal dark glands.

Capsule — The pattern of the vittae is similar in both species, but in *H. elodes* the ovary is unilocular above whereas it is said to be completely trilocular in *H. coadunatum*.

Seeds — *H. coadunatum* and *H. caprifolium* differ from the other species of Sect. *Montana* in having almost smooth seeds. The lines of pits are very faint. In this character *H. elodes* shows a greater resemblance to these other species, since its seeds were found to be occasionally foveolato-lineate. More often, however, each line of pits merges into a single longitudinal depression traversed by numerous small striae (Fig. 91).

Habitat — Both species grow in regions with an 'Atlantic' climate, and both frequent damp habitats — *H. elodes* in peaty pools and *H. coadunatum* over damp rocks and at streamsides. (Apart from *H. caprifolium*, all the other species of Sect. *Montana* grow in dry habitats.)

On the basis of the above comparison, it seems valid to regard *H. elodes* as an extreme development of Sect. *Montana* which has become adapted to an aquatic existence /
existence and has evolved a specialised type of flower. In many characters *H. ceadunatum* shows a tendency to approach *H. elodes*, while in others it is a typical member of Sect. *Montana*.

The chromosome number of *H. elodes* was found to be \(n = 16\), i.e. it is tetraploid in relation to all other species of Sect. *Montana* which have been counted (see Chap. V).

The Cyrenaican endemic, *H. decaisneanum* Coss. et Dav. (see Map 2), which also belongs to this section, has the general appearance of a small plant of *H. elodes* with crowded leaves. However it is neither stoloniferous nor aquatic.

The preceding discussion of the 'Elodes' group of *Hypericum* has yielded the following conclusions:

1. Sect. *Elodea* should not be included in *Hypericum*, but, as the genus *Triadenum*, it should be placed in the *Cratoxyleae*.

2. Sects. *Triadenia* and *Adenotrias* are related to the shrubby species of *Euhypericum* in the Mediterranean region (the *Triadenocioidea* group).

3. Sect. *Elodes* is an extreme development of Sect. *Montana*, one of the herbaceous groups of *Euhypericum*.

It will be shown later that the shrubby and the herbaceous species of *Euhypericum* belong to separate evolutionary lines of *Hypericum*. This fact, along with the possibility of relating *H. aegypticum*, *H. russegeri* and *H. elodes* to relatively advanced species of *Hypericum*, lends further support to the theory that the staminodes /
staminodes in these species are secondarily acquired — or rather, reacquired — probably in relation to the more specialised type of flower which they possess.
CHAPTER IV.

THE RELATIONSHIPS OF THE HYPERICUM SPECIES WITH AFASCICULAR OR IRREGULAR ANDROECIA.

(1) Sect. Campylopus.

It has already been shown that *H. rhodopeum* Friv., the only species in this section, does not have a truly afascicular androecium. The flowers of this herb from the Balkans and Asia Minor occupy an intermediate position in the trend from five fascicles and five carpels to 'three' fascicles and three carpels. They usually have three carpels, but Stefanoff indicates that four- or five-carpellary flowers are sometimes found, though less frequently. Likewise he describes the stamens as "triadelpha vel tetradelpha", although the flowers studied in the present work had five separate fascicles. The presence of fascicles and its herbaceous habit suggest that *H. rhodopeum* is a species of the 'herbaceous Euhypericum' type, while the variation in the numbers of floral parts indicates that its nearest relatives should be sought among the less reduced members of that group. The broad, entire, imbricate sepals resemble those of *H. olympicum* L., which occurs in the same area; and the numerous unbranched stems, each terminating in an inflorescence of a few, relatively large flowers, are also characteristic of that species and of several related ones from the same and adjacent regions (e.g. *H. orientale* L. and *H. origanifolium* Willd.). Like *H. rhodopeum*, *H. origanifolium* /
folium is densely pilose in its vegetative parts; and since the only species outside 'herbaceous Euhypericum' and H. elodes which have a tomentum are H. setosum L. (Spachium) and H. reflexum L. ('shrubby Euhypericum'), this character is another piece of evidence which suggests that the nearest relatives of H. rhodopeum are to be found among the large-flowered species of Euhypericum from the Balkans and Asia Minor.

(2) Sects. Myriandra, Brathydium and the 'Genus' Ascyrum.

The evidence from floral anatomy favours the idea that these species form a natural group in which the five stamen fascicles have condensed into a continuous ring. Gross morphology, too, suggests that the above sections are closely related. Indeed, it is difficult to find characters which will separate them satisfactorily.

Myriandra comprises shrubs whose flowers have a five- to three-carpellary ovary in which the placentation is rarely completely axile, more often incompletely axile or almost parietal. In Brathydium the species are mostly herbaceous, and the placentation of the tricarpellary ovary is usually completely parietal. Keller followed Spach in separating the two sections on whether the stamens are deciduous (Myriandra) or persistent (Brathydium), but this treatment results in some anomalies, e.g. the dwarf shrub H. buckleyi Curt. has axile /
axile placentation but its persistent stamens place it in Brathydium. Although there is a general trend from shrubs with axile placentation and deciduous stamens to herbs with parietal placentation and persistent stamens, the characters of Brathydium and Myriandra intergrade to such an extent that it may not be possible to draw a satisfactory dividing line between these sections, in which case they should be treated as a single section.

American species of Ascyrum have several characters in common with one or both of these sections. Like Sect. Myriandra they are shrubby and the carpels can be isomerous (they vary from four to two), but the placentation is always parietal as in Brathydium. All three groups have quadrangular or winged stems and minute stigmas, and the styles are partly or completely coherent during flowering. They also have overlapping geographical distributions. Brathydium has the most northern range, being confined to Eastern North America, while Ascyrum and Myriandra species occur in the same region, but are also found in Central and South America and the West Indies. Three gatherings of A. hypericoides in the Royal Botanic Garden Herbarium, Edinburgh, come from Brazil (Reineck, 1896 and 1899), and H. gallicoides Lam. s.l. (Myriandra) probably occurs in Ecuador (see below). These southern representatives of both groups are variable, but the narrow-leaved forms of A. hypericoides are very similar in general appearance to some forms of H. gallicoides v. pallidum Svenson. Again, A. amplexicaule Michx. from Florida differs essentially from /
from *H. myrtifolium* Lam. (a plant of the same region) only in the tetramery of the perianth.

The large pair of outer sepals which occurs in all species of *Ascyrum* except *A. microsepalum* Torr. et Gr. gives the flowers a characteristic form; but although the sepals of *Myriandra* species are also very unequal, their quincuncial insertion gives them a different appearance from those of *Ascyrum* species.

The remaining member of *Ascyrum* is *A. filicaule* (H.F. et Th.) Dyer, which occurs in the Himalayan region. A glance at the type specimen from Sikkim (at Kew) was sufficient to show that this species is very different from the American ones. In fact, practically the only point of resemblance to them is the tetramerous perianth. *A. filicaule* is a dwarf herb with stems ca. 7.5 cms. high, which "forms mossy clumps on the granite boulders of cascades" (Kingdon-Ward, No. 9882). Each stem bears a single flower which has three stamen fascicles and three divergent styles. On the other hand, it differs from small specimens of *H. monanthemum* H.F. et Th. only in the tetramery of the perianth. On the label from which the above quotation was taken, Kingdon-Ward also remarks: "This may be only a form of No. 9763", which number turns out to be a small specimen of *H. monanthemum*. We can conclude, therefore, that *Ascyrum filicaule* is related to Himalayan herbaceous species of *Euhypericum*, not to the American species of *Ascyrum*.

Vestal /
Vestal (l.c.) showed that there was no difference in wood anatomy between the American species of Ascyrum and Hypericum, and we have also seen that their flowers are anatomically similar.

In view of all these facts there appears to be no case for retaining Ascyrum as a separate genus. Indeed, owing to the reticulation of characters between Myriandra, Brathydium and Ascyrum, it is not certain whether it should be given full sectional status. Keller has already referred to it as a section of Hypericum (Keller, 1898), but he apparently changed his mind when making his 1925 revision, where it is treated independently as a genus.

The results from the studies of floral anatomy indicated that Sects. Myriandra, Brathydium and Ascyrum were related to the African Sect. Campylosorus and to Sect. Webbia from the Canaries and Madeira, and support for this idea is also provided by gross morphology. Thus some species of Campylosorus and all those in the other sections have a quadrangular stem; the styles are connate to a greater or lesser degree in all the sections except Webbia; the seeds of the species in Webbia are keeled, as are some of those in Myriandra, e.g. H. splendens Small; and the placentation in Webbia is semi-parietal, while in many of the American species it is completely parietal.

(3) Sect. Brathys.

It has been shown that the afascicular androecium in Sect. Brathys is produced by a lateral expansion of /
of the five stamen fascicles, in contrast to that of the Myriandra group where an analogous condition results from radial contraction of the fascicles.

As Keller recognised it in 1925 (i.e. excluding the shrubby species from New Guinea), Sect. Brathys consists of species with parietal placentation and afascicular androecia (except in flowers with a small number of stamens). In contrast to the previous group, the styles are always free and divergent. Keller includes two species from Ecuador with fused styles in Subsect. Eubrathys (H. nitidum Lam. and H. aciculare HK.), but Svenson (1940) treats the former one as synonymous with part of H. galioides agg. (Myriandra). No further information about H. aciculare has been discovered, but the fused styles and narrow leaves suggest that it is related to the same aggregate species and not to Brathys.

Brathys contains two subsections, Eubrathys and Spachium. Eubrathys species are shrubs with short internodes, imbricate leaves and few, usually large flowers. They grow in the American Cordillera from Peru and Bolivia to Guatemala, and also in the West Indies and the mountains of Guiana (Gleason, 1929). The species of Spachium, on the other hand, are mainly herbaceous with more numerous, smaller flowers. Members of the two subsections are usually easily differentiated, but some South American shrubs have intermediate characters and so prevent the two groups being given sectional status. Keller originally (1895) classified
a group of these intermediate species in a Subsect. Connatum, but he omitted this subsection in 1925. Although Spachium is best represented in the Americas, some species occur in Africa south of the Sahara and Madagascar, while others are found in E. Asia, Indonesia, Australia and New Zealand. In both subsections the number of carpels varies from five to three, and some of the species of Spachium with small flowers have only two.

A discussion of the relationships of Sect. Brathys involves consideration of Sect. Humifusoidum, and so it will suffice to point out here that some of the New Guinea species of Hypericum form a link between these sections.

(4) Sect. Humifusoidum.

At the present time, Sect. Humifusoidum consists of only two species, H. peplidifolium A. Rich. from Tropical Africa and H. natalense Wood et Evans from Natal and Cape Province. Reasons were given in Chapter II to show why H. aethiopicum Thunbg. from Cape Province and H. sonderi Bredell from S.E. Africa should also be included in this section, and further research has revealed several more species in the same circle of affinity. Keller's diagnostic characters for Sect. Humifusoidum — three stamen fascicles and five carpels — have been shown to apply to only certain forms of H. peplidifolium and H. natalense and not at all to the other species that were considered, and so the characters and limits of the section require to be redefined.

