A TAXONOMIC REVISION OF THE TRIBE

DESMODIEAE (LEGUMINOSAE - PAPILIONOIDEAE)

by

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PREFACE

The experimental work described in this thesis was carried out at the Botanical Research Unit, Durban and at the Department of Botany, University of Durban - Westville between April 1981 and December 1984.

This thesis, unless specifically indicated to the contrary is the author's own original work, and has not been submitted in any form to another University.

TO

MY   PARENTS

One of the reasons that science has achieved such stature in the late 20th century is its self-confident autonomy, the freedom of the scientific mind, Prometheus unbound, to go wherever it pleases .... In a way, science has replaced art as the art of the period, precisely because it shows no bounds .... "Art is a sign of life. There can be no life without change, as there can be no development without change. To be afraid of what is different or unfamiliar is to be afraid of life". People believe that. The trouble was that science soon proved itself more attuned to the different and unfamiliar than did art.

TIME. Special Anniversary issue October 5th, 1983.

It seems as one becomes older,
That the past has another pattern, and ceases to be a
        mere sequence -
Or even development: the latter a partial fallacy
Encouraged by superficial notions of evolution,
which becomes, in the popular mind, a means of disowning
        the past.
The moments of happiness - not the sense of well-being,
Fruition, fulfilment, security or affection,
Or even a very good dinner, but the sudden illumination -
We had the experience but missed the meaning,
And approach to the meaning restores the experience
In a different form, beyond any meaning
We can assign to happiness.

                                T.S. Eliot (The Dry Salvages)

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ABSTRACT

The tribe Desmodieae has a pantropical distribution and is
one of the most advanced tribes in the subfamily Papilionoideae.
Despite this fact, the tribe was already present in the fossil
record of the early Tertiary and so the Papilionoideae appear
to be much older than is currently accepted. With its greatest
centres of development in tropical Asia and America, Africa
is relatively poorly endowed and only four genera comprising
sixteen species occur in the Flora of southern Africa. Many
of these species are widespread in the Old World tropics
and the few African endemics appear to be closely related
to them. Desmodium is the largest genus with the bulk of
species belonging to the Asian subgenus Sagotia. Of the two
sections of Sagotia represented in Africa, section Nicolsonia
is clearly more derived than section Heteroloma, showing
many characters intermediate between Heteroloma and the con-
siderably more derived genera Alysicarpus and Lespedeza.
Other Desmodium species either of the Old or New World have
often become naturalised as weeds in Africa. Pseudarthria
is a genus derived by an aneuploid increase of the basic
x = 11 for the tribe rather than an aneuploid decrease as
in the case of Alysicarpus and Lespedeza. A re-count of the
chromosome number of P. hookeri (2n = 26) matches the count
obtained in another species of Pseudarthria for the first
time. Flowering strategy and flower structure in the tribe
are the result of intense coevolution with the ecological
requirements of skilled bee pollinators and although many
bees can trip Desmodieae flowers, only a relatively few high
energy demanding, traplining bees are able to bring about
effective pollination. The overall breeding system represents
a fine balance between the need for selfing and the need
for outcrossing in order to produce enough seed of sufficient
quality to survive in unstable environments.

CHAPTER 1

GENERAL INTRODUCTION

The Leguminosae is considered to comprise some 650 genera and approxi-
mately 18,000 species and is the third largest family of flowering
plants after the Compositae and Orchidaceae (Polhill, Raven and Stirton,
1981). The family is cosmopolitan in distribution and includes a
large number of economically important species. In spite of this
importance, knowledge of the family is insufficient and its taxonomy
is far from complete (Ohashi, 1971a). The family is divided into
three subfamilies, Mimosoideae, Caesalpinioideae and Papilionoideae.
The subfamily Papilionoideae is the largest and most advanced group
in the Leguminosea and it has been classified by different workers
into a variable number of tribes (de Candolle, 1825; Bentham, 1865;
Taubert, 1892-94 and Hutchinson, 1964). Polhill (1981) in the most
recent review of the subfamily, recognises 33 tribes.

The tribe Desmodieae comprising 27 genera with a mainly tropical
distribution (Ohashi, Polhill and Schubert, 1981) is distinguished
from the other tribes with jointed indehiscent fruits by the presence
of (1) - 3 - foliolate leaves with stipels (Ohashi, 1971a). It is
believed that the loment arose independently in a number of cases
(Ohashi et al. 1981) and the old tribe Hedysareae which included
all sections with such pods, was certainly not a natural group in
the evolutionary sense (Ohashi, 1971a).

Three subtribes have been recognised in the latest treatment of Ohashi
et al. (1981). The largest and most polymorphic of these is the
subtribe Desmodiinae which is represented in southern Africa by three
genera, Desmodium, Pseudarthria and Alysicarpus. The much smaller
subtribe Lespedezinae is only represented here by the naturalised
bush-clover genus, Lespedeza. The type genus Desmodium is the most
widespread and numerous of the tribe with about 300 species (Ohashi
et al. 1981). It occurs widely in the tropical and subtropical regions
of America, Asia, Australia and Africa with two major centres of
diversification. Firstly in Mexico and Brazil where there is perhaps
the largest number of species with the most diverse development of
plant parts (Schubert, 1963); also in Asia (Sino-Indian region down
through Malesia to Australia) where there are also large numbers

of species in many subgeneric groups. In addition the least specialised
subgenera and most archaic genera are   found in the Asian region
indicating a possible source of origin for the genus (Ohashi et al.
1981).

Africa is a subsidiary centre for development of the genus where
only a few representatives of some distantly related subgenera meet
(Schubert, 1952). Of the 10 species of Desmodium found in southern
Africa most have an Asian origin although there are a few that are
endemic in Africa.   Some too, are naturalised introductions from
the New World. Pseudarthria with 4 - 6 species and Alysicarpus
with 25 - 30 species are in the main, tropical Old World genera.
 These are represented in the flora of southern Africa by 1 and 4
species respectively.   Southern Africa contains the tail-end of the
tribe's tropical African distribution as well as a growing number
of naturalised introductions.

A number of important problems arising out of an initial survey of
the tribe Desmodieae are to be addressed in the following chapters.

The subgeneric treatment of Desmodium is not yet satisfactory (Schubert,
pers. comm.); and there is little or no indication as yet of how
the members of the genus in Africa are related to one another. Although
consideration of the former is beyond the scope of this study, it
is hoped that evidence from the study of comparative morphology will
provide information that will give a more natural grouping of species
in the taxonomic review.

A major problem with the taxonomy of the tribe is the difficulty
in imposing limits on the main genus Desmodium (Ohashi et al. 1981).
A number of obviously related genera are very similar e.g. Pseudarthria,
and the difficulty arises with how diverse the concept of Desmodium
should be.   An attempt will be made to prove whether Desmodium and
Pseudarthria are sufficiently different to be maintained as separate
genera, using evidence from a comparison of the morphology of the
four genera as well as a detailed study of breeding systems.

An attempt will be made to answer the need for an overall biological
view in plant taxonomy, through a study of the particular breeding
system in Pseudarthria hookeri. The many traditional taxonomic charac-
ters used to describe the flower, pollination, or indeed any aspect
                                        of reproductive/.....

of reproductive biology will be considered in structural-functional roles, as parts of linked functional systems which together markedly affect the ecology of the plant.

No formal attempt has yet been made to consider the overall phyto-geography of the tribe, from its origins through likely paths of migration to its present position. A synthesis of a wide range of geophysical and phytogeographical data will form the basis on which conclusions about the above are drawn. It is felt that no clear understanding of taxonomic relationships can be made without this information.

The final discussion will draw together the salient points derived during the study, and will be the section in which the above problems are tackled.

The major purpose of this study is to provide a taxonomic treatment of the tribe for the Flora of Southern Africa.

CHAPTER 2

TAXONOMIC BACKGROUND

2.1. History

The origin for the names that apply to our taxa goes back to the
pre-Linnaean classification system of de Tournefort. This purely
artificial classification is considered important for the development
of the modern concept of the genus (Stace, 1980). Many of these
names were later adopted by Linnaeus in his attempt to create a workable
system for the classification of plants. Linnaeus divided the plant
kingdom on the basis that reproductive features were more important
than other characters for taxonomic purposes. In the flowering plants
his prime divisions are based on the number of stamens that a flower
possesses (Radford et al, 1974) and in his class Diadelphia Decandria
the genus Hedysarum has been adopted from Tournefort and published
in Syst. Nat. (1735) and again in Gen. Pl. (1737).

von Haller (1742) published the name Papilionaceae to include similar
plants and Linnaeus (1751) in Philos. Bot. used the same name for
one of his 67 orders (families). An important facet of the Linnaean
system besides the classification is the consistent use of binomial
nomenclatureenabling the creation of a precise, referable and expand-
able system of nomenclature. This brought order to the large variety
of literature, systems of classifications and plants available during
the eighteenth century. Many plants had been known by a binomial
title long before Linnaeus, but the name might be and often was expanded
into a polynomial. Linnaeus made binary nomenclature a fixed rule
(Rendle, 1904) and the first consistent use of a binomial nomenclature
appeared in the Species Plantarum in 1753 (Stace, 1980). This was
a catalogue which listed all known plants, with synonyms, in a simple
logical system of classification. The first edition of Species
Plantarum is the starting point for the nomenclature of, among others,
the flowering plants and this means that all generic names accepted
and published by Linnaeus in the Species Plantarum, even if not accom-
panied by a description, are treated as having been validly published
on 1 May 1753 (Stafleu, 1967). Hedysarum L., ed.1.Sp.pl. : 745
(1753) was published along with two species occurring in our flora
area; H. gangeticum and H. vaginale. In 1759 H. barbatum was published
in Syst. Nat. From then until the early 1800's various authors ascribed

other species under present study to the genus. Aublet (1775), H. racemosum (= H. incanum); Swartz (1788), H. adscendens and H. tortuosum; Thunberg (1784), H. sericeum; Vahl (1791), H. repandum and H. glumaceum; Willdenow (1802), H. velutinum and H. rugosum and Poiret (1805), H. salicifolium. Owing to the arbitrary choice of characters in the classification system of Linnaeus there arose in the late 1700's the concept of creating a natural system based on the equal use of as many measurable features as possible (Radford et al, 1974). The empirical approach, that no greater emphasis should be placed on one character than another, was employed first by Adanson in Fam. Pl. (1763). He placed the group of plants most closely similar to Hedysarum in a section Coronilleae, which corresponds to the tribe in its present-day rank (Ohashi, 1971a). de Jussieu published his Genera Plantarum in 1789 and produced the first complete system of classification which can claim to be a natural one (Rendle, 1904). Here the family name Leguminosae was described and the previously separate Papilionaceae combined with the Caesalpineae and Mimoseae. de Jussieu divided the flowering plants into groups on the basis of monocotyledon vs. dicotyledon, ovary and stamen position, presence or absence of petals and degree of fusion of petals (Lawrence, 1951). The next step was the realisation that several different genera existed in Hedysarum and in 1803, Michaux described the genus Lespedeza and in 1813, Desvaux described Desmodium and Alysicarpus. Thunberg (1823), however, continued to use the broad concept of Hedysarum in the Linnaean system of Flora capensis.

de Candolle produced the next significant development in a natural classification by improving on de Jussieu's treatment of the dicotyledons. These were subdivided into more basic primary groups with apparent closer affinities (Lawrence, 1951). For example, they were divided first into two groups on the presence or absence of corolla; those with corollas were subdivided on gamopetally vs. polypetally; and the latter again divided on the basis of ovary position. It was in de Candolle's treatment of the Leguminosae in the Prodromus (1825) however, that real progress was made. In this publication the Papilionaceae was described formally as the subfamily Papilionoideae of the family Leguminosae. He divided the subfamily into tribes, one of which was called Hedysareae and this corresponded to and is a later synonym of Adanson's Coronilleae. This assemblage included

plants arbitrarily grouped on the indehiscent, jointed nature of the legumes (Ohashi, 1971a). He recognised three subtribes based on morphology of the inflorescences and legumes and he took the bulk of existing Hedysarum species and placed them under various genera, among others Desmodium (subtribe Euhedysareae) and Alysicarpus (subtribe Alhageae). One of the new genera he described was Nicolsonia and in 1836, Meyer described two species, occurring in the present study area, N. caffra and N. setigera. The genus Pseudarthria was established by Wight and Arnott in 1834 and was described again by Meyer (1836) as Anarthrosyne. Wight and Arnott described the species P. hookeri along with the genus in 1834.

Lindley in 1836 proposed an alternative name for the family Leguminosae, the Fabaceae, based on the type genus Faba. Although this name is valid according to article 18.1 of the International Code of Botanical Nomenclature (1978), the name Leguminosae is still treated as validly published and is sanctioned by long usage according to Art. 18.5. The name Papilionaceae as an independent family has also been sanctioned in Art. 51.2 (1978).

The last major natural classification was produced by Bentham and Hooker. Then as now, one of the major problems has been the circumscription of the genus Desmodium. In 1852 Bentham proposed a system in which the genus Desmodium as described by de Candolle, was split into five genera including Desmodium sensu Bentham. Other genera proposed by de Candolle i.e. Nicolsonia were placed as one of 11 sections in Desmodium. Bentham in his review of the Leguminosae in 1852, placed Hedysarum barbatum and Nicolsonia caffra under Desmodium calling the latter Desmodium dregeanum. In 1865, in the Genera Plantarum, new standards were set in descriptive botany because these were drawn up afresh from a wide study of British and continental herbarium specimens (Stace, 1980), and did not represent a compilation made from existing literature. The general outline was based on that of de Candolle and genera were subdivided into subgenera and/or sections, but greater stress was laid on the contrast between free and united petals. The Leguminosae was placed in one of three big sections of the Dicotyledons; the Polypetalae, and in one of three series of this section, the Calyciflorae. One of the five cohorts (equivalent to order) in the series, the Rosales, contained the Leguminosae with eight other families.

In 1865 however, Bentham greatly changed his previous concept of the genus Desmodium and its allied genera. He established the broader circumscription of the genus (Ohashi, 1973) including many genera described by previous authors and himself (1852). In his treatment the genus was characterised as "leguminis articuli polymorphi racemi terminales v. rarius subaxillares, simplices v. paniculati" (p 449) and was placed within the tribe Hedysarae. This was one of eleven in the subfamily Papilionoideae. Bentham considered six subtribes within the Hedysareae, one of which, the Desmodiinae (described as Desmodieae) contained all the genera under present study. Five of these subtribes represented quite a change from the concept of de Candolle's Euhedysareae and Alhageae. Harvey (1862) in revising the South African representatives of the tribe for Flora Capensis placed Nicolsonia setigera under Desmodium and described a new species, Alysicarpus zeyheri. The genus Nicolsonia was later put into synonomy with Desmodium. In his Genera of South African Plants in 1868, the genera under study were all included in the broad tribe Hedysareae sensu Bentham. In 1871 and 1876 Baker published accounts of the tribe Hedysareae in the Flora of Tropical Africa and Flora of British India respectively. He did not use Bentham's subtribes, but the concept of Desmodium was broadened in the latter publication to Bentham's of 1865 which included eight subgenera, the subgenus Desmodium having six sections based on differences in the legumes and loment articles (Ohashi, 1973).

German botanists were among the first to struggle with the concept of evolution regarding the development of a taxonomic scheme (Radford et al, 1974). Engler and Prantl are names associated with the system developed originally by Eichler in about 1875. It was modified by Engler and his associates but it was not a phylogenetic system in the modern sense (Lawrence, 1951). Engler's system distinguished between primitive and advanced conditions and accepted to a degree the principle of simplification by reduction, but it had the utility and practicality of a natural system. One of the reasons for the widespread adoption of theEnglerian system by many herbaria even today, is that it applied to the plants of the world in a twenty volume work, Die natürlichen Pflanzenfamilien. This illustrated work with modern keys provided a means for the identification of all known genera of plants from algae to the most advanced seed plants. Because of

the vast/.....

the vast literature that has adopted its principles it is still widely used. Despite changes in delimitations of taxa, Taubert in the Pflanzen_familien (1894) employed entirely, Bentham's treatment of the tribe Hedysareae in the revision of the Leguminosae. The system of Taubert in Engler and Prantl's Pflanzenfamilien and its successors, De Dalla Torre and Harms (1900-1907), used by most South African herbaria and Schulze-Menz (1964), introduced some changes in tribal position to indicate evolutionary trends but apart from new genera, the content of the tribes has remained much the same (Polhill, 1981). In the Englerian scheme of classification the Leguminosae are placed along with the families Platanaceae, Crossosomataceae, Rosaceae and Connaraceae in the order Rosales suborder Rosinae (Dickison, 1981). Schindler produced an important monograph on Pseudarthria in 1914.

The Bessey system of classification (1915), was definitely conceived to be phylogenetic and was based on a series of "dicta" (see Radford et al, 1974). It is these that have, with modifications, provided the theoretical base and guiding principles of most contemporary systems of angiosperm classification. The position of the Leguminosae did not change much in Bessey's treatment.

After Bessey, Hallier produced an independent classification developing ideas similar to those of Bessey. Here the dicots were regarded as more primitive than monocots. He realigned many families and defended the use of many kinds of characters, placing more significance on ovule morphology and position than other phylogenists (Radford et al, 1974).

As far as the flowering plants are concerned almost all classifications are loosely referable to either the Eicher-Engler system or the Hallier-Bessey system which is in turn derived from de Candolle, Bentham and Hooker (Stace, 1980).

Hutchinson followed the latter tradition but divided the dicotyledons into two main groups on the basis of a predominantly woody or herbaceous character. This is considered an unnatural division by most workers. A second objection to his system is the insistence on a monophyletic origin for the seed plants in general and the angiosperms in particular. There is also no explanation given for his disposition of orders and families (Lawrence, 1951). Regarding his treatment of the Leguminosae (1926), he was the first prominent twentieth century botanist

to elevate the legumes as three families of the order Leguminales (Polhill, 1981). This same treatment was followed in later publications and in 1964. In Hutchinson's opinion the family is derived from the Rosaceae (including Chrysobalanaceae). This system of classification was adopted for the Flora of West Tropical Africa (1928); as it was for Burtt Davy's Flowering Plants and Ferns volume 2 (1932). The tribe Hedysareae retained the artificial broad concept of Bentham, without the subdivision into subtribes, but Pseudarthria was removed to the tribe Galegeae. This is considered by later workers to be unacceptable. Hutchinson also retained the narrow concept of Schindler's Desmodium except that Meibomia and Nicolsonia were included.

In 1929 Baker updated the treatment of the family in Africa in his Leguminosae of Tropical Africa, enumerating additional species and providing abbreviated descriptions. Gams (1923-1924) began to look at the tribe Hedysareae as a polyphyletic assemblage deriving from a number of different tribes (Ohashi, 1971a) but this idea only developed later on. In 1926 Phillips revised The Genera of South African Flowering Plants using Engler's system but basing the tribal divisions of the Leguminosae on Bentham (1865).

An important modification to the broad generic concept of the genus Desmodium circumscribed by Bentham (1865) was made by Schindler from 1924-1928 (Ohashi, 1973). He restored a large number of formerly included genera and created three new ones. This treatment resembled closely Bentham's initial account in 1852. Among the rest Schindler recognised two major genera, Meibomia sensu Schindler and Desmodium sensu Schindler. This narrowest concept of the genus Desmodium with only three subgenera (Schindler, 1928) has scarcely been adopted by succeeding taxonomists. The name Meibomia is rejected because of the conservation of Desmodium by the International Botanical Congress of Vienna in 1905 (Schubert, 1950). Schindler's complete list 'Die Desmodiinen in der Botanischen Literatur nach Linne' (1928) is a thorough bibliographic study of the Desmodiineae as recorded in botanical literature from 1775-1928, and it remains a most important contribution to the study of the genus and its relatives (Schubert, 1952). Burkart (1939) further rationalised the subtribal divisions of the Hedysareae sensu Bentham by proposing two new subtribes and removing another. This system was adopted by Schulze - Menz in the updated Melchior edition of Pflanzenfamilien of 1964 (Ohashi, 1971a). Schubert in a series, Desmodium : Preliminary Studies (1940, 1941, 1950, 1963)

concentrated/.....

concentrated on checking nomenclature, and the taxa against type material of several groups within the genus. Species in these groups were described preparatory to revisions of the genus in Africa and the New World.

The problem with circumscribing Desmodium is aggravated by the lack of a sensible subgeneric treatment of the genus. Based on Bentham (1852, 1865) and Baker (1876), Ohashi (1973) has proposed a new system but Schubert (pers. comm.) still feels the subdivisions are too many. The subgenus Podocarpium (Benth.) Ohashi was treated in detail by Isely (1951) in his preparation for the treatment of Hedysareae in the Leguminosae of North Central U.S.A. (1955). While researching the American species he found that relationships with Asian members warranted a survey of the whole subgenus. However, D. repandum which occurs in Asia and in our flora area and belongs to the subgenus, is left out of the study with no explanation given. Isely (1955) again raised the question of the heterogeneity within Bentham's tribe Hedysareae (Polhill, 1981).

Phillips updated The Genera of South African Flowering Plants in 1951 but the position of the Hedysareae remained unchanged. Schubert (1952) and Leonard (1954) contributed valuable taxonomic knowledge of the tribe in Africa, and together (1954) they dealt with the Hedysareae in Flore du Congo Belg et du Ruanda Urundi. In 1958 the second edition of Flora of West Tropical Africa appeared with the Leguminosae updated by Hepper, but the position of the tribe remained unaltered. A census of Desmodium for Flora Malesiana was produced by Knaap-van Meeuwen in 1962, and in the same year White considered the tribe in the Forest Flora of Northern Rhodesia.

1964 represents the year in which the tribal concept of the Hedysareae changed radically. Hutchinson in The Genera of Flowering Plants stated, "Since Bentham published his conspectus of tribes the number of genera has nearly doubled and the number of 'ambiguous' characters correspondingly increased. In consequence I found it quite impossible to key out satisfactorily these comparatively few tribes as defined by Bentham". Hutchinson then decided to treat most of Bentham's subtribes as tribes, thus elevating the Desmodieae to tribal status for the first time. Although he placed them near the tribe Hedysareae sensu stricto it has come to be realised more and more that simply having jointed fruits in common is an artificial character, indicating

rather that/.....

rather that convergence has taken place. The subtribes originally included in the old Hedysareae are in fact not closely related to the Desmodieae. The major problem with Hutchinson's scheme was his earlier (1926) removal of Pseudarthria and Lespedeza as two separate entities from the Desmodieae. Most subsequent workers agree that they should be placed in the tribe.

Schulze - Menz (1964) revived the old name Coronilleae (= Hedysareae sensu Bentham) and considered the present group under study as the subtribe Desmodiinae. This system was followed by Ohashi (1971a) in a Taxonomic study of the tribe Coronilleae with special reference to Pollen Morphology. This detailed and valuable addition to literature is a review of the taxonomic concept of the tribe and its history, surveying all genera to determine generic boundaries especially between Desmodium and closely related genera. The study was based on a broad comparative study of pollen morphology. In his review of the subtribe Desmodiinae it is noted that the concept of Hutchinson's tribes is unacceptable due to the existence of intermediate species between them and Ohashi adopts the original concept of the subtribe created by Bentham (1865), recognising 24 genera.

Other treatments of the tribe in Africa during this period were made by Torre in the Conspectus Florae Angolensis (1966) and Schreiber in the Prodromus Flora of South West Africa (1970).

The most recent systems of classification have tended to be Hallier-Bessey based (Stace, 1980) i.e. Takhtajan (1969), Cronquist (1968), Dahlgren (1975) and Thorne (1976). Schulze - Menz (1964) considered the families Connaraceae, Leguminosae and Krameriaceae to be part of the Rosalean suborder Leguminosinae (Dickison, 1981) while Takhtajan and Dahlgren regard the legumes as an order Fabales in which the Leguminosae is the sole family. Takhtajan envisaged the Fabales as deriving from ancestors of Saxifragales. Dickison (l.c.) states, "In most contemporary systems of classification, the order Rosales is an extremely diverse assemblage both morphologically and anatomically. Cronquist (1968), while noting that the order is very difficult to define, recognised 17 families in his circumscription. Cronquist further observed that in his system there exists a basic dichotomy between the Rosaceae, Chrysobalanaceae, Leguminosae and other families". Thorne (1976) also placed the family within the Rosales although he too recognised difficulties. Dickison (l.c.) continues, "Very recently Professor Thorne (pers. comm.) has rethought the matter

of the/.....

of the relationships of the legumes and has come to the divergent
conclusion that they have little affinity with the Rosales or Rosinae.
Rather, Thorne now tentatively treats the families Leguminosae and
Connaraceae as the Fabineae of the order Rutales (Rutiflore), closely
related to the Sapindaceae of that order and superorder. In his
view the ancestors of the Legumes must be sought in protorutalean
stock. A closer relationship between the Leguminales and Sapindales
has also been suggested by Dahlgren (1977)".

According to Dickison (l.c.) a legume origin outside the Rosalean com-
plex was also sought by Corner, on the basis of seed morphology; and by
Gottwald, on the basis of wood anatomy. Nevertheless the Connaraceae
and Chrysobalanaceae are consistently recognised as families having the
closest relationships to the Leguminosae. Artificial divisions with-
in the subfamily Papilionoideae have also been criticised by other work-
ers and in particular the heterogeneity of Bentham's Hedysareae. This
is expanded on later in the chapter.

Modern taxonomic treatments of the tribe Desmodieae particularly
in Africa date from when Schubert and Verdcourt revised the group for
the Flora of Tropical East Africa (1971). Verdcourt had published
some subspecific names of Alysicarpus and Pseudarthria in preparation
for the Flora in the previous year. The in depth revision of the
tribe in East Africa provided valuable information on types and clarifi-
cation of taxa (particularly in Schubert's treatment of Desmodium).

Ohashi, interested mainly in Desmodium in Asia, published A Taxonomic
study of the subgenus Dollinera of the genus Desmodium in 1971(b).
This was followed by the most detailed account of Desmodium to be
published, The Asiatic species of Desmodium and its allied genera
in 1973. This large work is most important for its taxonomic treatment,
the historical review of the concept of Desmodium and allied genera,
and the new system proposed for the subgeneric categories within
the genus with its comparative observations of morphological characters.

In 1974 Verdcourt produced an account of the tribe in preparation
for Flora Zambesiaca and although it is taxonomically very similar
to the treatment for East Africa (1971), the localities, distrib-
utions, habitats and quoted specimens were of more direct use for
this present study. The separate tribes are again loosely referred
to here as the Hedysareae (sensu lato). The updated The Genera of
Southern/.....

Southern African Flowering Plants volume 1 by Dyer (1975) followed
Hutchinson's disputed treatment of 1964 and Compton (1976) briefly
considered the group in Swaziland.

The most comprehensive and authoritative work to cover all aspects
of the family was produced as a result of the International Legume
Conference held in 1978. Advances in Legume Systematics is directed
principally toward an improved classification of the Leguminosae
at generic and tribal levels. The first volume is devoted to general
introductory chapters considering evolutionary relationships and
biogeography with a detailed taxonomic treatment of the family, by
tribes to genus level. The second volume considers specialist views
on aspects of biosystematics from cytology, phytochemistry and anatomy
to pollination, seeds and defenses as they have been researched to
date in the Leguminosae. The contributions of Dickison (Evolutionary
Relationships of the Leguminosae), Polhill (introduction to chapter
on Papilionoideae) and Ohashi, Polhill and Schubert (treatment of
the tribe Desmodieae) were most pertinent to this section of the
study. In this treatment of the tribe the three authors agree to
circumscribeDesmodium on a slightly broader basis than Ohashi (1973).

Cronquist (1981) published a revised classification of flowering
plants. The Division Magnoliophyta (= Class Angiospermae) is considered
to comprise two classes, one of which, the Magnoliopsida (= Dicoty-
ledones) contains 4 major subclasses. One of these, the Rosidae,
contains 18 orders including 114 families. This natural assemblage
stems from the ancient subclass Magnoliidae. The Leguminosae is
again considered as three separate families within the order Fabales,
the present group under study falling into the Fabaceae (= Papilion-
oideae). In this thesis the major divisions to subclass follow Cronq-
uist, from order to family follow Thorne (1978) and the treatment
to genus follows Ohashi et al, (1981). Subgeneric treatment of
Desmodium follows Ohashi (1973) as closely as possible.

2.2. Classification

The subclass Rosidae Takhtajan (1966) comprising some 18 orders, 114
families and 58,000 species is a natural grouping based on a distinct
combination of chemical compounds, a centripetal sequence of stamens
when many, and typically tricolporate pollen (Cronquist, 1981). Fossil

evidence/.....

evidence indicates that the Rosidae began to diverge from the ancestral Magnoliidae near the middle of the Albian stage of the lower Cretaceous as a group with tricolpate pollen and pinnatifid (then compound) leaves. Sapindopsis is a good candidate for the earliest recognisable antecedent of the subclass; the implication being that the pinnate leaved habit so common in the Rosidae is basic to the group i.e. modern simple leaves have a pinnate ancestry (Hickey and Doyle, 1977 in Cronquist, 1981). Simple leaves have repeatedly been derived from compound ones with unifoliolate compound leaves as intermediates.

The family Leguminosae as a whole is linked by: often bearing nitrogen fixing nodules; having non-protein amino acids in the seeds and vegetative parts commonly together with tannins; generally producing proanthocyanins and often with some or other alkaloid especially pyridine, quinolizidine or indole groups; having petioles with a complex vascular anatomy, and the typical legume fruit with one-to-many ovules on a marginal placenta. In contrast to the long accepted theory of a Rosalean origin for the Leguminosae, evidence has accumulated to ally the family and others such as the Connaraceae with the Sapindales and more closely to the Sapindaceae (Dickison, 1981): "The most archaic genera of Leguminosae seem to be the diverse extra tropical woody Caesalpinioideae - Gleditsia - Gymnocladus, Ceratonia - Zenia and Cercis. The vegetative organisation (apart from stipules), chemistry and embryology of these genera are comparable to Sapindaceae and their wood is very similar". Gleditsia and Ceratonia occur as common introductions in our flora area and it is with these that the similarities to Sapindaceae can be seen. Evidence, however, is accumulating that even these genera are considerably derived (Stirton pers. comm.)

As yet there is little fossil evidence about the early evolution of the family, but it appears to have become large and diverse only during the Eocene 38-54 m.y. B P (Raven and Polhill, 1981). Quoting Raven and Polhill (l.c.), "The considerable differences between the few notably primitive genera of legumes that have survived, taken together with their biogeography and the known fossil record, certainly place the origin of the Caesalpinioideae in the Upper Cretaceous, but there is no evidence for any great antiquity within the period and no authentic fossil evidence older than 70 million years." Stebbins (1974) emphasises that over the length of evolutionary time, environ-

environmental/.....

mental changes are certain to cause many species and genera to become extinct. Imperfectly adapted forerunners of a particular evolutionary line are most likely to be eliminated by competition with more efficient successors. This is largely responsible for the wide gaps between successful families like the Leguminosae and their nearest living relatives. Elimination of these generalised forerunners makes virtually impossible the persistence in a modern flora of the direct ancestors of any major group. Extensive shifts in geographic distribution during angiosperm evolution have further aided this situation. Raven and Polhill (1981) in a detailed account of the biogeography of the family consider that the relative concentration of the most archaic genera of legumes in the Old World points to Africa as a prime centre for the earliest evolution of the family. The Papilionoideae are linked to the Caesalpinioideae through the Swartzieae, an essentially South American group, whose flowers resemble the latter subfamily; but in seed, chemical and wood features they are more papilionoid.

When compared with other subfamilies, the essential features of the Papilionoideae are: the typical papilionoid flower consisting of five petals, the uppermost (adaxial), called the standard borne externally to the others and more or less enfolding the other petals in bud, two lateral petals or wings, usually similar and mostly distinct and two inner petals also similar and mostly connate distally to form a keel enfolding the androecium and gynoecium. The androecium consists mostly of 10 stamens, nine of which are commonly connate into an open sheath around the pistil, the 10th (adaxial) usually partly or wholly separate from the other nine. The gynoecium consists of a single carpel with a terminal style and wet, papillose, capitate stigma. Ovules are one-to-many on a marginal placenta. The seed typically has a hilar valve which is a sophisticated mechanism for drying out seeds (possibly linked to the greater development of the embryo at that stage which is represented by a curved radicle).. The synthesis of quinolizidine alkaloids and isoflavones as well as unique non-protein amino acids such as canavanine as sophisticated defense systems.

The radiation of the Papilionoideae is complex but in recent years there has been a general recognition of several major components, with the Sophoreae as a diverse base group. One group, the genistoid alliance includes the traditional tribes Podalyrieae and Genisteae

divided into a number of regional tribes (Polhill, 1981). The centre of the subfamily is dominated by the huge galegoid complex (the traditional tribes Galegeae and Dalbergieae) which differs from the Sophoreae by union of stamens, by the general replacement of quinolizidine alkaloids by canavanine and by the stabilisation of the basic chromosome number of $x = 11$ and $x = 10$ in the woody tropical part including Dalbergieae, Tephrosieae and Robinieae. The Galegeae proper are now separated with a number of temperate tribes (Loteae, Vicieae, Trifolieae, Hedysareae etc.) as the epulvinate series, characterised by the loss of the basal pulvinus of the leaf, closure of the vascular system and the leaves tending to be distichous rather than spiral and with phloem transfer cells (Polhill, l.c.).

The residual pulvinate series is predominantly tropical and can be subdivided into a core, the Tephrosieae and Robinieae, and a number of more advanced tribes generally with a regional preference for either the Old World or New World. Advanced tropical tribes of the Old World, Desmodieae, Indigofereae, Psoraleeae and Phaseoleae display different characteristics to those centred in the New World, Aeschynomeneae, Adesmieae and Amorpheae. All have developed an elaboration of the flowers in many different ways associated with specialisation and greater constraints on the variability of root nodules, leaves, inflorescences, fruits, seeds and seedlings and many have become herbs. The regional differentiation of these groups is borne out by a number of characters. Pollen wall structure tends toward a marked thickening of the endexine and almost complete loss of a foot layer in the Old World tribes (reaching a peak in the Desmodieae) whereas the reverse is true of the New World tribes. Flowers tend to specialise developing a sophisticated explosive form of pollination (in the Desmodieae and Indigofereae) or having a nectary as intrastaminal disc as opposed to the nectary retained in the hypanthium of the New World tribes. In the Desmodieae nectar production has been lost. Flowers of the Old World group are often clustered on the rhachis to form a characteristic inflorescence, the pseudoraceme; in the others, the flowers are inserted singly. Canavanine is generally absent in the New World representatives and these are often characterised by lacking stipels and specialised hooked or biramous hairs (Polhill, 1981). The Old World features are on the whole well established in the Tephrosieae i.e. the presence of stipels and hooked or biramous hairs, and those of the New World in the Dalbergieae.

The tribe/.....

The tribe Phaseoleae shows the closest affinity with the Desmodieae but the latter differs in their relatively small, explosively dehiscent flowers with ephemeral petals, lack of nectar and mostly jointed fruits.

The tribe is dominated by the pantropical Desmodium and a varying number of rather controversial segregates (Ohashi et al, 1981) with some woody genera approximating towards the Tephrosieae from India to New Caledonia. It is felt by Ohashi (l.c.) that a sensible classification of the Desmodieae has been prejudiced by the traditional over-weighting of fruit characters. The fruit normally consists of indehiscent jointed articles but fruits that open have arisen a number of times. It has been mentioned that the major problem in classifying the tribe has been the circumscription of the genus Desmodium.

CHAPTER 3

MORPHOLOGY

3.1. Introduction

Morphological characters, exclusively, have been used as the basis
upon which all taxonomic conclusions have been drawn in the past.

In de Candolle's concept (1825), the tribe Hedysareae included all
genera with jointed pods. He recognised three subtribes based upon
differences in shape, texture and dehiscence of pod-articles together
with position and branching pattern of inflorescences. Use of these
characters led to his placement of Desmodium and Alysicarpus in separate
subtribes.

Delimitation of subtribes was altered by Bentham (1852) to include
all the genera investigated in the present study in a single subtribe,
Desmodieae. He based his altered circumscription upon consideration
of leaf, stipule, stipel, inflorescence, petal and stamen morphology.

Hutchinson (1964) on the basis of pod differences excluded Pseudarthria
and Lespedeza from Desmodieae, placing them in tribes of their own,
and raised Desmodieae to tribal status. All the genera were re-united
in the single tribe, Desmodieae by Ohashi (1971a) who considered
the comparative morphology of their pollen in great detail. Ohashi
(1973) in a study of Desmodium and its allied genera in Asia made
the most serious attempt to compare them in terms of habit, leaves,
inflorescences, bracts, stamens, pollen, pods, seeds and seedlings.
He also developed the subgeneric concept of Desmodium from that of
earlier workers. Ohashi et al, (1981) in the most recent treatment
of the tribe, illustrate how variable pod characters can be in the
Desmodieae and point out that their overstressed importance has prejud-
iced previous classifications of the tribe.

In this study many morphological, biological and ecological characters
are compared as the bases for drawing taxonomic conclusions in the
final chapter.

3.2 Materials and Methods.

3.2.1. Materials

Approximately 1400 herbarium specimens were examined from 15 herbaria (BLFU, BOL, GRA, J, NBG, NH, NU, PRE, PRU, SAM, STE, UDW, VENDA, WIND, ZULU). Of these 1265 southern African specimens have been quoted in the taxonomic review of the tribe (see appendix). Standard abbreviations of internationally recognised herbaria are taken from Holmgren, Keuken and Schofield (1981). Type specimens of taxa were seen in photographs from K, BM and LINN as well as from collected photographs of types in European herbaria from GH. Tropical African material was also examined at PRE.

Much of the morphological research and all of the plant descriptions were made from live plants grown in the Natal Herbarium garden. These were collected on a number of field-trips in Natal and eastern Transvaal. Plants of all species were stored in preservative to ensure access to fertile material through the whole year.

3.2.2 Methods

All herbarium specimens obtained on loan were first coded for each herbarium of origin to facilitate re-sorting later. They were then examined, with the pertinent information on the labels being put onto index cards.

Data on the collectors name and number, date of collection, herbarium where housed, major and minor locality and other notes, was placed on each card.

This systemprovided a flexible means of sorting information in order to, shuffle taxa around as their name determinations became clear; compile ecological notes; construct distribution maps; plan field-trips; store an accumulation of data and provide a list of authors quoted in the appendix.

Herbarium specimens were sorted into 'like' groups on the basis of observable structural features, and any anomalies were noted and kept aside. Extensive field work was undertaken over three years

to test/.....

to test each of the taxa isolated in the herbarium, and major anomalies were followed up in the field.

Fresh slide preparations of floral parts were made in the field (Stirton pers. comm.) by placing freshly dissected floral organs on to Scotch pressure-sensitive tape arranged with the adhesive surface upwards. Once the mount was completed, a small sheet of transparent perspex was pressed over the tape and any air bubbles removed. This method retained the floral structures in good condition for the duration of the study. Its real value lies in enabling the researcher readily to compare many characters of a number of taxa in the field.