From a study of the relevant material in the herbaria /
herbaria at Edinburgh, Kew and the British Museum (Nat. Hist.) it has become clear (i) that most of the Central and South African species of Hypericum apart from Sect. Campylosporus belong to Sect. Humifusideum, and (ii) that the characters which separate this section from Sect. Brathys are not so clearly marked as they were thought to be. Table 1 gives the distributions and some characters of the African species which appear to be related to *H. peplidifolium* and *H. natalense*, and so should be included in Sect. Humifusideum.

The specific differences between the various members of the enlarged Sect. Humifusideum are not always clear cut, and the whole group requires detailed taxonomic revision. Thus an examination at Kew of specimens of the three plants which Milne-Redhead (1953) treats as incompletely known species ("Species A, B and C"), shows that Species A and B appear to be intermediate between *H. kiboense* and *H. aethiopicum*, while Sp. C is near *H. peplidifolium* but has some characters which resemble *H. natalense*. A specimen in Hb. Mus. Br. labelled 'H. peplidifolium' (H.B. Gilliland, B.448) has numerous flowers, narrow, acute sepals which are covered with dark dots, as are the petals and the stem, and also three long styles — all of which are characters of *H. sonderi*; but its leaves are small and orbicular like those of *H. peplidifolium*. Another specimen, in Hb. R.B.G. Edin. (Buchanan, 140), has the dotted stems of *H. sonderi* and the habit and leafy inflorescence of *H. natalense*, while the fruit tends to be succulent as in *H. 
H. peplidifolium. Likewise H. oligandrum, with its more or less quadrangular stem, few dark glands, five carpels, unilocular ovary and tardily dehiscent capsule, appears to be intermediate between H. peplidifolium and the H. humbertii-H. scouianum group (see Milne-Redhead, 1948). Norlindh (1934) states that he has not been able to separate H. natalense from the very variable H. peplidifolium, since there appears to be a complete series of forms intermediate between the two extremes.

In all the species in Table 1 the androecium is usually more or less irregular, i.e. the presence of fascicles is not easily detected, and the filaments are all shortly connate at the base. Other features which are typical of the section are as follows:

(i) The terete stem of most of these species differentiates them from nearly all species of Sect. Brathys. The shrubby members of that section (Subbrathys and some S. American species of Spachium) often have stems which are terete in the lower, more woody parts, but the younger branches are nearly always more or less quadrangular like those of the herbaceous species.

Keller (1908) names four species of 'Spachium' with terete stems. Of these H. wilmsii Keller belongs to Humifusoidae, H. polyanthemum Klotzsch is one of the S. American shrubs mentioned above whose stems are terete below and quadrangular above (see Reichardt, 1878), and H. chamaecaulon Keller (from Guatemala) is a 'nomen nudum'. The remaining species, H. collinum Schl. et Cham. (from Mexico), will be discussed below.

(ii) Most of the species have dark glands on the leaves,
leaves, sepals, petals and anthers, whereas these are very rare in Sect. Brathys. They are said to occur only in one or two American species of Spachium (e.g. H. stigmatophorum Keller and H. melanostictum Keller from Mexico), but they are apparently scattered over the leaves and stem in those species, not confined to the margins of leaves, sepals and petals as they are in most of the Sect. Humifusicideum species. Keller separated H. madagascariense from H. lalandii Choisy (Spachium) owing to the presence of dark glands in the former species, but Perrier de la Bathie (1927) states that dark glands are absent from the Madagascar specimens of H. lalandii that he has seen. The 'pale' glands on the leaves of Hypericum species sometimes appear to be almost black after drying, and so some of Keller's references to dark glands in Sect. Brathys may refer to these. The absence of dark glands is a constant character of Sect. Brathys species seen by the author, but no specimens of H. stigmatophorum and H. melanostictum have been examined.

(iii) The inflorescence is either a bracteate cyme (e.g. H. sonderi), a foliar cyme where each leafy branch ends in a flower (e.g. H. natalense), or the terminal flowers may appear axillary as a result of the development of one axillary shoot, as in H. elodes (e.g. H. peplidifolium).

(iv) In contrast to those of Brathys species, the ovaries of Humifusicideum species nearly all have axile placentation.

(v) No species of Brathys has a baccate fruit such as /
as is found in *H. peplidifolium*. The capsule valves of most of the other species in Table 1 bear longitudinal vittae which are either narrow and entire or, more often, irregularly swollen. In a few specimens of *H. sonderi* there was no sign of vittae, the whole outer carpel wall being covered with swollen, resinous glands. On the other hand, the carpel walls of *H. humbertii* and *H. scoianum* are smooth like those of some *Brathys* species. Other *Brathys* species have faint, longitudinal vittae or, rarely, scattered vesicles (*H. pratense* Schl. et Cham.).

*H. collinum*, which Keller includes in *Spachium*, differs from members of that subsection in several characters. The herbaceous stems of this Mexican species are wholly terete and reddish in colour; there are dark glands on the leaves, sepals, petal margins and anthers; the ovary is trilocular and the styles are capitate but not peltate. Also the pale glands on the sepals and leaves are large and yellowish, unlike those of *Spachium* species.

Keller (1898) rightly points out that it differs from species of *Euhypericum* in having stamens which are not triadelphous but free or all connate at the base, although the ovary is trilocular. (To confirm this a flower from Pringle No. 8945 was dissected.) On the other hand, all these characters, as well as the lax, few-flowered inflorescence and foliar bracts, suggest that *H. collinum* belongs to Sect. *Humifuscideum* as enlarged above. Therefore it would appear that this /
this section is represented in Central America. A closer acquaintance with other species from that area may show that other members of *Humifusideum* are also present there.

Keller (l.c.) also says that his *H. collinum v. liebmannii* (which became *H. liebmannii* Keller in 1925) joins *H. collinum* and the *H. canadense-H. mutilum* group of *Spachium*. No specimens of *H. liebmannii* have been seen, but Keller's description (quadrangular stem, peltate stigmas, unilocular ovary, minutely longitudinally striate capsules etc.) suggest that this species does belong to *Spachium* and differs considerably from *H. collinum* in essential characters.

*H. scotianum* and *H. humbertii* resemble species of *Spachium* in several respects, viz. the quadrangular stem, the absence of dark glands, the tendency towards parietal placentation, and the smooth carpel walls; but the pseudo-axillary flowers of these creeping herbs at once distinguish them from species of *Spachium*, whose inflorescence is always a terminal cyme. On the other hand, they appear to be related to *H. peplidifolium* and *H. natalense* through *H. oligandrum* and *H. nigropunctatum* respectively. It is possible that the resemblances to *Spachium* in *H. scotianum* and *H. humbertii* indicate that these species have originated from hybridisation between the variable *H. lalandii* and *H. peplidifolium* or a related species, since all four plants grow in damp places; or the resemblances may be due to parallel evolution. Experimental work should throw some light on this problem.

Thus Sect. *Humifusideum* consists of low shrubs and /
and erect or creeping herbs which resemble Sect. Brathys in the variability of the number of carpels, in the free styles which mostly have capitate stigmas, and usually in the absence of clearly defined stamen fascicles. If H. humbertii and H. scolanum are excluded, it differs from Sect. Brathys in having axile placentation, terete stems, dark (usually marginal) glands on the leaves etc., and swollen carpel vittae or a more or less succulent fruit. The above species, and also H. peplidifolium and H. oliganthum, differ from Sect. Brathys in their pseudo-axillary inflorescence.

Axile placentation, spreading styles, and dark glands are also found in Sect. Euhypericum (shrubby and herbaceous), but Sect. Humifusoides is distinguished from these groups by the irregular androecium, the variable number of carpels, and the configuration of the carpel vittae (see Chap. II).

Therefore, although detailed investigations may lead to changes in the number of species which it contains, Sect. Humifusoides is a recognisable entity, at least in Africa. However, despite the differences mentioned above, it seems to be most closely allied to Sect. Brathys. Thus the conclusions reached in the floral anatomy studies are supported by investigations into the comparative morphology of this group as they were in the other groups discussed in this Chapter.
CHAPTER V.

GENERAL EVOLUTIONARY TRENDS IN HYPERICUM.

(1) Introduction.

The conclusions which have been reached in the previous Chapters with regard to morphological trends in the flower of Hypericum, and the various inter-relationships which have been revealed as a result of these, have an important bearing on the primary classification of the genus. It now remains to show how information from other sources (e.g. cytology and distribution) can be interpreted in the light of these conclusions to give an idea of the probable course which evolution has taken in Hypericum.

As in previous Chapters, the emphasis will be placed on similarities rather than differences, since only trends and general relationships will be discussed. Concentration on differences is essential when studying specific and lower taxonomic categories, but it may obscure relationships in higher categories. The discussion is based on the results of an examination of all the specimens of Hypericum in the herbarium of the Royal Botanic Garden, Edinburgh, and also many of those in the British Museum and Kew herbaria.

(2) The Articulated Leaf.

The studies in floral anatomy have shown that /
that Keller's primary divisions of Hypericum based on (a) the presence or absence of staminodes, (b) the arrangement of the stamens, and (c) the number of styles are unsatisfactory. Keller and Stefanoff also both lay emphasis on whether the corolla and the androecium are deciduous or persistent after anthesis, on the sculpturing of the testa, and on the pattern of the vittae on the fruiting carpel wall. It has already been shown that these characters are important in certain parts of the genus, but too much reliance on them has led to misclassification of some species (e.g. Stefanoff's separation of H. inodorum Willd. from his Sect. Pseucaandrosaenum on account of its persistent petals and stamens). Likewise the placentation, fusion of the styles, the shape of the stigmata, the presence of dark glands and of lines on the stem, as well as the habit and the form of the inflorescence, can all be employed in the classification of certain parts of the genus, but none of these characters alone provides a valid means of subdividing it initially. An improved classification of Hypericum will require a new approach to the morphology of the genus. In particular, none of the recent attempts to classify the 'Euhypericum' species (by Keller, Stefanoff, Gorschkova [1949] and Kimura) is entirely satisfactory, although each author has shed some fresh light on the subject.

A character which seems to be important in this connection is the presence or absence of an articulation.
articulation at the base of the leaf. Stefanoff drew attention to this character in his sectional descriptions, but he did not discuss it in detail. However, when members of all sections of Hypericum were examined, the presence or absence of articulated leaves was also found to be characteristic of certain sections and parts of sections in other parts of the world than Stefanoff's European-Mediterranean area. In typical examples this articulation takes the form of a deep groove round the petiole (Fig. 92, between pp.89-90) or between the leaf and stem where the leaves are sessile. All the species with articulated leaves are either shrubby or closely related to shrubby ones, but this leaf character is not merely a concomitant of the shrubby habit, since it is almost completely absent from the shrubs of Eubrathys, for example. Nevertheless, it tends to be less noticeable in the less shrubby members of the groups in which it is present, so that only occasional leaves may be articulated in those species.

Articulated leaves are characteristic of the following sections:

Eremmanthe Campylosporus Myriandra
Psorophytum Webbia Ascyrum

They are present in some species of:

Norysea/
Norysca Triadenoioidea series of Euhypericum
Androsaemum (including Stefanoff's sections —
Brathydium Adenotrias Triadenia Triadenoioidea
Arthophyllum Empetrifolia Ericoides
Serpyllifolium Cuneatum Haplophyllloides
Nummularia Ovalifolium Fragilia
Coridium Galiifolia Reflexa)

They are completely absent from:
Elodes The following (herbaceous) groups of Euhypericum —
Roseyana (i) Stefanoff's sections
Campylocpus Olympia Oligostema Grossophyllum
Thasium Bupleurcides Kelleria Modesta
Humifusoidium Montana Origanifolia Uniflora
Droserarpium Perforata (see Fig. 95, between pp. 89-90)
Pulchra Hyssopifolia Spectabiles

Hirtella Scabra
(ii) All E. Asian and N. American species, including H. concinnum.

It was thought at first that Sect. Brathys also contained no species with articulated leaves, but this character has been observed in H. chamaemyrtos Tr. et Pl., where it has probably arisen independently since this species is otherwise typical of Subsect. Eubrathys.

(3) The Four Main Groups of Species.

If the presence or absence of articulated leaves is regarded as a character of primary importance in /
A general characteristic of the group is the complete absence of dark, hypercin-containing glands.

Sect. Norysca occurs in South and East Asia, from Japan to Java and from Ceylon to the Himalayas and Afghanistan. 

**H. mysorensis** (Wight) Heyne is found in Socotra as well as S. India and Ceylon.

The styles in the species of this section vary considerably in length and in the degree of fusion, so that Kimura's genus *Takasagoya* (Kimura, 1936), in which they are long and completely fused, can be regarded as an extreme development of Sect. Norysca. *Takasagoya* agrees with *Norysca* in most other characters; but (i) the sepals are small and may be united at the base, (ii) the seeds are sometimes winged rather than merely apiculate, (iii) the anthers are basifixed, not versatile as in the rest of *Hypericum*, and (iv) the inflorescence usually consists of solitary flowers in the axils of the upper leaves. The characters of the styles, anthers and inflorescence were those which made Kimura give this group generic status. However, the styles of certain species of *Norysca* (e.g. *H. chinense* L.) are long and almost completely fused; and other species of that section (e.g. *H. longistylum* Oliver) have an inflorescence similar to that of *H. pallens* (c. Fig. 90), i.e. short shoots in the axils of the upper leaves, usually bearing a single flower, an arrangement which shows a tendency towards the *Takasagoya* type of inflorescence. The basifixed anthers appear to be unique in the *Hypericeae*. Nevertheless, even these may be regarded as a development from the normal, versatile type. Hence /
in the subdivision of *Hypericum*, so that the sections where they are present are treated as a unit, the interrelationships within the genus are made clearer. If, then, the distinguishing features between the *Euhypericum* and *Brathys* type of androecium are considered, it becomes possible to distinguish four main groups within the genus.

(1) *Norysca* and *Takasagoya*.

The central nucleus from which the other three groups have evolved is Sect. *Norysca*, the section which shows the largest number of apparently 'primitive' or 'unspecialised' characters. The most important of these are:

- **Habit** — Shrubby (tall to dwarf).
- **Leaves** — Sessile, containing translucent glands which are often short streaks rather than dots.
- **Flowers** — Usually large, in few-flowered, terminal cymes.
- **Sepals** — Free, slightly to very unequal, erect in fruit.
- **Petals** — Deciduous, very asymmetrical.
- **Stamens** — 5 deciduous fascicles, with numerous stamens in each fascicle.
- **Ovary** — 5 carpels with axile placentation.
- **Fruit** — Septicidal capsule, the carpel walls smooth or with numerous, narrow, longitudinal vittae.
- **Seeds** — Numerous, elongate-cylindrical, often apiculate at both ends, ecarinate, the testa smooth to reticulate-pitted.
Hence there seems to be no reason why this group in particular should be separated from the rest of Hypericum, since it is obviously a local evolutionary branch from Norysca, all its characteristics being foreshadowed in that section. However, the group is probably worthy of recognition as a section. It occurs in Formosa and the Philippines.

(ii) The Articulate Group.

This group represents a western development from Norysca, and falls into two main parts which correspond to Series II and Series III in the chapter on floral anatomy. Series II (the 'Androsaemum' Series) includes Sects. Eremanthe, Psorophyllum, Androsaemum and Inodorum Stef., while Series III contains Sects. Campylosporus, Webbia, Myriandra, Brathydium, Ascyrum and the shrubby species of 'Euhypericum' (i.e. the Triadenoidea Series and Sect. Reflexa Stef.). It has not been possible to find another character which, along with the articulated leaf, remains more or less constant throughout the whole group, but several characters which occur commonly in it are absent from the other groups. The following are the most important characters of the Articulate Group:

Habit - Mainly shrubby. (Herbs in Brathydium and some semi-herbs in the Triadenoidea Series).

Dark Glands - Absent from the Androsaemum Series, Webbia and the American sections; present /
present on the leaves, sepals or petals in some species of the other sections but then always marginal, never superficial (c.f. the Boreal Group).

Tomentum - Absent except on the stems of *H. reflexum* L. (c.f. the Boreal Group).

Sepals - Spreading or reflexed in fruit in the *Androsaemum* Series, erect in the others.

Petals - Deciduous in the *Androsaemum* group (except Sect. *Inodorum*), in the American sections and in some species of the *Triadenioides* Series, otherwise persistent.

Stamens - Deciduous in the *Androsaemum* Series (except Sect. *Inodorum*), in Sect. *Myriandra* and in some species of the *Triadenioides* Series, persistent in the others. The androecium consists of 5 free fascicles in *Campylosporus* and the *Androsaemum* Series, '3' fascicles in *Webbia, Reflexa* and the *Triadenioides* Series, 5 merged fascicles in *Myriandra* and *Brathydium* and 4 merged fascicles in *Ascyrum*.

Ovary - From 5 to 2 carpels; placentation axile in *Campylosporus, Reflexa* and the *Triadenioides* Series, semi-parietal /
parietal (i.e. the ovary unilocular above) in the Androsaemum Series, Webbia and Myriandra, and parietal in Brathydium and Ascyrum. Styles more or less connate in Campylosporus and the American sections. Stigmas usually small (very small in the American sections, c.f. the Austral Group).

Fruit — Septicidal capsule (except in Sect. Androsaemum, where it is baccate or tardily dehiscent), the carpel walls smooth or with entire, longitudinal vittae (rarely with diagonal, swollen vesicles in the Triadenioida Series).

Seeds — More or less winged or keeled in the Androsaemum Series (except in Inodorum), in Webbia, and in some species of the Triadenioida Series and of Myriandra, otherwise cylindrical. Papillose in some species of the Triadenioida Series, otherwise with a reticulate pitted or almost smooth testa.

The Androsaemum Series has a mainly Mediterranean distribution, i.e. Eremanthe — Pontus; Psorophyllum — Balearic Islands; Androsaemum — Mediterranean region and the Atlantic Islands (except for H. androsaemum L. itself, which reaches Gt. Britain in one direction and the Caucasus and S. Caspian regions in another).
another), and **Inodorum** - Pontus, Caucasus.

The **Triadenioidea** Series, as we have seen, is also a Mediterranean group, but species belonging to it also occur in the Middle East from the Caucasus to Socotra. **Campylosporus** is found in Africa south of the Sahara; **Reflexa** and **Webbia** in the Canaries and Madeira; while **Myriandra**, **Brathydium** and **Ascyrum** are centred in the south-east of North America but extend northwards to Canada and (apart from **Brathydium**) southwards to northern South America.

Text fig. II shows the suggested relationships in the **Norysca** and Articulate Groups. The subscripts indicate the structure of the androecium and gynaecium. From the figure it will be seen that none of the sections in the Articulate Group has the combination of deciduous petals, 5 fascicles and 5 carpels, completely axile placentation and free styles which is found in **Norysca**. Hence this combination of characters will serve to distinguish species of **Norysca** with articulated leaves from those of the Articulate Group itself. Also, the species of **Norysca** with more or less fused styles differ from **Campylosporus** in their deciduous petals and stamens, and from the American sections in their pentadelphous androecium.

**H. cernuum** Roxb., from North-west India, links Sect. **Norysca** to the **Androsaemum** Series, since it has five styles which usually diverge from the base and the sepals are sometimes spreading in fruit. Keller includes this species in **Eremanthe** along with **H. calycinum**, but it seems preferable to retain it in **Norysca**. It /
Text fig. II. Some Characters and Relationships of the Norysca and Articulate Groups.
It differs from *H. calycinum* in its taller, not rhizomatous habit, in its terete, not two- or four-lined stems, in its unarticulated leaves, and in its completely 5-locular ovary. In addition, the seeds of *H. cernuum* are narrow, spindle-shaped and apiculate as in Sect. *Norysca*, while those of *H. calycinum* are cylindrical, rounded at the ends and often more or less winged or keeled like those of the rest of the *Androsaemum* Series.

Likewise, *H. mysorensense* (Wight) Heyne from S. India, Ceylon and Socotra provides a morphological and geographical link between Sect. *Norysca* and the other series of articulate-leaved species. The leaves of this species are sometimes articulated, and they have a venation pattern reminiscent of that of some of the *Campylosporus* species (see Good, 1927). Also, like *H. lanceolatum* and some other species in *Campylosporus*, the stems have short internodes and the leaves are narrow and acute. However, *H. mysorensense* differs from all the species of *Campylosporus* in having deciduous petals and stamens, and from all except *H. socotranum* Good in its completely free styles. The five carpels of *H. mysorensense* distinguish it from the other Old World members of the Articulate Group.

The Socotran species of *Hypericum* are of importance in the study of the interrelationships of this branch of the Articulate Group. Thus *H. socotranum* has been classed in *Campylosporus* but has free styles like the Triadenicidea Series and *H. mysorensense*, while its leaves are small and tend to be somewhat obovate, thus /
thus approaching Sect. Arthrophyllum in the Triadenioideae Series. The Socotran species of this section, H. scopulorum Balf. fil. and H. tortuosum Balf. fil., have corymbose inflorescences of numerous, small flowers reminiscent of the inflorescences of H. glandulosum (Dryand. in) Ait. (Sect. Reflexa) from the Canaries and Madeira. This resemblance could denote relationship (see Text fig. II), but Reflexa may be more closely allied to Webbia from the same region.

Finally, it should be noted that all the species in the Articulate Group do not always have articulated leaves. In some species, e.g. H. ellipticum Hook (Brathydium), they are usually absent, while in others several leaves may have to be examined before an articulated one is found. On the other hand, apart from occasional specimens of Norysca species no members of the other groups have been found to have articulated leaves, the solitary exception being H. chamaemyrtos (see above).

The two parts of the Articulate Group (i.e. the Androsaemum Series and the Campylosporus Series) appear to have arisen from different parts of Sect. Norysca (see Text fig. II and also Map 3). We have seen that they differ in floral anatomy (Series II and III respectively) and in gross morphology; and it will be shown that they have different basic chromosome numbers, although this difference may not be constant. (No chromosome numbers have been counted in Sect. Campylosporus, for example). Hence the two series should /
should probably be kept separate in a classification of Hypericum. However, for convenience they have both been considered as parts of the same (Articulate) group in this work.

(iii) The Boreal Group.

The remaining species of Hypericum fall into two groups: a predominantly northern herbaceous one in which the androecium is always fascicular and the placentation nearly always axile (the Boreal Group), and a predominantly southern one comprising shrubs and herbs in which the stamens are rarely in fascicles and the placentation is often parietal (the Austral Group). Both these groups differ from Norysca and Takasagoya in having persistent petals and stamens, and the leaves are not articulated (apart from H. chamaemyrtos). The styles are always free and more or less spreading, except in some forms of H. ascyron L. (Roscyna).