On field-trips, rootstocks of species were dug out for morphological description and were retained for planting in the garden, at Natal Herbarium. Seed material was gathered where possible for germination and seedling description.

The preservative used for flowering material was F.A.G. or 'Kew Cocktail'.

Chemical proportion for 1 litre.

Formaldehyde	50mls
95% Ethanol	500mls
Glycerine	50mls
Water	400mls

Examination of morphological characters.

Relevant dried plant parts were examined and measured on herbarium specimens and compared with the equivalent live plants in order to draw up the overall details of size, shape, colour and vesture used in the individual plant descriptions. Colour contrasts and vesture in terms of glandular hairs are much better observed in fresh material. A Wild Heerbrugg dissecting microscope and handlens were used for observation.

In many cases in parallel with the above, dried samples of plant organs were obtained from herbarium specimens for comparison under the surface scanning electron microscope (S.E.M.). The instrument used was the PSEM 500, and untreated dried herbarium material was

mounted/.....

mounted directly onto brass stubs with nail varnish and sprayed with a fine coating of gold in a Polaron sputter coating unit (E.5000) to avoid electron beam damage to the material. Photographs (Plates 1 - 15) were taken at various magnifications from 20 x to 5000 x with a beam spot diameter of 640 A; an accelerating voltage of 25 K volts and a line time of 32m. secs per line, 1000 lines. S.E.M. work was used to describe leaf, petal, fruit and seed surfaces in great detail but also to give comparisons between size and shape of various other organs.

Drawings of leaf shapes, fruit characters and other organs were made to supplement the morphological descriptions; and photographs of good representative herbarium specimens are appended to the description of each taxon.

Distribution maps.

Distribution maps were plotted using the one-degree square system proposed for southern Africa and modified by Leistner and Morris (1976).

3.3. Results

3.3.1. Roots

Most species under present study are perennials and have two major types of rootstock. The majority have an erect, often thick, knotty or twisted woody rootstock which may be quite long and extensively dichotomously-branched below, to produce many cord-like woody roots. It is also much divided near the top (the stylopodial region of Stirton and Gordon-Gray, 1978) giving rise to a number of erect aerial stems as well as a number of horizontal rhizomes which are also cord-like and woody and tend to divide dichotomously and extend for some area around the parent. Erect leafy shoots and fibrous roots are produced at intervals from these rhizomes. Examples with this type of root system are generally herbs, suffrutices or subshrubs growing in open grassland or savanna conditions. Taking P. hookeri as representative, it is a perennial suffrutex or small shrub 0,3 - 3,0m tall producing a number of erect aerial stems as well as rhizomes. The rhizomes become very thick with age and eventually rot leaving individual plants separated from one another.

The second/.....

The second type of rootstock typified by D. adscendens is a thin
woody horizontal rootstock which gives rise to an extensive slender
fibrous root system and divides dichotomously into a number of rhizomes
which branch repeatedly often reaching the surface where they develop
leafy shoots. This type is also shared by D. salicifolium and
D. repandum. These species are either scandent herbs or subshrubs
of forest floors or in the case of D. salicifolium waterlogged mud
near lakes or streams, and they are able to cover extensive areas.
An unusual feature noted in D. setigerum and believed to occur in
other species is that the long slender cord-like roots may become
distally thickened a metre or more from the parent and give rise
to new shoot systems. The roots of many shrubs and trees form buds
which in some cases are an important means of vegetative reproduction
(Jamieson and Reynolds, 1967).

Finally A. rugosus subsp. rugosus and A. glumaceus are annuals having
slender daucate rootstocks.

3.3.1.1. Nodulation

Nodules have been noted in Desmodium, Pseudarthria and Alysicarpus
in Zimbabwe by Corby (1974). Corby (1981) distinguishes between
a number of different types of root nodule in legumes based on nodule
shape, size and whether they are branching or not. One type, the
desmodioid nodule (Corby, l.c.) is characteristic of the Desmodieae,
Loteae and Psoraleae but is common in some other tribes including
the Phaseoleae. These nodules have sometimes been referred to as
the Vigna or cowpea type (Allen and Allen, 1981). The desmodioid
nodule is described by Corby (1981) as being unbranched, invariably
oblate in shape, having obvious lenticels, by standing out roundly
from its parent root and not dimpling with age, not being subtended
by a fine rootlet and not being conspicuously numerous. They tend
to be large but rarely exceed 4,5mm in diameter.

3.3.2. Stems

Species are generally multistemmed if perennial (from the stylopodium
and often branch freely from near the base. In Desmodium and Pseudar-
thria stems are mostly woody and erect to suberect (particularly
if fire has not burned them back regularly). Exceptions are D. setige-
gerum and D. adscendens of the section Nicolsonia. In the latter

FIGURE 1

Leaf characteristics - Alysicarpus

Left half: adaxial surface;   Right half: abaxial surface

a)   A. glumaceus   x 2

b)   A. zeyheri   x 2

c)   A. rugosus subsp. perennirufus x 2

d)   A. vaginalis   x 2
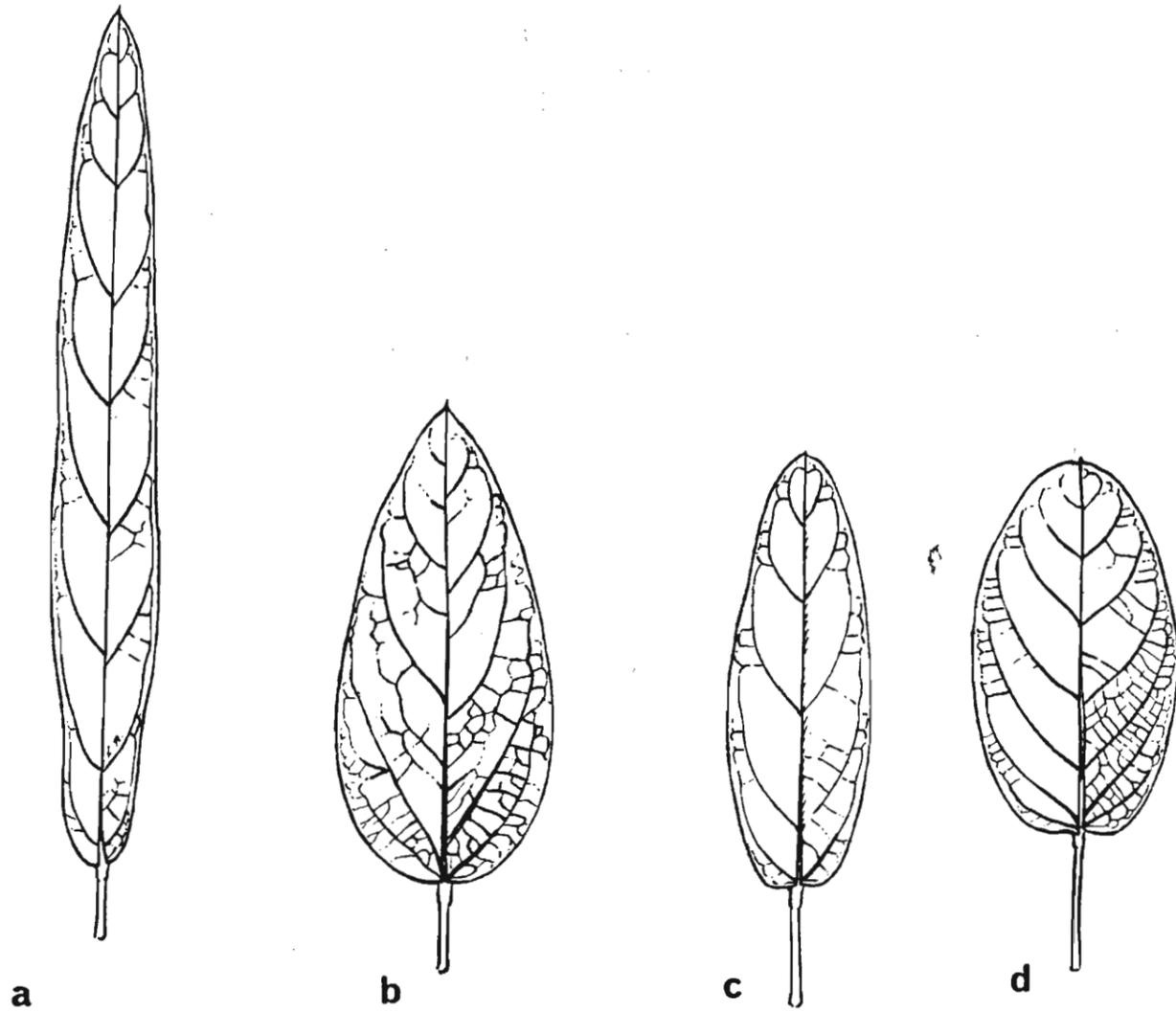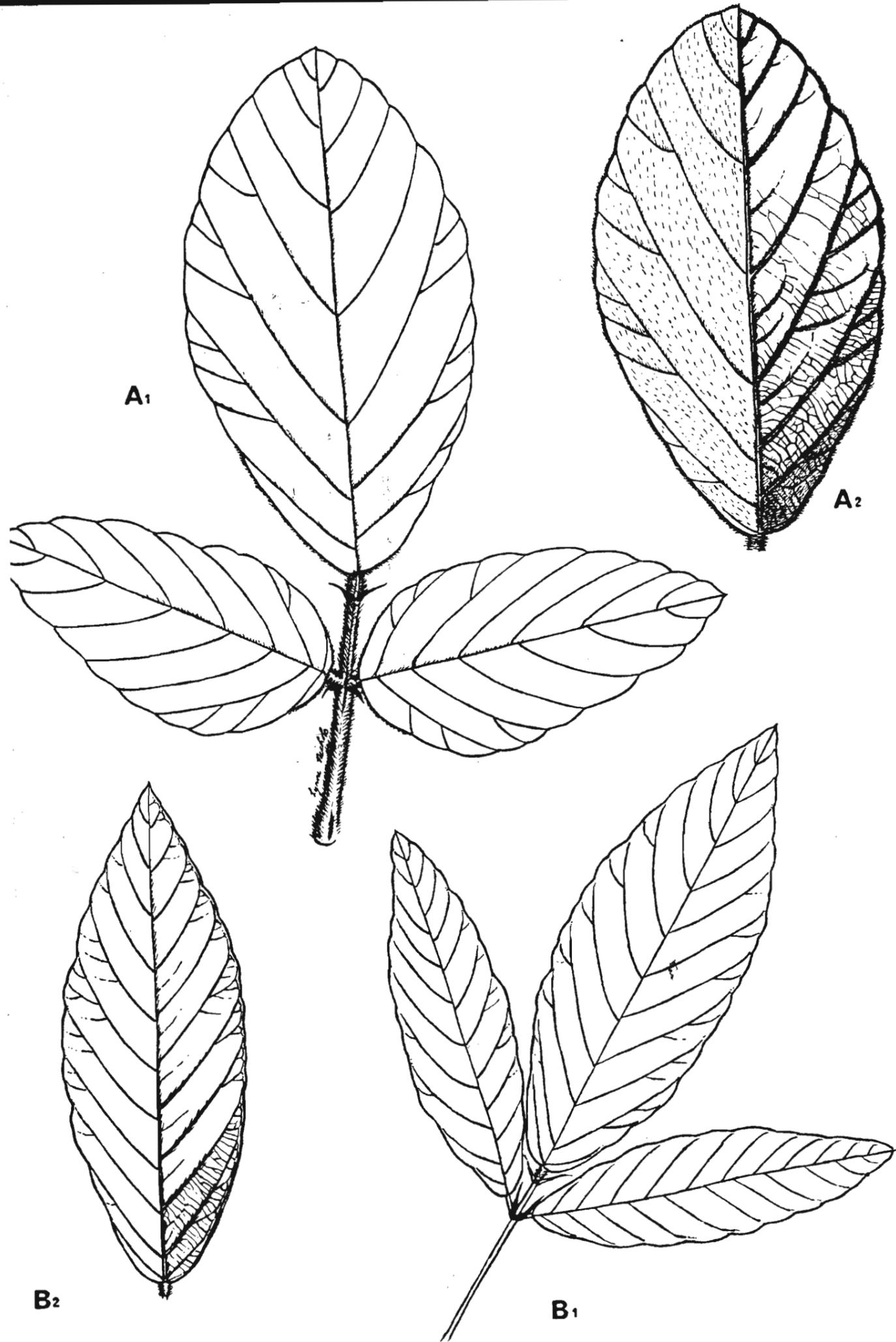
FIGURE 2

Leaf characteristics - Pseudarthria and Desmodium

Left half: adaxial surface;   Right half: abaxial surface

A1   Leaf of Pseudarthria hookeri   x 1

A2   Terminal leaflet of P. hookeri   x 1

B1   Leaf of Desmodium salicifolium   x 1

B2   Terminal leaflet of D. salicifolium   x 1
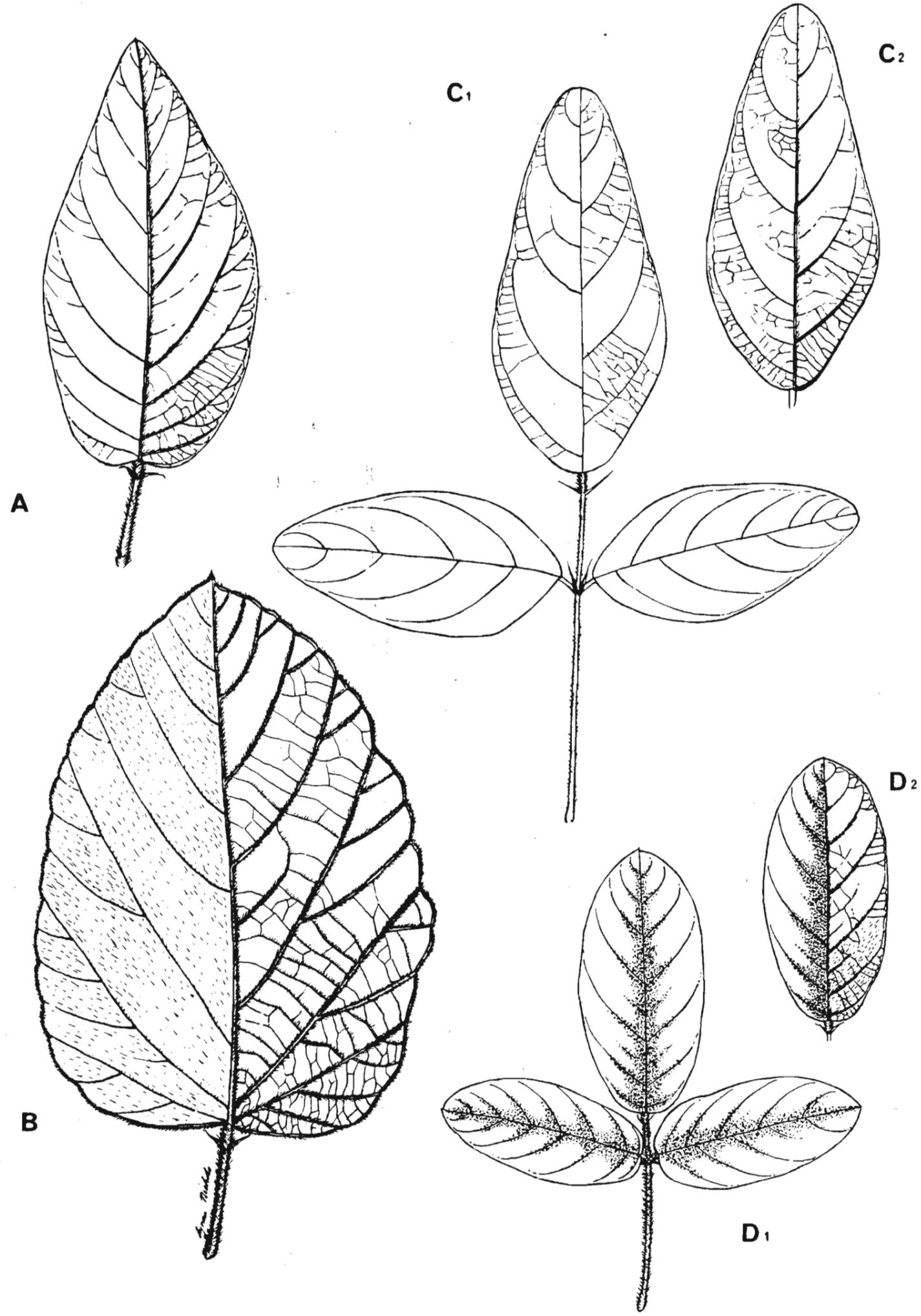
FIGURE 3

Leaf characteristics - Desmodium

Left half: adaxial surface: Right half: abaxial surface

A.	D. gangeticum		x 1
B.	D. velutinum		x 1
C1	D. tortuosum	leaf	x 1
C2	D. tortuosum	terminal leaflet	x 1
D1	D. incanum	leaf; note discolouration along midribs	x 1
D2	D. incanum	terminal leaflet	x 1
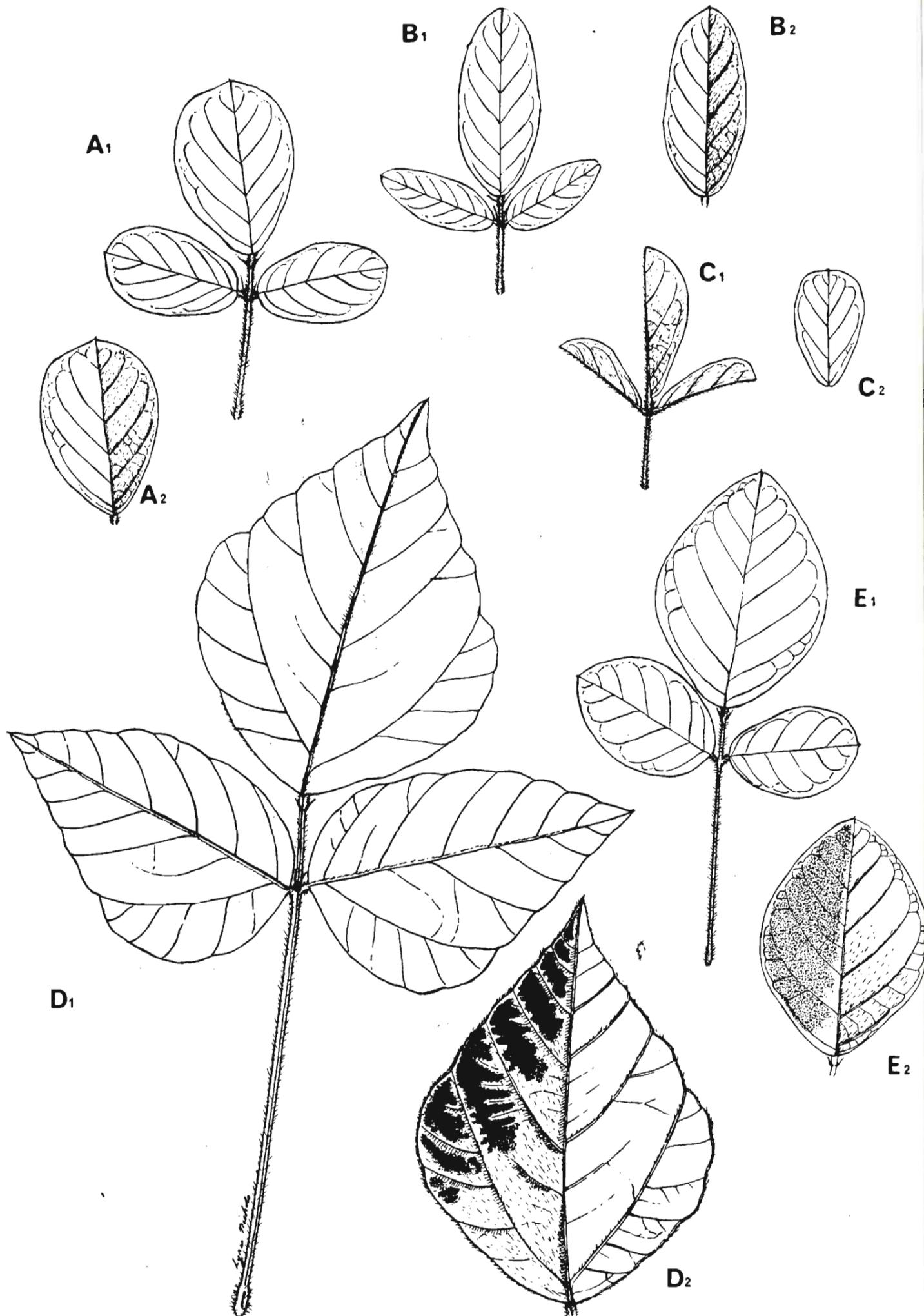
FIGURE 4

Leaf characteristics - Desmodium

Left half: adaxial surface;   Right half: abaxial surface

A1	D. setigerum	leaf	x 1
A2	D. setigerum	terminal leaflet	x 1
B1	D. barbatum	leaf	x 1
B2	D. barbatum	terminal leaflet	x 1
C1	D. dregeanum	leaf, note conduplicate leaflets	x 1
C2	D. dregeanum	terminal leaflet	x 1
D1	D. repandum	leaf	x 1
D2	D. repandum	terminal leaflet, note silvery dis-colouration along midrib and up lateral veins of adaxial surface	x 1
E1	D. adscendens	leaf	x 1
E2	D. adscendens	terminal leaflet, note silvery dis-colouration along midrib and around perimeter on adaxial surface	x 1

and in Alysicarpus and Lespedeza stems tend to become herbaceous and decumbent to ascending. The stems of Alysicarpus are characteristic in being slender, flexuous, conspicuously fine grooved and with many internodes.

This trend to a herbaceous habit is seen in those species which are indicated all the way through the morphological comparisons of this chapter as being more derived.

3.3.3. Leaves

Pinnately 3(5-7) or 1-foliolate; petioles sulcate and conspicuously grooved, terminal leaflet with rachide narrower but similar to petiole; pulvinate, petiolulate; stipules conspicuous, persistent, striate, scariose, often oblique, generally ovate - lanceolate to attenuate with ciliate margin; leaflets variable but laterals smaller than terminal; stipellate (except Lespedeza), one stipel subtending each lateral leaflet and two the terminal one, smaller but similar to stipules, subulate to linear, persistent.

Desmodium (1) - 3 foliolate (tending to be mixed 1 - 3 foliolate in D. barbatum and 1 - foliolate only in D. velutinum and D. gangeticum); stipules 0,3 - 16mm long but up to 25mm in D. repandum, 1,0 - 4,0mm wide but up to 6,0 - 7,0mm in D. repandum, D. tortuosum and D. salicifolium, usually auriculate at the base abruptly narrowing to a long caudate tip in D. velutinum; minutely puberulent to pilose abaxially; free or rarely partially connate along leaf-opposed margins when young (e.g. in D. incanum where stipules are erect and stem clasping, or in D. tortuosum with stipules spreading and occasionally forming a collar around the stem); erect or partially reflexed e.g. in D. repandum, D. tortuosum and D. salicifolium; leaflets variously shaped (figs.3 & 4) and very variable in size; generally larger in the section Heteroloma, 1,0 - 17,0cm long, 1,0 - 10cm wide and of different shape to the section Nicolsonia where leaflets are 0,5 - 6,0cm long, 0,3 - 3,5cm wide; vesture variable but characteristically silky pilose in D. dregeanum and D. barbatum and fulvo-velutinous in D. velutinum (not dissimilar to P. hookeri); thinly chartaceous in D. adscendens, D. setigerum and D. repandum to coriaceous in D. incanum, D. gangeticum and D. salicifolium to soft and velvety in D. velutinum; margins sometimes revolute, repand or sinuate in D. repandum, D. salicifolium and D. velutinum otherwise entire, often with appressed cilia; venation often prominent below and veins pallid in

D. tortuosum and D. velutinum; varying from dark green shiny above as in D. incanum, D. salicifolium and D. gangeticum to a paler dull green in the section Nicolsonia; D. incanum with a characteristic light discoloured streak along the midrib, and a silvery discolouration often around the perimeter of the adaxial surface in D. adscendens as well as up the midrib and along major lateral veins in D. repandum. This latter phenomenon is noticed in many shade-growing legumes e.g. Glycine wightii. Reversibly conduplicate leaves occur in D. dregeanum and D. barbatum; lateral leaflets smaller than the terminal leaflet and often oblique except in section Nicolsonia where lateral leaflets are smaller but symmetrical; stipels generally 0,5 - 6,0mm long and to 1,0mm wide except in D. salicifolium which are 4,0 - 8,5mm long and up to 2,0mm wide.

Pseudarthria 3 (abnormally 5 - 7) foliolate; stipules 5.0 - 12,5mm long and 1,5 - 5,0mm wide; free, sharply re-curved, densely tomentose abaxially, dark brown glabrous adaxially; leaflets characteristic (fig. 2) 2,5 - 16,5cm long, 1,3 - 10cm wide, thick, soft velvety, adaxially rugose appearing viscid scabrous due to dense uncinate puberulence and sparsely pilose, abaxially scattered pilose and densely grey-white tomentose; venation prominent beneath, pallid; margin repand to sinuate; stipels 0,5 - 70mm long, 0,2 - 1,0mm wide, lanceolate.

Alysicarpus 1 - foliolate (very rarely 3 - foliolate only in A. rugosus); petiole often winged; stipules 5,0 - 15mm long and 1,5 - 2,6mm wide in A. vaginalis and A. glumaceus but up to 30mm long and 4,2mm wide in A. zeyheri and A. rugosus; lanceolate - acuminate, oblique and extended at the base along the leaf-opposed margins and fused for a short distance at the base at least when young, often appearing free; generally glabrescent to minutely puberulent abaxially, margin ciliate (sparsely in A. vaginalis); leaflets variable in size and shape (typical shapes in fig. 1) 5,0-50mm long in A. vaginalis, 8,0 - 80mm in A. zeyheri, 6,0 - 110mm in A. rugosus and 6,0 - 125mm in A. glumaceus, usually 2,0 - 20mm wide although only to 11mm in A. glumaceus; upper leaf surfaces glabrous to minutely puberulent and isolated pilose, lower surfaces moderately puberulent and often scattered strigose; subcoriaceous to coriaceous; stipels 0,7 - 1,5mm long and to 0,2mm wide but 1,6 - 2,4mm long and to 0,6mm wide in A. zeyheri. Leaves usually with prominent venation; margin entire,

sometimes/.....

PLATE 1

Abaxial leaf surfaces
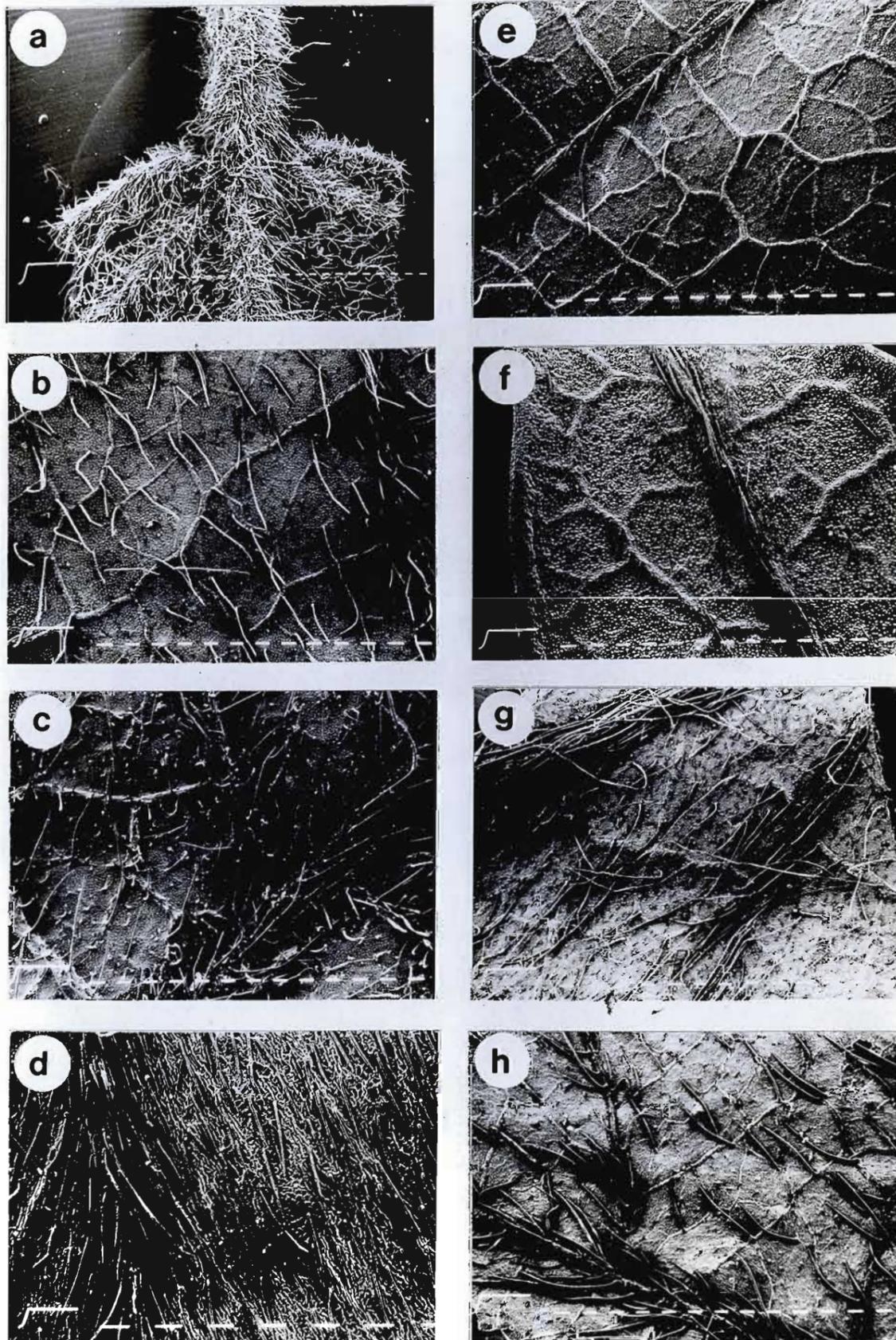
a)	P. hookeri	x 20,	tomentose vesture
b)	D. adscendens	x40,	tertiary percurrent vein off secondary vein at extreme right and quaternary branching
c)	D. velutinum	x40,	primary, secondary, tertiary and quaternary venation
d)	L. cuneata	x80,	sericeous vesture
e)	D. gangeticum	x40,	forked tertiary percurrent veins
f)	A. rugosus	x40,	weakly percurrent tertiary veins
g)	D. dregeanum	x40,	long silky-pilose vesture
h)	D. repandum	x40,	primary, secondary and simple tertiary percurrent veins

PLATE 2

Abaxial leaf surface detail
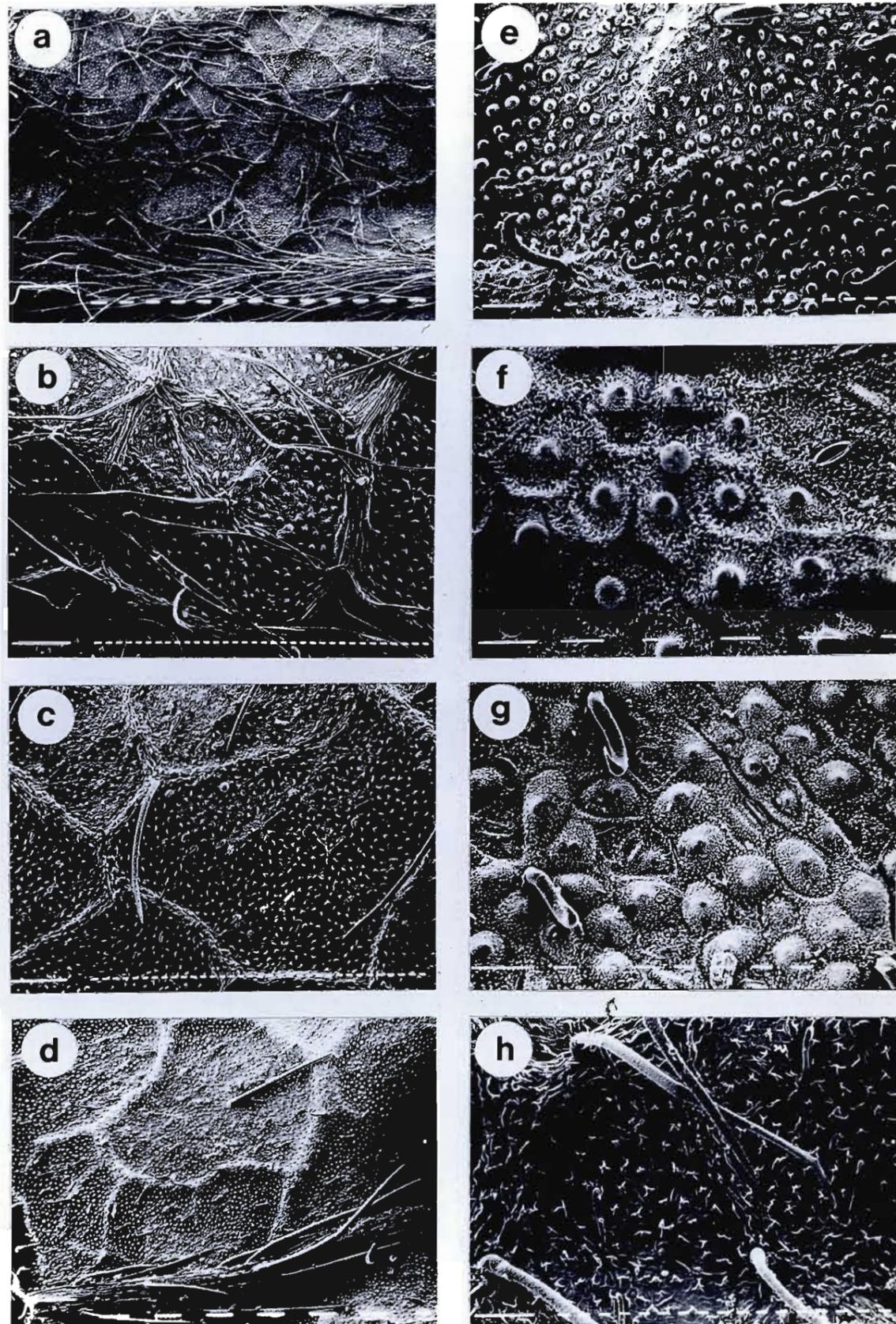
a) D. barbatum   x40,   vesture, to be compared
                                 with D. dregeanum Plate
                                 1 fig. g

b) D. barbatum   x160,   areole, bounded by tertiary
                                 veins bottom and right,
                                 quaternary veins top and
                                 left

c) D. gangeticum   x160,   leaf detail

d) A. vaginalis   x80,   areole

e) A. vaginalis   x320,   domes; pentagonal to hexagonal
                                 cell shape

f) A. zeyheri   x1250,   domes and cell shape with
                                 wax ridges; prominent anti-
                                 clinal walls; flat periclinal
                                 walls

g) A. rugosus   x640,   regular cell shape with
                                 prominent anticlinal walls;
                                 convex periclinal walls
                                 with apical domes; sunken
                                 channel between anticlinal
                                 walls and periclinal convexity

h) D. adscendens   x320,   irregular cell shape; promin-
                                 ent anticlinal walls; irregu-
                                 lar branched domes

PLATE 3

Adaxial leaf surfaces
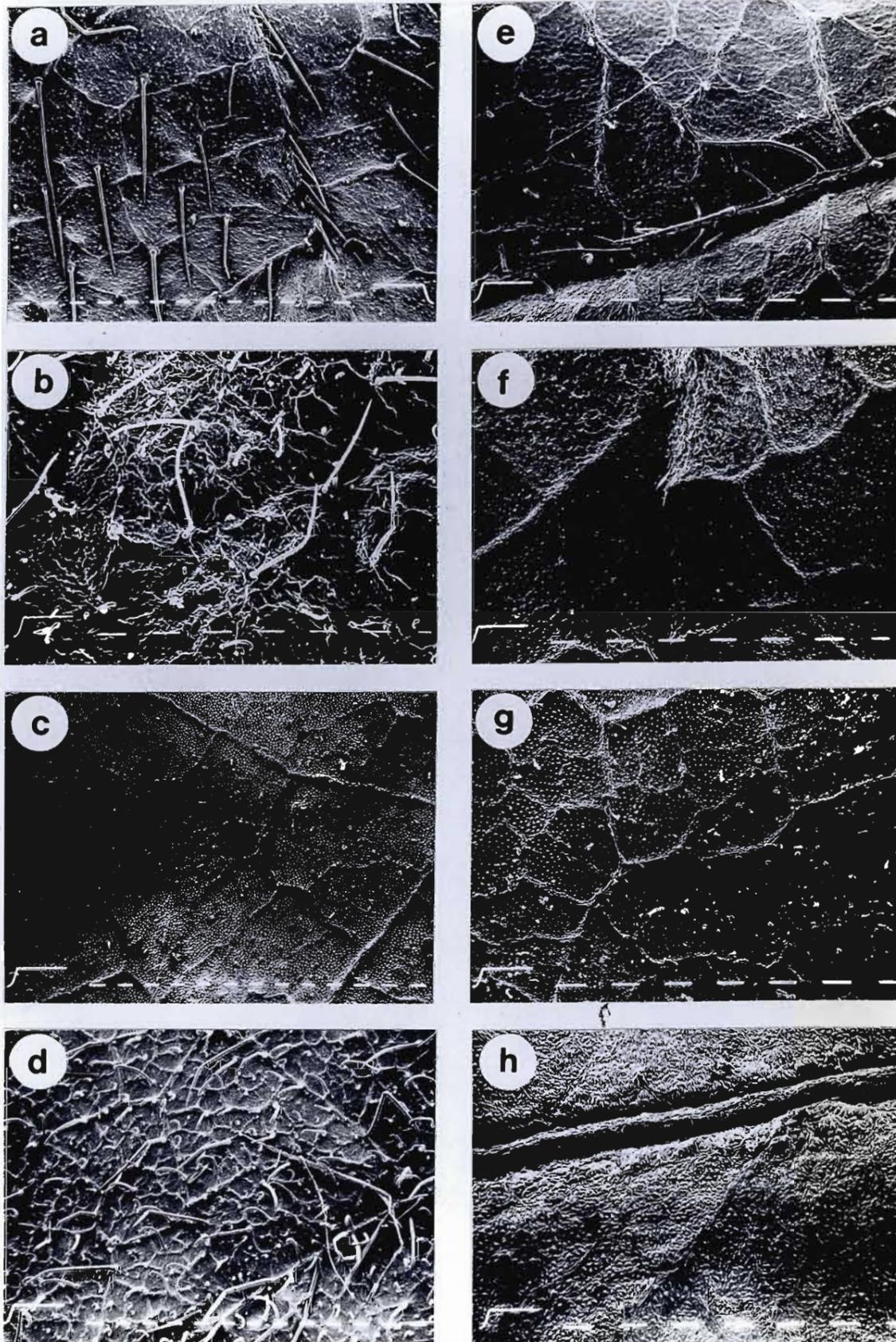
a)	D. repandum	x40,	strigose vesture
b)	P. hookeri	x80,	sunken tertiary and quaternary venation
c)	D. adscendens	x40,	tertiary and quaternary venation
d)	D. velutinum	x40,	quinternary venation prominent
e)	D. incanum	x80,	prominent midrib and indistinct epidermal cells
f)	A. vaginalis	x80,	sunken midrib and distinct epidermal cells
g)	D. gangeticum	x80,	tertiary and quaternary venation and epidermal cell detail
h)	D. barbatum	x80,	prominent midrib, tertiary and quaternary venation and visible areoles

sometimes revolute and with appressed cilia, A. rugosus often with a characteristic paler streak along the midrib adiaxally.