The Boreal Group corresponds to Series I of the floral anatomy section, in which tangential contraction results in the formation of two double fascicles and lateral carpel traces are always present. It has already been noted that flowers with a tetramerous perianth are rare in this group. They occur at all frequently only in H. humifusum L. and H. filicaule H.f. et Th. (Ascyrum filicaule Dyer), both of which are small herbs with small flowers. The rarity of tetramerous perianths in the Boreal Group when compared to the Articulate /
Articulate Group may be related to the wider torus of the former. In the Austral Group (Series IV and V), where the torus is even wider, no tetrramerous perianths have been reported.

The members of the Boreal Group include Sect. Roscyna, Campylopus, Thasium and Elodes, and the herbaceous species of Euhypericum. Roscyna is the section most nearly related to Norysca, but the characters which distinguish it from that section appear to be fairly constant. Thus, in contrast to the shrubs with deciduous petals and stamens in Norysca, the species of Roscyna are herbs (mostly tall) with persistent petals and stamens. An examination of more material may show that these distinctions break down occasionally, but it has usually been easy to decide to which section a given specimen belongs.

On the other hand, the dividing lines between Roscyna and herbaceous Euhypericum are not so easy to draw. The subdivision of the latter 'section' has also proved a difficult task. As we have seen, Keller placed H. elodes L., H. thasium Grsb., and H. rhodopesum Friv. in independent sections because they did not have the requisite characters for Euhypericum ('3' fascicles and 3 carpels and no staminodes). Euhypericum itself he divided into nine subsections, of which three belong to the Articulate Group. Three of the others contain single species or small groups of closely related species (Subsects. Olympia, Oligostema and Crossophyllum), while Subsects. Heterotaeniun (excluding H. perforatum L. and H. perfoliatum L.) and Drosocarpium (excluding H. sampsoni Hance) /
Hence) are equivalent to Stefanoff's Sects. *Origanifolium* and *Drosocarpium* respectively. All the remaining species — and also several which do not belong to the Boreal Group — Keller placed in Subsect. *Homotaenium*.

The relationships of *H. elodes* and *H. rhodopeum* have been discussed already, and so it remains to show that *H. thasium* and *H. modestum* also belong to the herbaceous *Euhypericum* group. *H. thasium* is a herb from the Balkans whose flower has five stamen fascicles and five carpels. However, if the numbers of these organs are ignored, it has all the characters of Stefanoff's Sect. *Drosocarpium*. Indeed it is almost indistinguishable from *H. rumelicum* Boiss., which grows in the same area. Likewise *H. modestum* Boiss., a species endemic to Cyprus, was placed in a monotypic section by Stefanoff because it, too, has five styles. However, this decumbent herb has the interrupted carpel vittae of Stefanoff's Sect. *Origanifolia*, and appears to be morphologically intermediate between *H. trichocaulon* Boiss. et Heldr. from Crete and *H. leprosum* Boiss. from Asia Minor, both of which belong to Sect. *Origanifolia*. Hence too much emphasis must not be placed on the number of styles in a classification of the Boreal Group. There is a general trend from the '5+5' flowers of Sect. *Roscyna* to the '3+3' ones of *Euhypericum*, but intermediate conditions occur, as well as the apparent reversions just mentioned.

Each /
Each author who has studied this group since Keller's account was published has classified the species of Subsect. *Homotaenium* in a different way. Stefanoff only considered the European, Mediterranean and Oriental species, Gorschkova the Russian species, and Kimura the Japanese species (although the last-named did include a 'skeleton' classification of the rest of the *Homotaenium* species). When all the herbaceous species of the *Euhypericum* type were reviewed, along with the others which have been shown to belong to the same circle of affinity, the problem of devising a valid classification of this group was found to be difficult owing to the presence of numerous cross-relationships and apparent intergrading. Hence no attempt will be made here to provide such a classification. It will suffice to mention some interesting aspects of the distribution of the Boreal Group.

As its name implies, this is essentially a Northern Hemisphere group. It has three main centres of diversity: (i) S. Europe and the Mediterranean region, (ii) E. Asia and (iii) N. America; and the occurrence of certain species or related species in two or all three of these areas suggests that the group at one time may have had a pan-boreal distribution. Thus the species of Sect. *Roscyna* are almost confined to China, Japan and E. Siberia; but *H. ascyron* s.l. also occurs in eastern N. America, and seeds which were referred to this species have been found in Pliocene deposits on the Dutch-German frontier (Reid and Reid, 1915).
1915). The E. Asian *H. attenuatum* Choisy and the other members of Kimura’s Grex *H. attenuatii* seem closely related to the western N. American *H. formosum* H.B.K. and its allies. Likewise *H. sampsoni* Hance (E. Asia) and *H. punctatum* Lam. (E. North America) bear a close resemblance to one another. *H. sampsoni* has been included in Sect. (or Subsect.) *Prosocarpium* on account of the vesicles on its capsules, but these are smaller than the vesicles on the capsules of the European species. On the other hand, similar vesicles sometimes occur in *H. punctatum*, which also resembles *H. sampsoni* in its black-spotted leaves and corymbs of numerous small flowers.

*H. bupleuroides* Grub., a species from the eastern Pontus region with perfoliate leaves, was placed in a monotypic section by Stefanoff, as it is distinct from all the other species he was studying. Its nearest relative appears to be *H. przewalskii* Max., a Chinese species of Sect. *Roscyna* which has a similar habit, leaves which, although not perfoliate, are broadly cordate, and a few-flowered, corymbose inflorescence. Although placed in *Euhypericum* by Keller, the flowers of *H. bupleuroides* sometimes have more than three styles.

A disjunction between the Pontus or Caucasus regions and E. or S.E. Asia occurs in the distribution of several other genera, e.g. *Pterocarya* Kunth has one species in Transcaucasia and three in China and Japan.

The close relationship between *H. olympicum* (Greece and Asia Minor) and *H. concinnum* Benth. (California)
fornia) has already been mentioned in Chap. II. Finally, *H. perforatum* L. occurs in all three of the centres of distribution of the Boreal Group. In fact, from the records given by Gorschkova it appears to have a continuous distribution from Europe to E. Siberia. It also occurs in China and Japan as well as N. Africa. In N. America it has usually been regarded as an introduction from Europe, as it is in Australia, New Zealand, South Africa etc.; but in view of the above facts, *H. perforatum* may be native to that region. Certainly it seems to be more variable in N. America than it is in Australia, where the introduced plants all belong to Subsp. *angustifolium* D.C.

(iv) The Austral Group.

This group, which consists of Sects. *Brathys* and *Humifusoides*, has already been discussed at some length. We have seen that Sect. *Brathys* has its centre of diversity in tropical South America. *Eubrathys* is practically confined to that region; but *Spachium* occurs throughout the New World, and also in Africa south of the Sahara, Madagascar, E. Asia from Japan to Ceylon, the Malayan Archipelago, Australia, New Zealand and New Caledonia. The centre of divergence of Sect. *Humifusoides* is in Africa south of the Sahara, but it has been shown that this section is also present in Central America. The Austral Group is absent from Europe, N. Africa and W. Asia, except for one or two apparently introduced species. Thus the N. American *H. mutilum* L. (*Spachium*) grows in Tuscany (*H. blentinense* Bertol., *Sarothra italic* Savi); this species has also /
also been reported from the Caucasus region (Gorshkova) and from Germany (v. Uechtritz, 1885) as has H. japonicum Thnbg. (v. Uechtritz and Ascherson, 1885); while H. canadense L. has recently been found in France (Bouchard, 1954). However, the fossil species H. cantalense E.M. Reid from Pont-du-Gail in France is referred to Spachium (Reid, 1923), and so some species of the Austral Group may have been native to Europe in the past.

The occurrence of the group in the Malaysian region remains to be mentioned. Apart from annual plants which have been included in H. japonicum, the species of Hypericum in New Guinea comprise a series of forms which links Sects. Brathys and Humifuscoideum. At one extreme H. papuanum Ridley and H. habbemense A.C. Smith are shrubs or suffruticose herbs with broad leaves, relatively long stem internodes, and 3- to 5-carpellary ovaries. A comparison of type material of these two species confirms Smith's surmise that they might be conspecific (Smith, 1941). The leaves are successively narrower and more crowded in H. hellwigii Lauterb., H. macgregorii F. v. M. and H. saruwagedicum Diels, each of which has a tricarpellary ovary. In all these species the androecium appears to be afascicular or irregular. The stamens are certainly free in H. saruwagedicum, and they are not arranged in obvious fascicles in specimens of the other species which have been examined (i.e. all except H. hellwigii). It was not possible to section ovaries /
ovaries of all these species in order to study the placentation, but descriptions in the literature show that it varies between axile and parietal. *H. macgregorii* is said to have axile placentation (Lauterbach, 1923) while in *H. hellwigii* and *H. habbemense* it is parietal. It has been confirmed that *H. saruwagedicium* has an intermediate type — parietal placentae which project into the ovarian cavity — as described by Diels, 1929.

Apart from the absence of dark glands and the parietal placentation, *H. papuanum* and *H. habbemense* resemble some of the species of *Humifusoideum* on account of their terete, more or less herbaceous stems with uncrowded leaves which bear protruding, resincous, yellow glands, their inflorescence consisting of single terminal flowers or a leafy cyme, and their capsules which sometimes have interrupted or irregular vittae. Likewise, we have seen that *H. saruwagedicium* has floral vasculature which is similar to that of species of *Brathys*, and its narrow, crowded leaves, shrubby habit single, terminal flowers are characters which also occur in *Brathys* species.

If the New Guinea species show an early stage in the differentiation of Sects. *Brathys* and *Humifusoideum*, other Malaysian species form a link with Sect. *Norysea*. *H. pulgensens* Merrill, a suffruticose herb from the Phillipines which resembles a large-flowered form of *H. natalense*, has three carpels, axile placentation and more or less interrupted carpel vittae; but the stamens are in five fascicles, not irregular as in *Humifusoideum*. Also, *H. consimile* Keller from Java is said/
said to be a shrub with five fascicles and three carpels which has deciduous petals like Norysca, but the stamens are tardily deciduous which suggests an approach to the persistent stamens of the Austral Group (see Keller, 1923).

Since the Malaysian species of *Hypericum* are relatively little known (most of the species mentioned above have been recorded only once), it would be inadvisable to try to lay down a hard and fast dividing line between Norysca and the Austral Group. It may be that no such line can be drawn. Nevertheless, a provisional distinction can be made between those species whose flowers have deciduous petals and stamens, five stamen fascicles and five carpels (Norysca), and those in which this combination of characters is absent (Austral Group). This is a negative differentiation and therefore unsatisfactory, but it will serve to distinguish the two groups for the present. The distinction between Sects. Brathys and Humifusoides, which is fairly clear when African and American species are compared, is not so obvious in the Malaysian region owing to the reticulation of characters, e.g. axile and parietal placentation. In general, *H. pulosense, H. habbemense* and *H. papuanum* are near Humifusoides, whereas *H. hellwigii, H. macgregorii* and *H. saruwagedicum* are more closely allied to *Habrathys*; but until specimens of *H. hellwigii* have been seen it is not possible to say whether a dividing line between the sections can be drawn at this point.
(4) Chromosome Numbers in the Hypericoideae.

Chromosome counts are available for only about one-tenth of the species of Hypericum and two species of the rest of the Hypericoideae, but it will be of interest to discuss them in the light of the main divisions of Hypericum outlined above.

As well as all the published numbers, Table II (below) includes chromosome counts of all the British native and naturalised species, which the author made in connection with another piece of work. One or two counts were made from pollen mother cells using the acetic carmine squash technique (Darlington and La Cour, 1947); but most of the results were obtained by placing stem apices in 0.2 per cent colchicine for two hours in light, and then fixing overnight in 1 : 3 acetic alcohol. The squash technique described by Meyer (1943) was adopted, but acetic laemoid was used for staining instead of leucobasic fuchsine which, in several attempts, did not give good results.

**TABLE II.**
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<tr>
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<th>Species</th>
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<th>Author and Source of Material</th>
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<td>Norysca Group</td>
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<td>Hypericum x Eremanthae x H. mosserianum Andre (?) (H. patulum x calycinum)</td>
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<td>H. densiflorum Pursh v. lobocarpum (Gatt.) Svenson (as H. lobocarpum)</td>
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<td>H. prolificum L.</td>
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<td>x H. dawsonianum Rehd. (H. lobocarpum x prolificum)</td>
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<td>16</td>
<td></td>
<td>Robson: Myndd Glew, Glamorgan.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>16</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>16</td>
<td></td>
<td>Robson: Steps Bridge, Devon.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>16</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>16</td>
<td></td>
<td>Robson: Coimbra E.G.</td>
</tr>
<tr>
<td>Group and Section</td>
<td>Species</td>
<td>n</td>
<td>2n</td>
<td>Author and Source of Material</td>
</tr>
<tr>
<td>-------------------</td>
<td>---------</td>
<td>---</td>
<td>----</td>
<td>-----------------------------</td>
</tr>
<tr>
<td>'Euhypericum' (European area) contd.</td>
<td>H. humifusum L.</td>
<td>8</td>
<td>16</td>
<td>Winge (1925): ?</td>
</tr>
<tr>
<td></td>
<td>H. tetrapertum Fr. (as H. acutum)</td>
<td>8</td>
<td>16</td>
<td>Robson: Italy (Davis 17459).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td></td>
<td>Nielsen: North Sealand.</td>
</tr>
<tr>
<td></td>
<td>(as H. quadrangulum)</td>
<td>8</td>
<td></td>
<td>Winge: ?</td>
</tr>
<tr>
<td></td>
<td>H. tetrapertum Fr.</td>
<td>8</td>
<td>16</td>
<td>Chattaway: Bagley Wood, Oxford.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td></td>
<td>Sugiura (1944): B.G.</td>
</tr>
<tr>
<td></td>
<td>H. undulatum Schousb. ex Willd.</td>
<td>8</td>
<td>16</td>
<td>Robson: Marburg, Germany.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td></td>
<td>Sugiura (1944): B.G.</td>
</tr>
<tr>
<td></td>
<td>H. maculatum Cr. ssp. maculatum</td>
<td>8</td>
<td>16</td>
<td>Robson: Whiting Bay, Arran.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td></td>
<td>Nielsen: North-Seeland.</td>
</tr>
<tr>
<td></td>
<td>(as H. quadrangulum)</td>
<td>8</td>
<td></td>
<td>Winge: ?</td>
</tr>
<tr>
<td></td>
<td>H. maculatum Cr. ssp. obtusiusculum (Tourlet) Hayek</td>
<td>32</td>
<td>32</td>
<td>Robson: Chailey, Sussex.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>32</td>
<td></td>
<td>&quot; : Loch Tay, Perthshire.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>32</td>
<td></td>
<td>&quot; : Drum, Aberdeenshire.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>32</td>
<td></td>
<td>&quot; : Munich B.G.</td>
</tr>
<tr>
<td>Group and Section</td>
<td>Species</td>
<td>n</td>
<td>2n</td>
<td>Author and Source of Material</td>
</tr>
<tr>
<td>-------------------</td>
<td>---------</td>
<td>----</td>
<td>----</td>
<td>-----------------------------</td>
</tr>
<tr>
<td><strong>Euhypericum</strong></td>
<td>H. desetangsdii x H. maculatum ssp. obtusiusculum x perforatum</td>
<td>16</td>
<td>32</td>
<td>Robson: Lewes, Sussex.</td>
</tr>
<tr>
<td>(European area)</td>
<td>H. perforatum L.</td>
<td>16 (17, 18)</td>
<td>40, 48</td>
<td>Winge: ?</td>
</tr>
<tr>
<td></td>
<td>H. elegans Steph. ex Willd.</td>
<td>16</td>
<td>32</td>
<td>Robson: Oxford B.G.</td>
</tr>
<tr>
<td></td>
<td>H. rumeliacum Boiss.</td>
<td>7</td>
<td></td>
<td>Nielsen: Copenhagen B.G.</td>
</tr>
<tr>
<td><em>Euhypericum</em></td>
<td>H. kamschatcum Ledebov. v. senanense (Max.) Kimura (as H. senanense)</td>
<td>16</td>
<td>1935</td>
<td>Matsuura and Suto: Mt. Zao, Japan.</td>
</tr>
<tr>
<td>(Asiatic area)</td>
<td>H. erectum Thunb.</td>
<td>16</td>
<td>1950</td>
<td>Suzuka: ?</td>
</tr>
<tr>
<td></td>
<td>H. elodioides Choisy</td>
<td>8</td>
<td></td>
<td>Sugira (1944): B.G.</td>
</tr>
<tr>
<td><em>Euhypericum</em></td>
<td>H. punctatum Lam.</td>
<td>8</td>
<td></td>
<td>Hoar (1931): Massachusetts and Vermont.</td>
</tr>
<tr>
<td>(American area)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
| Austral /
TABLE II (Contd.)

<table>
<thead>
<tr>
<th>Group and Section</th>
<th>Species</th>
<th>n</th>
<th>2n</th>
<th>Author and Source of Material</th>
</tr>
</thead>
<tbody>
<tr>
<td>Austral Group</td>
<td>H. mutilum L.</td>
<td>8</td>
<td></td>
<td>Hoar and Haertl; Massachusetts.</td>
</tr>
<tr>
<td>Brathys (Spachium)</td>
<td>H. boreale (Britton)</td>
<td>8</td>
<td></td>
<td>Hoar and Haertl; Vermont</td>
</tr>
<tr>
<td></td>
<td>Bicknell</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>H. majus (Gray) Britton</td>
<td>8</td>
<td></td>
<td>&quot;</td>
</tr>
<tr>
<td></td>
<td>H. canadense L.</td>
<td>8</td>
<td></td>
<td>&quot;</td>
</tr>
<tr>
<td></td>
<td>H. gentianoides (L.) BSP.</td>
<td>12</td>
<td></td>
<td>&quot;</td>
</tr>
</tbody>
</table>

(i) (?) after the name of a species or hybrid indicated that the number recorded is unusual and the identification of the material requires to be checked.

(ii) *H. polyphyllum* Boiss. et Bal. has been placed in quotation marks because the plant cultivated under that name in the author's experience has always turned out to be *H. olympicum* L. The true *H. polyphyllum* is a rare Syrian endemic.

(iii) Darlington and Wylie (1955) interpret Suzuka's *'H. electum Thunb.'* as *'H. elatum';* but *H. erectum* Thunb. is a Japanese species which would be likely to have 2n = 16, whereas *H. elatum* (Dryand. in) Ait. grows in the Canaries and belongs to Sect. *Androsaemum*, and the author has found its chromosome number to be 2n = 40.
Nielsen (1924) concluded that, since the haploid numbers which he had counted in species of *Hypericum* (7, 8, 9, 16 and 20) are not multiples, there is no one basic number for the whole genus; he also said, rightly, that to postulate three phylogenetic series based on 4, 7 and 9 would cut across other phylogenetic evidence. Winge (1925) preferred to think of the fundamental series for the genus as a 4-system, from which the numbers 7 and 9 have arisen by aberration. Chattaway (1926) pointed out that, although the numbers are not all multiples, yet they are not so entirely irregular as those in *Carex*. He suggested that the situation resembled that of *Crepis*, i.e. polyploid series arising from a few basic numbers. Sugihara (1936) commented that the addition of the number \( n = 18 \) (*H. patulum*) filled a gap in the series, so that the numbers 7, 8, 9, 10, 12, 16, 18 and 20 suggest that *Hypericum* resembles *Carex*. In a later paper (1944) he went even further and, with a complete disregard for systematic groupings, proposed that Sects. *Roscyna*, *Androsaemum* (sic!), *Euhypericum* and *Myriandra* should be placed together in any classification because the number 9 occurs in all of them. He was then of the opinion that there were two series, based on 3 and 4, from which the numbers 7 and 9 had been derived.

From Table II it is clear that Chattaway is correct, and that in *Hypericum*, as in *Crepis*, there are several basic numbers, most of which give rise to a polyploid series. Thus the *Androsaemum* series has the basic number 10, the species of Sects. *Androsaemum* and *Inodorum* /
Inodorum being tetraploids. The only species of the Norysca Group which has been examined is a tetraploid of the basic number 9; while the American articulate species and the sole representative of the Triadenicida Series all have \( n = 9 \). The basic number 9 is also found in some of the members of the Boreal Group, the rest of which are nearly all diploids or tetraploids with the basic number 8. The exception is \( \text{H. rumeliacum} \), which has \( n = 7 \). The irregular somatic numbers in \( \text{H. perforatum} \) are attributable to the pseudogamous apomictic method of reproduction in that species (see Noack, 1939). The chromosomes of only a few members of the Austral Group have been counted, and all of these belong to Subsect. Spachium. The basic number 8 occurs in all but one of these species, the exception being \( \text{H. gentianoides} \) \( (n = 12) \). It will be recalled that this much-branched annual with only scale leaves has very much reduced flowers in which each 'fascicle' usually consists of only one stamen, and sometimes only two carpels are present. Hence the number 12 should be regarded as a derivative of the 8-series. Two explanations of this number present themselves. Either (i) it is a triploid of the 8-series, which must 'breed true'; or (ii) the basic number may have undergone reduction like the plant itself, in which case \( \text{H. gentianoides} \) is a tetraploid in a series with a basic number of 6. Until the chromosomes of other related species have been counted, it will be impossible to tell which, if either, of these explanations is correct. To summarise, the known basic numbers of the four groups are /
are as follows:

Norysca Group - 9
Articulate Group - 10 (Androsaemum Series), 9 (Campylosporus Series)
Boreal Group - 9, 8, 7.
Austral Group - 8, 7.

From these figures it is apparent that Hypericum resembles Crepis in having a descending series of basic chromosome numbers. The highest recorded number does not occur in the Norysca Group, but since only one species in that group has been studied cytologically too much emphasis must not be placed on this fact. The mechanism by which basic chromosome numbers are reduced differs from that which would lead to a series of increasing numbers (see Stebbins, 1950), and so it is unlikely that the basic number in the Androsaemum Series has increased from 9 to 10 when in the rest of the genus it has undergone reduction. It is also worth noting in this connection that the known numbers in the Theaceae are all multiples of 10 (see Darlington and Janaki Ammal, 1945).