Lespedeza 3-foliolate; stipules 0,4 - 7,0mm long, triangular to subulate, abaxially scattered strigose leaflets 0,5 - 32mm long, 1,5 - 10,5mm wide, narrowly obovate to cuneiform, glabrous or isolated strigose above, densely strigose to subsericeous below; dull green above with lateral veins parallel, conduplicate, lateral leaflets oblique; stipels 0.

3.3.3.1. Leaf surfaces

Venation (terminology from Hickey, 1979): Pinnate, craspedodromus in P. hookeri, D. repandum and D. velutinum (figs.2,3,4), mixed craspedodromus in D. salicifolium (fig. 2), eucamptodromus in D. incanum, D. tortuosum, D. gangeticum, Alysicarpus and Lespedeza, brochidodromus at least distally in the section Nicolsonia of Desmodium (fig. 4). Distinct marginal vein around the entire leaf, visible abaxially; primary midrib straight or very slightly curved, unbranched; secondary veins diverging at 40 - 60° (moderate), uniform, curving upwards, occasionally branched distally; tertiary venation, percurrent (termed scalariform in Ohashi et al, 1981) in Desmodiinae and reticulate in Lespedezinae. In Desmodiinae percurrent veins (Plate 1 fig.f) often convex, oblique. Higher vein orders of the 4th degree are distinct usually on both surfaces (Plate 1 fig. b; Plate 3 fig. g). 5th degree orders are rare but present in D. velutinum (Plate 3 fig. d). Quaternary venation more or less orthogonal reticulate, often the smallest veins bounding well developed areoles (except when quinternary veins present). Areolar shape is generally irregular pentagonal and medium sized being between 1 - 0,3mm. (Plate 2 fig.b,d; Plate 4 fig.a)

Epidermal cells. Abaxial; generally irregular in shape in Desmodium (Plate 2 fig. h), becoming more distinctly pentagonal or hexagonal in Alysicarpus (Plate 2 fig. f); isodiametric to slightly oblong. Anticlinal walls straight or often curved in Desmodium, predominantly straight in Alysicarpus, generally slightly prominent (Plate 4 fig. d), occasionally indistinct (Plate 4 fig. e). Adaxial; cell shape trends are similar to the abaxial cells except in the section Nicolsonia. Anticlinal walls are markedly undulate, being prominent in D. adscendens and D. setigerum (Plate 5 figs. a and b) but sunken in D. barbatum and D. dregeanum/....

Adaxial leaf surface detail
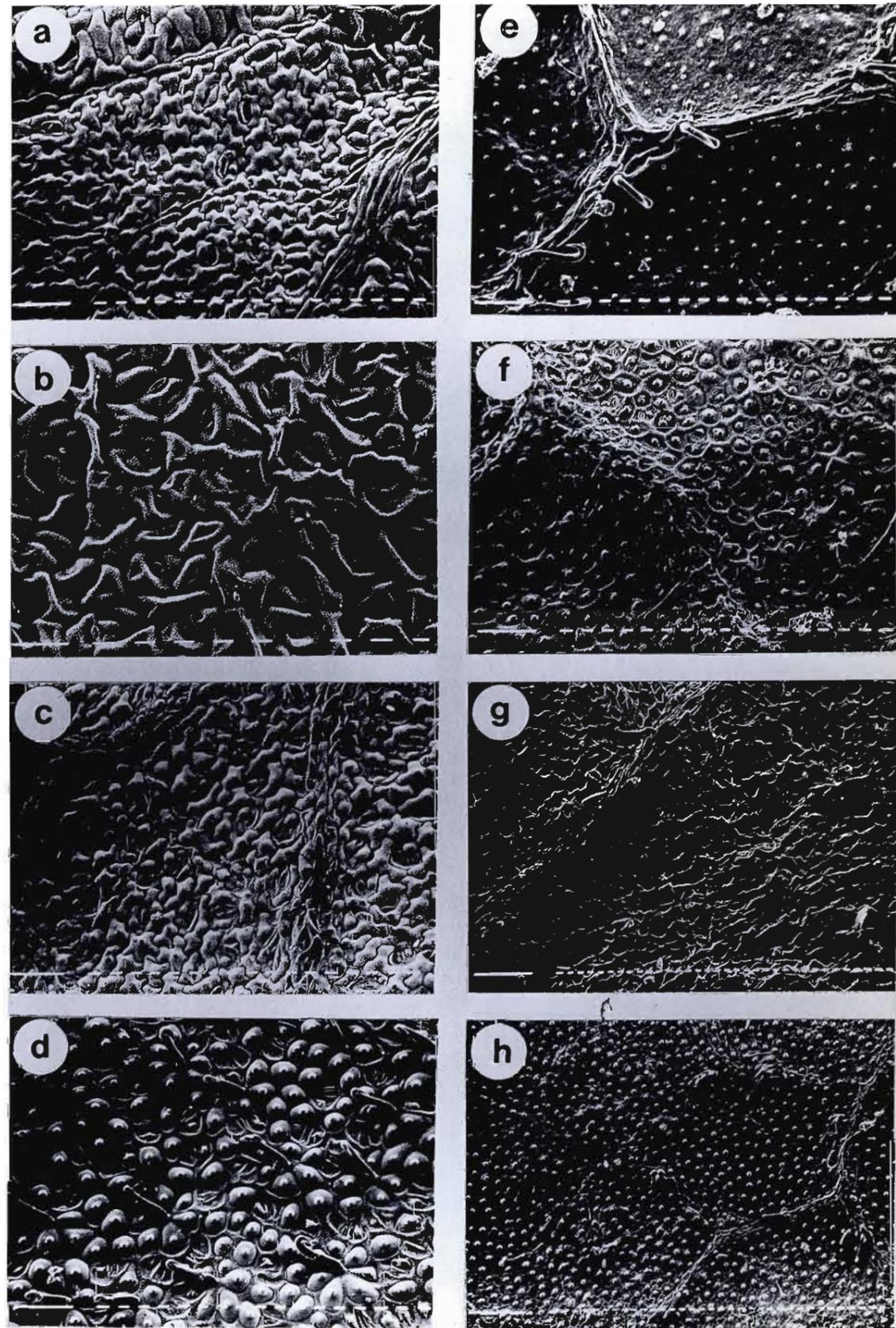
a) *D. barbatum* x320, markedly undulate, sunken anticlinal walls; convex periclinal walls with apical dome features; stomata with very unequal subsidiary cells

b) *L. cuneata* x640, anticlinal walls sunken, stomata surrounded by sunken channel (anticlinal walls of hidden guard cells) and flanked by two unequal convex subsidiary cells (paracytic)

c) *D. dregeanum* x320, note similarity to *D. barbatum* (fig. a)

d) *A. rugosus* x320, clear regular cell shapes with marked differences visible between ordinary epidermal cells and subsidiary cells; note clear ridges parallel to and flanking stomata, representing anticlinal walls of hidden guard cells; also regular uncinate trichomes giving puberulent vesture

e) *D. gangeticum* x80, areolar detail; indistinct cell shape; regular dome formations

f) *A. vaginalis* x320, prominent anticlinal cell walls and regular cell shape and regular domes; subsidiary cells around stomata again distinct in having reduced domes

g) *D. salicifolium* x160, glabrous surface with irregular cell shape but distinct prominent anticlinal walls; scattered stomata

h) *D. adscendens* x160, markedly undulate, prominent (as opposed to sunken, figs. a and c) anticlinal walls, with regular domes

PLATE 5

Leaf epidermal cells

a to d: adaxial surface; e to h : abaxial surface
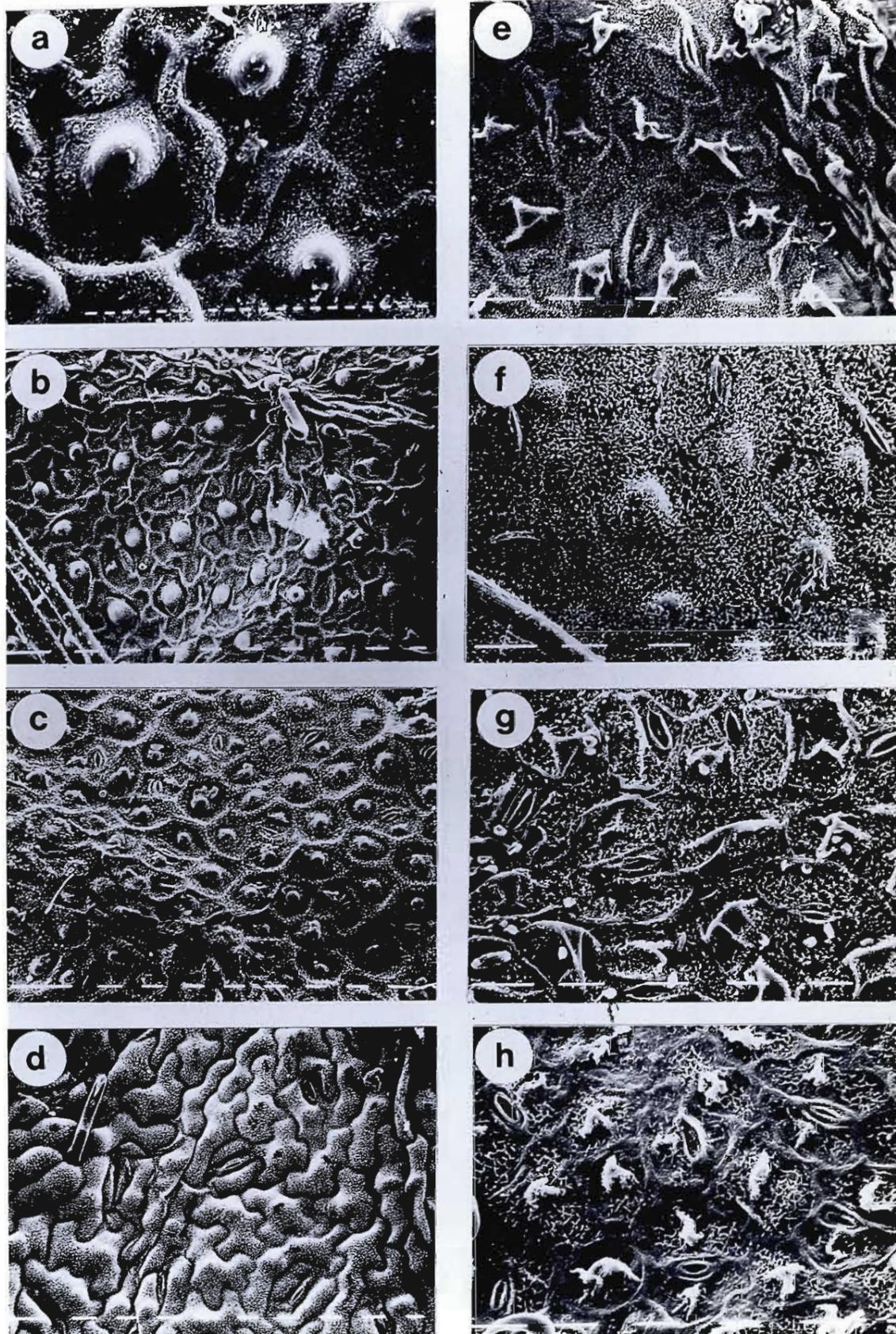
a) D. adscendens   x2500, prominent anticlinal wall detail

b) D. setigerum   x640,   note similarity to D. adscendens

c) A. vaginalis   x640,   cell detail

d) D. barbatum   x640,   note two often unequal subsidiary
                             cells and sunken lines flanking
                             stomata, representing anticlinal
                             walls of hidden guard cells

e) D. adscendens   x1250, irregular cell shape outlined
                             by slightly prominent anticlinal
                             walls; irregular branched domes;
                             compare with adaxial surface
                             (fig. a)

f) D. barbatum   x1250, cell outline indistinct but domes
                             present; compare with adaxial
                             surface (fig. d)

g) D. salicifolium x1250, subsidiary cells clearly visible
                             on either side of the stomata,
                             often unequal in size; note
                             cell in the middle with a simple
                             ridge, becoming branched and
                             domed in other cells.

h) D. gangeticum   x1250, subsidiary cells again visible
                             on either side of stomata; wax
                             deposits different to other species
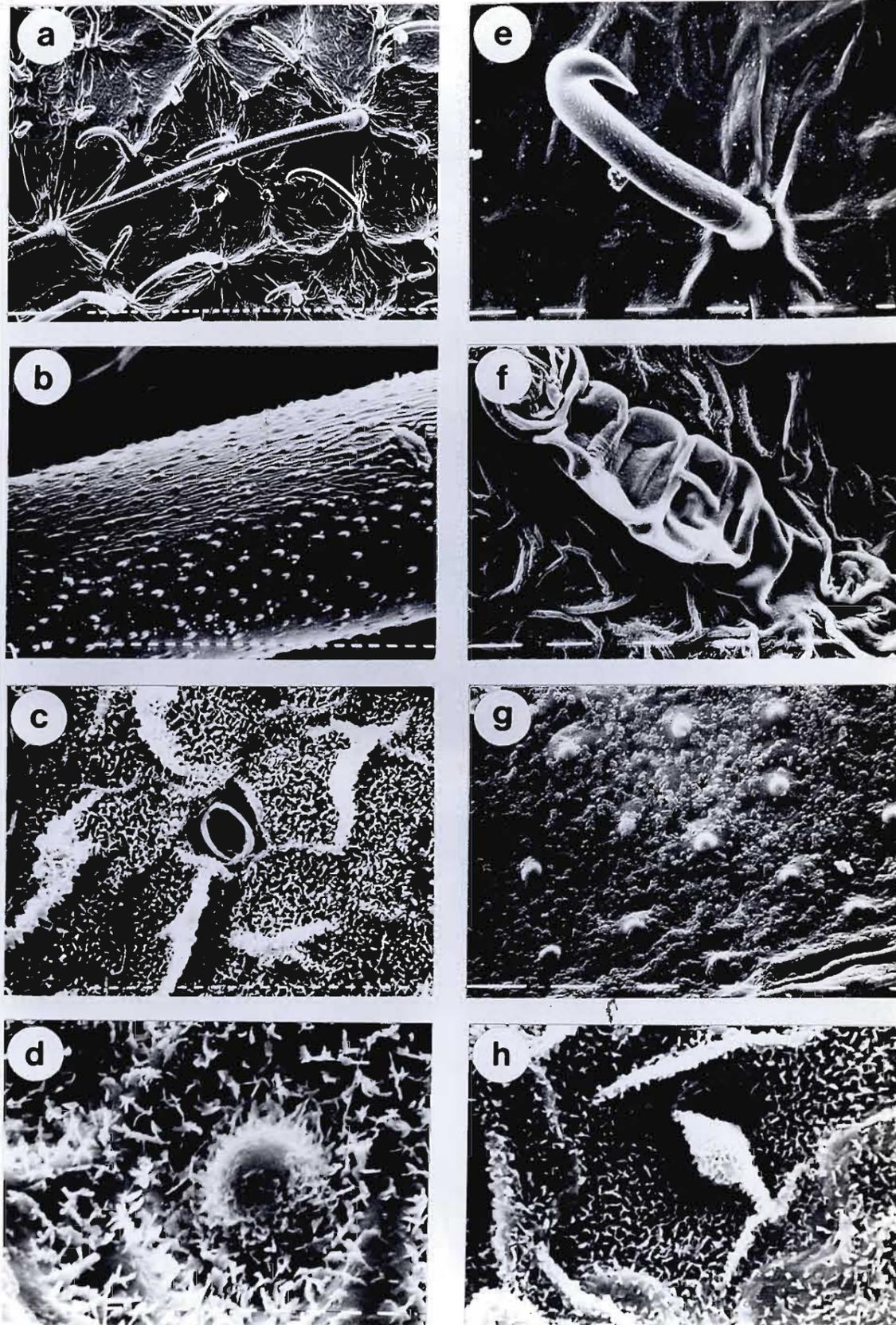
PLATE 6

Trichomes and domes

a) D. velutinum   x160,   long hair detail

b) D. velutinum   x2500,   warty sculpturing on long hairs

c) D. gangeticum x2500,   stoma detail showing presence of the
two guard cells in the stomatal cavity,
the prominent outer stomatal rim and
the two flanking ridges representing
the anticlinal walls of the partially
visible guard cells

d) A. zeyheri   x5000,   sunken outer periclinal wall; regular
domes and short, branched ridges of
wax

e) D. gangeticum x1250,   uncinate hair detail indicating base
cell and unicellular trichome

f) A. glumaceous x1250,   uniseriate multicellular glandular
trichome detail

g) D. gangeticum x1250,   crustose flake deposits of wax on
adaxial leaf surface

h) D. repandum   x5000,   detail of irregular dome and wax
features

and D. dregeanum (Plate 4 figs. a and c), resembling pieces of a jigsaw puzzle. In the section Heteroloma anticlinal walls are similar to the abaxial surface being slightly raised (Plate 4 fig. g) or indistinct (Plate 4 fig. e). Anticlinal walls in Alysicarpus appear more strictly pentagonal or hexagonal. In Lespedeza the anticlinal walls are sunken but cell outline is indistinct (Plate 4 fig. b).

Stomata. Present abaxially only, in P. hookeri, D. gangeticum, D. repandum, D. adscendens, D. setigerum and D. velutinum but present both abaxially and adaxially in D. salicifolium, D. barbatum, D. dregeanum, Alysicarpus and Lespedeza. Using the terminology of Wilkinson (1979), stomata are broadly elliptical (L:W ratio 1 - 1.5:1) e.g. Lespedeza, to narrowly elliptical (L:W ratio 1.5 - 2:1). Size rather uniform 12 - 22 m long, 5 - 8 m wide in Desmodium and Alysicarpus; usually with a slightly raised outer stomatal rim which is highly cutinised and conspicuous (Plate 6 fig. c). Flanking the outer stomatal rim is a pair of conspicuous folds occurring most frequently as ridges (Plate 4 fig.d, Plate 5 fig. h) but sometimes as furrows (Plate 4 fig. b, Plate 5 fig. d). The folds represent the anticlinal walls of the guard cells and part of these may be viewed through the open stoma (Plate 6 fig.c). Subsidiary cells are paracytic (Plate 4 fig. d, Plate 5 fig. d) usually two, variably shaped, and parallel to the long axis of the stoma and guard cells. Frequently cells are very unequal in size (Plate 4 fig. a).

Cuticle. Both surfaces non striate, occasional ridges on adaxial leaf surfaces appear to be artifacts due to drying shrinkage (Plate 4 fig. b). Non glandular trichomes; on all surfaces, of three major types; long filiform hairs tapering to a point, relatively thin walled, collapsed and variously kinked (Plate 10 fig. h), giving the tomentose or sericeous appearance to P. hookeri, D. dregeanum and D. barbatum (Plate 1 fig. g, Plate 2 fig. a); long to short hairs tapering to a point but turgid and rigid (Plate 6 fig. a), either ascending or appressed, giving the pilose or strigose appearance respectively to leaves (Plate 1 figs. b,c,d,e,f and h, Plate 3 fig. a), occurring also along veins, and as cilia on calyces (Plate 7 fig. f); short to longish uncinate hairs (Plate 6 fig. e), often the most prevalent trichome giving the characteristic puberulence to Desmodieae surfaces (Plate 1 fig. g, Plate 4 fig. d), not present in Lespedeza (Plate 1 fig. d). Frequently uncinate hairs of both sizes can be mixed
(Plate 10/.....

FIGURE 5

Uniseriate, multicellular gland

Plate 10 fig. f). All three hair types can be warty sculptured (Plate 6 fig. b) and uncinate hairs are particularly dense on pedicels and calyces (Plate 7 figs. c,d,g,h) and fruit surfaces (Plates 8,9 and 10). <u>Glandular trichomes</u>; simple uniseriate, multicellular, erect glands (see fig. 5) with uppermost cell globose, (Plate 6 fig. f) collapsed view. Occurring most frequently on pedicels and calyces (Plate 7 figs. c,d,h), fruit surfaces (Plate 10 fig. b) and sometimes on leaf surfaces.

<u>Papillae</u> Various domes occur as projections of the outer periclinal wall of individual cells and such papillae are not known to comprise more than one cell (Wilkinson, 1979). There appears to be a trend in the Desmodieae towards development of a single, centrally located dome in each cell of leaf surfaces. In Plate 5 fig. g the trend is initiated with a central ridge in the middle cell on the photograph. To the right of this cell and next to it can be seen a number of branches on the ridge. Below these cells are further developments where the centre of the ridge complex has been raised into a dome. Such domes are very irregular in shape in most <u>Desmodium</u> spp. and <u>Pseudarthria</u> (Plate 2 figs. c,h, Plate 5 figs. e,g,h, Plate 6 fig. h) but in the section <u>Nicolsonia</u> there is an indication that domes are becoming more symmetrical (compare Plate 2 fig. b, Plate 5 figs. a and b). Also in <u>D. gangeticum</u> (Plate 6 fig. g). In <u>Alysicarpus</u> domes are regular and symmetrical (Plate 5 fig. c). Another feature of comparison is the relationship of the periclinal wall to the dome. In <u>A. rugosus</u> (Plate 4 fig. d), the periclinal wall is convex with the typical dome feature at the central apex. It is noted that although the anticlinal walls are raised a sunken channel is found between the central feature and the anticlinal walls (Plate 2 fig. g). A very noticeable parallel occurs between <u>A. rugosus</u>, and <u>D. barbatum</u> and <u>D. dregeanum</u> (Plate 4 figs. a,c). The latter pair have sunken anticlinal walls but the entire outer periclinal walls are also convex with the apical dome feature visible. The periclinal wall may be slightly sunken as in <u>A. vaginalis</u> (Plate 5 fig. c) or <u>A. zeyheri</u> (Plate 6 fig. d). Subsidiary cells are often highlighted because domes are either reduced in size or absent.

<u>Wax</u> Wax features are common on Desmodieae leaves. Frequently wax occurs as short branched ridges and they only begin to appear under X300 magnification with the S.E.M. They densely clothe both surfaces (Plate 5 figs. a and g) and are seen in detail in Plate 6 fig. d.
<div align="right"><u>D. gangeticum</u>/....</div>

D. gangeticum does not have the usual branched ridges of wax but rather crustose particles scattered over the surface (Plate 6 fig. g).

It is understood that the above comparison of S.E.M. characters of Desmodieae leaves is very limited because no transverse sections or cleared epidermal samples were made. Scanning work has been used purely as a tool to provide additional taxonomic information.

3.3.4. Inflorescences

The basic inflorescence type of the Leguminosae is the polytelic synflorescence (Weberling, 1965). Here there is no terminal flower at the summit of the primary axis as in monotelic inflorescences, and hence the shoot apex remains indefinite after having developed a smaller or greater number of lateral flowers, the last of which often do not complete their development. The term florescence applies to the whole apical system composed of lateral flowers (Weberling, l.c.). Below the florescence terminating the main axis, there may be some branches which repeat the structure of the main stem by producing florescences themselves. These are co-florescences (Weberling, l.c.) and this entire system of florescences is called a synflorescence.

In the tribe Desmodieae this basic pattern is highly polymorphic and some extreme forms seem very different in appearance (Ohashi, 1973). In the part of the tribe under present study, all are characterised by a pseudoracemose inflorescence which is composed of a central axis bearing fascicles of flowers on the distal portion (Lackey, 1981). The origin of this form of inflorescence is seen (fig. 6) in terms of being derived by reduction from a panicle. Even on the pseudoraceme, fascicles may vary according to their degree of reduction (fig. 7) and this can provide useful taxonomic differences and show phylogenetic trends; i.e. the general trend of reduction supports other evidence that the section Nicolsonia of Desmodium is more derived than the section Heteroloma as is the genus Alysicarpus.

The typical pseudoraceme is generally elongate and spike-like with the length of the inflorescence rhachis varying from 5,0 - 30cm in most species of Desmodium, Pseudarthria and in Alysicarpus. In

D. dregeanum/.....

FIGURE 6

Detail of inflorescence reduction
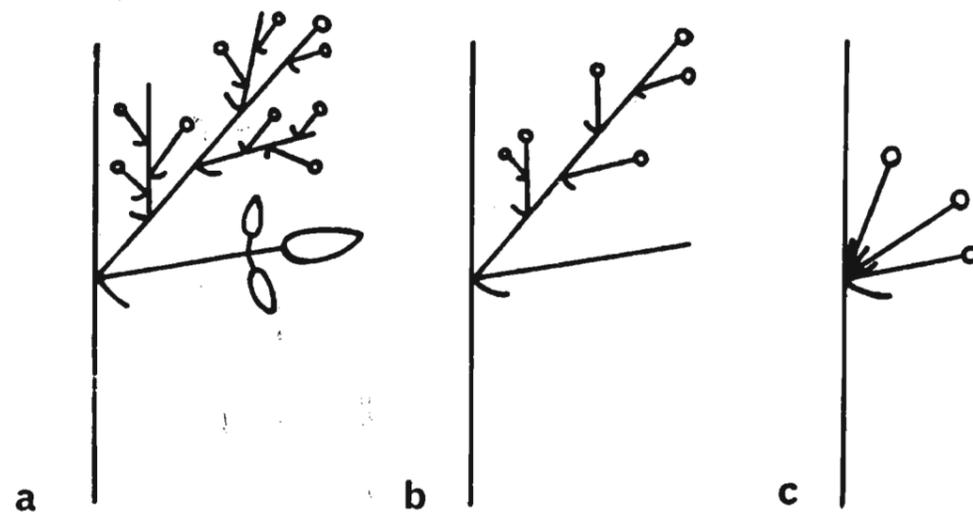
a) Hypothetical axillary paniculate ancestor

b) Reduction of the panicle side branches to eventual single flowers
    producing a raceme, and reduction of the subtending leaf. Both are
    seen in primitive members of the tribe in Asia (Ohashi, 1973)

c) Reduction of the raceme axis to fascicle, each pedicel subtended by
    a floral bract representing the remnants of secondary branches from
    the base of the panicle, and reduction of the subtending leaf to an
    inflorescence bract.

Inflorescence detail in Lespedeza
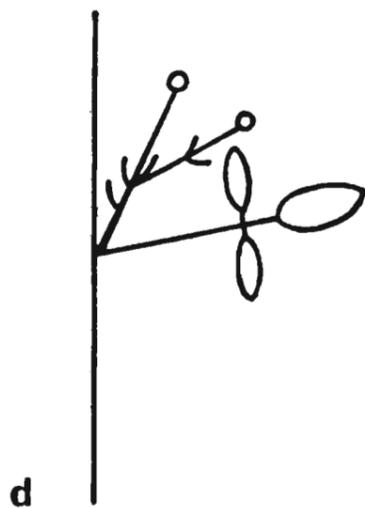
d) One, or more often two flowers appear on a short rhachis in the axils
    of leaves. This tight fascicle is subtended by an unusual arrangement
    of bracts. At the junction of the rhachis and pedicel of one flower
    there are three bracts close together although one is usually slight-
    ly lower than the others (possibly the inflorescence bract).
    Another two floral bracts occur somewhere on the lower half of the
    pedicel of the other flower. This axillary fascicle most probably
    represents an extremely reduced pseudoraceme.

D. dregeanum and D. barbatum however, the rhachis averages 1,0 - 4,0cm and pseudoracemes are densely capitate or shortly spicate. In Pseudarthria and section Heteroloma of Desmodium, the terminal pseudoracemes are often laxly branched appearing paniculate while in D. incanum, some of the section Nicolsonia and in Alysicarpus, pseudoracemes are unbranched. The degree of density or laxity of flowering fascicles also varies, with D. repandum, D. tortuosum, and D. setigerum and D. adscendens all having relatively few flowered very lax inflorescences with pedicels generally over 1cm long (fig. 9) while Pseudarthria, Alysicarpus and other species of Desmodium have dense spike-like inflorescences with pedicels most frequently well under 1,0cm long.

The period of flowering in a pseudoraceme is extended by the lower flowers opening first, followed by others at daily intervals as they open progressively upwards along the rhachis. Flowering time can also be prolonged in those species which have buds present between the outer two flowers in a fascicle. These have been noted to elongate and flower sometime after the first two have completed flowering.

Inflorescences are either terminal at the ends of branches; axillary and developed to varying degrees along the length of the branch; or leaf-opposed where growth has continued past the inflorescence by the new stem growing sympodially in the axil of the leaf immediately below the inflorescence. As the stem develops the inflorescence now appears to lie opposite the leaf. This latter type is found in Alysicarpus, again suggesting it is a more derived type. All or any of these may be observed in one species.

Finally it is worth noting that inflorescence contraction from panicle to pseudoraceme is part of a complex series of reduction and secondary aggregation of inflorescences that can occur in Papilionoideae, and because of this range of possibilities, inflorescence structure tends to be very labile in the subfamily. In the Genisteae, Polhill (1976) traces the following development, "The flowers are most often in terminal racemes. These tend to become leaf-opposed as growth continues, but they are often contracted to varying degrees, sometimes just to heads or reduced to single flowers. The inflorescences are quite often borne on short lateral shoots which may bear leaves like those of the main branches or reduced to varying degrees. Axillary

FIGURE 7

Detail of fascicle reduction
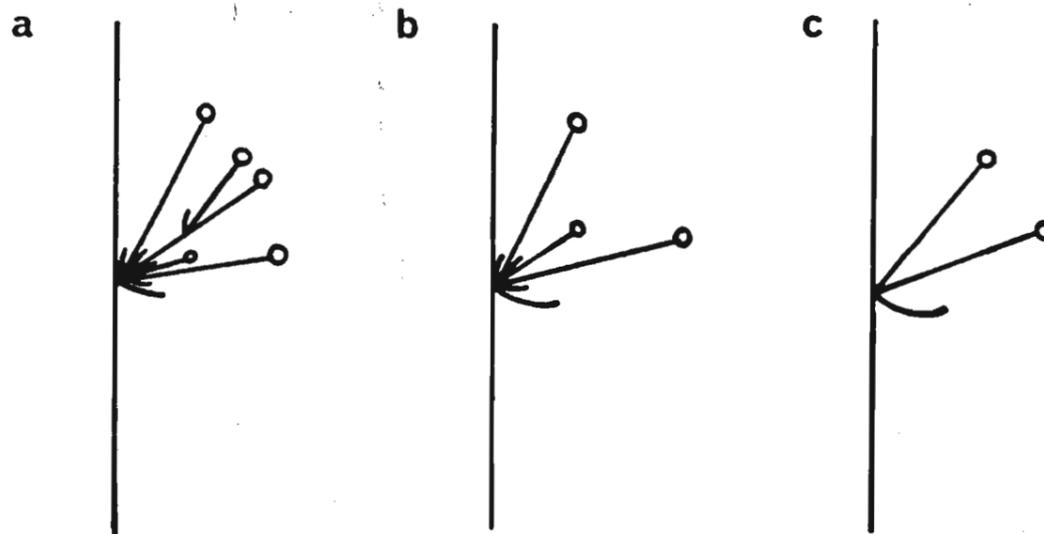
a) Fascicles of 3 to 5 pedicels - a median one remaining a bud. Rarely
    one pedicel may be seen as a branch of another in D. repandum show-
    ing incomplete reduction of the raceme to the fascicle. Floral bracts
    subtend each pedicel base including the bud.

b) Fascicles of 2 pedicels enclosing a median bud each subtended by a
    floral bract at the base. The floral bract is inserted slightly
    higher in the median bud than the flanking pedicels; at the junction
    of the rachilla of the reduced raceme and the minute pedicel of the
    median bud. These median buds often elongate and produce a flower
    some time after the outer two which mature together. This occurs
    widely in the section Heteroloma and in P. hookeri.

c) Fascicles of 2 pedicels with the loss of the median bud (often re-
    duced to a tuft of hairs) and the loss of floral bracts. In the
    section Nicolsonia both these trends are apparent although traces of
    both are still present in differing proportions in some species. In
    Alysicarpus, floral bracts are retained except occasionally in A.
    rugosus.

inflorescences seem generally to originate in this way and in some genera where this occurs the morphological sequence of leaf reduction and loss can be traced in different related species .... This sequence is often followed by secondary aggregation of the axillary inflorescences at the ends of the branches and if the subtending leaves then become suppressed, terminal leafless panicles or pseudoracemes are obtained."

3.3.5. Bracts

Inflorescence bracts are generally glumaceous, striate and early caducous, averaging 4,0 - 10,0mm long in Alysicarpus where they are trullate to rhomboid in shape. In Desmodium they average 1,5 - 7,0mm long being generally ovate-lanceolate and attenuate although often cochleariform in section Nicolsonia. Floral bracts when present average 0,5-3,0mm in length although A. rugosus and A. zeyheri can have floral bracts to 8,0mm long. Bracteoles from 0,5 - 1,5mm long are seen occasionally in D. velutinum, D. setigerum and D. incanum but are generally present in P. hookeri and L. cuneata.

3.3.6. Flowers

Flowers of most Desmodieae average 6,0-9,5mm in size with D. repandum appreciably bigger, from 8,0 - 14,4mm in length. Flowers of D. tortuosum, D. gangeticum, D. setigerum and D. adscendens are smaller, averaging 4.5 - 6,0mm long. Flowers of Alysicarpus are orange, apricot, pink buff to magenta while those of Pseudarthria and Lespedeza are pink, and white with purple markings respectively. In Desmodium, D. repandum is strikingly different from other species in having bright red flowers. D. incanum is also different with uniformly mauve flowers. The rest of the species are pink with varying degrees of white and purple.

3.3.6.1. Calyx and pedicels

Pedicels are densely hairy, puberulent and glandular (Plate 7 figs. b.c.h). In Desmodium calyces are broadly campanulate or cupulate and scariose when dry. Teeth 5; 4 or 5 lobed, the upper two sepals mostly appearing nearly connate and bifid only for the upper 0,1 - 0,4mm. In D. repandum the upper sepals are bifid to 0,5mm and in the section Nicolsonia, D. adscendens to 0,5mm, D. setigerum from 0,7 - 0,9mm/.....
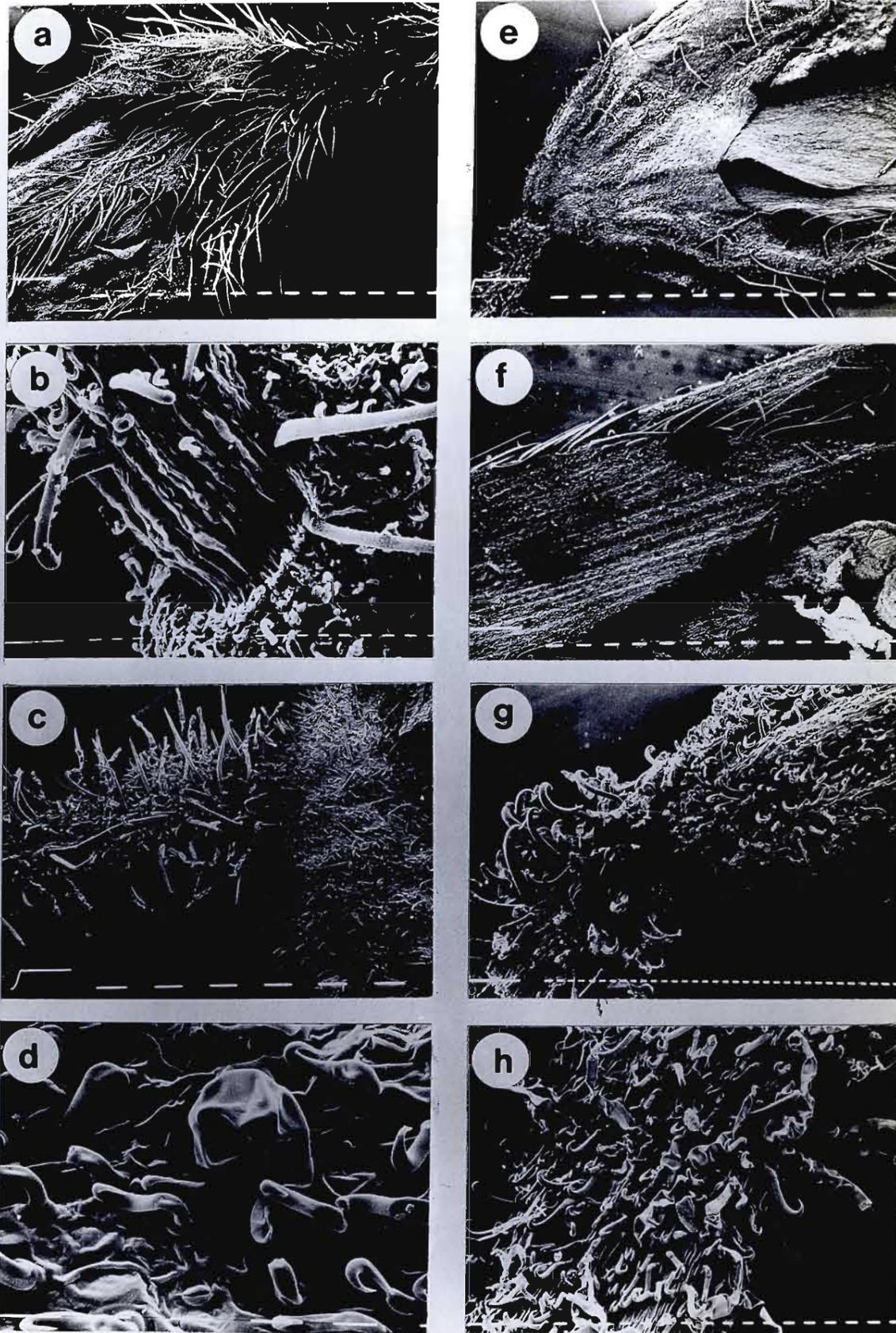
PLATE 7

Calyx and Pedicel detail

a) P. hookeri   x40,   calyx detail indicating the dense covering of trichomes and ciliate teeth

b) P. hookeri   x320,   calyx and pedicel

c) D. repandum   x80,   dense uncinate puberulence and gland on the pedicel

d) D. adscendens   x1250,   calyx tube

e) D. adscendens   x40,   calyx indicating triangular lateral tooth and longer beaked lower tooth

f) A. zeyheri   x40,   glumaceous, persistent calyx teeth with strongly ciliate margin

g) A. vaginalis   x160,   calyx & pedicel

h) D. adscendens   x320,   pedicel, glands and uncinate puberulence

0,7 - 0,9mm and in D. dregeanum and D. barbatum calyces are subequally 5-toothed, the upper pair of sepals bifid for over half their length i.e. from 2,0-3,0mm. The lower tooth is often longer (though not always) than the rest and narrowest, the upper widest and the two laterals usually shorter than both. In D. dregeanum and D. barbatum the lower tooth is often shorter and more narrowly attenuate. The calyx is 2,0-4,0mm long in most species with a tube length of 0,8-1,6mm. In D. repandum the calyx is larger, 4,0-5,4mm with a tube length of 1,4-2,6mm and in D. tortuosum the calyx is 3,5-4,8mm long. In D. dregeanum and D. barbatum calyces are (3,0) 4,0-6,0mm long. Teeth are variable in size from 1,0-2,4 (2,8)mm in most species, the lower tooth extending to 3,6mm long in D. tortuosum. In D. dregeanum and D. barbatum the teeth are from 2,5-4,2mm long. The tube is densely puberulent and glandular (Plate 7 fig.c). The teeth are triangular, ovate-lanceolate to narrow lanceolate and acuminate, puberulent and scattered pilose often more so on the teeth (Plate 7 fig. e) or densely silky pilose in D. dregeanum and D. barbatum.