Now, Triadenum virginicum has the gametic number 19, which has not been recorded in Hypericum. Thus cytological evidence supports the conclusion that it should not be included in that genus. The number 19 may have arisen through tetraploidy in a 10-series, with a subsequent reduction of one, i.e. \( (10 + 10) - 1 = 19 \).
This explanation seems more likely than the derivation from \(10 + 9 = 19\). Only one other species in the Cratoxyleae (\textit{Cratoxylon formosum}, \(n = 7\)) has been studied cytologically, and so no pronouncements on the relationship between \textit{Triadenum} and \textit{Cratoxylon} can be made at present from this point of view.

(5) The Course of Evolution in \textit{Hypericum}.

(i) Morphology.

It has been shown that Sect. \textit{Norysca} has many characters in common with the hypothetical primitive species from which \textit{Hypericum} has evolved. This plant probably had a large, regularly pentamorous flower with deciduous petals and stamens, axile placentation and free styles. It was probably a tall shrub with sessile, coriaceous leaves in which there were no aggregations of hypericin, although this substance may have been present in solution in the cell sap.

From this central type it is suggested that three principal evolutionary lines and one subsidiary one (to Takasagoya) may be traced. In each of the principal ones there is an overall trend:

(a) from shrubs to herbs,

(b) from androecia with free stamen fascicles to androecia in which the fascicles merge in some way,

and (c) from axile to parietal placentation.

There is also a general trend towards reduction in size and
and in numbers of floral parts in each line. However, the length to which these trends are carried varies from line to line. Thus there are few herbs in the Articulate Group, the Boreal Group is wholly herbaceous but has only one or two annual members (in E. Asia), while the Austral Group contains shrubs, perennial herbs and several annual species. Again, in the Boreal Group parietal placentation is practically absent and, apart from some flowers of Hypericum, only in one of the most specialised members (Hypericum elodes) does one find a partly unilocular ovary. Such an ovary occurs fairly frequently in the Articulate Group, some of whose species have completely parietal placentation, while this type of placentation is found in the majority of species in the Austral Group. In both the Articulate and Boreal Groups species have evolved in which the flower is pseudo-tubular with nectaries and 'lodicules', and in which the stamen filaments in each of the 'three' fascicles are fused for most of their length.

Table III gives a summary of the main characters of each group.

(ii) Distribution.

Since Sect. Norysca contains the species which approach most nearly in morphology to the basic type of Hypericum, the distribution of this section may help to determine the centre of origin of the whole genus. Now, Norysca is found within the area bounded by Java, Japan, Afghanistan and Ceylon, and also in Socotra, i.e. mainly in the lands which form the northern and eastern shores of the Indian Ocean (except Australia). Sect. Campylosporus,
<table>
<thead>
<tr>
<th></th>
<th>Norysca and Takasagoya</th>
<th>Articulate Group</th>
<th>Boreal Group</th>
<th>Austral Group</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habit</strong></td>
<td>Shrubs.</td>
<td>Mostly shrubs,</td>
<td>Perennial and</td>
<td>Shrubs, per-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>a few perennial</td>
<td>one or two</td>
<td>ennial and</td>
</tr>
<tr>
<td></td>
<td></td>
<td>herbs.</td>
<td>annual herbs.</td>
<td>annual herbs.</td>
</tr>
<tr>
<td><strong>Leaves</strong></td>
<td>Articulated in a few</td>
<td>Usually articu-</td>
<td>Never articu-</td>
<td>Very rarely</td>
</tr>
<tr>
<td></td>
<td>species.</td>
<td>lated.</td>
<td>lated.</td>
<td>articulated.</td>
</tr>
<tr>
<td><strong>Tomentum</strong></td>
<td>Absent.</td>
<td>Very rare (H.</td>
<td>Frequent.</td>
<td>Very rare</td>
</tr>
<tr>
<td></td>
<td></td>
<td>reflexum L.)</td>
<td></td>
<td>(H. setosum</td>
</tr>
<tr>
<td>**Dark</td>
<td>Absent.</td>
<td>Absent or</td>
<td>Usually pres-</td>
<td>Rare in Brath-</td>
</tr>
<tr>
<td>glands**</td>
<td></td>
<td>marginal, dots</td>
<td>ent, marginal</td>
<td>ys, supe-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>only.</td>
<td>and superfi-</td>
<td>ricial; fre-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>cial dots or</td>
<td>quent in Humi-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>streaks.</td>
<td>fusoidem, mar-</td>
</tr>
<tr>
<td><strong>Petals</strong></td>
<td>Deciduous.</td>
<td>Mostly decidu-</td>
<td>Persistent.</td>
<td>Persistent.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ous.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Stamens</strong></td>
<td>5 fascicles,</td>
<td>5-‘3’ fascicles,</td>
<td>5-‘3’ fasci-</td>
<td>Rarely 5-‘3’</td>
</tr>
<tr>
<td></td>
<td>deciduous.</td>
<td>or 5-4 fascicles</td>
<td>cles,</td>
<td>fascicles,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>merged, decidi-</td>
<td>persistent.</td>
<td>usually 5 fa-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>nous to persis-</td>
<td></td>
<td>scicles mer-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>tent.</td>
<td></td>
<td>ged or irregu-</td>
</tr>
<tr>
<td><strong>Carpels</strong></td>
<td>5</td>
<td>5-2</td>
<td>5-3</td>
<td>5-2</td>
</tr>
<tr>
<td><strong>Styles</strong></td>
<td>Free to completely</td>
<td>Free to complete-</td>
<td>Nearly always</td>
<td>Always free</td>
</tr>
<tr>
<td></td>
<td>connate, never (?)</td>
<td>ly connate, often</td>
<td>free and</td>
<td>and divergent</td>
</tr>
<tr>
<td></td>
<td>divergent from the</td>
<td>divergent from</td>
<td>divergent</td>
<td>from</td>
</tr>
<tr>
<td></td>
<td>base.</td>
<td>the base.</td>
<td>the base.</td>
<td>the base.</td>
</tr>
<tr>
<td><strong>Stigmas</strong></td>
<td>Small.</td>
<td>Very small to</td>
<td>Small to</td>
<td>Always ± capi-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>medium-sized,</td>
<td>large, often</td>
<td>tate, peltate</td>
</tr>
<tr>
<td></td>
<td></td>
<td>rarely capitate.</td>
<td>capitulate.</td>
<td>in Spachium.</td>
</tr>
</tbody>
</table>

**TABLE III.**

CHARACTERS OF THE FOUR MAIN GROUPS OF HYPERICUM.
<table>
<thead>
<tr>
<th>TABLE III (Contd.)</th>
</tr>
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<tr>
<td></td>
</tr>
<tr>
<td>Placentation</td>
</tr>
<tr>
<td>Carpel Vittae</td>
</tr>
<tr>
<td>(when visible)</td>
</tr>
<tr>
<td>Seeds</td>
</tr>
<tr>
<td>Known Basic Chromosome Numbers</td>
</tr>
<tr>
<td>Species</td>
</tr>
<tr>
<td>---------</td>
</tr>
<tr>
<td>H. aethiopicum Thunbg.</td>
</tr>
<tr>
<td>H. sanderi Bredell</td>
</tr>
<tr>
<td>H. nigropunctatum Norling</td>
</tr>
</tbody>
</table>

Specimens not seen. Information obtained from Bredell (1939) and Perrier de la Bathie (1927, 1951).

Stem, L(aves), Se(pals), P(etals), A(nthers). Brackets indicate that the glands are few in number or sometimes absent. For synonymy see Milne-Redhead (1933), Bredell (1959) and Perrier de la Bathie (1927, 1951).
Campylosporus, a group of tall shrubs and small trees which is an immediate derivative of Norysca, occurs in the lands on its west coast (Africa, Madagascar and the Mascarenes). Taken together, these two sections are distributed practically right round the Indian Ocean. There is no evidence, paleobotanical or otherwise, which suggests that species in these sections have ever occurred in regions far from those in which they are found at the present day, and so we may assume that the centre of origin of the whole genus was somewhere in the lands bordering the Indian Ocean, or in a region which is now covered by the Ocean itself.

The distributions of the other tribes in the Hypericcoideae are relevant to this problem. In the Vismieae, Vismia occurs in Africa and tropical America, Psorospermum is confined to the African mainland, and Harungana is found in Africa and Madagascar. In the Cratoxyieae, Eliaea is endemic to Madagascar, Cratoxylon occurs in S.E. Asia, and Triadenum in E. Asia and N. America. It seems likely from these facts that the Vismieae and Cratoxyieae both originated in the Madagascar region, and migrated in north-west and north-east directions respectively. Apart from Triadenum (a temperate derivative of Cratoxylon), these genera are confined to warm countries, like many other groups which seem to have originated in the same area (see Croizat, 1952).

Croizat believes that the dispersal tracks of all modern Angiosperms start in three centres in the Southern Hemisphere which he calls the African, Western Polynesian and Magellanian Gates, respectively. He regards /
regards these three areas as the last remnants of a once continuous Antarctic continent. Unlikely though this hypothesis may appear at first sight, the evidence which Croizat brings forward in favour of it is very impressive. It is true, as Matthews (1955) has said, that he has not given as much attention to recent geological changes in the Northern Hemisphere as he might have done; but the morphological and geographical evidence from Hypericum supports his ideas. Only in the Boreal Group would these geological and climatic changes have had an appreciable effect on present day distribution (see below).

If two tribes of the subfamily have originated in the South African region, the third is likely to have done so, too. In contrast to the previous tribes, the Hypericeae (Hypericum, including 'Ascyrum') is most abundant in cool regions, and is almost confined to the higher altitudes in the tropics. Hence it probably originated to the south of the Madagascar region, in what Croizat calls the Afroantarctic Triangle (the area bounded by Natal, the Kerguelen Islands and Tristan da Cunha) (Map 3). This area fulfils both conditions for the centre of origin of Hypericum: (i) Africa, India and Malaysia may be reached from it quite easily and (ii), according to Croizat, groups which are thought to have originated there are not usually essentially tropical.

From the centre of origin, the evolving genus would appear to have spread in a north or north-east direction. The tracks shown in Map 3 are almost certainly /
Map 3. The main migratory routes of *Hypericum*

I. The *Norysca* and Articulate Groups.

- Centre of origin (or dispersal) of *Hypericum*.
- Dispersal lines of Sect. *Norysca* and of *Takasagoya* (T).
- Dispersal lines of the Articulate Group, *Androaemum* Series.
- Centre of origin of the Articulate Group, *Campylosporus* Series.
- Dispersal lines of the Articulate Group, *Campylosporus* Series.
- Centre of origin of the Boreal Group.
- Centre of origin of the Austral Group.
certainly over-simplified, but they will serve to give some idea of the distributional relations of the parts of Norysca to the other groups of Hypericum. One series of forms can be traced from Ceylon and S. India (H. mysorense) through the N.W. Himalayan species, (H. cordifolium Choisy and H. cernuum Roxb.) to the Androsaemum Series, which appears to have spread through Asia Minor and the Mediterranean area to the Canaries, the Azores, N. Africa and up the Atlantic coast to Britain (H. androsaemum L.). All these species are shrubs with five stamen fascicles and free styles. A second series starts with the large-flowered Malaysian species of the H. hookerianum group, e.g. H. triflorum Blume in Java. From these forms stem the Norysca species in which the styles tend to be at first appressed at the base (H. hookerianum etc.), then more or less connate (H. chinense L.), and eventually completely united (Takasagoya). The Austral Group appears to have originated in the Malaysian region as an offshoot from this series, probably from H. patulum Thunbg. or a species resembling it. Also, a semi-herbaceous form with partly fused styles probably gave rise to Sect. Roscyna (Boreal Group) in China.

The third series originating in Sect. Norysca starts, like the first, with H. mysorense, but its primary centre of diversity is in Socotra and the adjacent parts of Africa. From there two lines of dispersal can be traced. To the north there developed a /
a group of shrubby 'Euhypericum' species — the Triadenioidea series — which spread from the E. Mediterranean westward to the Pyrenees, W. Alps, Spain and N. Africa, and eastward to the Caucasus region. Unless Reflexa belongs to this series, it does not appear to have reached any of the Atlantic islands. The other branch of this series of the Articulate Group spread into the Mascarenes, Madagascar, Central Africa and the north of S. Africa (Campylosporus) and across to W. Africa. This section, or an ancestral form, gave rise to the American species of the Myriandra, with Webbia (and possibly Reflexa) occupying an intermediate stage both morphologically and geographically (in the Canaries and Madeira). The centre of diversity in America appears to have been the south-east of N. America, from which Myriandra and Ascyrum extend into eastern N. America, Mexico and the north of S. America. Myriandra also gave rise to Brachydiium in eastern N. America.

The Boreal Group (like e.g. Crepis) seems to represent a fairly typical example of dispersal (or probably redispersal) from an area in Central Asia such as the Altai region (Map 4). The earlier sections of the group occur disjunctly over the whole of its range — Roscyna in Central and E. Asia, N. America, and as a fossil in Europe, the related H. bupleuroides Grif. in Asia Minor and Olympia in Asia Minor and California. The E. Asian and N. American 'Euhypericum' species of this group are closely related, but the species in the European-Mediterranean area are almost completely distinct from them. The only ones which link /
Map 4. The main migratory routes of *Hypericum*.

II. The Boreal Group.

- Centre of origin of the Boreal Group.
- Probable centre of dispersal in the Altai region.
- Secondary centre of dispersal in Asia Minor.
- Dispersal lines of the Boreal Group.
- Alternative crossing of the Pacific Ocean in the Hawaiian region.
link the two areas geographically and the two sets of species taxonomically are some of those in Stefanoff's Sect. Perforata, one of which (H. perforatum L.) extends over the whole area, while another (H. maculatum Gr.) occurs from Central Asia to W. Europe.

The eastern species (Kimura's Series Bilineata and Blineata) have spread to the Himalayan region, Malaya, China, Formosa, Japan, and across the Pacific Ocean region to the west and east of N. America as far south as Mexico. The western species fall roughly into two groups, (i) a northern one comprising Stefanoff's Sects. Perforata (excluding the tomentose species) and Drosocarpium, which appear to have undergone speciation in S. W. Europe and the Balkans respectively, and (ii) a southern one which can be derived from Sect. Olympia. The second group has its centre of diversity in Asia Minor, from which three main series can be traced. Of these, Sect. Origanifolia, is confined to Asia Minor and the immediate surroundings. The second series, Sect. Montana, spread into the Balkans, and H. montanum L. itself reached Britain; but the main line of evolution of this section (which should include the tomentose species in Stefanoff's Sect. Perforata) seems to have been across the Mediterranean, ultimately giving rise to H. elodes in the Atlantic region. Sect. Montana must also have migrated southward into Africa, since two closely related species occur in the E. African mountains, one of which is found also in Sardinia (H. annulatum Moris.). The third series includes Sect. Pulchra.
Pulchra, Hyssopifolia, Spectables, Hirtella and Scabra. Apart from H. pulchrum L. and H. hirsutum L., which occur to the north-west of the Asia Minor centre, and H. hyssopifolium Chaix ap. Vill. (s.s.), which has a disjunct Mediterranean distribution, the dispersal trends in this group have been mainly east and south-east from Asia Minor into the Caucasus region, Iraq and Iran.

Owing to the recent geological and climatic changes mentioned above, the interpretation of evolutionary trends on the basis of present day distribution is more liable to error in the Boreal Group than in the rest of Hypericum. However, although the variations in the outlines of the Obic and Tethys Seas during the Tertiary period may have obscured some of the evidence, the overall picture does not appear to have been obliterated. Thus the earlier species were pan-boreal, but now occur disjunctly in N. America, E. Asia, Asia Minor and (as a fossil) in W. Europe. Two centres of diversity seem to have developed — in Asia Minor and E. Asia — the component groups of each being almost entirely different. One species, H. perforatum, appears to be related to species in both regions, and is also the only one whose distribution includes both regions. Hoar and Haertl (1932) suggest that H. perforatum may be a natural hybrid, and unpublished work by the author supports this view. It seems possible that it is a pseudogamous amphidiploid which resulted from a cross between the diploid H. maculatum Cr. subsp. maculatum (from Europe and W. Siberia) and one of the E. Asian species /
species of **Euhypericum** belonging to Kimura's Grex **H. attenuati**, maybe **H. attenuatum** Choisy.

The lines of dispersal of the Austral Group (Map 5) are mostly less obvious than those of the other groups. It seems likely that it originated in the Malaysian region because (i) the forms nearest Sect. **Norysea** (e.g. **H. consimile**) occur there and (ii) the component sections, **Brathys** and **Humifusoides**, are less distinct in this area than they are elsewhere. From Malaysia Sect. **Humifusoides** probably evolved in a westward direction towards Africa, where it has undergone most of its speciation. As we have seen, it has also reached Central America (**H. collinum**).

However, Sect. **Brathys** poses a problem from the outset, viz. how to interpret the disjunction in **Eubrathys** between New Guinea and South America. Now, both the absence of this subsection from Africa, and the westward direction taken by Sect. **Humifusoides**, suggest that **Eubrathys** migrated eastwards across the Pacific region. Croizat (l.c. p. 178) explains the absence of **Rhododendron** from Africa as the result of a trans-Pacific migration rather than a trans-Atlantic one. He argues convincingly in favour of a 'land-bridge' across the Pacific Ocean in Cretaceous times, without which some present-day plant distributions could be explained only by more involved hypotheses such as lowering of the whole bed of the ocean. Hence we may accept the trans-Pacific migration hypothesis as more likely under the circumstances than, for example, the westward /
Map 5. The main migratory routes of *Hypericum*.

III. The Austral Group.

- Centre of origin of the Austral Group.
- Secondary centre of dispersal for Sect. *Brathys*.
- Original dispersal line of Sect. *Brathys*.
- Possible dispersal line for the fossil *H. cantalense* (? aff. *H. canadense*), or for *H. canadense* itself (see text).
- Dispersal lines of Sect. *Humifusoidem*. 
westward migration of a Brathys-Humifuscoideum stock with subsequent differentiation in S. America and Africa respectively.

In S. America we find the secondary centre of diversity of Brathys. Although speciation has taken place there in Eubrathys, that subsection has not spread further than the tropics. However, it also gave rise here to Spachium, which has extended its area much further. From its S. American centre a series of forms can be traced up through Central America and the Antilles to N. America. The reference of the fossil H. cantalense to H. canadense suggests that this N. American species may have crossed the Atlantic, but the evidence is too slender to make a definite pronouncement on this point. However, it is clear that Spachium has crossed the Atlantic region further south, because it is possible to match exactly specimens of the very variable African H. lalandii Choisy with various American species. For example, the small form of H. lalandii which grows in dry habitats is morphologically identical with small forms of H. chilense Gay from the Andes, while larger specimens which were also named H. lalandii are very similar to H. pauciflorum H.B.K. Milne-Redhead (1953) found it impossible to subdivide H. lalandii in Africa since all the forms seem to intergrade. He thought that the Indian and Chinese forms of this species might be separated as a variety, but that they were very close to the African ones. In both regions the species is said to smell of rotten orange peel! It seems clear, then, that there is a trend from /
from S. America through Africa to the Himalayas and China. *H. gramineum* Forst. from Australia, New Caledonia and New Zealand also appears to belong to this group because, like *H. lalandii* s.l., it has an erect, sparingly branched habit, long leaves with a cordate base, a bracteate inflorescence and acute sepals. It can be matched almost exactly by some specimens of *H. lalandii*.

The other African species of *Spachium* is confined to Madagascar. Previous authors have thought it to be allied to the E. Asian *H. japonicum* Thunbg., and Keller named it *H. japonicum* subsp. *pseudocrispum*. However, it is a perennial while the rest of *H. japonicum* is annual; and since we shall see that the immediate relatives of *H. japonicum* are N. American, it would be a reversal of the trend if the perennial Madagascar plant were derived from the E. Asian species. In fact, its relationships appear to be with S. American species, and in particular with *H. thesiifolium* HBK. Thus we have here another link between Africa and S. America.

On the other hand, *H. japonicum* and its related E. Asian species, (*H.*) *Sarothra saginoides* Kimura and *H. laxum* Blume, appear to be derived from the N. American *H. gymnanthum* Engelm. et Gray and *H. anagalloides* Cham. et Schl. Another American species in the same circle of affinity, *H. mutilum* L., also occurs in E. Asia, and two examples of this species from Hawaii have been seen. This may indicate the route by which the *H. japonicum* group /
group reached Asia, but *H. mutilum* has been introduced into other regions of the world and so it may not be native to Hawaii. However, a specimen from Formosa (Tanaka and Shimada, No. 11063), labelled 'H. japonicum', is indistinguishable from *H. gymnanthum*, which suggests that the 'Hawaiian bridge' has in fact been used by this group. From the Formosa region it has spread to Japan, India and Ceylon, and also through Malaysia to New Guinea, Australia and New Zealand.

Two points remain to be mentioned in connection with this account of the evolutionary and migratory trends in *Hypericum*.

(i) It may be thought that the author has been rather dogmatic in his assertions regarding the interrelationships and migratory tracks of certain groups of species, especially since their detailed taxonomy has not been studied. However, in the course of the work it has become clear that in general there is a striking correlation between the morphological trends discussed above and the distributions of the various groups. Also, when the genus was examined as a whole, certain species and groups were found to show similarities which had not been stressed before, because (a) the species or groups occurred in different parts of the world, and so were not both examined by the same regional monographers (e.g. *H. sampsoni* and *H. punctatum*), or (b) they had been classified in different parts of the genus by Keller (e.g. *H. wilmsii* and *H. peplidifolium*).
To explore the implications of all these similarities would require monographic treatment, and it was thought that a broad view of the general relationships — morphological, cytological and geographical — would be preferable at present.

(ii) Some of the migratory tracks shown in Maps 3, 4 and 5 imply a different configuration of land and sea from that of the present day. A difference there must have been, for it is setting the bounds of probability too widely to attribute all, or even most, of these disjunct distributions to chance, long-distance dispersal. Continental drift could be invoked to explain the Atlantic and Indian Ocean disjunctions, but Wegener's theory has never been able to provide a satisfactory solution to the problem of trans-Pacific disjunctions. Therefore, for these at least, one is forced to postulate some sort of land connection between Asia and America in the warmer latitudes. Further, more and more evidence is accumulating to show the improbability of continental drift on the scale that Wegener envisaged. Hence some land-bridge or submerged-continent theory is also necessary to explain the Atlantic and Indian Ocean disjuncts.
CHAPTER VI.