Pseudarthria (Plate 7 fig.a) Teeth 5, appearing 4 lobed, the upper two sepals partially connate and bifid for upper 0.5-1,0mm. Lobes are subequal. The calyx is 5,0-5,7mm long with a tube length of 1,9-2,2mm. The teeth are 3,2-3,5mm long. The tube is densely puberulent and glandular hairy, the teeth lanceolate-attenuate and puberulent and scattered pilose.

In Alysicarpus calyces taper narrowly to the base, are glumaceous, persistent and striate. Teeth 5, appearing 4 lobed, often splayed out in flower, the upper two sepals partly connate and bifid for upper 1,0-2,0mm. The lobes are subequal, the lower often the longest and narrowest and slightly keeled for support, the upper widest and the laterals usually shorter than both. The calyx is 6,0-9,0mm long in A. zeyheri, A. rugosus and A. glumaceus but 4,5-6,5mm long in A. vaginalis; with a tube length of 1,0-2,5mm. Teeth are 2,5-4,0mm long and conspicuously narrow in A. vaginalis, 5,5-7,5mm long and wider in the others. The tube is narrow and densely puberulent and glandular haired (Plate 7 fig. g). Teeth are ovate-lanceolate to lanceolate and acuminate, densely puberulent and ciliate on the lower tooth. The margin is strongly ciliate (Plate 7 fig. f).

Lespedeza Teeth 5. The calyx is 4,5-5,1mm long with a tube length to 2,1mm./....

to 2,1mm. The teeth are 3,2-3,8mm long, lanceolate-attenuate with densely spreading appressed tapering hairs, striate and with ciliate margins.

3.3.6.2 Corolla

The morphology of petals is discussed in detail in chapter 4, in terms of their structural-functional role in pollination. A uniform trend is for the keel petals to be slightly longer than the wing petals.

3.3.6.3. Androecium

The staminal column of most species averages 3,5-5,5mm long with exceptions being, P. hookeri up to 7,0mm, A. zeyheri up to 7,5mm and D. repandum up to 12mm long. The vexillary stamen is most often free and slightly shorter than the staminal column but in A. zeyheri and A. rugosus the vexillary stamen may be partly coherent to the column for at least half its length. The same is true with D. repandum. In L. cuneata the vexillary stamen is at least 1,0mm longer than the staminal column. Filaments are mostly alternating in length although equal in L. cuneata and anthers are uniform and basifixed.

3.3.6.4 Gynoecium

The ovary of most species is 2,0-4,0mm long with section Nicolsonia of Desmodium at the shorter end, averaging between 2,0-2,7mm. Alysicarpus is also small, from 2,0-3,0mm long. L. cuneata has the shortest ovary, from 1,0-1,2mm long. This trend indicates a reduction in ovary size in more derived species. Larger than average ovaries occur in P. hookeri up to 5,5mm and D. repandum, up to 8,0mm long. Usually concomitant with a short ovary is a longer style. Desmodium section Heteroloma which has ovaries averaging 3,0-4,0mm long have short styles, 1,0-2,0mm long flexed from 45° to erect almost immediately distal to the ovary. P. hookeri is an exception becoming flexed upwards only halfway along the style. In Alysicarpus, Lespedeza, D. dregeanum and D. barbatum where ovaries are smaller i.e. from 1,0-3,0mm long the styles are longer, averaging 3,0-6,0mm and styles are invariably flexed only at the distal ends. Alysicarpus is characterised by often having the distal flexed portion incrassated. In a few species of Desmodium the point of flexure

may/.....

may also be thickened. The stigma in all species is capitate.

3.3.7. Pods

Fruit characters in the Leguminosae have traditionally been one of the most important in the classification of the family (Ohashi, 1973). They are however, exceedingly variable and fruits show a great diversity of morphology in response to varying selection pressures in the breeding system. The over-weighting of fruit character importance has led to much confusion about the real relationship that the tribe Desmodieae has to other tribes which have similar fruits (Ohashi et al, 1981). Ohashi (1973) notes that fruit characters are insufficient to distinguish taxa at the tribal rank although they are most certainly useful in separating genera and species.

The general type of fruit in the family is a superior, unilocular, monomeric apocarp with submarginal placentation (Dudik, 1981). In the Desmodieae this has developed into a loment with (1)-2-many, one seeded indehiscent or tardily dehiscent articles, which separate easily from one another at maturity. D. velutinum and D. barbatum are examples with tardily dehiscent articles. Pseudarthria differs in having a narrow linear oblong pod with the sutures often sinuate between the seeds (fig. 8) but not articulate and it is 2-valved, dehiscing abaxially.

The following trends indicated by Dudik (l.c.) to be advanced or derived characters in the Leguminosae, occur in the Desmodieae. Legumes have a persistent style, they are few seeded to one seeded as opposed to many seeded; two-valved to indehiscent, moniliform and jointed; and the pericarp becomes adnate to the seed in D. repandum only (Plate 11 fig. a). These criteria for specialisation of the pod indicate possible evolutionary trends (Dudik, l.c.). The pod probably originated from a multi-follicle which specialised to form a type of pod, the multilegumen as found in some primitive Leguminosae (Dudik, l.c.). Evolution proceeded by decreasing the number of carpels to the oligolegumen and then to the legumen of one carpel. The specialisation of the legume then proceeded in various ways with changes in the type of dehiscence, and reduction of the number of seeds (Dudik, l.c.). The typical jointed and mostly indehiscent pods of many Desmodieae are seen as the culmination of strong selection pressures due to parasitism (compartments protecting neighbouring seeds being att-

attacked/.....
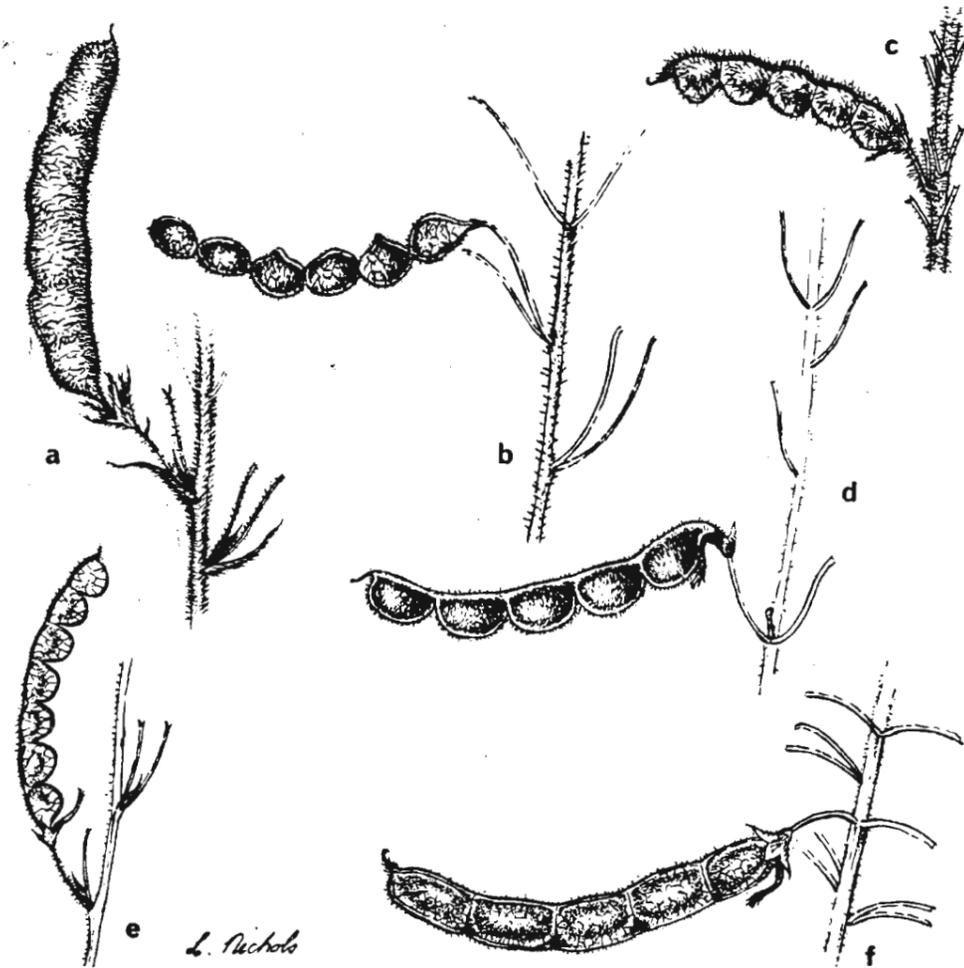
FIGURE 8

Inflorescence rhachides, pedicels, calyces and fruit

Pseudarthria and Desmodium

a) Pseudarthria hookeri

b) Desmodium tortuosum

c) D. velutinum

d) D. incanum

e) D. gangeticum

f) D. salicifolium
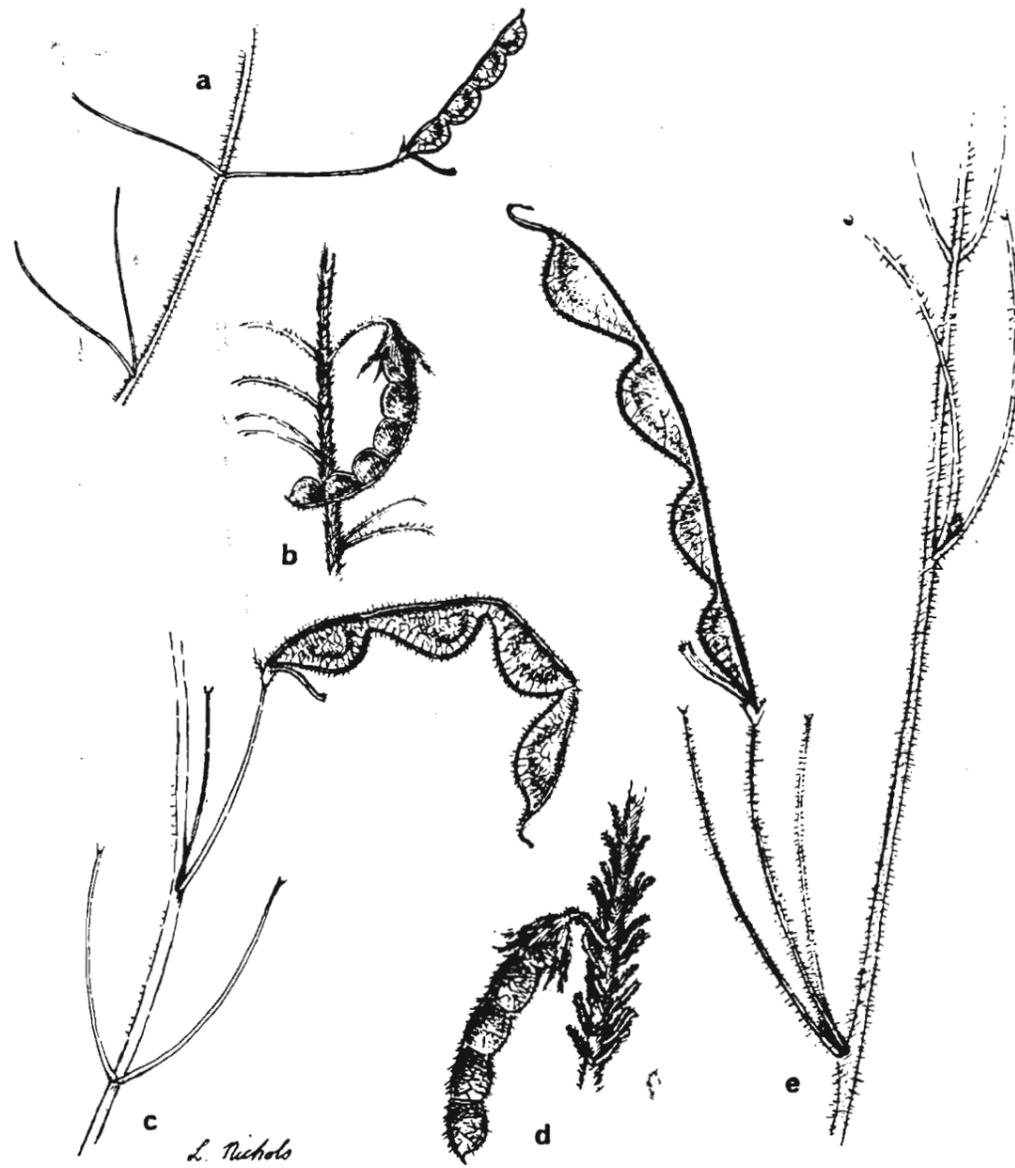
FIGURE 9

Inflorescence rhachides, pedicels, calyces and fruit

Desmodium

a) D. setigerum

b) D. barbatum

c) D. adscendens

d) D. dregeanum

e) D. repandum

L. Nichols

FIGURE 10

Inflorescence rhachides, pedicels, calyces and fruit

Alysicarpus and Lespedeza
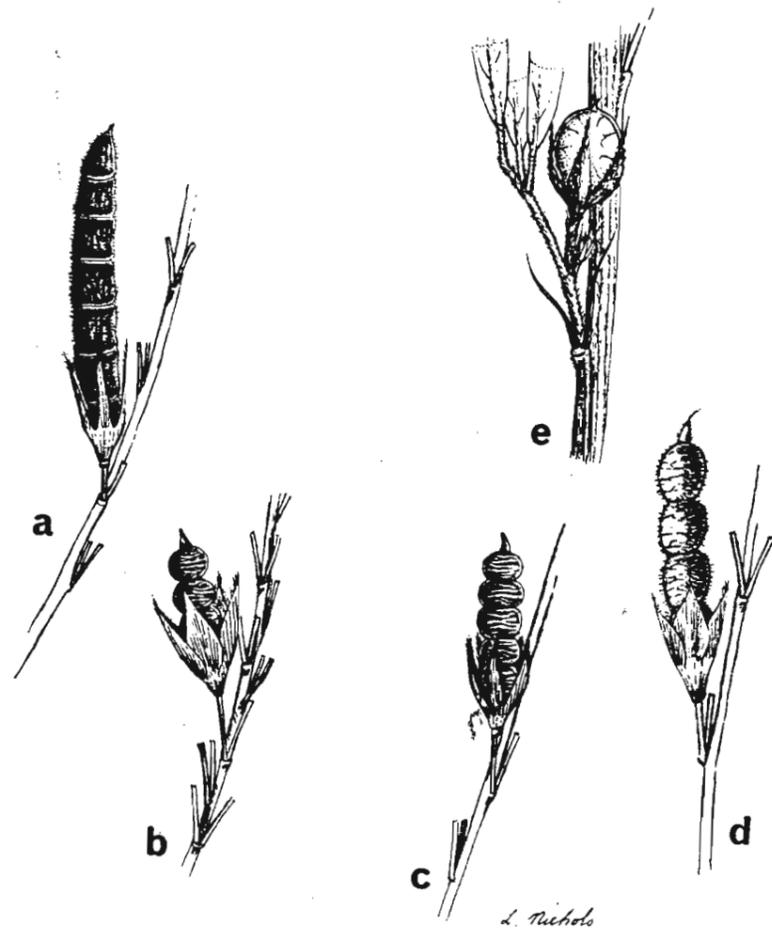
a) Alysicarpus vaginalis

b) Alysicarpus rugosus

c) Alysicarpus glumaceus

d) Alysicarpus zeyheri

e) Lespedeza cuneata

attacked) and seed dispersal (indehiscent, easily separating articles facilitate wider dispersal).

In Desmodium (figs. 8 & 9) the calyces are senescent and inconspicuous in fruit except in D. barbatum and D. dregeanum and it is doubtful that they play a significant role in dispersal. These two, however, together with Pseudarthria and Lespedeza have persistent hairy calyces which definitely aid dispersal (Plate 15 fig. d and h). This trend is carried even further in Alysicarpus which have large glumaceous, persistent calyces with long stiff cilia (Plate 7 fig. f). Pods are held away from erect and outwards in Desmodium (fig. 9), the conspicuous vesture of uncinate and other hairs as well as the persistent style being relied on principally to aid dispersal. In Alysicarpus however, pods are held erect and are generally smaller and more compactly arranged than in Desmodium. Dispersal will rely very much more on the calyx with uncinate hairs and cilia and the persistent style, although pods are also densely uncinate puberulent and glandular.

The shape of the mature pod is determined by the article's shape, size and number, and the width of the isthmus between them. In Desmodieae pods, articles are variously shaped from almost circular in outline e.g. D. tortuosum (fig. 8 and Plate 8 fig. h) to essentially linear e.g. in D. salicifolium (fig. 8) and A. vaginalis (fig. 10). Most frequently in Desmodium articles are essentially straight above and more or less deeply indented at the isthmi along the lower suture (Plate 8 fig. g); 3 - 8 in number and between 1,0-8,0mm long and 1,0-4,0mm wide. In Alysicarpus, pods are linear-oblong and mostly moniliform comprising 2 - 7 'stacked' articles 1,0-3,0mm long and 1,5-3,0mm wide (fig.10 and Plate 9 fig. f). Articles of most Desmodieae fruits have a prominent reticulate venation pattern (Plate 9 fig. d) and in two species of Alysicarpus (Plate 9 figs. e and f) the articles are strongly ridged. Individual cells have prominent anticlinal walls and are easily visible on most fruit surfaces (Plate 10 figs. b,e and f). Stomata commonly appear sunken and partially surrounded by a peristomial rim (Plate 10 fig. c). Wax deposits also sometimes occur (Plate 10 fig. b). All except Lespedeza are densely uncinulate puberulent, often glandular (Plate 10 fig. b) and scattered pilose (Plate 8 fig. b); tomentose (Plate 8 fig. a) or silky pilose (Plate 9 fig. c). Many have a persistent style (Plate 8 fig. g) or an apical tuft of long hairs (Plate 10 fig. g) to aid dispersal.

3.3.8. Seeds/....
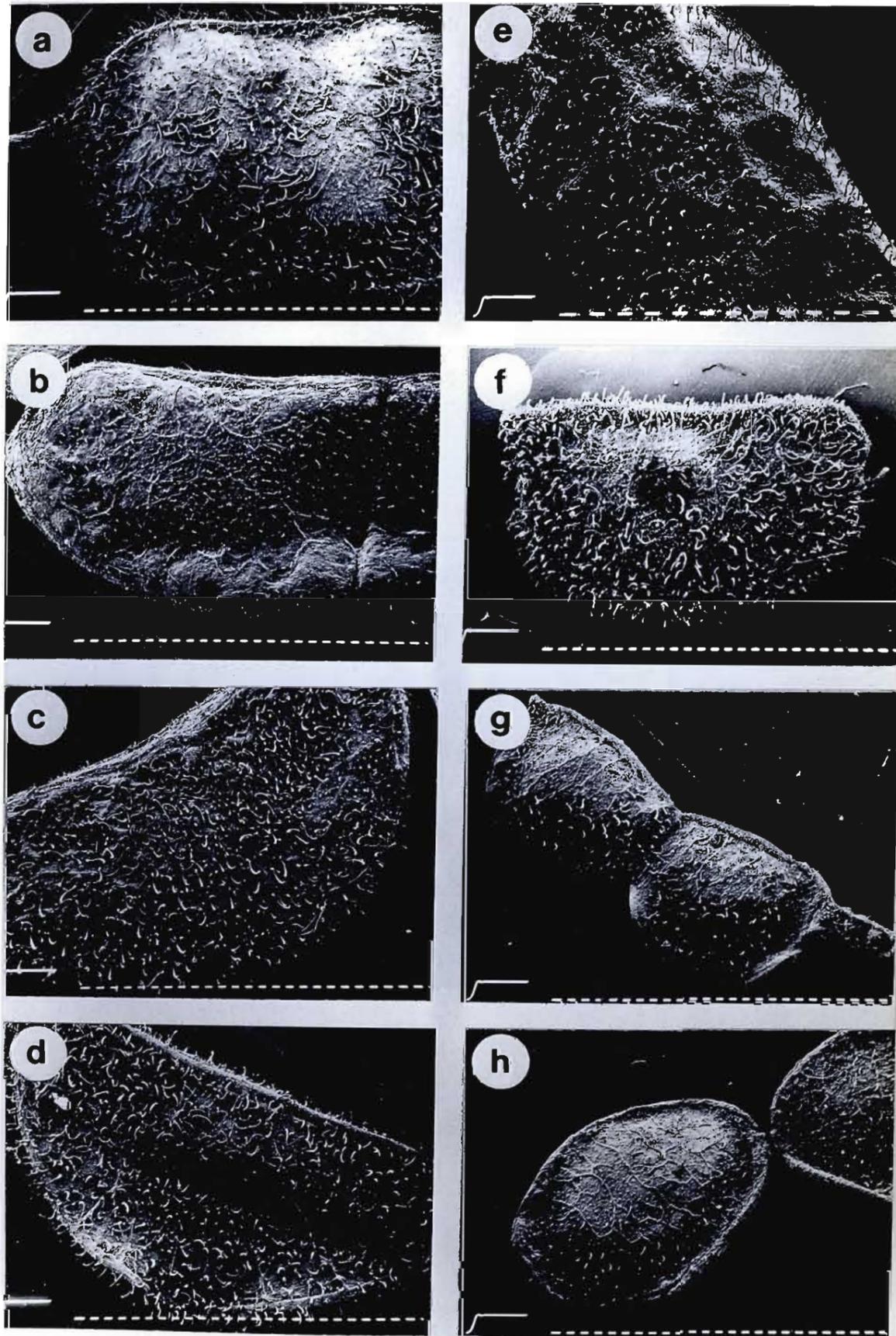
PLATE 8

Pods and articles

a) P. hookeri — x20, pod only constricted slightly between seeds, not separating into articles; note reticulate venation and dense vesture

b) D. salicifolium — x20, clear line of separation between articles; reticulate venation obvious

c) D. repandum — x20, dense puberulence

d) D. adscendens — x20, reticulate venation and prominent margin

e) A. vaginalis — x40, reticulation and puberulence

f) D. incanum — x20, very dense puberulence with two distinct sizes of uncinate hairs

g) D. setigerum — x20, two articles and persistent style

h) D. tortuosum — x20, unusually shaped articles and clear reticulate venation
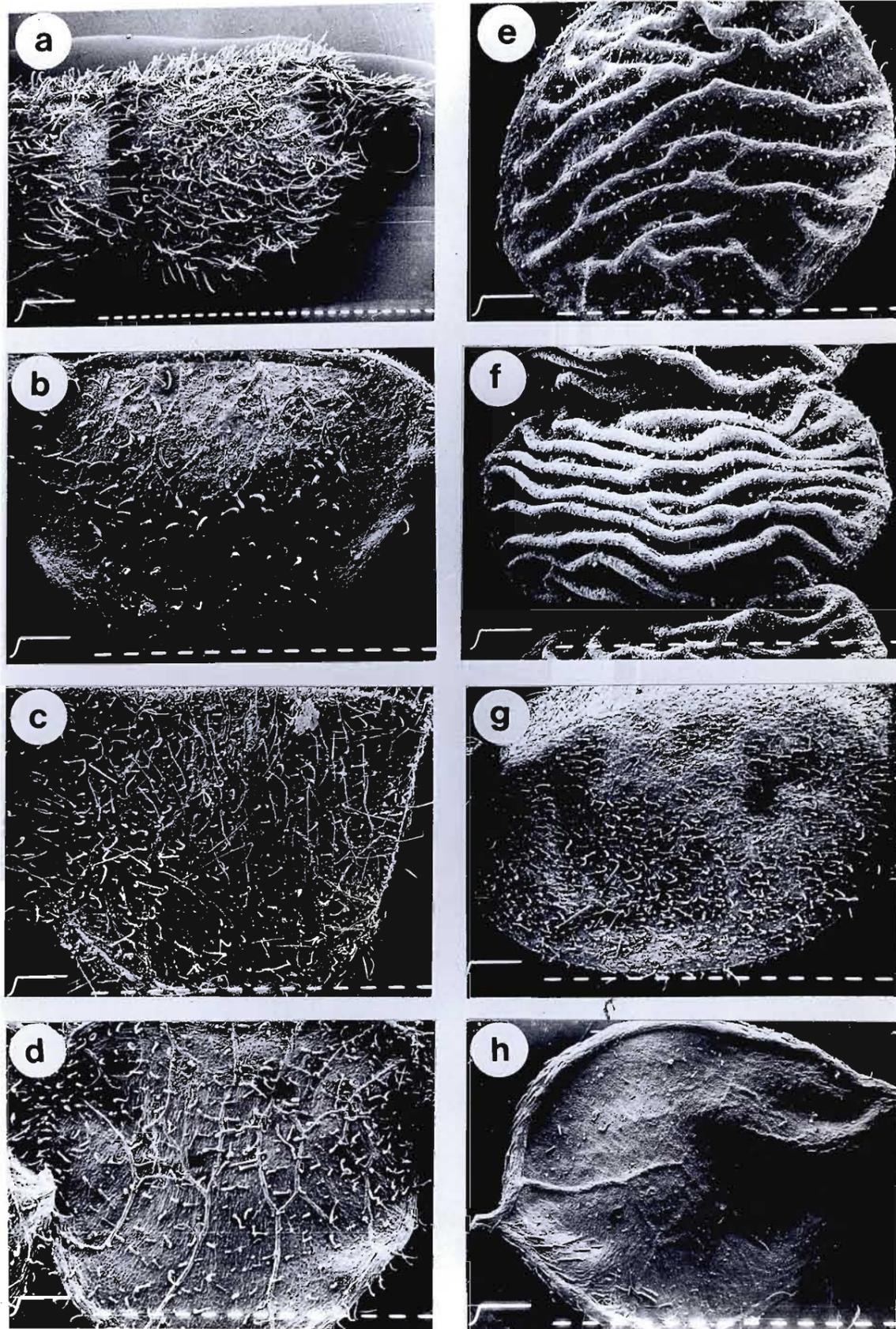
PLATE 9

Articles

a) D. velutinum   x20,   articles separating, tardily
                            dehiscent, velutinous

b) D. setigerum   x40

c) D. dregeanum   x40,   article with silky-pilose
                            vesture

d) D. gangeticum   x40,   reticulate venation and
                            individual cell outlines

e) A. glumaceus   x40,   article with prominent ridges

f) A. rugosus   x40,   articles similar to above in-
                            dicating close relationship

g) A. zeyheri   x40,   subglobose articles, densely
                            puberulent, without ridges

h) L. cuneata   x40,   single articled pod
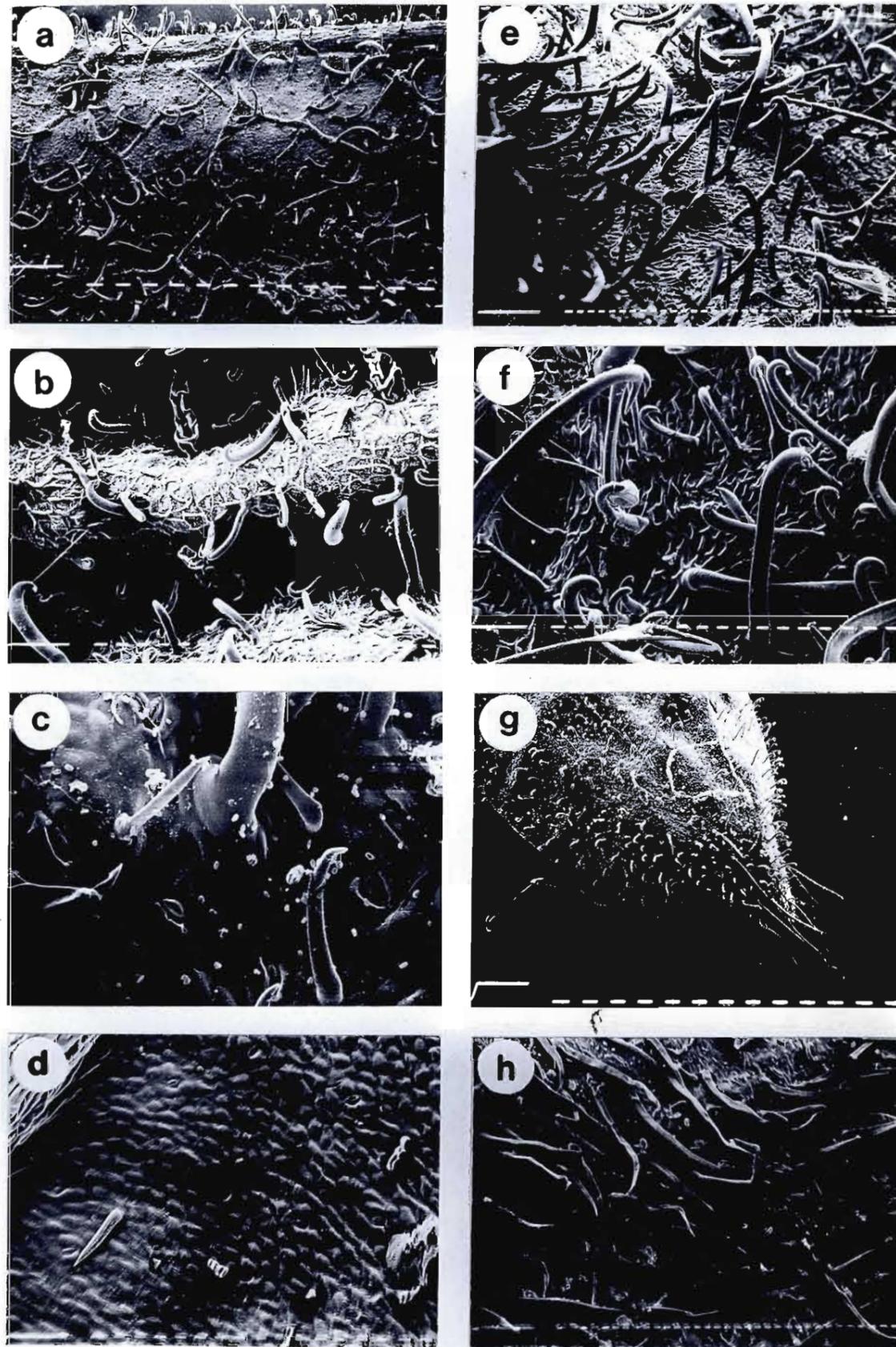
PLATE 10

Fruit surface detail

a) D. adscendens   x40,   reticulation and puberulence

b) A. glumaceus   x320,   ridge detail showing cell shape with prominent anticlinal walls, multicellular glands and wax deposits

c) D. incanum   x640,   smaller uncinate hairs and stomata which are tending to become sunken and surrounded by a peristomial rim

d) L. cuneata   x320,   cell shape, prominent paracytic stomata and subsidiary cells

e) P. hookeri   x160,   irregular cell shape with prominent anticlinal walls; variously sized hairs

f) D. velutinum   x320,   similar to fig. e but indicating collapse of long velutinous hairs above the basal cell

g) A. vaginalis   x40,   fruit tip indicating aggregation of long hairs to aid in dispersal

h) D. dregeanum   x160,   long silky-pilose vesture

3.3.8. Seeds

External morphological features shared by legume seeds are a cuticle, testa, hilum and sometimes an aril, all derived from maternal tissue. Internal morphological features include two cotyledons which are usually straight and an embryonic axis with a well defined radicle, poorly defined hypocotyl and poorly defined epicotyl. A plumule arising from the epicotyl may be present or absent and endosperm varies from large amounts to absent.

In D. repandum the inner layer of the fruit wall is adnate to the cuticle of the testa which is considered an advanced, derived character by Dudik (1981), (Plate 11 fig. a). Below the cuticle, the testa of papilionoid seeds is complex and composed of a number of layers (Gunn, 1981). The hilum is also complex and has a separation in the palisade layer known as a hilar groove, a characteristic feature of Papilionoideae (Plate 13 fig. d). This groove may be concealed under a funicle or funicular residue (Plate 15 fig. g). The hilar groove acts as a hygroscopic valve by obstructing the entrance of water when the seed is surrounded by moist air, but permitting water to leave the interior of the seed when it is surrounded by dry air (Gunn, l.c.). This contributes to the hard seededness and the impermeability of the testa. Three non arillate features may be included in the hilar region; a micropyle, lens and hilar rim (see fig. 11). The micropyle is a plugged opening in the mature seed representing the passage in the ovule stage between the integuments for the pollen tube (Plate 13 fig. a). The micropyle is on the opposite side of the hilum from the lens. The lens is commonly a mound of tissue (often discoloured) on the cotyledonary lobe and has been shown to be an area of weakness or a partial opening in the testa. This is the area where water initially penetrates the otherwise impenetrable testa (Gunn, l.c.). The hilar rim or corona, a feature restricted to papilionoid seeds is a collar-shaped mound around the hilum. Most seeds have an externally visible radicular lobe best seen in lateral view (fig. 11). The testa surface is usually smooth at low magnifications (x 30 or less) and glossy. At higher magnifications under surface scanning electron microscopy (S.E.M.), minute patterns are observed on the surface (Plate 12). The funiculus usually remains attached to the fruit after abcissing from the mature seed and exposing the hilum. The head of the funicle is expanded into the hilum like a stopper. Corner (1951) likens the hilar rim to a rudimentary aril and terms the whole hilar rim a rim aril. Using
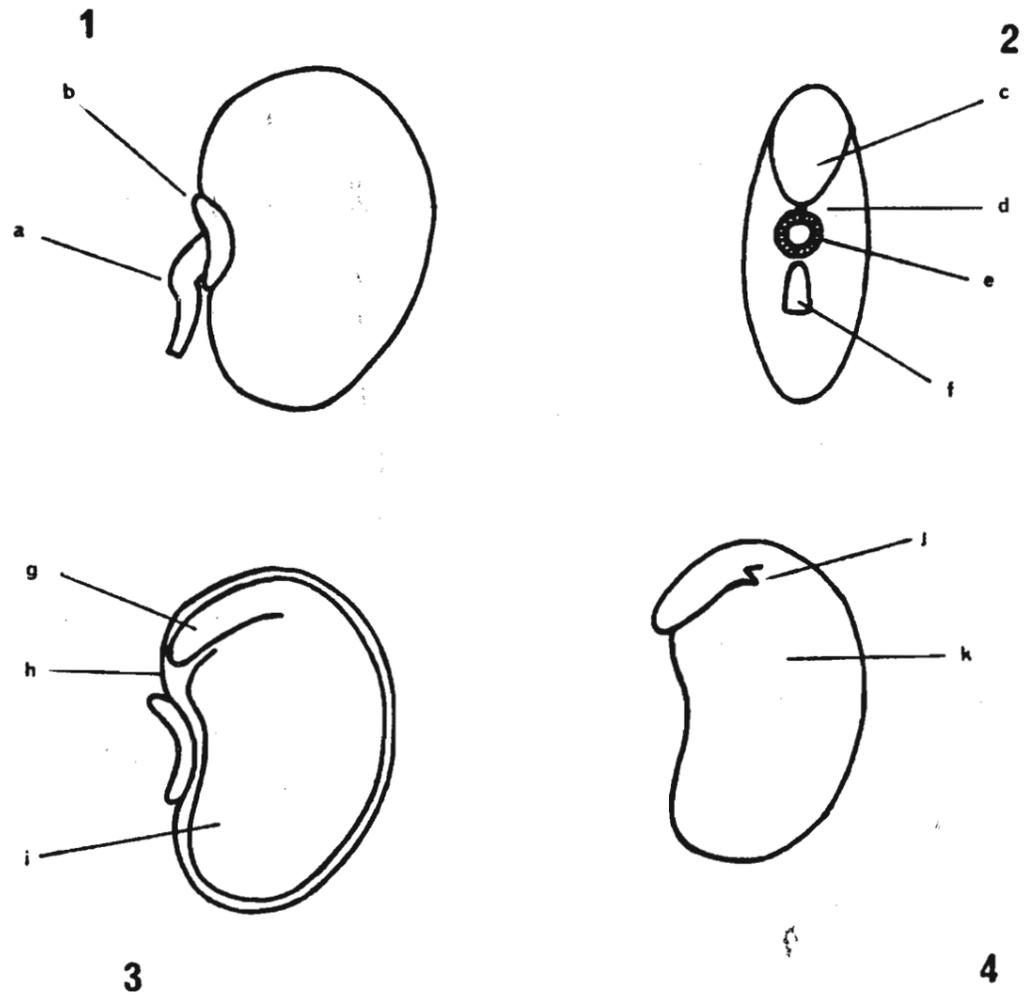
FIGURE 11

Desmodieae seeds

1) Lateral view   a) funicle, b) aril

2) Front view   c) radicular lobe, d) micropyle,
                                          e) hiler rim and aril, f) lens

3) Longitudinal transverse
    view   g) radicular lobe of embryo
                                             (radicle and hypocotyl)
                                          h) testa, i) cotyledons