SOME MORPHOLOGICAL IMPLICATIONS OF THE FLOWER OF THE HYPERICOIDEAE.

It has been shown that the flower of Vismia is pentacyclic, isomerous, pentamerous, and has a diplo-stemonous androecium of which the inner members are fascicles of stamens and the outer are staminodes. From such a flower it is possible to derive all the other floral structures in the Hypericoideae by elimination of staminodes, fusion of adjacent pairs of stamen fascicles (pseudo-trimery) or merging of all the fascicles into a continuous ring, and reduction in the number of carpels. In 'Ascyrum' there has been a combination of meioimery in all whorls and merging of the stamen fascicles.

From the same basic floral structure one can derive the flowers of the Moronoboideae, the Calophylloideae and the Garcineae. In the Moronoboideae the staminodes merge to form a five-lobed or entire disc, and the fascicles fuse to produce a staminal tube. The staminodial whorl is absent in the Calophylloideae as in Hypericum, and the fascicles merge as a continuous ring of 'free' stamens. The Clusioidae are of special interest because in one species of this subfamily the outer androecial whorl consists of fertile fascicles. This plant — Decaphalangium peruvianum Melchior — has characters /
characters which link the tribes Clusieae and Garcineae (Melchior, 1930), and from it one can derive all the floral variations in these tribes. Thus, in the Garcineae the outer whorl of stamens becomes staminodial and then disappears, while in the Clusieae one or both whorls may be present in various forms. We can therefore postulate that the plants ancestral to the Guttiferae had regular, pentamerous flowers with two diplostemonous whorls of stamen fascicles.

Other authors have come to similar conclusions with regard to the basic structure of the flower in related families. Brown (1935) showed that the flower of Saurauja subspinosa has a diplostemonous androecium which comprises an outer whorl of five single stamens and an inner whorl of five groups of stamens. He observed that the latter arose by division of five single primordia, and suggested that the original condition for the whole of the Theaceae (in which Saurauja has sometimes been classified) had been two diplostemonous whorls of single stamens. However, in the light of our conclusions regarding the ancestral condition of the Guttiferae, it seems more likely that the Theaceae and the Guttiferae had a common ancestor with an androecium of two pentamerous, diplostemonous whorls of stamen fascicles, and a gynaeceum of five carpels. Rao (1952) derived the Malvales from a similar ancestral floral type except for the androecium which was obdiplostemonous. Saunders (1936a) showed that the 'polyandrous' /
'polyandrous' androecium of the Cistaceae results from the merging of an antepetalous whorl of fascicles, the antepetalous whorl being absent. Wilson's investigations of floral anatomy (Wilson, 1937) revealed that the androecia of other families in Engler's Parietales are basically fascicular, although they often appear to be polyandrous.

Corner (1946) dismissed the whole idea that the stamen fascicle is a branching system as a 'reductio ad absurdum'. He admitted that it was possible to find all transitions in the Dilleniaceae from the massive centrifugal androecium to the fascicular state which, he claimed, was produced by humping or lobing of the torus in the early stages of development; but he thought this lobing was related to a diminution in size of the floral bud. Now, we have seen that the flowers of Hypericum which have 'afascicular' androecia (in Sect. Myriandra etc.) are not the largest ones in the genus. That title belongs to members of the sections Norysca, Eremanthe and Campylosporus, whose flowers have five stamen fascicles and five carpels. Furthermore, it seems clear that the afascicular, not the fascicular condition is related to a diminution in size of certain toral dimensions in Myriandra, Brathydium and Ascyrum.

The results from the study of the floral anatomy and morphology of Hypericum Sect. Brathydium are relevant in this connection. It will be remembered that a morphological trend can be traced from Sect. Norysca (with five separate fascicles) to the very small 'Sarothra'.
'Sarothra' type of flower in Subsect. Spachium, in which each fascicle is sometimes reduced to a single stamen. The intermediate stages in the trend are occupied by flowers in which the androecium is apparently afascicular or irregular. This condition has apparently been attained by the tangential spread of the stamen fascicles until a continuous ring of stamens was formed. When the number of stamens becomes too small to form a continuous ring, the arrangement appears irregular; but with a further decrease in number five separate fascicles can be detected again. In Sect. Brathys, then, the 'indefinite' androecium represents an intermediate stage between fascicles of numerous stamens and fascicles of few stamens.

It must be emphasised that a fascicle in such a 'polyandrous' androecium has not lost its individuality, any more than a petal loses its identity in a tubular corolla, although it may appear to have done so.

It is significant that those workers who have studied the floral anatomy of Hypericum or related groups all favour one or other of the theories which regard the stamen fascicle as a morphological unit (e.g. Wilson favoured the Teloxue Theory and Saunders the 'Dédoublement' Theory); while most of those who have studied their floral ontogeny (e.g. Hirmer and Corner, but not Payer) took the view that the fascicle is an aggregate structure. If the stamens are numerous it may /
may be impossible to detect the presence of fascicles by an ontogenetic study, because the anthers may be crowded so that they assume a pseudo-spiral arrangement. It may even be possible to draw parastichies through them in the bud, e.g. in *Wormia suffruticosa* (Dilleniaceae) (see Corner l.c., p. 430, fig. 4). Nevertheless, a study of the floral anatomy of another species of *Wormia* (*W. burbridgei*) revealed that the stamens, which are apparently spirally inserted, obtain their vascular supply from branches of a small number of trunk traces (Wilson, 1937). This situation should be contrasted with that found in, for example, the Ranunculaceae, where the stamens are in fact spirally inserted so that the trace for each stamen emerges from the stele separately and forms its own 'gap' (Smith, 1926; Brouland, 1935).

From these considerations it will be apparent that an investigation of the floral anatomy of a plant may reveal a fundamentally symmetrical organisation which was unsuspected on morphological or developmental grounds. On the other hand, it seems highly probable that the centrifugal development of the androecium in a polyandrous flower may indicate the presence of stamen fascicles even if they are not outwardly visible. The converse does not necessarily hold, however, since species in the Myrtaceae for example, have stamen fascicles which are said to develop centripetally (Hirmer, l.c.; Corner, l.c.). It will be recalled that the successive whorls in the flower of *Hypericum* are initiated /
initiated centripetally, but that the stamens on each fascicle primordium develop centrifugally. This is not so unexpected as Corner suggests if it is realised that there is a fundamental difference involved. It is a question of the origin on the one hand of whole organs (sepals, petals, stamen fascicles and carpels) and on the other of subdivisions or branches of organs. Hence it is understandable that the rate of development or the method of subdivision of members may vary (centripetal or centrifugal), though the initiation of whorls is usually centripetal.
SUMMARY.

(1) The floral vasculature of representative species of Hypericum L., Ascyrum L., Vismia (Velloz. ex) Vand. and Cratoxylum Blume (all in Guttiferae, Hypericoideae) as well as Ploiarium alternifolium (Vahl) Melch. (Theaceae, Bonnetiaceae) has been investigated by a method involving the clearing of whole flowers.

(2) From a basic pattern which occurs in some specimens of Hypericum Sect. Norysca, it was found that variations in the configuration of the floral vasculature in Hypericum (excluding Sect. Elodea) and Ascyrum formed five reduction series. The differences between the series can be correlated with variations in the dimensions of the torus. The basic vascular pattern implies that the most primitive type of androecium in Hypericum consists of five separate fascicles of stamens. From this type the 'three'-fascicled androecium results from merging of adjacent pairs of fascicles (i.e. 2+2+1), while the 'polyandrous' or 'afascicular' condition has been derived in two different parts of Hypericum independently by the merging of all five fascicles to form a ring. In the pentandrous androecium (Sarothra type), each fascicle is reduced to a single stamen. These variations are best interpreted in terms of the Telome Theory, i.e. each fascicle is a reduced branching system.

(3) /
(3) In Vismia an outer whorl of sterile fascicles (staminodes) alternates with the five fertile ones. In Cratoxylon two of the staminodia are absent. The floral vasculature of Hypericum Sect. Elodea resembles that of Cratoxylon rather than of other sections of Hypericum, the staminodes having a vascular connection with the stele. In H. elodes L. and H. aegypticum L. there is no such vascular connection, and the petal appendages are non-vascular.

(4) Sect. Elodea also differs from the rest of Hypericum in the petal colour, the corolla aestivation, the equal number of stamens per fascicle, the form of the inflorescence, the stomatal type and the basic chromosome number. It should be classified in the tribe Cratoxyleae as the genus Triadenum.

(5) H. aegypticum L. and H. russeggeri Fenzl are related to the shrubby Mediterranean species of Euhypericum. H. elodes L. is allied to herbaceous 'Euhypericum' species in Sect. Montana Stef. All three species have pseudo-gamopetalous flowers which show specialisation for insect pollination, unlike the rest of the genus. The staminodes, nectaries and connate filaments have been acquired secondarily and independently in the two groups. Their presence does not imply relationship to tropical shrubby Hypericoidae.

(6) H. rhodopeum Friv. (Sect. Campylopus) does not have a truly afascicular androecium; it is related to Sects. Olympia and Origanifolia among the herbaceous species /
species of Euhyperioum.

Sect. Myriandra is allied to Sects. Webbia and Campylosporus, and from it Sect. Brathydium and the American species of Ascyrum have evolved. Ascyrum is apparently reticulately related to Myriandra, and so there is no reason for separating it from Hypericum as a genus. The Himalayan species (A. filicaule [H.f. et Th.] Dyer) is related to herbaceous species of Euhyperioum from the same region.

Sect. Humifusocordum should be enlarged to include most species of Hypericum in Africa south of the Sahara, apart from Sect. Campylosporus. At least one species occurs in America. The section appears to merge with Sect. Brathys in Malaysia.

(7) The articulated leaf is an important taxonomic character in Hypericum, since it is a valuable indicator of affinity.

Four main groups of species have been distinguished. These correspond to the series based on floral anatomy, as follows: Norystal, I, II and III, IV and V. Norystal is the central group, from which Kimura's genus, Takasagoya, is a local development, and which has also given rise to the Boreal, Articulate and Austral Groups respectively.

(8) Hypericum species show a descending series of basic chromosome numbers from 10 to 7 (or possibly 6). Triadenum has $n = 19$. Several new chromosome counts of Hypericum species are listed.
(9) All three tribes of the Hypericoideae probably originated near South Africa, the Vismieae and Cratoxylaeae in the Madagascar region and the Hypericeae (= Hypericum) further south. From there the Norysoa Group spread into south and east Asia and Malaysia. The Articulate Group evolved to the west of this area, the Boreal Group to the north, and the Austral Group to the south-east.

(10) The ancestral flower of the Guttiferae was probably isomerous, pentamericous and diplostemonous, each whorl of the androecium being composed of fascicles of stamens. From this type of flower it is possible to derive all the floral variations in the family. The Theaceae probably had a similar ancestral flower, and the Malvales one which differed only by having an obdiplostemonous androecium. Polyandry is not necessarily a primitive condition, but may be an intermediate stage in a reduction trend from a number of separate fascicles each with many stamens to the same number of single stamens (c.f. Hypericum Sect. Brathys), especially if the androecium develops centrifugally.
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