4) Upper cotyledon removed   j) plumule, k) lower cotyledon
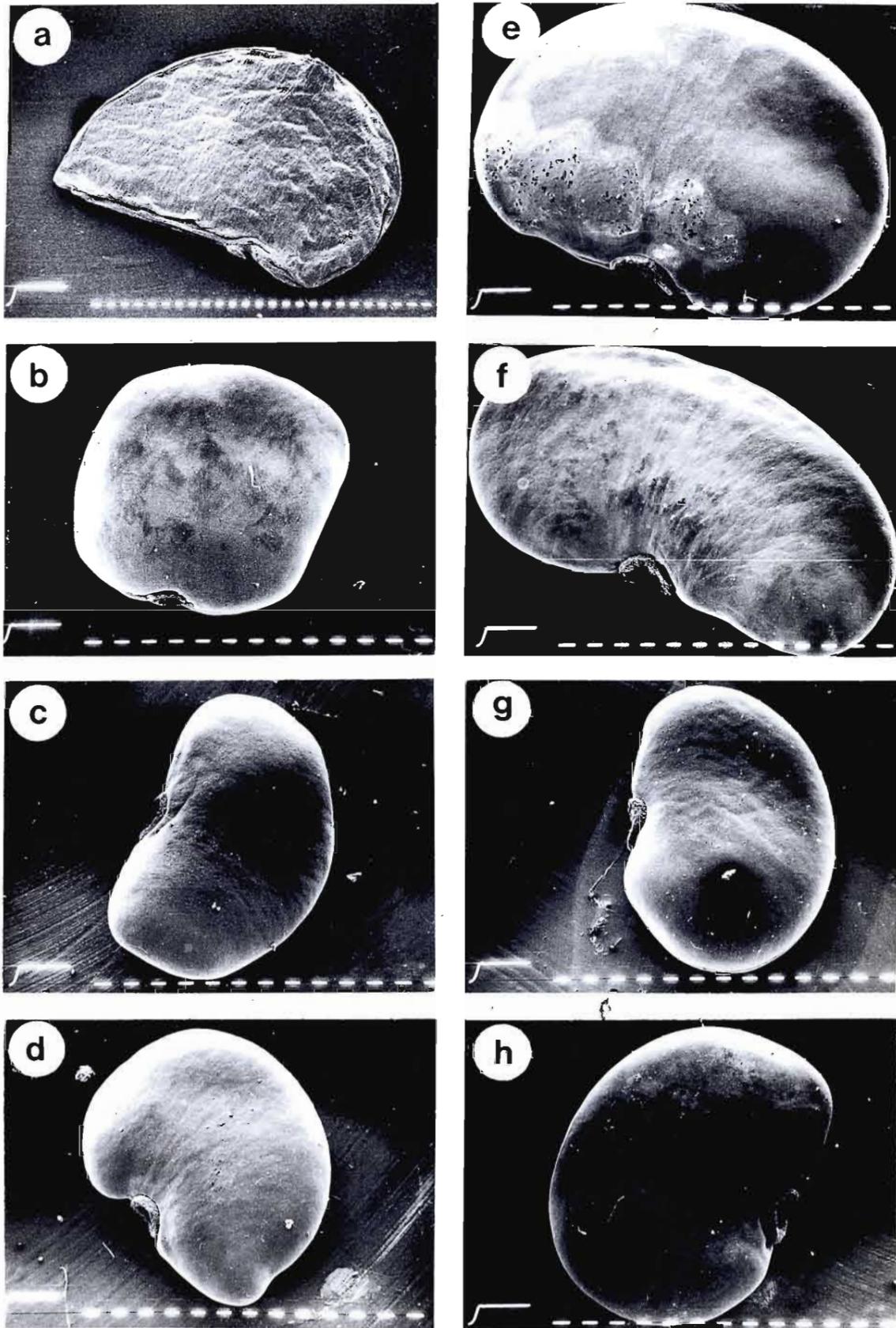
PLATE 11

Seeds

a)	D. repandum	x20,	inner layer of pericarp adnate to seed
b)	A. zeyheri	x40	
c)	D. setigerum	x40	
d)	D. gangeticum	x40	
e)	D. incanum	x40	
f)	D. salicifolium	x40	
g)	P. hookeri	x40	
h)	D. velutinum	x40	
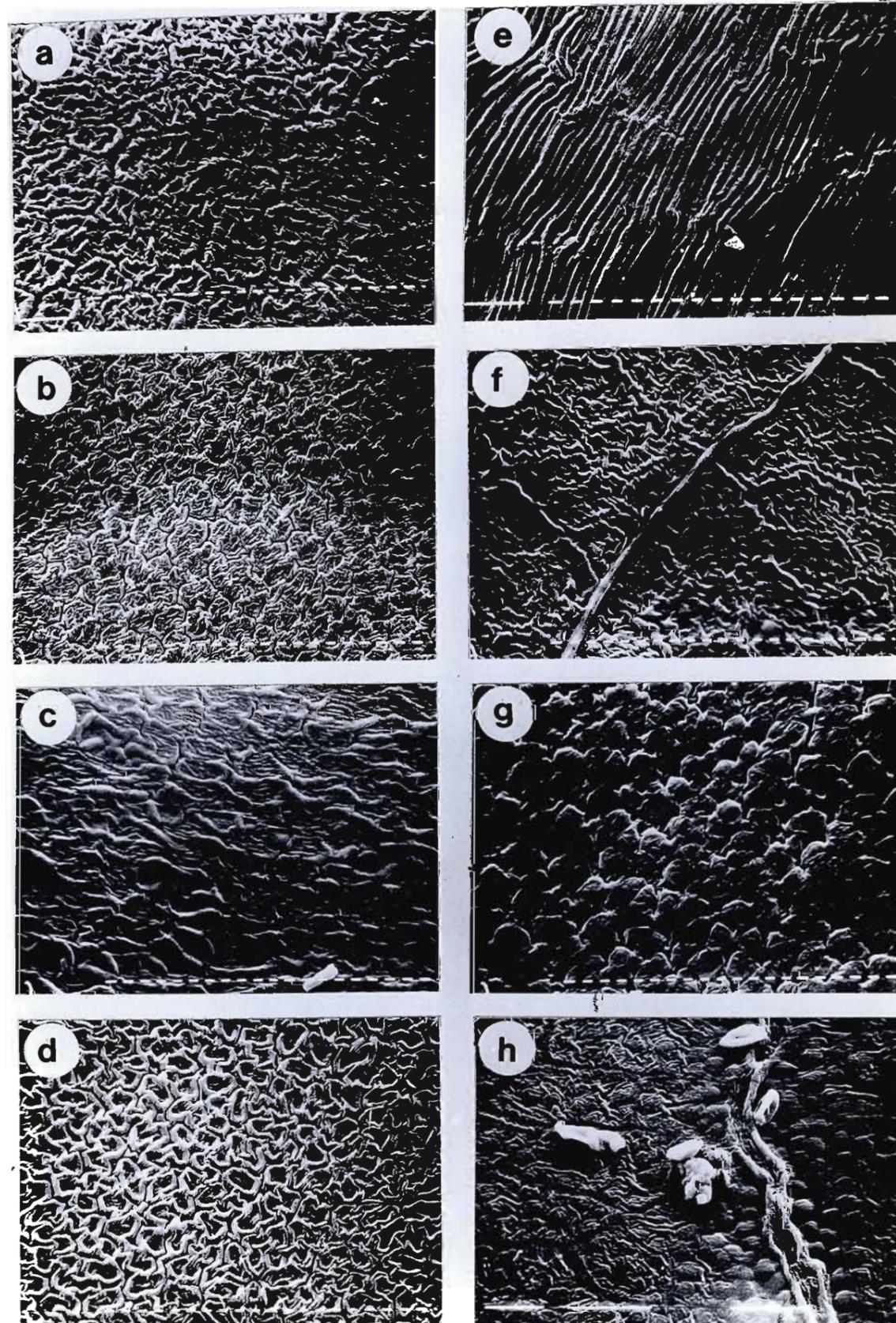
PLATE 12

Seed surfaces

a) P. hookeri   x2500,   ridges and raised rims of anti-
                               clinal walls of testa due to
                               drying shrinkage

b) A. vaginalis   x2500,   individual cells ridged but
                               margins not prominent

c) D. velutinum   x2500

d) A. zeyheri   x2500,   anticlinal walls very prominent

e) D. repandum   x320,   inner layer of pericarp

f) D. salicifolium   x2500

g) D. gangeticum   x2500

h) P. hookeri   x2500,   spores and mycelium of fungus and
                               its effect on seed surface topo-
                               graphy

Hilar region, seed arils
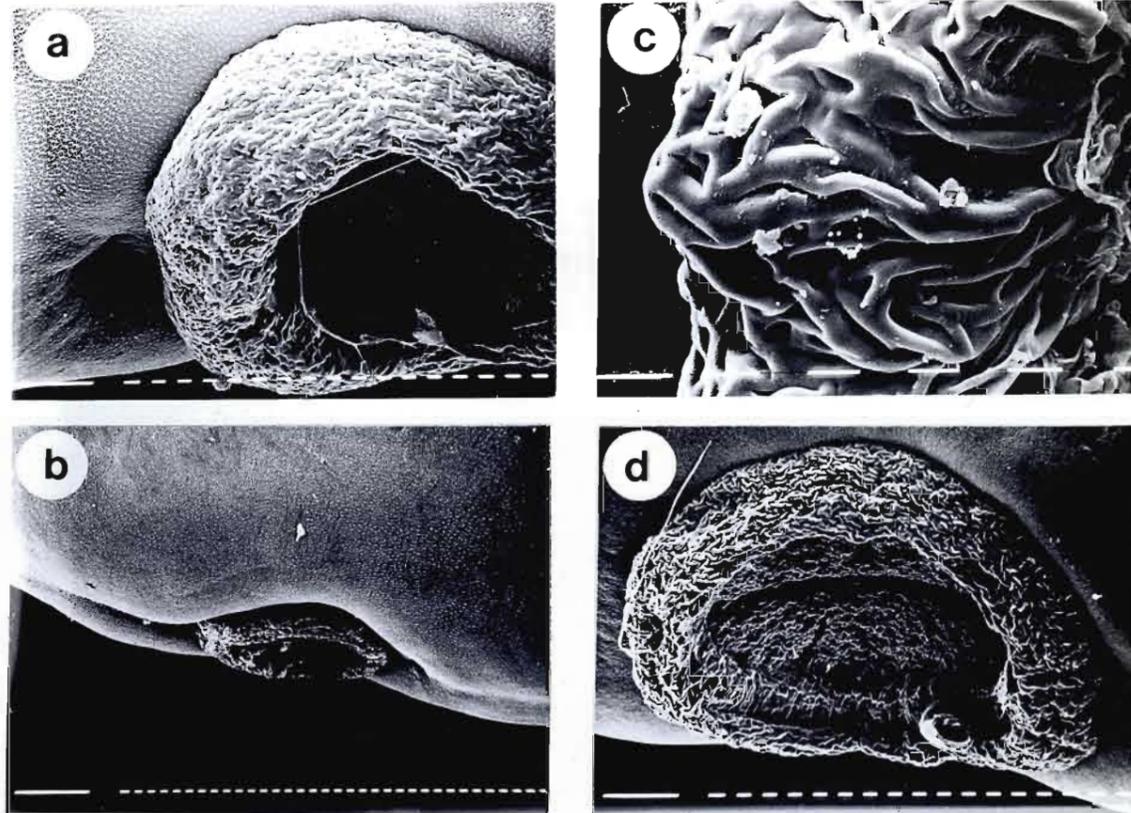
a) D. velutinum   x320,   aril and micropyle to left
                                of picture

b) A. zeyheri   x160,   aril

c) P. hookeri   x1250,   aril detail

d) D. setigerum   x320,   aril and hilum

the classification of Gunn (1981) the aril represents a dry collar
(Plate 13) of material attached to the hilar rim and depending on
whether the funicle remains attached or not, it is termed elongate
or inconspicuous-regular respectively.

Seed size varies from 1,5 - 3,0mm long, 1,2 - 2,0mm wide and 0,5
- 1,0mm thick in most species of the tribe and the shape is generally
reniform, ellipsoid - oblong or squarish (Plate 11).   In D. salici-
folium, D. adscendens and D. repandum seed length increases to 4,0;
5,0; and 7,0mm respectively and up to 3,0mm wide.   The shape of the
seed of D. repandum is obliquely lunate (Plate 11 fig. a).   The endo-
sperm when present is usually hard and dry and somewhat glassy (Gunn,
1981) and may encase the embryo and cotyledons.   The legume embryo
is composed of two cotyledons and an embryonic axis.   In the embryonic
axis the radicle is fully exposed and inflexed.   The two cotyledons
are easily separated and one can be removed by a slight twist reveal-
ing the embryonic axis still attached to the other cotyledon (Gunn,
l.c.). A slight scar is present on the inner surface of the removed
cotyledon showing where it was attached to the apex of the hypocotyl.
With the removal of one cotyledon, the radicle, hypocotyl and epicotyl
(including plumule) are exposed (fig. 11).   Fresh green seed before
seed coat hardening and desiccation, was measured in P. hookeri to
be 3,9 (4,0)mm long and up to 2,8mm wide.   Dry seed only measured
2,0mm by 1,2mm.

3.3.9. Seedlings

Since the seedling stage is a critical phase in the life cycle of
of a plant and because the microhabitat of the juvenile is often
different from that of the mature plant, a better knowledge of seedlings
may provide valuable information about the ecological and evolutinary
history of the group (Duke and Polhill, 1981).

In the Desmodieae as with many legumes, germination commences with
the emergence of the radicle. This is pushed out of the envelopments
by the elongating hypocotyl (de Vogel, 1980), and during and after
establishment of the seedling the hypocotyl usually continues enlarge-
ment. It is first curved in a loop above the soil with its tip and
base subterranean but ultimately the hypocotyl straightens drawing
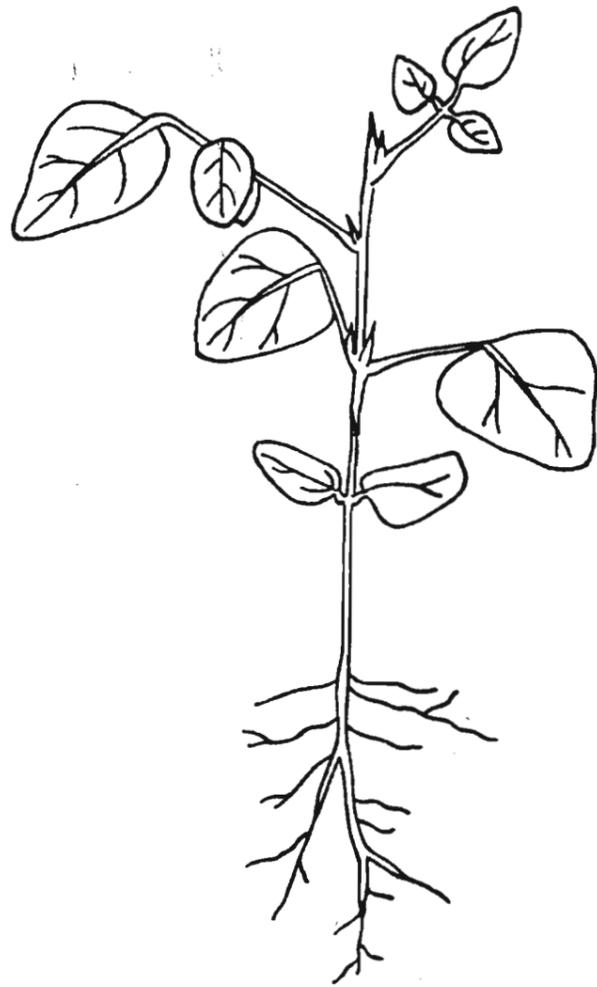
FIGURE 12

The Desmodieae seedling

From the bottom upwards note the dichotomously branching root; the foliar cotyledons; the opposite, unifoliolate eophylls and the alternate spirally arranged trifoliolate metaphylls.

the cotyledons and plumule from the soil and bringing them erect (de Vogel, l.c.).

A number of terms are applied to this kind of germination. Where the cotyledons spread some distance above ground level as in the case of Desmodieae germination is epigeal (Duke and Polhill, 1981). Another distinction is made by adding the prefix phanero - if the cotyledons when they emerge have thrown off the testa. In some seeds (not Desmodieae) coverings remain because cotyledons have an haustorial action withdrawing nutrients from surrounding endosperm in the seed. In seeds with little or no endosperm, after emergence of the root and hypocotyl, and after a short resting period, the cotyledons expand and throw off the testa (de Vogel, 1980). The cotyledons of Desmodieae are foliar being relatively thin, green and leaf-like and they expand soon after germination. They are relatively large and long-persistent, remaining functionally photosynthetic until a number of leaves have developed. No additional foodsource is present on the seedling once the foliar cotyledons are produced. Seedlings may further be categorised by the arrangement of the seedling leaves termed eophylls as distinct from the adult leaves termed metaphylls (Duke and Polhill, 1981).

According to the classification of de Vogel (1980), Desmodieae are classed as having a Macaranga type of seedling i.e. phaneroepigeal with foliar cotyledons (see fig.12). Seedlings of this type developed from small seeds predominate in open habitats in the tropics and temperate areas. Characteristic of these seedlings are two temporary rest periods during development. First when the cotyledons are still enclosed by envelopments with the root and hypocotyl exserted and second when the entire seedling is free of envelopments and only the foliar cotyledons are developed, i.e. before the epicotyl expands (de Vogel, l.c.). Cotyledons are without stipules but the first two eophylls produced are simple, unifoliolate, stipulate (lacking stipels), opposite and well differentiated from true leaves. Although this combination of characters is not uncommon, Duke and Polhill (1981) note that more frequently eophylls tend to be less differentiated from true leaves and alternate in typical phaneroepigeal seedlings with foliar cotyledons. The next leaves are true metaphylls being trifoliolate, alternate and spirally arranged.

Ecologically,/....

Ecologically, seedlings derived from a breeding system producing many small seeds with long viability and irregular germination have a considerable period of assimilation by the first foliar organs before aerial growth can continue in open exposed places (Duke and Polhill, 1981).

Quoting Duke and Polhill (l.c.), "To the extent that distinctive natural genera may have evolved as a result of a significant adaptive shift in their ecology, indications of this may be rather readily apparent in seedling structure, behaviour and biochemistry." They note that in a few studies of generic and infrageneric relationships that have used seedling characters as components of a more general survey, significant correlations have been revealed.

3.3.10 Cytology

According to Goldblatt (1981) the Papilionoideae appear to be fundamentally tetraploid with a basic $x = 14$. Aneuploid reduction is widespread and in most of the tropical papilionoid lines the base numbers are $x = 12$, 11 or 10. In the Desmodieae, Desmodium has $n = 11$ which equals the base number for the tribe although D. salicifolium has been recorded as $n = 10$ by Turner and Fearing (1959). Alysicarpus has $n = 8$ and is a more derived aneuploid genus. Lespedeza is also an aneuploid genus with L. cuneata being recorded as $n = 10$ by Hanson and Cope (1955). Pseudarthria is more difficult to interpret since the three species counted so far (Bolkhovskikh et al, 1969) have different chromosome numbers. P. hookeri has been reported by Riley and Hoff (1961) as having $n = 17$, a number difficult to correlate with the overall $n = 11$ especially since P. hookeri so closely resembles many Desmodium spp. A recent recount of P. hookeri (Spies pers. comm.) of $n = 13$ refutes this and allies it for the first time with a count of $n = 13$ for P. fagifolia.

CHAPTER 4

BREEDING SYSTEMS

4.1. Introduction

A discussion of constraints theory (4.3.), developed largely by Stirton
in Polhill et al (1981), introduces an interesting means of examining
the overall biology of breeding systems. It will be used as far as
possible in the final chapter to isolate the central features that
are unique in the tribe.

The flower is the basic unit of reproduction and as such, is a function-
al system (see 4.3.) that may be considered as the compromise that
best satisfies the following selection pressures (from Polhill et
al, 1981).

a) Balancing the advantages of a heterogamous with an autogamous
    breeding system
b) Maximising the traffic of pollen to a receptive stigma
c) Attracting and rewarding suitable pollinators
d) Limiting and protecting the energetic resources of the flower
    to discourage opportunists and robbers
e) Repelling mammalian and other herbivore attack
f) Providing adequate protection to developing seeds

Some or all of these requirements are satisfied in any one type of
flower and can be achieved in any number of ways. In the following
sections an attempt is made to trace trends in the Papilionoideae
leading to the Desmodieae flower, and then to discuss all its components
from a structural-functional viewpoint. The whole is considered
throughout in the biological context of pollination (pollinator behav-
iour and pollinator-plant relationships), reproductive strategies
and seed dispersal. Specific experiments on Pseudarthria hookeri
and some species of Desmodium are used as examples to illustrate
the discussion.

4.2. Materials and Methods

Flowers of several species of Desmodieae were tested for the presence
of/.....

of osmophores or active sites of attractant odour production using the following procedure.

A 1% solution was made up of neutral red dye powder in distilled water adapting the method of Vogel (1963) as suggested by Stirton (pers. comm.). Neutral red is a vital stain which is taken up by actively secreting tissues.

The solution which was thoroughly stirred to ensure no remaining undissolved solids, was dispensed into Polytops vials in sufficient quantity to completely immerse a section of inflorescence rhachis with flowers. In the early morning when flowers were fully opened but not tripped, portions of inflorescence containing 3-4 flowers were removed from the plant and immediately placed in the vials. Flowers were collected only on sunny days because osmophore activity was expected to be minimal in overcast conditions (Buchmann, 1983). They were also handled carefully to avoid any bruising as damaged areas also take up the dye. Once immersed, the vials were gently upended a few times to ensure proper wetting of the petal surfaces. Vials were left to stand for 6 to 8 hours after which the flowers were removed, dried between tissue paper and examined under a dissecting microscope.

Flowers of two different species of Desmodium were viewed under an ultraviolet (UV) lamp to see if additional visual cues became apparent. The UV lamp used was a 125w, Woods Glass, Mercury lamp with a UV range of 300 - 400nm peaking at 360nm. The lamp was switched on half-an-hour before viewing, to warm up, and flowers were examined for patterns of either UV absorbance or reflectance. The materials and methods employed during the breeding system experiment on Pseudarthria hookeri are described under that section.

Black and white drawings have been made to illustrate certain concepts described and histograms are used to summarise data on seed production in P. hookeri.

4.3. Constraints theory

For the purposes of this study, a functional system is defined as any set of interacting structural characters that function together as a relatively discrete and autonomous unit. (The functional structural complex of Stirton pers. comm.).

The crucial/.....

The crucial points in the radiation of the family Leguminosae are marked by certain functional systems becoming fixed in a unique way i.e. the papilionoid flower, hilar valve or plant herbivore defense systems (Polhill, Raven and Stirton, 1981).

With a greater awareness of biological interactions, the more tradition-ally used 'characters' in taxonomy, like stamen arrangement, flower colour or stigma type are seen as each playing a role in a particular functional system (Polhill et al, 1981).

Quoting Polhill et al (l.c.), "Such a system is an evolutionary compro-mise between numerous external and internal selective pressures acting on its components. These components are simultaneously a) under contemporary design constraints b) under contemporary budgetary constraints c) temporal and spatial anachronisms d) multifunctional and therefore e) optimal (not maximal) in performance rate and func-tion." Stirton (pers. comm.) goes on to say, "This compromise between push-pull conflicts is set up by chemical and physical constraints during ontogeny, each imposed by the various needs of homeostasis, deterrent-defences or attraction mechanisms."

It is therefore better to picture a functional system as representing only one of many possible compromises between its individual characters. Some of these characters may be quite variable without significantly affecting the system e.g. the number of flowers in the inflorescence. These can be considered as more marginal characters. Others cannot vary however, and are central or fixed in that system. Considering the functional system of the Desmodieae flower, the tripping mechanism is a critical central feature without which the whole breeding system would change.

Considered genetically, components either become fixed that in combin-ation are evolutionarily successful and confer advantage in offspring, or are simply carried along with others because they don't confer any disadvantage. Successful systems are dependent on many genes and their interaction is co-ordinated and protected from disruptive mutation by control and switch mechanisms in the genetic code (Stebbins, 1974). It is for this reason that fixed components in a functional system actually limit and channel the possibilities for further adap-tation (canalisation in the sense of Stebbins, l.c.). Since adap-tation is likely to be channelled along the path of least resistance, options become dependent on previous decisions (Polhill et al, 1981),

and the number of possible compromises between individual characters
is restricted. As components become canalised and constrained, the
more parsimonious adaptation is likely to be (Polhill et al, l.c.).
This resistance due to the accumulative effect of previous adaptations
gives rise to the process of systemisation in the sense of Riedl
(1978).

Whenever selection pressures (either genotypic or phenotypic) interact
strongly enough to disrupt the orderly process of systemisation,
even strong constraints may be broken and a repatterning of the charac-
ters within the functional system may lead to the development of
new compromises with different adaptive properties. This is termed
ontogenetic switching (Stirton, pers. comm.).

In this way various fixed characters are accumulated at different
stages in the evolutionary line. These carry a 'burden' (Polhill
et al, l.c.) which is all the other characters dependent on them,
like links in a chain. Accumulated burden is indicated by a tighter
interlinking between individual characters and between different
functional systems with a consequent decrease in the relative autonomy
of each system.

The importance of this concept of burden is that it begins to guide
further change the more it builds up, i.e. becomes an ontogenetic
director (Stirton, pers. comm.). Quoting Stirton (l.c.), "Higher
order taxa such as family or genus are characterised by whole shifts
in constraints which take place early in ontogeny while speciation
is characterised by constraint shuffles which take place later in
ontogeny."

The value of the constraints approach is that it considers the overall
biology of the plant and that by looking for functional systems and
determining fixed characters, markers are found that give an insight
into the evolutionary development of each system and hence the phylogeny
of the taxon. Stirton (pers. comm.) adds, "By isolating, identifying
and placing functional systems in a hierarchy of development we can
produce a profile which can be compared to other taxa."

4.4.   Trends and adaptations in Papilionoideae leading to
       the Desmodieae flower.

The flowers of Leguminosae are evolutionarily successful because
                                            they have/.....

they have had the capacity to radiate into different lines, each
of which shows increasing specialisations in structure and function
(Polhill, Raven and Stirton, 1981). Floral efficiency has been in-
creased by separating the responses to conflicting demands so that
contingencies can be met independently to a greater extent (Stirton,
mss). This is apparent in the specialisation of different parts
of the flower e.g. in the tendency towards the zygomorphic "butterfly-
like" flower typical of the Papilionoideae. Here, due largely to
pollinator and breeding system selective pressures, a compromise
has been met between two major trends in legume flower evolution.
There is either a trend towards a more tubular flower with better
protection of the fertile parts (as in the Mimosoideae) or a trend
towards a greater radial display (as in the Caesalpinioideae). The
Papilionoideae have met both contingencies in their attractive 'flag'
petal and in their fertile parts being protected by keel petals.
(Polhill et al, 1981).

In spite of the seemingly similar appearance of many papilionoid
flowers, very different strategies have evolved as various sequences
of constraints accumulated in the basic flower type. However, the
very fact of this similarity is proof that certain major features
became fixed from early on and that these constraints considerably
limited further change.

In the direction from which the Desmodieae arose, inflorescence-type
became fixed quite early on. Panicles in the earlier base-groups
became reduced to the typical pseudoraceme which itself is subject
to various degrees of reduction. Even true racemes may occur with
further reduction. Some measure of secondary aggregation of axillary
and terminal pseudoracemes is found to augment display.

One of the consequences of the indeterminate pseudoracemose strategy
of flower presentation is that it allows a major shift to occur in
flowering regime. This is from a massive - 'big bang' or intermittent
type flush as for example in Delonix to a more continuous protracted
flowering period which has considerable bearing on pollinator special-
isation. In many of the advanced papilionoid legumes this longer
period of flowering is combined with more complex flowers that have
hidden rewards which require sophisticated methods of reaching them.
Pollinators are thus reduced to a relatively narrow band of highly

advanced/.....

advanced (social or semi-social) skilled bees, particularly in the Desmodieae. Prospective pollinators need not only the skill to trip flowers, but also to memorise the locality of flowering individuals and to have sufficiently high energy requirements to fly between them even though they may be some distance apart. This characteristic of traplining (Heinrich, 1983) where bees will often follow a set route from memory between widely dispersed individuals is only made possible by a protracted flowering regime which offers high energy rewards for a long time. Insect visits therefore become long and infrequent.

Two distinct trends can be seen in the continuous flowering regime and these again lead to very different strategies. In one, a number of flowers are produced in an inflorescence, and they have a relatively long life span, with adaptations for making pollen transfer economical. These will have either the simple valvular, pump (piston) or brush arrangement methods of repeatable pollen representation to pollinators (Leppik, 1966). Nectar is often offered as a reward. In the other which occurs in nearly all the tribe Desmodieae, only a few flowers open every day in ascending order along the pseudoraceme and these are short-lived having an explosive method of pollen release. Instead of being repeatable these flowers make only one effective visit possible after which the petals become disorientated and caducous. Even if the flowers are not visited, self tripping occurs during the day and flowers wilt by nightfall. Here pollen is most often the reward with flowers losing the ability to produce nectar. Rapid colour change of flowers and loss of attractiveness or resupination are characteristic of both strategies once fertilisation has occurred to avoid pollinator revisits which may be wasteful of energy. A further trend is noticeable in the switch from self incompatible breeding systems to self compatible ones in more advanced groups including the Desmodieae.

In the flower, specialisation has been towards smaller size, and calyces with the upper lobes more connate; tending to become more subequally arranged or two-lipped. The calyx is small, senescing in fruit or is glumaceous, prominent and persistent as in Alysicarpus. They play a role ultimately in fruit dispersal. The corolla increases in complexity with the standard developing small appendages on either side of the midline above the claw, particularly in Alysicarpus.

These are/.....

These are seen as playing a role in maintaining petal configuration and are the focal point for the pollinator to unlock the tripping mechanism during pollination. Wing petals develop auricles, transverse pockets, transvenal wrinkles and intervenal crescent-shaped folds, often aggregated proximally to peg into the keel petals. The pattern produced is again more observable in Alysicarpus than in other members of the tribe and is also closely linked to providing pollinator footholds. Keel petals become more firmly joined distally and interlocked with the wings and the whole structure folds tightly over the staminal column holding it under tension. The vexillary stamen tends to be free or become more coherent (not fused) with the rest of the staminal column as a result of the loss of nectar production. Anthers are uniform with the pollen developing a marked thickening of the endexine and loss of the foot layer. This is a trend occurring only in the advanced Old World tropical tribes and must play a role in pollen grain metabolism. The style becomes more elaborate, thickened and variously hairy.

In Lespedeza breeding system selection has resulted in a very different strategy. Flowering is more like the former continuous type. A number of flowers are produced in axillary fascicles representing reduced axillary racemes and they lack the explosive method of pollen release and secrete nectar at the base of the corolla. Flowers however, only tend to open for one day. Unusual in this group is that two types of flowers are produced. Cleistogamous and chasmogamous flowers occur on separate racemes, the former having the appearance of remaining in the bud stage since the petals never unfold (McGregor, 1976). In these, the ovary becomes receptive to fertilisation and the style recurves until the stigma rests on one or more anthers, the filaments of which do not elongate (Clewell, 1966). Pollen grains germinate within the anthers on which the stigma rests and the tubes grow through the indehiscent anther wall into the stigma (cleistantheric pollination). The style is persistent on mature pods and reflects its mode of development by being sharply recurved (Clewell, l.c.). Styles persistent on chasmogamous pods are longer and either erect or variously curved but not sharply recurved. Cleistogamous pods can be distinguished from chasmogamous ones by being shorter and more orbicular rather than elliptic, by the shape of the style and by having a slightly shorter calyx (Clewell, l.c.).

4.5/.....

a

b
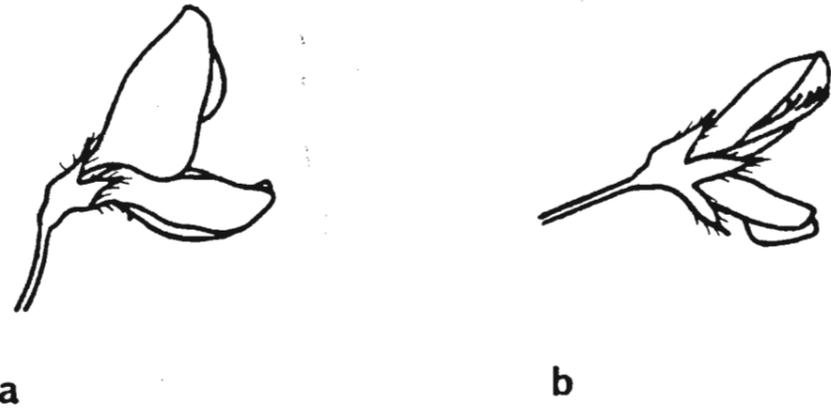
FIGURE 13

The untripped versus the tripped flower

a) The untripped flower in D. incanum.

b) The tripped flower in D. dregeanum.

Note the larger calyx than a); the staminal column blocking the orientation cues on the standard, and the keel and wings deflexed with petals disorientated.

4.5. The Flower as a functional pollination unit

The single most important functional feature of the papilionoid flower is the tripping mechanism (Arroyo, 1981). Both pollen and nectar (where produced) are concealed in the keel and become available only after tripping. Not only has this led to greater pollen and nectar economy (Leppik, 1966) but it has allowed the development of relationships with increasingly specialised pollinators capable of working successively more complex mechanisms (Arroyo, 1981).

Few features have dominated architecture of the flower more directly than those associated with tripping. Connate stamens affording greater precision by directing pollen release, a bilabiate-type calyx providing greater support to the keel as it is tripped, the elaborate interconnections between standard, wing and keel petals and thickening or elaboration of the style are all examples of interacting floral components constrained by the selection pressures associated with the tripping mechanism (Arroyo, l.c.). Explosive tripping as it occurs in the Desmodieae is considered to be the most advanced method of pollen release. Here the staminal column and stigma are held under tension and emerge from the keel eruptively when the configuration of petals is disturbed (see fig.13).

The structure of a typical Desmodieae flower corolla is as follows:- (see fig.14).

4.5.1. Standard

The standard is either sharply deflexed or held erect with a short claw attaching the petal to the receptacle. Immediately above the claw at the base of the lamina are two poorly to well developed (in _Alysicarpus_) appendages which may simply be small folds or developed into calluses of tissue flanking a small channel along the midline.

4.5.2. Wings

The wing is described as being generally cultrate (knife-shaped) with a claw at the base attaching it to the receptacle. The lamina is broadly oblong, rounded at the apex and produces an auricle proximally above the claw. The auricles which are slightly flexed

relative/.....

FIGURE 14

The Desmodieae corolla
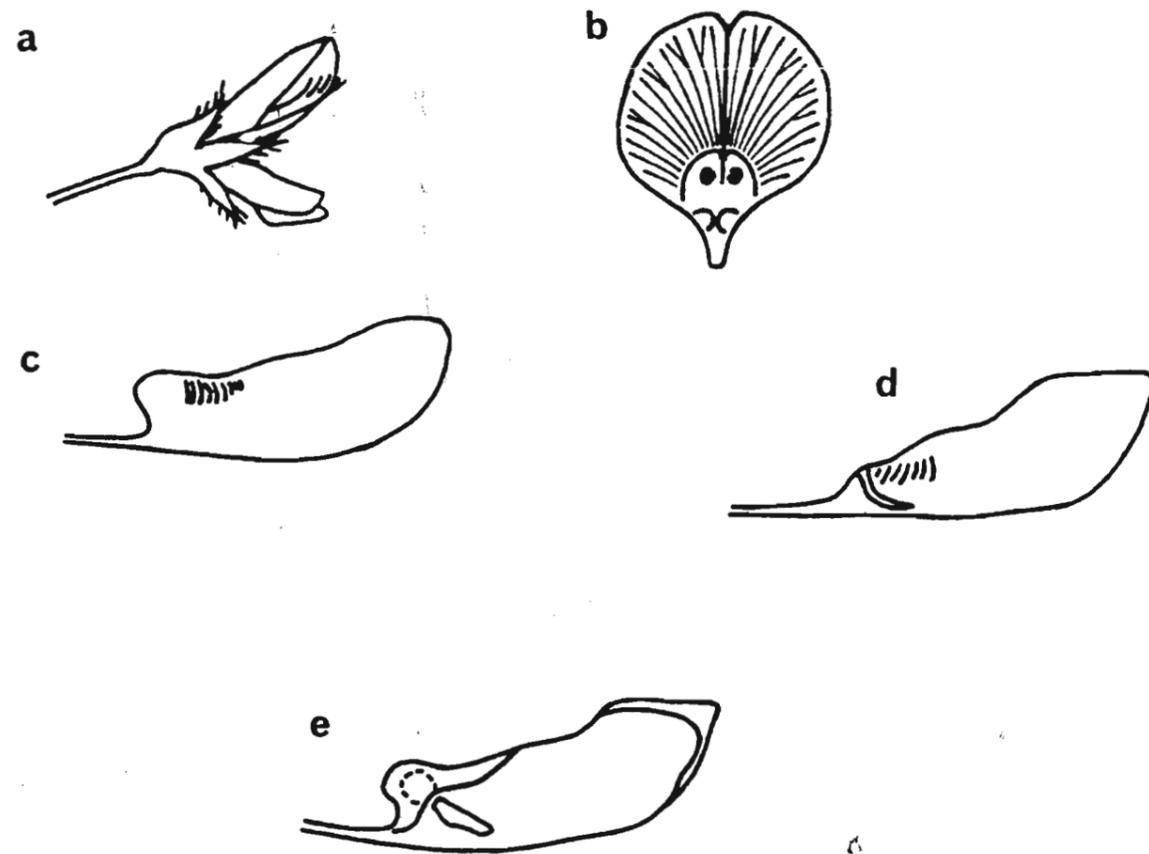
a) Whole corolla in an open, tripped flower.

b) Standard petal. From the base upwards note the claw, the two
    appendages for holding the wing auricles together; the nectar guide
    region with two differently coloured orientation patches and the
    rest of the lamina with translucent venation visible in the back-
    ground colour of the petal.

c) Wing petal. From the left note the claw, the auricle at the proximal
    end of the lamina and the wing petal sculpturing region for insect
    footholds.

d) Keel petal. From the left note the long claw; the transverse ridge
    or 'peg' applied closely to a corresponding socket in the wing and a
    region of transvenal wrinkles also for closer contact with the wing.

e) Wing and keel petals juxtaposed.

relative to the rest of the lamina fit in between the appendages of the standard and hold the wings tightly together at the base. Wing petal sculpturing is visible in most members of the tribe in southern Africa. According to the terminology of Stirton (1981) the region of sculpturing is in the upper basal and upper central portion of the wings i.e. in the area immediately in front of the auricle, and the type of sculpturing is lamellate. These epidermal foldings serve predominantly as footholds for insect pollinators. The lamina of the wing is also 'dimpled' proximally, constricting the base of the staminal column and keel petals. The rest of the lamina folds over and under the keel providing support, and various methods are employed to interlock keel and wing petals more firmly.

    i)   petal surfaces are finely sculptured and these are
         applied as closely to one another as possible.
    ii) an area of minute folds on the keel petal provides
         greater surface contact with the wing which has mirror-
         ing intervenal puckering.
    iii) Proximally, near the hyaline base of the keel lamina,
         often at the region between 'wall' and 'floor' of
         the keel, is a definite pocket or ridge protruding
         outwards and pegging into the wing. Other dimples
         or corresponding sockets may occur as well.

4.5.3. Keel petals

Keel petals are complex in shape representing in their entirety the view of the front end of a ship being cut back gradually, starting a distance behind the 'bow'. At the distal end the petals are fused to one another and are tightly folded over the staminal column, the truncate uppermost parts and distal extremity protruding beyond the wings. The proximal third of the keel is represented by long claws attached to the receptacle, forming the floor of the keel. In this area the walls of the keel are provided by the wing petals.

The chief source of tension for the tripping mechanism is the petal configuration of the keel pulling down on the staminal column. The typical picture after tripping is the disarrangement of wing and keel petals with the sharp deflexing of the keel. The staminal column may lift only marginally.

Tripping is brought about by the pollinator digging its head into
                                                        the base/.....

the base of the standard and moving it backwards. This releases the base of the wing petals. The forelegs placed on the wing sculpture pattern and the hindlegs scrabbling for a hold distally on the wings quickly open the rest of the keel releasing the staminal column against the underneath of the insect. In slow motion it is observed that in the truly diadelphous members, the vexillary stamen appears first as the keel begins to open out. Only when the distal parts of the keel are forced open will the whole column be exposed.

All the factors combined, select to some extent for a particular type of pollinator that 'fits' the mechanism most closely.

4.6. Melittophily

Quoting Arroyo (1981), "The legume family, as borne out by Leppik's (1966) statistical survey of floral syndrome types, is principally a bee-pollinated family, and in constituting one of the largest of angiosperm families, is a major food source for bees. Bees and legumes have been intimately associated with one another throughout their evolutionary histories and this association reaches its climax in the Papilionoideae. The very success of the Leguminosae is reflected in the utilisation of bees as pollinators, and the evolution of the highly complex papilionoid flower has in turn exerted a profound effect on the sensory development and tropheclectic activities of bees themselves."

In the Papilionoideae the mechanism of tripping tends to exclude all but bees, however the flowers tend to be visited by numerous species, representing many different genera. Since there is no parti- cular specialisation in Desmodieae flowers seriously restricting the type of bee that can operate the tripping mechanism, they share polylectic pollinators with a wide range of host plants. The small size of the flower excludes the larger Xylocopa species which are pollinators of many South African papilionoids and the more sophisti- cated tripping mechanism and trapline flowering regime encourage highly skilled semi-social to social bees that show an ability to learn. These bees are able to build up complex behavioural patterns such as territoriality and group foraging, allowing a high degree of constancy to one species of foodsource at any one time despite being polylectic overall (Faegri and van der Pijl, 1971). Such bees

also tend/.....

also tend to be relatively independent of their environment compared to solitary bees and more active over the whole year. Solitary bees tend towards oligolecty and hence are more tightly tied to the life cyle of the 'host' plant. The semi-social and social bees are also more physically active with a much greater energy requirement. Although the subject of pollination energetics is dealt with in detail later, this becomes a critical point in limiting the choice of foodplants available to the potential pollinator. Those plants with the highest energy reward will be selected above others, and the ability of the insects to perceive and remember a number of similar plants enables them to build up the trapline pattern of foraging behaviour, that temporarily at least, provides a high degree of constancy to one species of food source.

Social bees have also developed a communication system permitting them to inform each other about the location and sources of food (see 4.11.1.). This may take the form of odour trails, odour marks on blossoms, a different buzz tone, zigzag return flights which communicate information on food sources to departing workers, and even the use of radar has been suggested. Bees exhibit many adaptations for manipulation and packing of pollen for transport, from structures normally used in grooming e.g. combs and scrapers to unique scopae (brushes) and corbiculae (fringed plates). The more primitive scopae in female bees of the Halictidae (e.g. Nomia) are located on the trochanter through the tibia of the hind leg, with accessory scopal areas elsewhere on the body (Thorp, 1979). Females of the Anthophoridae (e.g. Braunsapis) have scopal hairs restricted primarily to the hind tibia and basitarsus. The most specialised pollen transport structures are the corbiculae of the hind tibia in female pollen-collecting Apidae (e.g. Apis) (Thorp, l.c.). All bees also possess densely packed, branched, body hairs which readily collect pollen.

Quoting Faegri and van der Pijl (1971), "The hoarding instinct of higher social hymenoptera, especially the genus Apis, is of great importance for the effectivity and assiduity of these insects as pollinators ... the instinct to stop collecting when a certain point is reached, does not exist."

Biotic pollination relies on establishing a definite relationship between the agent and the flower to be pollinated (Faegri and van der Pijl, 1971). The pollinator has to visit the flower regularly

as part/.....

as part of its life activity and such a relationship is built up
around attraction devices and energy yielding rewards on the part
of the flower. The effectiveness of this combination manifests itself
in a succession of visits to a flower of the same species. This
sense of 'purposefulness' in which pollen must incidentally be trans-
ferred from flower to flower so that effective cross-fertilisation
can occur, constitutes a true pollinating visit.

4.7. Attraction

Attractants in flowers of the tribe Desmodieae can be considered
under two major categories, a) odour and b) visual attraction.

4.7.1. Odour

Early in the evolution of the angiosperms, pollen must have been
the original attractant and reward of insects; exploited most probably
as a high protein, energy rich food (Buchmann, 1983). In cycads
pollen is known to be eaten and carried by beetles (Faegri and van
der Pijl, 1971). When functioning as an attractant however, pollen
is generally well exposed and is available for rapid collection by
both generalised and specialised insects. In the Desmodieae pollen
cannot be considered as an attractant because it is well hidden and
is only accessible to bees after tripping.

i) Pollen odour

Buchmann (1983) and Faegri and van der Pijl (1971) note many workers
who have observed that certain pollen has a specific odour, either
different from or the same as the overall scent produced by the peri-
anth. Since nearly all the Desmodieae lack nectar, pollen is most
probably the overall reward to pollinators, and such specific pollen
odours might be important in directing bees at close range. Pollen
contains phytosterols that may attract insects because of the odour
they give to pollen grains (Buchmann, l.c.). In the final stage
of pollen wall development, lipoids and other substances may be accumu-
lated on the exine surface. This material which is collectively
called pollenkit imparts colour and odour to the pollen (Buchmann,
l.c.). Simpson and Neff (1983) note that Apis is known to be attracted
to specific components of some pollen, particularly octadeca - trans-
2, cis-9, cis-12 - trienoic acid. They suggest that this is a case

where/......

where a chemical does appear to be a good candidate for a specific substance produced in direct response to selection for pollinator attraction. Little about its taxonomic distribution or physiological function is yet known. Stanley and Linskens (1974) quote substances like 24-methylene cholesterol which bees are unable to synthesise and an ester of the flavone pigment lutein as being found to be specific attractants.

It is very likely that volatile substances in pollen play an important role in learning-conditioning during the larval development of bees because pollen is provided as the major food source.. As bees visit certain flowers they learn by experience the meaning of certain odours in relation to sources of food. A different odour may put off a bee perhaps misled by morphological similarities. This may explain the many instances observed where prospective pollinators approach a flower but will turn away at a short distance, apparently because some feature produces an antagonistic effect (Faegri and van der Pijl, 1971). It should be remembered this may also be due to a 'wrong' visual cue.

The more long lived polylectic, social and semi-social bees exhibit a high degree of adaptability for maximising energy returns from foraging behaviour. Since the quality of returns is in constant flux in any environment, individuals tend towards a high level of fidelity to one pollen source at least on a given trip in spite of being 'generalist' overall (Heinrich, 1983). In addition bees must be able to track floral resources as plants come into bloom and fade so that they can shift to other species to satisfy their nutritional requirements. Specific odours or phagostimulants must therefore be present in pollen for recognition and bees must obtain some chemo-sensory and mechanical feedback from sensory appendages. This in turn would initiate the behavioural response for grooming pollen from body areas and packing it into appropriate transport devices (Buchmann, 1983).

ii) Perianth odour

Floral fragrance is both an attractant and releaser of feeding behaviour (Williams, 1983) and is generally produced in actively metabolic sites in the perianth called osmophores. This is a term coined

by/.....

by Vogel (1962) from two Greek words meaning scent-bearers, and it appears to refer more to a region of function than to specific organelles. They have been noted in several families (Williams, 1983) and because they are metabolically active they stain with neutral red. The region of scent production is characterised by a generally increased surface area over that of the rest of the petals (Williams, l.c.). A study of the microstructure of Desmodieae petals has shown that areas on the standard, wings and tip of the keel are intricately patterned with finely sculptured intervenal crescent-shaped folds but these will also be considered in the next section in their relation to petal colour. It has been shown with orchid work (Williams, l.c.) that the structure of the osmophore region varies from species to species or from genus to genus. The mechanism of fragrance production is not clearly known. One alternative is an accumulation of minute droplets of monoterpenes in the perianth epidermis which diffuse through the cuticle to the outside. There has also been the more widely accepted suggestion that the plant accumulates starch reserves that are actively metabolised to floral fragrance compounds in the tissue immediately below the epidermis, and these are then released through the cuticle (Williams, l.c.). It seems most probable that fragrance does not accumulate in the osmophore but is actively produced and released from the flower. It is believed that ambient temperature is important because floral fragrances are not produced in large quantities on cool overcast days (Williams, l.c.), and it has been observed in the field that there is minimal pollinator activity on such days.

The most common chemicals produced by osmophores are monoterpenes, aromatics, aminoids or hydrocarbons. It seems reasonable (Williams, l.c.) that bees are able to perceive floral fragrances over a distance of at least several meters.

Arroyo (1981) notes, "Explosive pollen release is associated with loss of nectar secretion in Genisteae, and although nectar is not offered, bees have been observed to linger in Genisteae flowers. If these flowers should contain osmophores, as such observations suggest, the legume family provides another example of pollination based on compounds with intoxicating effects." Esau (1965) quotes two examples in the Genisteae, Spartium and Lupinus as having osmophores; located on the wings in the former and on the standard in

the latter/.....

the latter. This suggests that odour is very important in short distance recognition because osmophores are localised in particular areas of petals.

4.7.1.1. Osmophore experiment

In an experiment to determine whether active production of attractant odours occurs in the Desmodieae, flowers of D. incanum, D. velutinum and D. gangeticum were immersed in a neutral red dye solution according to the procedure outlined in section 4.2.

When examined, although areas of the petals frequently showed some uptake of dye in the form of conspicuous red dots or splotches, these never followed a set pattern and in quite a few flowers they were absent altogether. These areas of uptake of dye are considered to be artifacts due to petal damage.

In nearly all flowers tested dehisced anthers stained a deep purple. Undehisced, immature anthers did not, nor did the anthers from abnormal flowers that had not opened fully.

Since the dye was absorbed by some and not by others it is assumed that some form of active secretion must be occurring in the dehisced anthers of normal open flowers. This evidence seems to suggest that attractant odours are produced by the anther contents and not by osmophores in the perianth.

4.7.2. Visual attraction

Flowers attract insects by providing visual stimuli which are interpreted as guides to food rewards and these may be in the form of colour and shape - inclusive of size (Faegri and van der Pijl, 1971). Recognition of flowers which they have perhaps learned to manipulate to extract rewards also promotes temporal flower constancy through which the plant benefits by intraspecific pollen flow and greater efficiency in pollination (Kevan, 1983).

The insect visual spectrum is shifted entirely towards the shorter wavelengths of daylight and shows three peaks of optical sensitivity i.e. in the ultraviolet, blue and yellow parts of daylight corresponding to blue, green and red as the insect sees it (Kevan, l.c.). Equal

proportions of the three appear to the insect as white. Insects are most sensitive to UV light, the light least abundant in their visual spectrum and they boost its importance relative to the other primary wavebands of their colour vision (Kevan, l.c.). However, UV reflectance is no more important than any other primary colour in terms of providing a full picture and if no UV pattern exists one cannot conclude that no pattern of interest to insects is present (Kevan, l.c.). Ultraviolet light reflectance mixes blue with the other colours and superimposes differing shades of colour onto the background. Kevan (1978) has elegantly shown that the number of floral colours visible to the human eye is greatly expanded to the insect so that many more colours become distinct. Insect blue reflecting flowers for example stand out from the background more visibly by being differently brightly visible rather than by being just bright. White (insect yellow) however, reflects brightly across both the insect and human visible spectrum and is thus a good background colour.

Colour functions as a long distance signal especially if flowers are aggregated in inflorescences and many are in flower in a population. This gregariousness of individuals is a common feature in species of the Desmodieae owing to their ability to propagate vegetatively. This array of floral colours allows insects to distinguish species at a distance and whereas the human eye tends to recognise flowers of the same colour by their shape, bees recognise the indefinitely resolved shape at a distance by its distinctive colour. To the bee, flowers are brighter than the soil and vegetation (which is a dull yellow-grey) and darker than the sky (Kevan, 1983).

As yet the full colour vision capability of bees is unknown. Kevan's (l.c.) detailed work on colour perception by insects unfortunately falls short with regard to the many leguminous flowers that are not yellow, blue or violet in colour. By excluding the red end of the spectrum it is difficult to understand for instance how bees perceive the carmine coloured flowers of many Indigoferae, unless it is the blue component of these colours only, that is observed.

These flowers together with the small pink and magenta flowers of many Desmodieae are too small to be pollinated by Xylocopa species which Kevan notes are unusual in being able to sense red colouration. Xylocopa is undoubtedly involved with the larger pink and mauve flowered Tephrosia, Canavalia and Vigna species. Mention must be made though of the unusual flowers of Desmodium repandum which are larger than

the other/.....

the other Desmodieae and are bright red in colour. Faegri and van der Pijl (1971) make the suggestion that most red to pink flowers contain a blue component especially if supplemented by UV. Whatever colour is ultimately perceived from Desmodieae flowers they are certainly recognisable from a distance and the large pink inflorescences of <u>Pseudarthria hookeri</u> were observed to attract numbers of <u>Apis</u> within the first minutes of daybreak.

Higher insects have been noted (Faegri and van der Pijl, l.c.) to react to contrast either between flower and surroundings or within the flower. Floral guides which act as near-goal orientation cues are well reported in Leguminosae (Kevan, 1983). Ultraviolet light absorptive or reflective guide lines on the standard converge on a blotch or patch of a different colour at the base of the petal. This patch is usually a darker pink and is also UV light absorptive or reflective. The insect most probably perceives this as a dark patch against a pale background. Frequently two smaller spots, often yellow, provide a target pattern in the centre of the patch on the standard. These all mark the entrance to the flower where the insect's head initiates tripping by pushing back the standard. The tips of the wing and keel petals are also frequently a darker colour than the rest and provide a more precise orientation cue leading to the standard.

4.7.2.1. <u>Ultraviolet lamp experiment</u>

Under ultraviolet (UV) light, two different types of <u>Desmodium</u> flowers showed up different patterns of UV absorption. No UV reflection was noted. In fig. 15 the standard petals of <u>D. incanum</u> and <u>D. velutinum</u> are compared. <u>D. incanum</u> has a dark coloured flower (mauve) with two light coloured yellow spots towards the base of the standard. Around the yellow spots and between them along the midline of the petal is a darker mauve area which is UV absorbent. Under the UV lamp the lighter spots are highlighted by the UV absorbent margin around them. The rest of the petal does not respond to UV light.

<u>D. velutinum</u>, like many other <u>Desmodium</u> species has much paler flowers with the standard generally a pale pink with two small darker markings towards the base. Under UV light the standard shows two large 'hemispheres' of absorption on either side of a non absorbent midline. The radiating/.....

a

b

FIGURE 15

Ultraviolet light absorption patterns

The standard petal

a) Desmodium incanum. The major part of the petal surface is non
   absorptive except for the rim of the nectar guide and the mid-
   line, in this region. The two areas so demarcated are much lighter
   in colour than the rest of the petal.

b) Desmodium velutinum. Two large hemispheres are ultraviolet light
   absorptive because the petal is a very pale colour in visible light.
   The midline is not absorptive.

The radiating veins visible along the standard in normal light do
not react to UV.

The keels and wings of most species are a darker colour than the
standard, especially towards the tips, and this area is strongly
UV absorbent.   These provide UV reinforced orientation cues towards
the standard. The interaction between visual and UV patterns greatly
increases the possibility for species recognition by pollinators.

4.7.2.2. Petal surfaces

A feature noted by Stirton (mss.b.) and confirmed by petal scanning
in the Desmodieae (see Plate 14), is the highly variable and changing
structure of fine sculpturing across any petal surface. It is suggested
(Stirton, l.c.) that differences in colour in petals are due largely
to diffraction, refraction and reflection of light on these variously
sculptured surfaces.   Both anthocyanins and UV absorbing flavonoids
appear to be substantially confined to the epidermis in the majority
of species (Stirton, l.c.) and the mesophyll layer is the fundamental
reflecting layer in the petal.   Quoting Stirton (l.c.), "The primary
function of the papillate epidermis of petals is to act as a light
trap for incident light and in conjunction with the reflective meso-
phyll, to guide incident light through the pigments contained in
the epidermal cells and return it to the exterior by a combination
of external reflection, refraction and internal reflection.   Another
function may be that of providing a tactile or visual recognition
stimulus to insects." It has been noted earlier that certain regions of
this papillate epidermis may function as osmophores.

Colour changes have also been mentioned earlier as occurring in the
banner markings and overall colour of the petals so as to decrease
the attractiveness and conspicuousness of fertilised flowers to pollin-
ators.   Colours may change so that they are outside the perceptual
range of insects or to match the background.   Pollinators are clearly
able to recognise these floral changes and they only visit the viable
or unpollinated ones. In making this distinction pollinators increase
their foraging efficiency since flowers that have undergone change
invariably offer no food rewards (Gori, 1983). This has selective
advantages to the pollinator, in maximising rates of energy intake,
as well as preventing wastage of energy by visiting non-rewarding
flowers/.....

PLATE 14

Petal surfaces
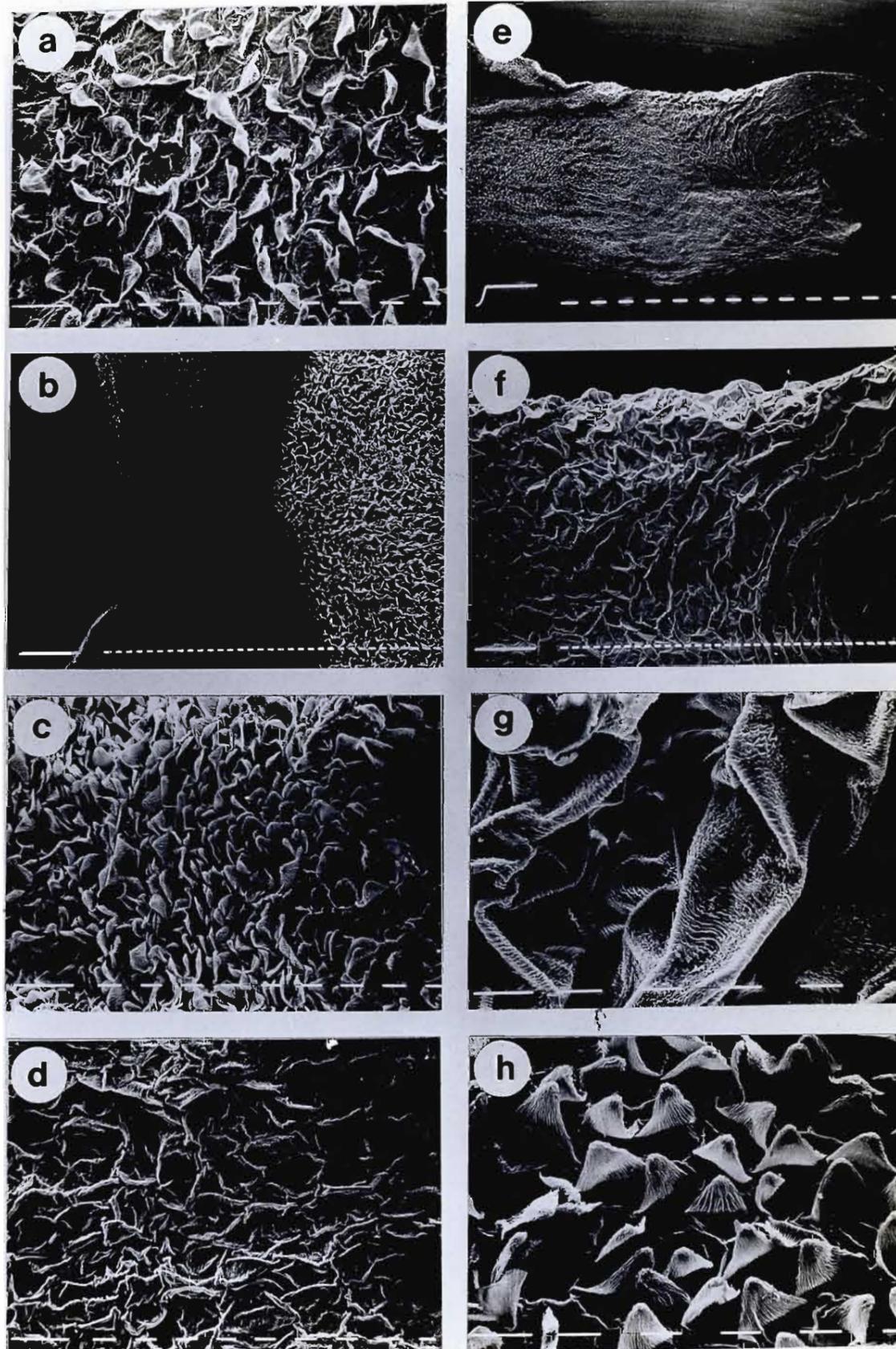
a) P. hookeri   x640,   standard petal near claw at entrance to flower, indicating collapsed (due to drying) conical papillate cells with intricate striations, together these function to trap incident light

b) P. hookeri   x160,   keel and wing apex indicating density of papillae on these surfaces which are regions of darkest colour

c) P. hookeri   x640,   keel surface detail at apex, papillae turgid and conical in fresh state

d) P. hookeri   x640,   keel surface below wing therefore lack of papillae; petal cell outlines and striations

e) P. hookeri   x40,   basal half of wing petal showing auricle and claw (top right and bottom right respectively); also upper central region of intricate folds for insect holds

f) P. hookeri   x160,   region of folds on wing surface

g) P. hookeri   x1250,   furrow detail with striations in this region

h) P. hookeri   x1250,   outer wing surface with papillations and striations

flowers.   Selective advantages to the plant include prevention of wastage of incoming pollen on nonviable flowers as well as increasing pollinator residence times on plants because pollinators have assessed them to be high energy yielding.   This results in greater seed set and pollen donation (Gori, l.c.).

5.6. Rewards

Advanced pollen flowers which are strictly melittophilous, offer a pollen surplus to female bees whose activity is exclusively directed to this reward (Vogel, 1978). The thorough dusting of pollen obtained sternotribically on the bee by the explosion of Desmodieae flowers ensures that some pollen is left even after most has been groomed out of the body hairs and stored. Pollen is a convenient food source and has the advantage of requiring relatively little specialisation on the part of the pollinator to make use of the reward.   This is an example of co-evolutionary adaptation along lines of least resis- tance.

Chemically, pollen has often been described as an excellent food source. Faegri and van der Pijl (1971) quote the following analysis; 16-30% protein; 1-7% starch; 0-15% sugars, 3-10% fat and 1-9% ashes. Stanley and Linskens (1974) state, "For many insects and especially bees, pollen is the principal source of normal non liquid food. Pollen contains most, if not all, the essential nutrients for production of royal jelly, which nourishes the larval queen and young worker larvae. Pollen is the ultimate source of protein and lipid for larvae and imagos of all species and genera of Apidae. Older worker bees use protein directly from pollen; queen imagos, larval queens and the young larvae of both sexes receive protein in the royal jelly produced by nurse bees supplied with pollen. Bee collected pollen is stored in the hive in cells in the combs; changes during storage result in the formation of bee-bread." The quantity of pollen carried on the body hairs of honey bees is larger than that on other hairy insects. Apis and Bombus may carry a load of 100 - 120mg, equal to half their own body weight.

The exine of pollen is considered to be indigestible to bees (Simpson and Neff, 1983) and their patterns of digestion do not require mechan- ical destruction or damage to the exine.   Osmotic differences in
the crop/.....

the crop of the insect most likely burst and release the cell contents. While pollen may be a high quality food source, the relative slowness of the digestive process for the large quantities needed for nutrition, and the fact that more than half of the caloric value of the grain is tied up in the indigestible exine, means that pollen alone is unlikely to be an adequate sole energy source for bees with high energy requirements. It is most probable that bees will supplement pollen by collecting nectar from other plants in the environment.

4.9. Pollen structure in relation to function

The basic pollen type widespread throughout the Leguminosae is a spheroidal tricolporate, finely reticulate-tectate, single pollen grain of about 30μm in diameter with typical angiosperm exine stratification consisting in the mesocolpial zone of a well defined endexine layer about equal in thickness to the foot layer, with a columellate interstitium where the columellae are well spaced and equalling or slightly exceeding in height the combined thickness of endexine and foot layer. There is a distinct tectum, the thickness being less than half the height of the columellae (Ferguson, 1984).

Considerable variation occurs within the Papilionoideae in pollen morphology. The apertures and exine stratification are considered conservative characters (Ferguson, l.c.) consistently of the greatest value in tribal classification while size, shape and exine ornamentation are of secondary importance, at the generic and specific level.

The tricolporate aperture with an equatorial, usually small, circular or elongate thinning of the endexine is the most common type. Apertures are specifically delimited, generally thin walled areas in the outer pollen wall or exine through which the pollen tube usually (but not always) emerges at the time of germination. The major function is to allow for volume change accommodations (harmomegathy) as a result of water relation dynamics (Walker and Doyle, 1975). With regard to shape, two different types of apertures are found. a) elongate, furrow-like apertures or colpi and b) round pore-like apertures or pori. The three colpi are either long or short and are located equidistantly at the equator running meridionally and bisected by the equatorial plane. The three pori, slightly elongated along the equatorial axis are also located equidistantly on the equator at the centre of each colpus. See Plate 15 figs. d and e.

Pollen/.....

Pollen grains of Desmodieae are either prolate with the polar axes longer than the equatorial axes or more often spherical to oblate with the polar axes shorter than the equatorial axes. The pollen of Desmodium varies from 25 - 40μm in size while in Alysicarpus grains are up to 70 μm. (Ohashi 1971).

4.9.1. Exine stratification

The exine stratification as far as most Leguminosae is concerned consists of two basic layers, the inner endexine and outer ektexine both composed of resistant sporopollenin. (Fig.16)

This is a section in the mesocolpial zone as in many species the aperture membrane is mostly just endexine. Above the foot layer is a region of internal, upright rod-like elements called columellae covered by a roof-like layer, the tectum (Walker and Doyle, 1975).

One of the major trends away from this general exine stratification occurs in the Desmodieae. A considerable thickening of the endexine with reduction to eventual loss of the foot layer is associated with a marked increase in complexity of the ektexine (Ferguson, 1984). In P. hookeri the trend is seen with a thick endexine, very narrow foot layer and short columellae covered by a densely perforate tectum (Ferguson and Skvarla, 1981). Grains with the exine complete, containing columellae and tectum are called tectate. Tectate grains may be further categorised as tectate imperforate (without any holes in the tectum or tectum perforate (with small holes or tectal perforations) Walker and Doyle (1975). In tectate grains the possibility exists for elements to be formed upon the roof or tectum which then constitute the sculpturing (Walker and Doyle, l.c.). The sculpturing in Desmodieae however, arises not from supra-tectal elements but from the way tectal perforations pattern the surface. If the diameter of the perforations becomes larger than the breadth of the pollen wall between them, an open network or reticulum may result. In reticulate pollen the tectal perforations become spaces or lumina and the walls which make up the reticulum are known as muri. Trends in Desmodieae are from perforate, fine-reticulate, as in D. velutinum and D. gangeticum (Ohashi, 1973) to entire smooth as in Alysicarpus zeyheri (Ferguson and Skvarla, 1981) which has specialised by losing the foot-layer altogether and developing an entire, very thick tectum
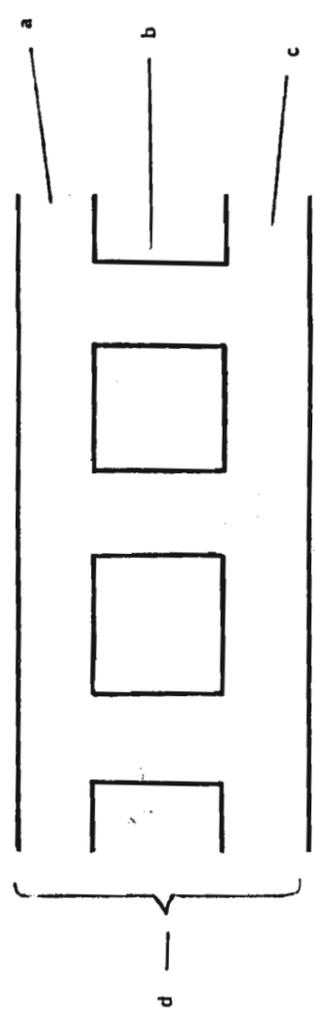
FIGURE 16

Pollen wall stratification of a typical angiosperm pollen grain

after Walker and Doyle, 1975.

a) Tectum

b) Columellae

c) Foot – layer

d) Ektexine

over dense columellae. A trend also to finely rugulate is noted in one species of Desmodium (Ferguson and Skvarla, 1979). Columellae are often short and dense with a thick, perforated or not, tectum.

Desmodieae and Indigofereae pollen differs from the Phaseoleae type, denying a close relationship which many other characters suggest. Ferguson (1984) makes the important observation that pollen morphology in these two advanced tribes has been evolved in a secondary adaptive role because the Desmodieae and Indigofereae are the only two advanced tropical tribes with an explosive pollination mechanism. Arroyo (1981) suggests that the widespread development of self-compatibility in these tribes may also affect pollen morphology. Phaseoleae differs from the other two tribes in that the aperture type found, i.e. the tricolporate condition, occurs only in grains where the footlayer is present. (Ferguson, 1984).

4.9.2. Pollen walls as adaptive systems

The essential function of the pollen grain and the tube that emerges from it, is to deliver a pair of gametes to the embryo sac (Heslop Harrison, 1979). This functional objective of double fertilisation is dependent on a whole sequence of adaptations from dispersal, inter-action with the stigma and style, nutrition, growth and target finding (Heslop Harrison, l.c.). The pollen grain wall is the most critical feature in the journey between the anther and receptive stigma, and in some cases there is co-evolution between wall structure and polli nator type. It is concerned not only with protection and dispersal but with the hydrodynamics of the gametophyte within it, and also in various ways with interactions (pollen recognition) on the stigma. The pollen grain is another example of a functional system which is an evolutionary compromise between many external and internal constraints (Ferguson, 1984). The large diversity in pollen form can therefore be better understood especially since similar functional ends can usually be attained by many different morphological and physiological devices (Heslop Harrison, 1979). An important consequence of this is that a number of elements may not readily be interpreted in adaptive terms at all, being related to lineage and the evolutionary events of a remote past, or being simply the products of fortuitous change. (Heslop Harrison, l.c.).

4.9.3. Harmomegathy

Harmomegathy is the term applied to the structural adaptations concerned with accommodating to volume changes in pollen grains. These occur through the loss or gain of water and it is in the control of this that one of the main physiological functions of aperture mechanisms is to be found. (Heslop Harrison, l.c.).

4.9.3.1. Desiccation

Water is removed from grains immediately before and during anther dehiscence. Afterwards desiccation proceeds further but at a rate determined by the pollen type. In Desmodieae anther dehiscence occurs up to twelve hours before anthesis probably since pollen must be dry and powdery enough to fly out in a cloud after tripping. Some 15-30 percent loss in fresh weight can be expected during dehydration. During the first phase of partial dehydration in the anther, pollen lies immersed in locular fluid (Heslop Harrison, l.c.) and water is withdrawn by deficits developed elsewhere in the anther or filament. Longitudinal slits appear in the basifixed anthers as dehiscence begins. As soon as pollen is released and comes into contact with the air, the second phase starts as a new set of gradients is established. Resistance to over-desiccation builds up with simple infolding or buckling of the colpi; by interleaving shutters of sporopollenin plates reducing the permeability of the wall and by the desposition of lipid surface materials which are synthesised in the tapetum and transferred to the exine during the final phase of pollen maturation (Heslop Harrison, l.c.). These become entrapped in the margins of the colpi as they draw together during the final dehydration of the grain.

4.9.3.2. Rehydration

Successful pollen must land on a suitable receptive stigma. This is discussed further in the next section, but all stigmatic surfaces must provide conditions for rehydration of compatible pollen as an essential preliminary to germination (Heslop Harrison, l.c.). Water uptake and consequent dilation of the grain is the reverse procedure of dehydration. As the grain expands the surface lipids are dispersed into the medium. The apertures open and because, as the grain hydrates there is less hydraulic resistance to further inflow of water, uptake

is accelerated (Heslop Harrison, l.c.).   With more of the intine
exposed as the colpi gape, a tube begins to emerge from the grain
and germination has begun.

4.10. Style - stigma structure in a functional role

Taxonomically, the stigma surface is as variable as other morphological
features of the flowering plants but all papilionoids fall into
the category of the wet stigma type with the receptive surface consist-
ing of low to medium length papillae (Heslop Harrison and Shivanna,
1977). The style was determined to be solid in P. hookeri (see Plate
15, fig. c) and the principal source of secretion for the wet stigma
is the stigma cells of the receptive surface which secrete copiously
into the interpapillate spaces (J. and Y. Heslop Harrison in Cutter,
1982a). See Plate 15, fig. b. The mature stigma however, appears
to be smooth, non papillate and dry because the surface is ensheathed
by a thin (75-100nm) but highly impermeable pellicle which encloses
the papillae of the receptive surface. These are immersed beneath
the pellicle in their secretory products (J. and Y. Heslop Harrison,
1983). Pollen cannot become hydrated on the intact surface so in
the untripped flower pollen can surround the receptive stigma without
germinating and thereby prevent premature selfing. The pellicle
is ruptured when the flower trips because it is very easily dislodged,
and in springing up, the stigma is likely to come across non-self
pollen first on the insect's body (see Plate 15, fig. a). Self-pollen
however, is likely to be present as well and is now capable of germinat-
ing on the receptive surface in the stigmatic exudate. Inhibiting
reactions to self-pollen must be present slowing down their growth.
It is this that must extend the life of the repeatable presentation
type flowers whose pellicle is broken on the first tripping and also
gives foreign pollen the edge in the explosive method. The secretion
forms a lipid-rich emulsion with a mucilaginous aqueous phase which
reacts cytochemically for protein and carbohydrate and has esterase
activity (J. and Y. Heslop Harrison, l.c.). Pollen grains hydrate
within 5 minutes and germination begins in the next 10-20 minutes.
The site for any inhibitory reactions to self-pollen tubes is likely
to be in the style as growth proceeds from the stigma. Pollen tubes
grow through the intercellular spaces of a specialised transmitting
tissue in the solid style (J. and Y. Heslop Harrison, 1982b) and
intercellular fluids secreted by style cells provide a medium for
pollen/.....
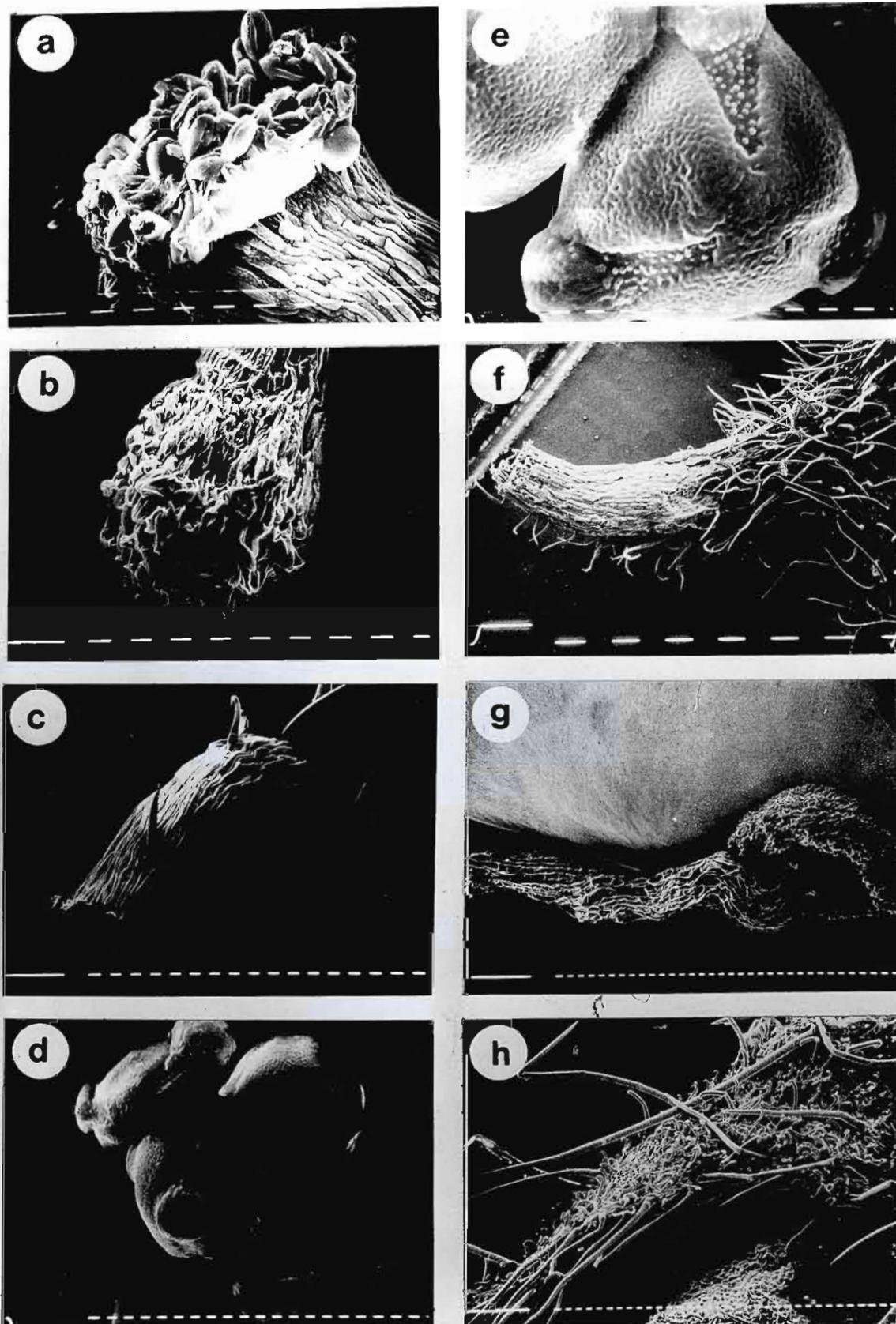
PLATE 15

Stigma, style and pollen

a) P. hookeri   x640,   tripped stigma with pollen grains on
                              the surface

b) P. hookeri   x640,   untripped stigma from a bud with
                              pellicle destroyed by drying; papill-
                              ate surface visible

c) P. hookeri   x320,   solid style and style hairs

d) P. hookeri   x2500,   pollen grains with swollen artifacts
                              in the position of the pori; note
                              colpi and perforate tectum

e) P. hookeri   x5000,   pollen grain detail

Aids for fruit dispersal

f) P. hookeri   x80,   dried persistent style on fruit tip

g) P. hookeri   x160,   hilum with funicle attached

h) P. hookeri   x160,   calyx tooth with cilia

pollen tube-growth and nutrition. Work by J. and Y. Heslop Harrison (1982c) has shown that in protein spectra of stigma eluate and stylar fluid in Trifolium pratense, although the two were similar, two glyco-proteins were peculiar to the stigma and one to the style with minor variations elsewhere. It was felt that since the stigma was incapable of discriminating between self and other pollen, if discrimination did occur, it must be in the stylar fluid and it may be linked to the constituent not found in the stigma eluate. An interesting feature to come out of their work was that the difference in protein composition indicated a considerable degree of independence between the secretory system of the stigma and style.

4.11. The Pollinator

4.11.1. von Frisch's experiments on bee behaviour (von Frisch, 1966)

Observations on animals, and ants in particular, have shown that they move at a certain angle to the position of the sun and consequently go in a straight line, doing the reverse on the return journey. This method has limitations over long periods because the sun changes position. Bees however use the sun as a reliable compass as well as taking the time of day into consideration. In an experiment, an established feeding pattern was built up in a colony of bees and the hive was then removed to a completely different locality. Food sources were placed in a number of different directions from the hive but the majority of bees only used the food source that lay in the same direction used the previous day. This and further work showed that bees are so familiar with the sun's position at any hour of the day that they still found the direction to the feeding place to which they had been trained previously in the evening, although the morning sun is in a different relative position. They can only do this after they have learned the daily course of the sun from several days spent in free flight and this continual adjustment by learning and memory enables bees to follow the sun's changes. The ability to grasp the full daily course of the sun and fly in trained directions is of vital importance in bee survival.

Bees recognise localities in a number of different ways. Colours, of which blue and yellow, and black and white are the most contrasting, are recogised easily. Nearby objects are used as landmarks and distance is memorised between them and the hive. Scent is produced by scent organs and can be used to direct individuals to a food source or back to the hive. Bees' eyes are also particularly sensitive to

polarised light and its wavelengths. This light comes from the blue
sky and its intensity and wavelengths depend on the position of the
sun. They not only keep position by using the tiny portion of the
eye that faces directly towards the sun, but the many facets take
in different patterns of light distinct for each point of the compass
and representing many different intensities. In this way, colours
and contrast patterns are greatly expanded to the bees senses. Navi-
gation only fails when skies are heavily clouded and can't transmit
polarised light. (A marked drop in bee activity was noted in P.
hookeri pollination studies on very overcast days). The relative
importance of landmarks or sun orientation in guiding bees depends
on how crowded or open environments are.

A high quality control food source, initially unattended, was later
seen to attract a few scout bees. Within a few hours large numbers
of bees had arrived, generally from the same colony. The first scouts
collect pollen or nectar from the source and return to the hive.
They disgorge the mixture from the stomach onto the comb where it
will be used by nurse bees and then proceed to perform a 'round dance'
whirling around in a narrow circle constantly changing direction,
right and left in quick succession describing one or two circles
in each direction. This dance infects surrounding bees who with
outstretched feelers attempt to keep in contact with the dancers'
body so that the central bee appears to trail a 'comet tail' of other
bees. This continues for a minute or so after which the 'dancer'
breaks loose and flies out of the entrance to the particular foodsource
to bring back another load. Since the hive is in darkness fellow
bees only follow the dancer through a sense of feeling and smell.
Each time the scout flies out a number follow to the food source
and as they return and perform the same ritual, greater numbers of
bees become involved. New comers do not actually follow the dancer
directly but learn from the symbolic gestures of the 'round-dance'
where to locate the food source outside the hive. If due to cloudy
weather or if the food runs out, the dance stops and bees remain
in the hive. Whenever a plant newly come into flower is discovered
by the scout bees, they announce their discovery by means of a dance
and their fellows are able to go straight to the source. While a
forager is collecting, scent from the pollen or flower remains on
the bee. While dancing on her return, a trace of the scent remains
on the body and the other bees pick this up by means of their feelers

(organs/.....

(organs of smell) as they touch the body of the dancer. This is committed to memory and flower scent is the clue for bees to be able to recognise the kind of flower which is the food source as opposed to all other flowers of a similar colour. As a food source runs out, even though bees may still be present, no more dancing is performed and no newcomers are attracted. Every worker bee has a scent gland near the tip of the abdomen which can be protruded as a moist glistening pad. If a worthwhile amount of food makes the help of more bees desirable, foragers also use the scent organ during their flights to flowers. This was proved by experiment where on removal of scent glands, bees still danced and located food sources but were not able to attract many more bees to the source.

Distance to the food source is important and bees foraging near the hive perform 'round dances' while those foraging at a distance return and perform a figure of 8 'wagging dance'. This is done by the bees running straight forward for a little way, returning to the starting point in a semi-circle and then describing another semi-circle on the other side in a figure of 8. This can go on for minutes at the same spot. The most striking difference between this and the 'round dance' is a rapid shaking movement of the abdomen which is always performed during the straight part of the forward movement (wagging-runs). At the same time the dancer makes a noise of very short repeated vibration impulses (30 per second) indicative of the sound produced by wing buzzes. Bees are very sensitive to vibrations on the ground but not through the air. The dance and straight 'wagging-runs' are closely attended by other bees. At distances of 50 to 100 metres away from the hive 'round dances' are replaced by 'wagging-dances' so that distance can be communicated. Information however is much more precise and a regularity in the course of the 'wagging-run' is observed. For a distance of 100 metres between hive and food source, the straight line part of the dance sequence is performed 9 or 10 times in 15 seconds; for 500 metres roughly 6 times; for 1000 metres 4 or 5 times; for 5000 metres 2 times and for 10,000 metres little more than 1 turn per 15 seconds. Therefore the decisive signal for distance is given by the period of time for the 'wagging-runs' i.e. by the wagging time which is sharply emphasised by the abdomen movements and noise production. Bees are able to transmit if they have been into a headwind by indicating a greater distance than if there was no wind, and a shorter distance is indicated if there is a following wind. Calculation of distance thus depends on the time taken or the strength exerted.

The direction of the good source is also contained in 'wagging-runs' during the figure of 8 dance. For showing the right direction, bees use two different methods depending on whether the dance takes place (as it usually does) inside the hive on the vertical comb or outside on a horizontal surface. In the latter, if a bee flies to a food source with the sun at an angle of 40° to the left and front, this angle is kept in the 'wagging-run' indicating the direction of the food source. The bees follow after the dancer and notice their own position with respect to the sun as they follow the 'wagging dance' and by maintaining the same position on their flight they can locate the source. This applies only if the dancer can see the sun or at least a blue sky. Inside the hive however, the sky is invisible and the comb surface is vertical. Instead of using the horizontal angle with the sun they followed during their flight to the food source, scouts indicate direction by means of gravity in the following way. Upward 'wagging-runs' mean that the food source lies towards the sun, downward movements away from the sun. An upward 'wagging-run' 60° to the left of vertical points to a food source 60° to the left of the direction of the sun (fig. 17). Information passed on to bees by means of their delicate sense of gravity is transformed to a bearing on the sun once they are outside. In the tropics when the sun is directly overhead there is no foraging activity but even an angular distance of 2-3° is sufficient for bees to recognise the direction from the sun's position and to announce it correctly in dancing. The faceted eyes rigidly fixed in the head, constructed out of thousands of slightly diverging single eyes are extremely suited for measuring angles. In hilly or mountainous or in other obstructed terrains, the 'wagging-run' indicates the shortest route not the intermediate changes of direction and the indirect route is given rather by distance information.

Pollen odour in exclusively pollen collecting runs has been proved to be a critical attractant in locating the food source. In an experiment where pollen in two flower types with a strong perianth smell were swapped around, bees went unerringly for the recognised pollen odour. (This reinforces the hypothesis of pollen odour being the major attractant in Desmodieae).

4.11.2./......

a

hive ●———————→ reward
      60°

b

reward ←——————— ● hive
              120°
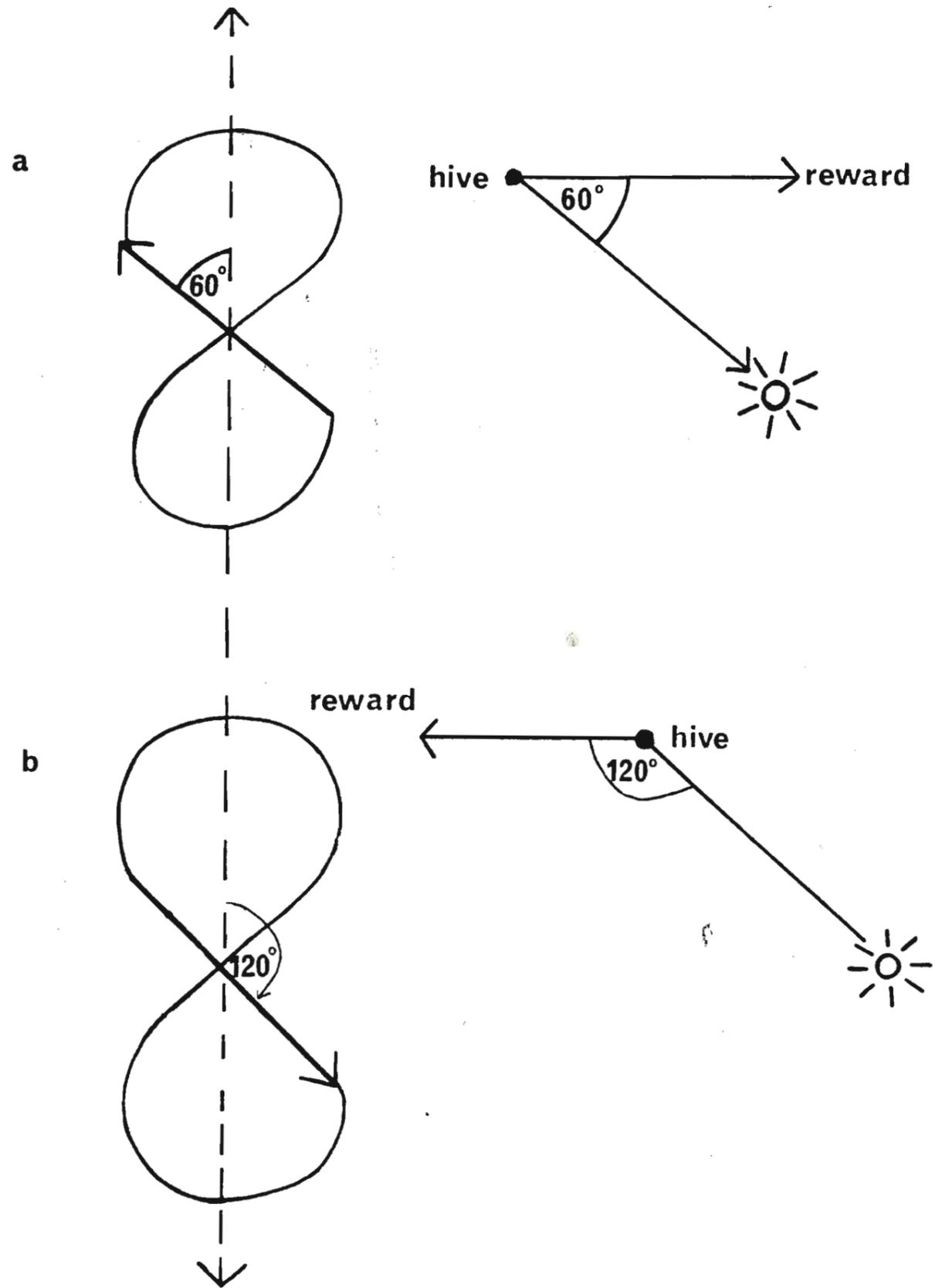
FIGURE 17

The figure of 8 'wagging' dance in Apis mellifera (von Frisch, 1966)

a) 'Wagging run' (thick line indicated with an arrow in the figure 8) made 60° to the left of vertical in the hive.

   As the bee leaves the hive it flies toward the reward which is 60° to the left of the suns direction.

b) 'Wagging run' made 120° to the right of vertical in the hive.

   As the bee leaves the hive it flies toward the reward which is 120° to the right of the suns direction (and directly opposite to the previous direction)

4.11.2. Foraging strategy and energetics

While making attractants and rewards as attractive as possible, a restriction on the amount produced is needed because of the cost to the overall energy budget of the plant. A careful balance is also required to make sure insects move on to other plants to effect cross pollination (Heinrich, 1983). Economy is practised by restricting foragers to a select clientele of pollinators. This has been accomplished in the Desmodieae by hidden rewards requiring specialised techniques for access. Quoting Heinrich (l.c.), "The plant's strategy is to be selective in its rewards. The foragers' strategy has been to circumvent the plant's mechanisms that limit access. The plant has evolved flowers with design and reward complexities to use the forager to the plant's best advantage. The ensuing coevolutionary relationships with food energy as the primary payoff to pollinators for cross pollination service, has evolved as an intricate game of strategies and counterstrategies."

There is considerable selective advantage to pollinators in the ecossystem in which a concentrated flowering period is found in some plants and protracted periods in others, as well as spacing through the season of the flowering periods of different species. This together with the adaptive radiation of flowers to the range of available pollinators (and vice versa) creates a great complexity of niche opportunities for foraging strategies (Proctor, 1978).

A specialised type of pollination syndrome is a relatively narrow ecological niche limited to only one or a few species of insect, and this occurs commonly in the families Orchidaceae and Asclepiadaceae. Another is found in the Desmodieae where although foragers are limited to a specific type of bee able to effect tripping, flowers are available to large numbers of different genera and species of bees.

The following are important aspects of foraging behaviour that affect foraging returns.

Pollinator foraging should be concentrated in habitats where the expectation of yield is greatest. They have to choose between a number of potential food plants which vary enormously in density and ease of handling (Levin, 1978). They must feed upon pollen which is most efficiently harvested (a feature very much in favour of Desmodieae flowers), and which has a sufficiently high nutrient return in terms of calories (Levin, l.c.). All flower visits require energy

and are energetically inefficient if expenses exceed gains. Negative items in the energy budget are the need to maintain a temperature differential between the body and air in cold weather, predator avoidance, long flying distances between flowers and between nest and foraging area and the work entailed in obtaining the reward (Faegri, 1978). Desmodieae are principally summer flowering in the warmer tropics and subtropics so temperature differential is not a major loss. As indicated above, rewards are relatively inexpensive to the right insect in terms of harvesting, except when bees hover. The big expenditure is in long distance flying between flowering patches. A plant will therefore only be exploited if the amount of time spent in travel and extraction is more productive than the same time devoted to another species in the same habitat (Levin, 1978).

Natural selection favours individuals genetically predisposed for efficiency in feeding. This favours increased ability to choose the best plants, to locate them and to manipulate their flowers (Levin, l.c.). The optimal foraging strategy may then be defined as that which yields the greatest net energy and nutrient gain per unit foraging time. Pollinators should differentiate between different plant species by forming 'search images' of the most favourable ones. The tendency of individual pollinators to forage for a period of time within a plant species rather than foraging at random among several suitable species (flower constancy) is a typical form of this behaviour (Levin, l.c.).

Analysis of pollen loads collected by bumblebees (Heinrich, 1983) indicated that individual bees sometimes visit numerous species of flower on any one foraging trip. These should not be interpreted however as 'inconsistant' generalists because this largely ignores the sophistication of foraging energetics. Whether a bee is a specialist or generalist must be assessed not only by the kinds of flowers it visits but also by the number and sequence of different flower visits relative to flower availability (Heinrich, l.c.). Bees could collect relatively pure pollen loads not because they are flower constant but because they have site-fidelity to an area; where at a particular time there are no other acceptable plants in bloom (Heinrich, l.c.). Individual bees of one or more species may utilise the flowers of different plant species in different proportions while

foraging/.....

foraging at a particular site, e.g. bumblebees are generalists as species but as individuals they specialise. A great variety of different pollen loads is returned to the colony at one time but each individual carries a relatively pure load. In the field <u>Bombus</u> is not as strongly programmed genetically as for example is <u>Apis</u>, to search for a specific flower that is likely to be rewarding (Heinrich, l.c.). With honeybees new foragers are directed by the dances of scouts from the hive to rewarding flowers. Site-specifity reduces a forager's random movements permitting it to maximise its energy return for energy investment. Foraging space is minimised by moving from a plant to one of its near neighbours (Levin, 1978). A further development in site-specificity with a memorised 'search image' is the tendency for some pollinators to repeat specific foraging paths. Bees are not attracted to the flowers as such but to the location where they expect and remember flowers to be. Traplining can best be examined as a modification of site-specificity. After a bee has found large concentrations of food at one site it will return again and again to that site until the food is exhausted (Heinrich, 1983). For example honeybees restrict visits to specific foraging areas, often several miles from the nest. Individual bees active at one site some distance from the hive, normally do not switch immediately to new superior food rewards as they come into bloom closer to the hive; but the hive constantly tracks new food rewards by way of the scouts that direct new recruits to them (Heinrich, l.c.). When the food rewards at a site are renewable (replenished each day) as well as limited (only a few available each day) then the traplining forager must visit several sites in succession on any one trip, increasing the opportunity for cross pollination. Visiting the different sites in a specific sequence may be the best strategy for remembering all of the sites. In addition it may be the best strategy for enhancing foraging returns at specific flowers; there is little payoff in revisiting flowers before they have had time to be 'replenished' (Heinrich, l.c.). This strategy is employed most obviously in the Desmodieae, and insects are guided within a patch by tripped flowers becoming immediately unattractive, with the standard collapsing over the staminal column and blocking the orientation cues. Colour changes follow shortly after.

Traplining pollinators should be relatively large in size with high energy demands, since resources are highly dispersed in time and

space/.....

space although they are predictable.   Faegri (1978) mentions thatlong flights are more likely to occur with relation to pollen collecting
than nectar gathering.   Flowers with small energy rewards cannot
be utilised by higher energy demanding pollinators and this restricts
them to those visitors with lower energy requirements (Faegri, 1978).
Selection thus promotes tighter linkage between high energy yielding
rewards and high energy demanding pollinators.

The relatively high degree of constancy to floral species at the
individual bee level when foraging for pollen, reduces time and effort
in learning to locate new resources and to manipulate diverse mechanisms
(Thorp, 1979).

In the field bees sample the available reward spectrum at any one
time and rank it from richest to poorest and specialise on the most
rewarding flower type (Heinrich, 1983).   With time, levels become
reduced to that of others in the environment. Heinrich (l.c.) describes
the theory of 'majoring-minoring' in bumblebees to account for a
behaviour pattern observed to enhance foraging uptake.   A strict
major on a 'good' flower is always the best strategy for a reward,
however minoringis a necessary compromise required to sample and track
resources changing over time.   Net rewards are presumably measured
by averaging the returns from many flowers visited.   If so, then
bees may have to make 'runs' periodically, switching from one kind
of flower to another in order to assess reward. Such 'runs' or tempor-
arily 'pure' majors in an overall majoring-minoring strategy accounted
for the general pattern observed (Heinrich, l.c.).

From the plant's perspective, it is advantageous to make the pollinators
runs as long as possible so that pollen is deposited on receptive
stigmas of the same rather than different species.   A corollary of
this is the periodicity of flowering in plants both within and between
years and also their presentation of pollen at specific and limited
times of the day, usually when rewards are highest (Faegri, 1978).
P. hookeri may flower over many months of the year depending on
where it is growing and what the rainfall pattern has been.   Generally,
however, at a particular locality, flowering occurs at the same time
each year for up to six weeks. Flowering is continuous with only
a relatively few flowers opening in each inflorescence every day.
The time of flowering is very specific with anthesis occurring an
hour before dawn and the bulk of tripping over by 11.00a.m.   This
predictability enables pollinators to specialise when the density
and quality/.....

and quality of the resource plants is high. This time factor, further increases pollinator fidelity. If sampling is a major criterion for making runs of varying lengths, then the predictability of rewards should determine the length of the runs (Heinrich, l.c.).

Specialisation and flower constancy are evolutionary and behavioural responses to the absolute abundance of different food plants. In this regard it is interesting to contemplate that the uniformity in papilionoid flower shape as a whole may provide similar "imprint" expectations of rewards to bees who recognise the generalised pattern.

Even within limited daily foraging periods a complex of bee species may partition a pollen resource with distinctly separated diurnal peak foraging times, although their foraging periods overlap (Thorp, 1979). This was clearly observed in the pollination strategy of P. hookeri where perhaps feeding periods were restricted due to competition. Two separate peaks were noted for Apis and Nomia. Thorp (1979) mentions that the time sense of Apis has been demonstrated frequently, returning to a food source in synchrony with its presentation.

The aspect of 'skill selection' is also important. Not all bees in the field are equally skilled (Heinrich, 1983). Individual variation in foraging skill has been shown in honeybees foraging from vetch (Heinrich, l.c.). Handling accuracy of complex flowers is a function of experience, and inaccurate handling is energetically expensive i.e. takes a longer time. It should be noted that the potential profits available from 'difficult' flowers are often enormous in comparison with those that require no skill to manipulate, since fewer bees are capable of handling them (Heinrich, l.c.). This selection force has been very much in evidence in the development of Desmodieae, considering the large amount of pollen directed accurately onto the bee.

Possibly the largest investment of energy for flower handling that a forager can make is to hover, but hovering is also the mechanism of visiting the most flowers per unit time. This was observed in P. hookeri inflorescences with Apis only. As an approximation hoverers visit three to four times more flowers than the fastest non-hoverers and can collect a large quantity of pollen for passing on to different plants. With energy expenditure so critical to the pollinators it is easier to understand why tripped flowers immediately become unattrac-

unattractive/.....

unattractive. Desmodieae flowers have also overcome the problem of a pollinator staying too long at one flower by their explosive dehiscence. Bees were seen to be constantly active and moving in amongst P. hookeri inflorescences.

Bee foraging is only optimal in terms of a balance of compromises that sometimes have to be made in the face of conflicting selective pressures (Heinrich, l.c.). Some bees are able to forage more optimally than others because they have fewer conflicting constraints e.g. sterile workers do not 'need' to make the compromises of seeking mates or concerning themselves with oviposition. More time can be devoted to pollen gathering in social bees, where labour is divided, than in solitary bees.

Pollinator foraging behaviour has a profound effect on the breeding structure of populations because neighbouring plants are likely to be close relatives. Pollinators are much more sensitive to spatio-temporal fluctuations in plant sociology than are the breeding or genetic systems of plants. They may considerably alter the level of inbreeding in a population (Levin, 1978).

4.12. Reproductive strategies - with particular reference to Pseudarthria hookeri

The Desmodieae are recorded as having predominantly self-compatible breeding systems (Arroyo, 1981) particularly in the more widespread members of the tribe. This is part of an overall trend towards self-compatibility in more herbaceous groups as opposed to woody ones (Arroyo, l.c.). Tropical herbaceous legumes as a whole are more commonly self-compatible than their temperate counterparts. Many tropical herbaceous species inhabit fire-prone savannas subject to marked seasonal fluctuations in climate, often in open and semi-disturbed areas. Greater selection for this type of breeding system is found in more unstable habitats (Arroyo, l.c.).

Autogamy is a commonplace result of self-compatible breeding systems. Many papilionoids including Desmodieae however, retain the ability to outcross by means of the tripping device. In making tripping a requirement for fertilisation, there is a good chance that outcrossed pollen will reach the stigma first if the flower is visited. Careful observation over a number of days determined that the bulk of outcross-ing occurs relatively early in the morning, but even after repeated

counts/.....

counts no more than 20% of flowers which opened on a day were tripped by visitors. The vast majority of flowers self-tripped as the heat of the day and environmental disturbance increased. Even in the 20% visited by bees, a large proportion were geitonogamously selfed because pollinators usually made many within-plant forays and visited genetically identical inflorescences.

A characteristic demographic pattern in P. hookeri, as well as in a number of other Desmodieae, is the clumped nature of the populations. Numbers of individuals occur in dense patches which are often some distance apart. P. hookeri has an effective method of vegetative reproduction, producing rhizomes and reproductive roots which give rise to genetically identical individuals for some distance around the parent. The occurrence of vegetative reproduction as well as a considerable capacity for autogamy suggests that individual clumps of P. hookeri are genetically similar. It has also been noted that in traplining a group of bees arrive together at a clump, either direct from the hive or from another population. The only real opportunity for cross-pollination therefore occurs in the first few flowers visited by each bee from a previous patch. It is also expected that after tripping a few flowers in the new patch, bees will again become saturated with 'same' pollen.

The question of how variable a population of P. hookeri really is, could be tested by gel-electorophoresis of crushed leaf extracts from a large number of individuals in the population using the elegant technique of Brain (pers. comm.) for Acacia karroo. Here an enzyme system profile is chosen which has at least a polymorphic expression for one of its enzymes. In the example, the pyroxidase profiles of A. karroo gave very good insight into how similar or different genotypes could be within a population by comparing observed gene frequencies within one polymorphic pyroxidase. Extrapolated to different populations compared in the same way this technique has provided an extremely valuable tool for understanding population dynamics as well as improving phytogeographical theories. This technique was not used for P. hookeri because a preliminary enzyme scan of leaf extracts did not reveal any significant pyroxidases. Other enzyme systems will have to be investigated.

The Desmodieae can thus be considered as predominantly autogamous.

Trends/.....

Trends towards autogamy are seen most obviously in the cleistogamous flowers of Lespedeza. Even if self-tripping does not occur to break the pellicle, it has been proved that in P. hookeri the membrane ultimately breaks down and allows self fertilisation. This was proved in the bagged experiment described in the next section. A trend also shown in the Desmodieae is that autogamous papilionoids generally have flowers that are reduced in size compared with predominantly outcrossing species (Arroyo, 1981). It is possible that selection for self-compatibility came about as a result of the tripping mechanism. Since tripping maintains high levels of outcrossing in many legumes, it is only by virtue of bypassing the need for insects that autogamy becomes possible (Arroyo, l.c.). Tripping could therefore be viewed in self-compatible papilionoids as a relic character which because of its complex morphological basis would only disappear with time, following the loss of self-incompatibility (Arroyo, l.c.). It is more than likely however that selection still operates to retain tripping because of its widespread occurrence and advantages, and so it is better to view tripping as having been responsible for the build-up of self compatibility in the Papilionoideae. Quoting Arroyo (l.c.), "While tripping and associated maintenance of outcrossing in the absence of self-incompatibility might be seen as casual factors for loss of genetically inherited self-incompatibility in Papilion- oideae, it is also evident that the same accumulation of self-compat- ibility has pre-adapted papilionoids for rapid segregation of autogamous lineages in those situations in which selection favours selfing. Selfing thus perhaps arises more readily in Leguminosae than in many families in which the change is directly from an obligate out- crossing system. This feature might also partially explain the success of papilionoid legumes as early pioneers, weeds and desert and savanna dwellers living in highly unstable habitats where either pollinators are unreliable or where rapid population turnover is desirable. The real evolutionary effect of the tendency towards self-compatibility in the Leguminosae will also become evident upon sophisticated analyses of speciation rates, niche diversity and levels of heterozygosity."

Lloyd (1980) illustrates two ways in which self-fertilisation increases the number of gametes contributed to the next generation. a) a plant contributes two gametes to each self-fertilised zygote but only one to each cross-fertilisation. This presumably provides new individuals with all the genetic qualities that have adapted the parent particularly well to that specific habitat. Self-fertilisation thus has an invari-

invariable advantage in individual selection because of the increased success in fertilisation. This is not true of group selection however. b) self-fertilisation increases the total seed set in many circumstances and hence contributes to an increase in the number of offspring. Quoting Lloyd (l.c.), "It has been confirmed in natural populations of a number of genera that autogamously fertilised flowers produce a greater seed-set than allogamously fertilised flowers." Many cross-fertilising species achieve only low levels of seed production in terms of seed set divided by fruit set (Lloyd, l.c.) so selfing has the advantage of increasing this amount.

In the bagging experiment with P. hookeri the seed count in the two bagged (hence completely selfed) inflorescences proved to be between 6 and 18% higher than in the two unbagged normally outcrossing inflorescences. These figures not only represent a quantitive measure of the enhanced effect of selfing on seed set, they also reflect conversely the equivalent percentage reduction in seed-set in the outcrossing situation. This could therefore be equated to the percentages of cross fertilisation occurring in each inflorescence and the method provides a useful way of determining this.

According to Lloyd (1980) two types of selfing are evident in the Desmodieae.
1) 'Competing' self fertilisation occurs when a fraction of the ovules are self fertilised either autogamously or geitonogamously by the action of the pollinating agent at the same time as cross fertilisation. 2) 'Delayed' self fertilisation which occurs when a fraction of the ovules are spontaneously self-fertilised usually after all opportunities for crossing have passed.

The important aspect however is the balancing of the numerical advantages of self-fertilisation with the qualitative superiority of the progeny arising from cross-fertilisation. Therefore even though crossing is less efficient and more costly than selfing, selection retains the process at a relatively low percentage in the average population of P. hookeri. The greater fitness which results from outcrossing is considered to arise more from heterosis or hybrid vigour than from increased genetical variability (Lloyd, l.c.).

The breeding system influences the variation pattern of the population (Grant, 1971). Given two or more homozygous individuals differing
with/.....

with respect to two or more genes, outcrossing generates a much greater amount of individual variability by recombination and maintains a heterozygous condition for at least one gene in most of these recombinational types. Continued selfing has the opposite effect decreasing the amount of heterozygous individuals. A strictly autogamous population is expected to consist of a small number of true breeding pure lines, but these expected results of selfing may not be realised in actual populations (Grant, l.c.). Even a low level of crossing regenerates new variability. Furthermore continued selfing will not lead to a decline in the proportion of heterozygotes at the expected rate if the heterozygous types have a selective advantage over the homozygotes. Such persistent genic heterozygosity due to heterozygous advantage has been found in Phaseolus lunatus (Allard and Workman, 1963) and in Acacia karroo (Brain, pers. comm.). The actual composition of populations in many autogamous plant species is thus a good deal more complex than would be expected on the basis of extrapolations from the pure-line concept (Grant, 1971). The populations of these predominantly autogamous species approach in most aspects those of regularly outcrossing species by containing a greater store of variability (Grant, l.c.). The relative fitness of selfed derived plants always decreases as the level of stress or competition increases, and heterosis increases as selection becomes more severe. These factors may promote the 'heterozygous advantage (Lloyd, 1980).

Overall selection of mating patterns can thus be viewed as effecting a compromise in individual selection between the advantages of selfing and those of outcrossing. In the former the number of successful gametes contributing to zygotes is increased as is the number of seed set. This is required in a colonising situation. In the latter the advantages are in maintaining heterosis and increasing the average fitness of the zygote in group selection. The critical difference appears when the advantages of increased colonising ability are outweighed by the disadvantages of genotype-dependent elimination under harsher environmental stresses. Autogamy is thus an advantageous 'autogamy of conquest' in a colonising situation.

It should be noted that the ultimate balance between the two is dependent on many adaptive mechanisms linked to it e.g. pollination and seed dispersal syndromes, adaptive strategies relating to reproductive effort and phenology.

In many plants self fertilisation by geitonogamy may be unpreventable.

According to the theory of r- and k- selection (MacArthur and Wilson, 1967), genotypes that allocate a greater proportion of their resources to reproductive strategy (r- strategists) will be favoured in environments with high density independent mortality, while genotypes that allocate a low fraction of resources to reproduction in favour of vegetative growth, vigour and competition (k- strategists) are favoured in crowded environments where most mortality is density dependent (Solbrig, 1980). The crucial factor in the r- and k- selection argument is the magnitude of density independent relative to density dependent mortality (Gadgil and Solbrig, 1972).

Density independent mortality environments are unsaturated or unpredictable and they favour opportunistic strategies in plants. There is a minimum investment of energy in vegetative functions and survival is maximised during favourable periods while enough seed is produced to overcome the unfavourable periods. Mortality is most frequently due to environmental unpredictability such as drought, floods, temperature extremes, fire and substrate instability.

Density dependent mortality environments are saturated and more predictable and they favour considerable investment of energy in vegetative functions to reduce mortality, or a high seed production level to reduce the losses due to mortality. Here vegetative reproduction, competitive seedlings and a perennial growth habit help to cope with these biological interactions. Mortality is most frequently due to the more predictable effects of resource competition, pathogens and predation.

The environment favoured by P. hookeri is saturated in that it represents a particular successional stage in the grassland component of bushveld savanna and open woodland (Ward, pers. comm.). The plants associated with P. hookeri which include among others Cymbopogon sp., are a grassland precursorial stage to woodland regeneration (Ward, l.c.). This is a fire controlled succession which is found if fires are infrequent enough to reduce grassland to a shorter mixed Themeda-type or even Aristida-type grassland (Ward, l.c.). The presence of P. hookeri so often near bushclump or forest margins is the result not of its integral association with these margins but of the effect of fire being lessened by the margins' proximity (Ward, l.c.). This

is also/.....

is also the prime site for woodland regeneration. If fires are removed for long enough, the P. hookeri - Cymbopogon association gradually becomes the site of bush encroachment and these species are pushed out. Conversely if fires are too fierce and frequent P. hookeri is prevented from gaining a foothold in open grassland. Most commonly however, clumps can be seen scattered in grassland as typical pyrophytes.

Vegetatively P. hookeri is a k- strategist surviving competitively by being able to quickly produce aerial stems from a large underground rootstock, and being able to reproduce vegetatively by means of rhizomes and reproductive roots. Aerial stems that survive burning produce copious new shoots from every node. They are able to survive in relatively high density clumps and have a high frequency of flowering individuals. These factors indicate a high competitive ability. A large percentage of individuals show varying degrees of predation mostly on the leaves, and very high levels of parasitism by bruchid beetles of the seeds. Parasitism must therefore play an important role as a negative selective factor in the reproductive strategy. Although seed dispersal mechanisms are discussed in the next section it appears that seed dispersal strategy is extremely opportunistic and dependent very much more on a series of chance events than the more precise strategy of pollination. The reason for this becomes more apparent when one considers the ephemeral nature of the successional sere in which P. hookeri grows, and the unpredictability of its environment. The area best suited for the growth of the plant is constantly changing owing to the push-pull effects of a fire controlled sere, the effects of forest and grassland dynamics and the semidisturbance factor caused by man and his grazing animals. P. hookeri can thus be considered as an habitually colonising species consisting of an extended genepool within which alternative phenotypes are selected in alternating residential and colonising episodes (Lloyd, 1980). It is this that most likely maintains a high level of heterzygous advantage even in a predominantly autogamous breeding system.

The overall fitness of the phenotype is equal to its probability of establishing new populations. P. hookeri thus has an r- strategy-type reproductive phase increasing seed set and the chance to establish new populations. Large numbers of seed are produced at the expense of seed size and a strong seed coat has led to the development of efficient and enduring mechanisms for maintaining the seed in a state of enforced dormancy. This production of large quantities of seed

gives/.....

gives the plant a competitive edge in an uncertain environment as well as in escaping the large amount of seed and seedling predators. The number of seed produced by individual plants is generally also higher in perennials with a vegetative means of life prolongation. This makes for greater success in this type of environment. Seeds have an advantage in P. hookeri of often being dispersed in a pod containing up to 6 seeds. If this should arrive in a suitable locality and two or more plants can become established, then the ability to self-fertilise and vegetatively reproduce at a later stage provides a distinct advantage in starting new colonies in spite of the inherent uncertainties of long distance dispersal. Even so with biotic dispersal of seed from the parent there is a low probability of seed reaching a favourable locality in space and time for germination. Even lower is the chance of success for a seed to develop into a new individual. With all the opportunities for mortality during germination and seedling establishment, a staggered seed germination (progressive breakdown of dormancy) is the optimal strategy to maximise seedling survival is an unpredictable environment. Seed is also held over in the pods until a suitable environment exists for dispersal and germination, usually at the onset of the summer rains.

In spite of this reproductive strategy, P. hookeri is not a weed or ruderal colonising new open habitats. It is tied to a relatively specific seral stage in succession. The main difference between true weeds and the colonising role of P. hookeri within its niche, is that in the latter, sites are relatively saturated by other species. As such they are typical k- strategists adopting an r- strategy- type reproductive capacity. The plant does often occur in various degrees of disturbance such as old cultivated lands, roadsides etc. where vegetation is regenerating but not in open or waste sites.

It may be better under final consideration to use the narrower defini- tions of r- and k- strategies given by Gadgil and Solbrig (1972) for the sake of greater clarity. The biotype with the higher values of population growth at low population density is the r- strategist while the biotype with higher values of population growth under con- ditions of high population density is the k-strategist. Even though P. hookeri is under strong selective pressures to cope with density independent mortality factors such as fire and an uncertain environment, it is also under strong selective pressures to increase its fitness in the density dependent situation of its particular niche. The

reproductive strategy of P. hookeri may therefore be interpreted as increasing its fitness under unfavourable conditions by diverting some of its resources to combating these conditions, i.e. a high seed production to reduce losses due to mortality, both density-dependent and independent. A large number of seeds is not sufficient evidence for r- selection. It must be shown that the difference is genetically fixed, that it represents an actual difference in resource allocation between reproductive and non reproductive tissue and that these changes are correlated with increased density independent mortality (Gadgil and Solbrig, 1972).

The overall reproductive and survival strategy of P. hookeri can therefore be considered in terms of coping adequately with the major factors of competition, predation (and parasitism) and environmental uncertainty. In the end, once woodland encroachment has proceeded to the stage of shading out P. hookeri, its competitive ability is cut drastically and it can no longer survive.

4.13 A specific case: The breeding system of Pseudarthria hookeri

4.13.1. Aim I

To determine flowering strategy, and pollination strategy in a natural population of P. hookeri.

4.13.1.1. Objectives

A natural population was selected and observations made over one night and two days. The experiment was commenced on the first day by selecting a number of inflorescences and removing all previously opened flowers and young developing ovaries. This was done in order to a) avoid confusion about flowers remaining from the previous day and b) ensure the seed produced was the result of the following treatments. Half the inflorescences were bagged in order to remove the element of parasitism and to ensure self-fertilisation. During the first day the timing of anther dehiscence in buds due to open the next day was observed and night observations were made for any pollination activity as well as to note when anthesis occurs. From the onset of pollination activity samples of pollinators were collected for identification and counts were made at regular intervals of the numbers of flowers tripped; these were then removed from the inflores-

cence to facilitate counting. The cause of tripping whether by pollinator or self was noted and a count of flowers removed at the end of the day gave the total opened for that day.

4.13.1.2. Methods

Only one large clumped population of P. hookeri was examined here and it is realised that a more intensive study is needed next season to compare interclump data and also populations from different localities.

Four inflorescences were selected and previously opened flowers and young developing ovaries removed. Two inflorescences were placed in light muslin bags which were tied around a wad of cottonwool at the base of the inflorescence. From the afternoon of the first day various buds likely to open the following morning were opened every hour to check for anther dehiscence. At the start of pollination activity various insects, both pollinators and others, were captured on the plant in large plastic bags drawn suddenly over an inflorescence. Insects were placed in vials containing a little formalin and later sorted and sent for identification. Records were kept of how many flowers tripped at half hourly intervals after anthesis in all four inflorescences. Tripped flowers were removed and totalled up for the day. Results were compared and tabulated (see table 1).

4.13.1.3. Results and Discussion

Stamens are very much shorter than the style-stigma, with large turgid anthers in the bud stage prior to anther dehiscence. Rapid elongation of stamens precedes anther dehiscence which was noted in flower buds from 17.00 onwards the evening before anthesis was due. Chow (1974) noted in Alysicarpus vaginalis that when the anthers started to dehisce a very narrow fissure started in the middle of each anther sac. Anther dehiscence was caused by the pollen sacs contracting and shedding the pollen and it took about two hours from the beginning of anther dehiscence to complete pollen shed. Chow (l.c.) records that anther dehiscence started shortly after midnight in A. vaginalis. Early dehiscence is considered to be maximising the chance of pollen transfer in a suitable dry and powdery state as soon as the flower is visited, but it is also recognised as possibly being a remnant of a protandrous situation in Leguminosae. Early anthesis is commonly seen in legumes (Stirton pers. comm.). No insect activity was observed during the

night/.....

TABLE: 1 Inflorescence bagging experiment in

Pseudarthria hookeri

NO.   OF   FLOWERS   TRIPPED

TIME	UNBAGGED INFLORESCENCES		BAGGED INFLORESCENCES	
	1.(full sun)	2.(Partial shade)	1	2
05.00	0	0	0	0
05.30	1	0	0	0
06.00	0	10	0	0
06.30	21	11	0	0
07.00	18	15	1	0
07.30	24	10	0	0
08.00	13	10	0	0
08.30	25	5	0	0
09.00	1	0	0	0
09.30	1	0	0	0
10.00	0	0	0	0
10.30	0	0	0	0
11.30	23	0	0	0
16.00	1	4	0	0
UNTRIPPED	6	3		
TOTAL FLOWERS OPENED	134	68		

night but anthesis occurred from 04.00 onwards with vexillum reflexion. The first indication of dawn was at 05.25 on a cloudless morning and the first pollinator activity was seen by <u>Apis mellifera</u> from 05.30 while still fairly dark. Sunrise was at 06.05 and bee activity was noted to be modest.   Counting of tripped flowers began by 05.30 in the unbagged inflorescences. This gradually built up until 07.00am, a period when the bulk of tripping may be said to have been due to pollinator activity.   Tripping continued at a high rate until 08.30 but this was due mostly to self-tripping by loss of turgor as heat and wind disturbance increased.   A further suggestion is made by Chow (1974) that self-tripping occurs after petals have expanded to their full size i.e. self-tripping becomes part of the developmental process.   It was proved however that bagged flowers, which were more protected from the environment did not self-trip.   Between 08.30 and 09.00 <u>Apis mellifera</u> activity tailed off rapidly to be replaced by a smaller bee of the genus <u>Nomia</u>. By 09.00am the weather became cooler with cloud and a breeze.   Near 10.30 this cleared and the period is marked by a distinct drop in flower tripping again indicating that heat and possible water deficits are the major cause of self-tripping.   Between 10.30 and 11.30 with the full heat of the sun again, all but 10% of the open flowers tripped.   Hutton (1960) concurs in that by 11.00am flowering was completed in <u>Desmodium uncinatum</u>. <u>Nomia</u> activity continued at a low level until late afternoon and by 16.00 a number of the remaining flowers were still untripped because they were either deficient, partly eaten by insects or protected in the centre of the inflorescence from atmospheric disturbance. The adaxial stamen was often presented for a while as the flower began to self-trip.   <u>Apis mellifera</u> which is a highly social and advanced bee is considered as the major pollinator, foraging at the ideal time when maximum rewards are available.   <u>Nomia</u> is a semi-social bee of the family Halictidae and burrows in sandbanks.   It utilises resources after <u>Apis</u> at a time when less rewards are present because many of the flowers have self-tripped.   There is good evidence from observation that <u>Nomia</u> only arrived as <u>Apis</u> was leaving thus indicating avoidance of competition by <u>Nomia</u>.   Flowers in the bagged inflorescences failed to trip at all because of the 'protective' nature of the bag shading flowers and preventing wind disturbance.   The flowers wilt in the bags at the end of the day and self-fertilisation occurs anyway. Other insects collected off the plants were a preponderence of a small semi-social bee <u>Braunsapis facialis</u> of the sub-family Xylocopinae. One of a group of allodapine bees which nest and burrow in the pith of stems and twigs (Michiner, 1974;   Skaife, 1979), it is very small,

up to/.....

up to 3 or 4mm in length and was found foraging on pollen left behind after flowers had tripped. They were too small to activate the tripping mechanism. A small wasp, Ormyrus sp. was collected which is parasitic on gall forming chalcid wasps (Imms, 1970). Seed of legumes is widely parasitised by beetles of the family Bruchidae which lay their eggs on the young fruit, and the larvae burrow through into the seed (Johnson, 1981). A possible connection between the two may exist but no bruchids were captured. Johnson (1.c.) reports the presence of Bruchidius sp. parasitising seed of P. hookeri. Many thrips and a scarab beetle of the genus Leucocelis were found foraging on flower material.

4.13.2. Aim 2

a) To determine the effects of enforced self fertilisation on seed production and to observe the effect of insect predation in unbagged inflorescences.

b) Long term germination tests were performed on both bagged and unbagged seed to test how long seeds took to germinate and to see how effective impermeable seed coats are as a dormancy factor by providing ideal conditions for germination. Seeds remained untreated in order to determine the above.

4.13.2.1. Objectives and methods

250 pods in each of the two bagged and any two unbagged inflorescences were sampled for number of seed produced per pod. The seeds in each pod were counted, including, but noting separately, the number of parasitised and aborted seeds in each. The pods were arranged into a number of seed classes using the number of seeds per pod e.g. 14 pods have 1 seed, 37 pods have 2 seeds etc. Four histograms were drawn comparing the total pod number for each seed class for the 250 pods of each inflorescence, comparing the two bagged with the two unbagged inflorescences (see figs.18 &19). Two further histograms combining the information of two like inflorescences were drawn so 500 bagged pods were compared with 500 unbagged pods (see fig. 20). Two histograms were also drawn to compare the number of pods and number of parasitised seed contained in each for the combined situation of 500 bagged pods and 500 unbagged pods. (See fig. 21). Finally 100 seeds each from bagged and unbagged inflorescences were germinated four months after maturing in sterile petridishes on moist filter paper. Each lot of 100 seeds was separated into

5 batches/.....

Inflorescence II Unbagged

No. of pods

Seed classes

No. of seeds per pod

Inflorescence I Unbagged

No. of pods

Seed classes

No. of seeds per pod
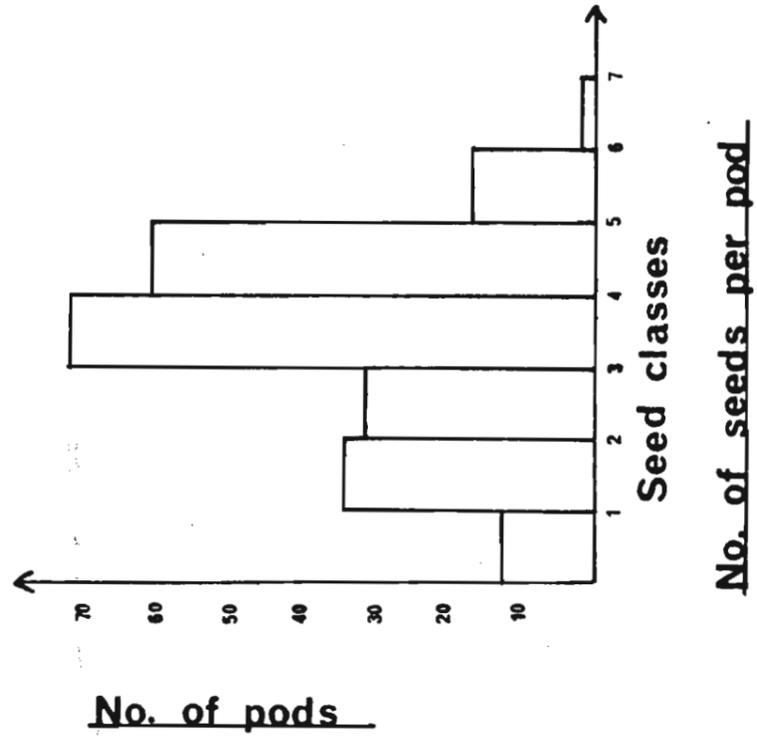
FIGURE 18

Pseudarthria hookeri

Histograms comparing numbers of pods with numbers of seeds contained in each.

The number of pods contained from 1 - 7 seeds respectively is compared for two unbagged, normally outcrossing inflorescences (250 pods each).

FIGURE 19

Pseudarthria hookeri

Histograms comparing numbers of pods with numbers of seeds contained in each.

The number of pods containing from 1 to 7 seeds respectively is compared for two bagged inflorescences (250 pods each).

Inflorescences I & II Bagged.

No. of pods

Seed classes

No. of seeds per pod
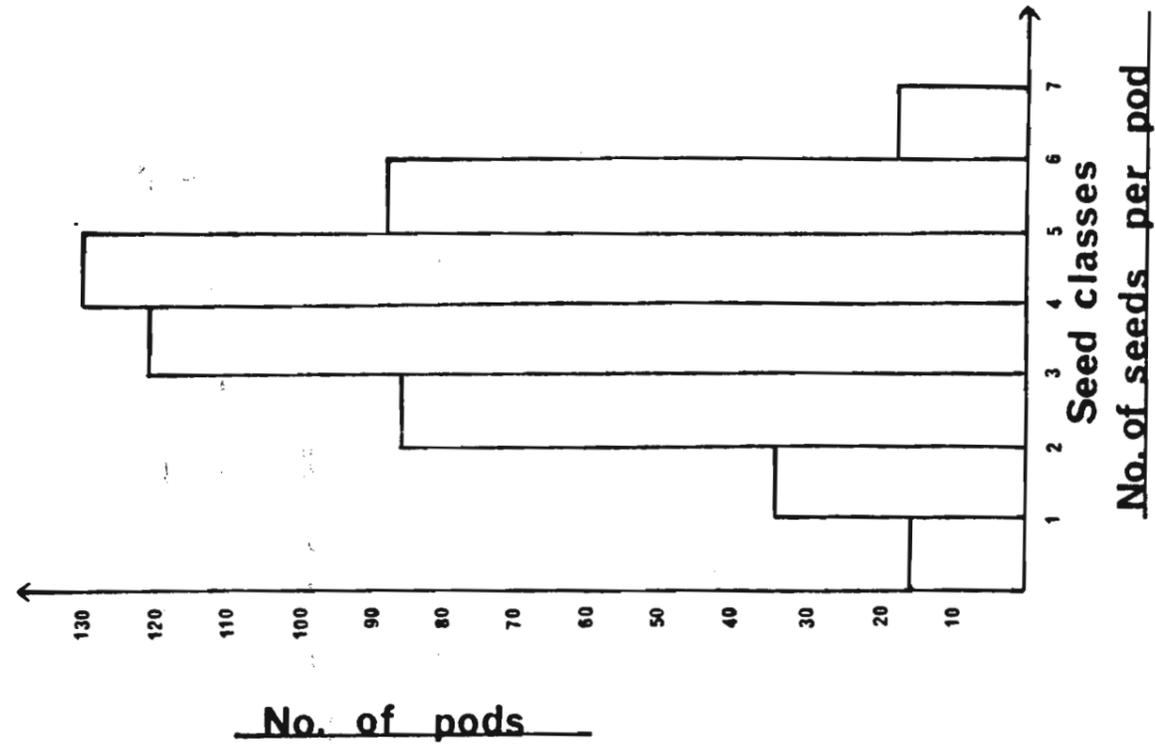
Inflorescences I & II Unbagged.

No. of pods

Seed classes

No. of seeds per pod
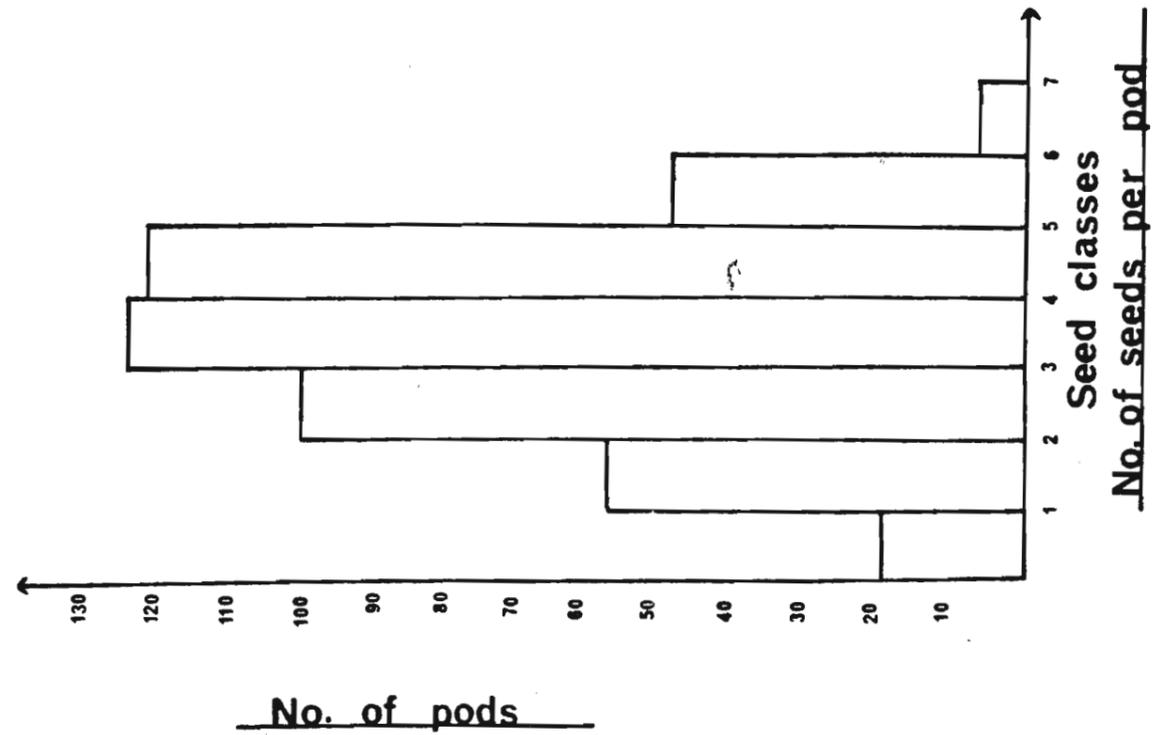
FIGURE 20

Pseudarthria hookeri

Histograms comparing numbers of pods with number of seed in each

The number of pods containing from 1 to 7 seeds respectively is compared for two inflorescences (500 pods) in each of the following treatments.

1) Unbagged - normally outcrossing

2) Bagged - completely selfed.

5 batches of 20 to counteract the effect of any fungal infection. Each was maintained at between 20°C and 30°C for alternating twelve hour periods and moistened regularly so the filter paper remained wet. A constant high humidity was maintained using a water bath at the bottom of the germination chamber. Seeds were counted at 10 day intervals and the germinated ones removed.

4.13.2.2. Results and Discussion

The total seed count in the bagged situation is slightly higher than in the unbagged inflorescence i.e. enforced selfing has increased the quantity of seed produced by between 6 and 18%. Reasons for this are discussed in the previous section. Bagging reduced parasitism tenfold. Seeds that are parasitised in bagged inflorescences may be due to larvae emergent from eggs layed on the inflorescence prior to bagging. It has been observed that levels of seed parasitism may vary considerably and other populations visited have indicated much higher levels of parasitism than shown here. This breeding system experiment is preliminary to a more extensive investigation and as yet the overall sample sizes are too small to draw any further conclusions from the results.

The results of the germination experiment are summarised in Table 2). After 80 days, extremely few seeds germinated under the constant high humidity, plentiful water and warm temperature conditions. It is interesting to note though that seeds from the bagged inflorescences appear to have germinated a little more readily. Again the sample size is too small to draw any valid conclusions from this.

The low level of germination could be due either to a very low viability or a strong inherent dormancy factor. Chow (1974) in germination experiments with Alysicarpus vaginalis and two species of Desmodium, found well over 90% viability in all of them with seeds that had been properly scarified.

A random sample of P. hookeri seed was tested under the same germination conditions as outlined in 4.13.2.1. but they were lightly damaged by piercing the testa with a needle point. This allowed water uptake by the seed and the germination percentage was very high.

This weakening of the seed coat was found to be essential for a good germination percentage to occur. In addition Chow (l.c.) found that

newly/.....

TABLE: 2 <u>Germination of P. hookeri seeds at 10 day intervals</u>

X 10 day intervals	Number of seeds germinated	
	Bagged	Unbagged
0		
1	1	-
2	1	-
3	3	1
4	1	1
5	2	1
6	1	1
7	2	-
8	3	-
Total out of 100	14	4

newly matured, treated seeds would germinate immediately. Since there was no need for a resting period it is believed that dormancy is not chemically controlled but rather due to the hard impermeable seed coat. This is gradually weakened over time by fire or microbial action in the soil and this provides the staggered germination discussed earlier as being an optimal strategy for survival in a seasonal savanna-type ecosystem.

An estimate of the number of seeds produced by a population of P. hookeri has been made based upon my own observations and those of Chow (1974).

In six overall pod counts of separate inflorescences the number of pods per inflorescences varied from between 250 and 800. In observations of 3 species of Desmodieae, Chow (l.c.) averaged out pod formation at roughly 50% of flowers produced. It could therefore be expected that an inflorescence produces in excess of 1600 flowers. Since the number of flowers opened in a day on any inflorescence varied from 68 to 134, taking an average of 100, this gives 16 days of flowering for the average inflorescence. This appears to fall within expected observations of P. hookeri populations considering that many inflorescences flower out of phase with one another to provide a flowering period of 4 to 6 weeks. Since the number of seeds for 6 counts of 250 pods averaged out at 1000 one can expect at least 3200 seeds per inflorescence. If a population averages between 50-200 inflorescences, even if 20% are parasitised or aborted this still leaves in excess of half a million seed available for dispersal.

4.14.1. Seed dispersal in P. hookeri

P. hookeri pods mature within 20-30 days after which they dehisce along the upper suture and open partially or fully, like a book. The seeds which remain firmly attached to the central lower suture are exposed either upwards or outwards. After fertilisation Chow (1974) found that seeds of Alysicarpus vaginalis and two species of Desmodium reached maturity within 14-28 days. It was noted that hard impermeable coats were formed some days before colour change and final weight indicated full maturity. Seeds are either light brown, yellow, khaki or green and are not markedly contrasted against the pod background.

The most challenging aspect of seed dispersal in P. hookeri is the length of time seeds are retained exposed on the plants before they are dispersed. Providing there has been no fire, the bulk of seed is still seen exposed and attached to the pods four to five months after maturing. There are two possible explanations for this phenomenon. 1) A selective presentation of seed is made to specific seed dispersal agents utilising seed as a food source. 2) Seed is best protected and held over in the standing-crop situation to await dispersal during more favourable conditions after winter i.e. in time for the rain and windy season.

Although the former possibility seems more likely at first because seed is presented in an opened pod from an early stage, close observation and the experience of a number of naturalists has proved otherwise. Seed may be considered as a valuable food source to mammals (particularly rodents) and to both granivorous or omnivorous seed-eating birds. Seed is produced in bulk and has a high protein content. Climbing rodents such as Dendromus and Mastomys may reach seed by climbing up the stems of plants, but they play no role in dispersal since all seed is broken and chewed before swallowing. Although the bulk of seed remains attached to the pods, some always drop off and filter down to the ground. Terrestrial rodents are common and a few (Saccostomus) are known to carry seed in cheekpouches and store them underground in their burrows (Smithers, 1984). Some P. hookeri seed therefore, besides providing an important basis of a large food chain, may escape being eaten and may germinate in the ground. Rodents do not tend to move very far away from their territory however, so long distance dispersal by this method is unlikely. Seed eating birds which superficially might appear to be the most obvious choice of dispersal agent from a standing-crop population of P. hookeri in fact play a minimal role. According to Maclean (pers. comm.) and Clancey (pers. comm.) seed of the size and type of P. hookeri which are presented in this manner, are not usually taken by birds. Close observation of a population seemed to support this, as no bird activity was ever noticed near plants. The high proportion of seeds per pod counted two and a half months after the first count again supports the fact that little seed was removed from the standing-crop. The only possibility conceded was that certain weavers of the genera Ploceus or Symplectes which are omnivorous (Clancey, 1964), may take and disperse seed which has passed undamaged through the gut. Forest weaver (Symplectes bicolor) has been seen to collect Acacia robusta seed from forest margins (Ward, pers. comm.).

Ground/.....

Ground feeding birds alternatively, may account for some dispersal. A prerequisite would have to be that ground cover was not too dense. After a fire for example, yellow or green seed might contrast strongly against a burned background and Francolins of the genera Pternistis and Francolinus, Guinea-Fowl of genera Numida or Guttera and Doves of the genera Turtur or Aplopelia would certainly distribute seed for some distance. It is felt though that any dispersal accomplished in the above manner is opportunistic and seed must escape the digestive process undamaged.

It can be seen therefore that seed is relatively well protected in the standing-crop situation. The hard seed coat makes parasitism difficult and although there may be a small loss due to rodents and groundfall, it now appears likely that the interpretation of holding over seed attached to pods to await more favourable environmental conditions is the correct one.

P. hookeri pods appear to play an integral part in seed dispersal. The calyx tube and pedicels appear densely covered with hooked hairs under S.E.M. (Plate 7fig.a). The calyx teeth are dry and sharp and are also covered with hairs and are ciliate (Plate 15 fig. h). The pod itself is open presenting a large surface area and is densely covered with hooked hairs. The style is often persistent, dry and hooked (Plate 15 fig. f). Mature pods although secure on the plant become very easily detached and stuck to hairy bodies. It is presumed on this basis that the primary seed dispersal mechanism of P. hookeri involves the large browsing ungulates such as Bushbuck, Nyala and Kudu (Tragelaphus sp.). These animals will collect pods on themselves while moving through populations to browse on other plants. Seed has a distinct advantage being transported this way because if one pod lands in a suitable locality, up to six seeds may germinate and start a new population. In addition it has been observed that seeds quite frequently detach from the pod if brushed past, the funicle acting as a hook (Plate 15 fig. g). Small branches of inflorescences also become broken off and attached to mammalian skins because of the densely packed hooked hairs on pedicels and peduncles, and this indicates that many pods could sometimes be transported together.

Another method of dispersal observed in the field which gave a possible clue to the adaptive significance of open pods was wind dispersal. During the winter-spring seasonal change which is normally accompanied by gusting winds, it was noticed that when inflorescences hit against

one another open pods became detached in large numbers and floated considerable distances. As was expected, a significant spread of P. hookeri was found along the route of the prevailing wind direction. The strength of these gusts was anything from 30 to 45 knots per hour (Durban Weather Office), and the open 'wing-like' nature of pods enabled them to float quite easily in spite of containing a number of seeds.

Another very important abiotic phenomenon which may aid dispersal is fire. For most of its range, at some time during the seed bearing period P. hookeri is likely to succumb to a veld fire. Most fires are exceedingly hot but of very short duration so while the above ground organs are largely destroyed, the seed may only be superficially scorched before it falls down to the relative safety of the root bases. Fire plays an important role in reducing ground cover and perhaps exposing many seeds to ground feeding birds. It also weakens the seed coat prior to the first rains.

P. hookeri seed does not float but pods may be carried for some distance by strong rain wash or indeed by flowing water in streams or rivers.

Seed dormancy appears therefore to be broken either by fire or by gradual breakdown of the testa by microbial action in the soil. Occasionally, passing through the digestive system of a bird may also weaken the testa and promote germination.

4.14.2. Dispersal in the rest of the tribe

The bulk of species in the tribe depend entirely on the fruit for dispersal. In most cases the lomentum consists of a number of one-seeded indehiscent or tardily dehiscent articles which can separate easily from one another at maturity. The pericarp is densely clothed with straight appressed and patent hooked hairs which together with the persistent curved style and calyx, make the fruit ideally suited to epizoochorous dispersal by mammals (van der Pijl, 1982). They are also adapted to hydrochory, being able to float, particularly in the case of D. salicifolium which is likely to deposit its fruit in water. van der Pijl is noted by Ohashi (1973) as suggesting that the seeds of Desmodieae are dispersed by ants due to the presence of the relic aril. No evidence of this has been observed and the aril appears to be too hard and dry to serve this purpose.

ORIGIN, EVOLUTION AND DISTRIBUTION

5.1. Introduction

In order to achieve better understanding of legume taxonomy, it is
necessary to attempt to pinpoint the place of origin of the group
concerned and to trace the paths of migration followed subsequently.
Conditions at the time when the group arose and diversified were
almost certainly very different from those of today. Under changing
conditions, over long periods of time, it is likely that changes
have occurred in taxa which may have obscured many of the features
which might otherwise serve to indicate relationships.

In the following study an attempt is made to build a scenario for
the origin and migration of the tribe Desmodieae to its present posi-
tion. Evidence from a number of geophysical phenomena such as plate
tectonics, orogenesis, ice ages, impact theory and continental drift
will set the scene of the Mesozoic world in which the angiosperms
evolved. The evolution of the tribe Desmodieae will be traced from
this origin.

The present distributions of the three subtribes, the large pantropical
genus Desmodium, and the most archaic genera, will be used as evidence
for past migrations and for a possible centre of origin for the tribe.
Tied into current theories of continental drift with probable times
for landbridges or major discontinuities, a putative pattern of mig-
ration will be suggested considering the most likely methods of disper-
sal.

Finally the geophysical history of Africa is discussed as a background
to the present distribution and ecology of the tribe in southern
Africa.

5.2. The Mesozoic World - a geophysical setting

Before examining the origins of the tribe under study, it is necessary
to look back to the world of the Mesozoic Era and lead up to the
Jurassic - Cretaceous border when the angiosperms began their ascent
to dominance.

Firstly it is useful to consider some of the basic geophysical cycles

which underlie and control natural events.

5.2.1. Plate Tectonics

Tectonic events appear to be cyclic with periodic thermal mantle convections providing pulses of heat to the crust from within the earth (Fairbridge, 1978). The essence of tectonic plate theory is that plate patterns themselves follow a cyclic development, the present pattern having lasted some 200m.y. with significant changes in direction and rate of movement of the major plates (Dott et al, 1976).

Continental masses are observed to consist of two tectonic subdivisions; those relatively most stable areas or blocks known as cratons, and adjoining areas of instability called mobile belts which are loci for volcanoes, regional metamorphism and earthquakes (Dott, l.c.). These mobile belts or orogenic centres can be the birthplaces of geosynclines, which are elongated belts of relatively thick strata of collected depositional material. The mobile belt is itself the cause of later subsidence of the geosyncline, often by means of crust compression causing downward buckling, which may fold and compress depositional material and cause mountain building (Dott, l.c.). This crust compression is due to the movement of tectonic plates against each other caused by sea floor expansion from lava flows emanating from oceanic ridges. Mobile belts are also sites for volcanic lava flows through the crust to the surface of continental masses; as well as major fault planes (e.g. African rift valley system) and also sites of subduction zones where ocean flooring is consumed. It can be seen then that mobile belts and oceanic ridges are orogenic centres playing major roles in the dissipation of energy generated by the planet.

It is these belts (Dott et al, 1976) that also represent where two ancient plates were compressed together. The present plates consist of mosaics assembled from pieces of different age, broken apart and glued together in a quilt-work pattern, a mixture of cratons surrounded by mobile belts. Plate boundaries and patterns of motion have changed drastically several times; six or seven episodes of extreme mountain building on a nearly worldwide scale probably record wholesale reorganisations of plates and the average duration of a plate pattern appears to be around 300-500 m.y. (Dott, l.c.).

The mobile belts in Africa began due to the convergence of lithosphere

plates which culminated in the collision of a mosaic of continental cratons to form the Gondwanaland supercontinent by Ordovician or Silurian time, 400-440 m.y. BP. This coincided with one of the major mountain forming periods (Dott et al, 1976) whose features are mostly eroded away today.

5.2.2. Orogenesis

Hercynian orogenesis which took place around 250 m.y. BP at the end of the Permian, coincided with the collision of northern continental masses into Laurasia. Collisions also occurred between Africa and America (Appalachian - Mauritanide revolution) and the extent of this orogenesis which was far reaching also resulted in the Cape Fold Mountain series (Davies et al, 1980).

Soon after the beginning of the Mesozoic Era - 220 m.y. BP, sometime after the Cape mountains were formed, igneous activity started in one or other part of Gondwanaland on a large scale (Davies, l.c.). The pouring out of lavas that built up the Drakensberg and Lebombo mountains and highlands of Lesotho occurred at this time.

This volcanic action through mobile belts was a result of 'membrane stresses' (Davies, l.c.) which came about as a direct consequence of the rotation and movement of Gondwanaland across different earth curvatures. It was to be a prelude to the breakup of the supercontinent, as these stresses sought new lines of weakness. At about 180 m.y. BP,West Gondwanaland (Africa and South America) began to separate from India and East Gondwanaland (Australia and Antarctica).

Despite the Hercynian mountain building phase affecting areas in northwestern and southern Africa there was no extensive mountain building over wide areas of Gondwanaland (Fairbridge, 1978). The size of the continents compared with the oceans was relatively small owing to the existence of only two supercontinents, and the sea level was much higher due to the lack of ice caps.

The widespread extinctions of both plants and animals during the late Mesozoic is well known but the reasons are far from clear. Many organisms adapted to the preceding relatively stable conditions of most of the early to mid Mesozoic were unable to cope with the sudden changes that coincided with the initiation of widespread breaking up of continents and continental drift.

5.2.3. <u>Ice Ages</u>

Another intimately linked geophysical phenomenon recurring throughout global history is the occurrence of ice ages. The cycles of ice-cap formation also appear to be loosely linked to periods of great orogenies following continental drifting. The late Carboniferous and early Permian iceage appears to be linked to a major orogeny. In the Cenozoic, continental drifting and sea floor expansion led to an increase in continentality with respect to oceans (Fairbridge, 1978). Former fragments of supercontinents forged new links with one another or drifted apart and formed both longitudinal and latitudinal barriers to the movement of warm moist air. In addition chains of volcanic islands helped to form these barriers. With the Alpine phase of mountain building being initiated in the early Eocene airflow was further disturbed forcing it to drop its moisture (and hence latent heat). As drier areas became established a change in the earth's albido would lead to more reflection of solar radiation (Fairbridge, 1978). Since the earth's heat balance is mainly related to heat loss this blockage in the global temperature regulating system led to an ice-age. The first sign of the approaching ice age of the Pleistocene was visible by the beginning of the Oligocene 37 m.y. BP (Fairbridge, 1978) when a sharp drop in the temperature (some 4 - 5° C) occurred in the oceans of both hemispheres. It is of general interest, that the present distribution and topography of continents are to a considerable extent responsible for the established Quaternary pattern of cyclic glacial initiation and termination. Fairbridge (1978) quotes the following in connection with the pattern exhibited by repeated glacial cycles. "Glacial initiation and/or rapid development is associated with a warm North Atlantic, coupled with an orbital pattern yielding minimum seasonal contrasts around 50 - 65°N - i.e. summer solstice approaching aphelion with relatively high eccentricity and minimum obliquity. Glacial retreat on the other hand is associated with approaching maximal seasonal contrast, ideally summer solstice approaching perihelion with high eccentricity and/or high obliquity. When this orbital condition for retreat is associated with extensive sea-ice and cold conditions in the northern Atlantic, then retreat is likely to proceed to termination."

5.2.4. <u>Impact Theory</u>

According to the researches of Alvarez <u>et al</u> (1984a) tantalising correlations are being found between periodic cratering on the earth's

surface, climatic change and mass extinctions. Studies (Alvarez, l.c.) on the appearance and extinctions of more than 500 families of marine animals revealed 12 peaks of mass extinction in the past 250 m.ys. With a few exceptions these seemed to fit a 26 million year cycle and at present we are at the midpoint of one cycle, the last event having been 13 m.y. ago (Kerr, 1984). Ancient impact craters on earth have also tended to fall at times corresponding to the periodic extinctions, at cycles of roughly 28 m.y. Added to this is the coincidence of the reported times of comet showers with mass extinctions. The most recent comet shower occurred 13 $\pm$ 2 m.y. ago, the same age reported for the most recent extinction events. Evidence exists that marked climatic oscillations occurred immediately preceding the largest mass extinctions of 65 m.y. ago as well as 38 m.y. ago at the beginning of the Oligocene. Stanley (1984) correlates extinctions of marine organisms to major periods of cooling, and evidence from glacial gravels agrees with this although cooling need not always be accompanied by glaciation. The Maastrichtian ($\pm$ 70 m.y. ago) was the coolest phase of the Cretaceous and it is also the time of the earliest known fossils of Leguminosae (Raven and Polhill, 1981). It was a period associated with widespread deterioration of global marine environments during large scale eustatic fall and epicontinental regression (Alvarez et al, 1984b) with rapid shifts in circulation patterns and rapid climatic changes. The coincidental periodicity of many of these features has been attributed by some to the solar systems orbital passage through the mid-plane of the disk of the galaxy, and its encountering medium-sized galactic clouds which are bunched near the galactic plane.

The great area of controversy however, lies with the interpretation of the impact theory. In 1978 anomalous concentrations of irridium, a platinum group rare on earth but common in meteorites, were found in precise correspondence with the Cretaceous-Tertiary (K/T) boundary as defined by a very abrupt change in calcareous microplankton in pelagic limestone sequences. These irridium anomalies have been found worldwide and at different times in the geological sequence corresponding to other periods of major extinction (Alvarez et al, 1984b). They note that marine organisms in particular show a very sudden extinction of small to large numbers of taxa in precise correspondence with the irridium anomaly at the K/T boundary. In their words, there can be little doubt that these extinctions resulted in some way from the inferred impact, with its consequent effects on the environment.

Not so says Stanley (1984). Since the rapid extinctions referred
to by Alvarez et al (1984b) i.e. from 1 to 1000 years, are correlated
mostly with animals, significant cooling of the oceans would be
sufficient to cause these. He emphasises that the Cretaceous crisis
was not a single brief event and that different groups of organisms
declined and became extinct at different times over at least 2
m.y. before the irridium layer is found.

Assessment of the validity of the various theories at this stage
is difficult but it seems that global cooling is directly related
to extinctions and that this may be associated with the periodicity
of the sun's orbit through the galaxy. Comet showers and impacts
are also directly associated with the sun's periodicity and extinction
events. It is very difficult however to directly correlate most
impacts with being the cause of climatic cooling or of actual extinc-
tions and indeed this does not seem to be the case (Stanley, 1984).
It is more likely that the two are superimposed cycles resulting from
similar astronomical phenomena.

5.2.5. Continental drift

By the start of the Cretaceous, 135 m.y. BP until about 50 m.y.
BP a gap of some 3000km separated the nearest land masses of Austra-
lasia from those in Asia. During the same time a gap that was
initially as large between South America and North America closed
to half that distance. Meanwhile Africa was in contact with Eurasia,
rotating and moving westwards with continuing compression until
about 63 m.y. BP (Raven, 1983). Africa diverged from Eurasia until
53 m.y. BP, finally moving 10°N and re-establishing connections
about 17 m.y. BP (Raven, 1979). Raven (1983) states, "These relation-
ships indicate unequivocally that during the first half of Angiosperm
history, the only relatively direct connections between the northern
and southern hemispheres were those involving Eurasia and Africa."

The following summary of tectonic events and possibilities for
more or less direct migration of plants is given by Pielou (1979)
adapted from Raven and Axelrod (1974).

a) Triassic   180 m.y. BP   West Gondwana (Africa and
                                           South America) separated
                                           from East Gondwana (Austra-
                                           lia and Antartica)

b) Early Cretaceous   135-125 m.y.   South America separated from
                            BP   Africa in the south

c) Mid Cretaceous   110-100 m.y.   (1) South America and Africa
                            BP   separated; Africa separated
                                           from Madagascar which separated
                                           from India; Africa, India
                                           and Australia all drifting
                                           northward.

                                           (2) Last direct migration
                                           possible for warm temperate
                                           and sub-tropical plants between
                                           West Gondwana and Australasia;
                                           also $\pm$ 10 m.y. - last direct
                                           migration between Africa and
                                           South America; Africa and
                                           Madagascar and India.

d) Late Cretaceous   80 m.y. BP   North America separated from
                                           (Europe and Greenland); (Antarc-
                                           tica and Australia) separated
                                           from (New Zealand and New
                                           Caledonia)

e) Very late Cretaceous   70 m.y.   Contact made between north-
                            BP   western North America and
                                           north-eastern Siberia.

f) Early Paleocene   63 m.y.   Africa separated from Europe
                            BP   temporarily. End of migration.

g) Eocene   49 m.y.   Dispersal route between North
                            BP   America and Eurasia being
                                           now predominantly through
                                           Beringia as it becomes wider
                                           and warmer.

h)	Eocene	$\pm$ 49 m.y. BP	Australia separates from Antarctica.
i)	End of Eocene	45 m.y. BP	India abuts against Asia.
j)	Oligocene	$\pm$ 38 m.y. BP	Last direct migration possible between South America, Antarctica and Australia.
k)	Oligocene	$\pm$ 34 m.y. BP	Last direct migration across atlantic between Europe and North America (Wolfe,1975).
l)	Miocene	17 m.y. BP	Europe and Africa rejoined; re-establishment of migration.
m)	Miocene	15 m.y. BP	Narrowing gap between Australasia and southeast Asia and appearance of stepping stone islands permits plant dispersal.
n)	End of Miocene	$\pm$ 10 m.y. BP	Cooling makes Berengia unsuitable for dispersal of subtropical to warm temperate plants between North America and Asia.
o)	Pliocene	$\pm$ 5-6 m.y. BP	North America and South America joined by a land bridge.

Geological Time Scale (Raven & Axelrod,1974)

Million years BP.	Period		Epoch		Stage
2.5	Quat		Pleistocene		
20	T E R T I A R Y	10 (Neogene)	Pliocene		
			Miocene		
		27			
40		38 (Paleogene)	Oligocene		
			Eocene		
		54			
60			Paleocene		
65		65		65 (Senonian)	
	C R E T A C E O U S		Upper	70	Maastrichtian
80				80	Campanian
				85	Santonian
				90	Coniacian
100				100	Turonian
					Cenomanian
120		110	Lower	110	Albian
				122	
				125	Aptian
				127	Barremian
				130	Hauterivian
				132	Valanginian
135				135	Ryazanian
140	J U R A S S I				Tithonian
160					
180					

5.3. Origin of the Angiosperms

Although there is no consensus on when, where or how the angiosperms originated or even whether they are monophyletic (the majority opinion) or polyphyletic; the overall views of Raven and Axelrod (1974) are accepted here, with a few modifications.

The dates put forward for the origin of the angiosperms range between two extremes; from the early Cretaceous when the flowering plants can be identified with certainty from the oldest fossils - or back to the end of the Triassic or beginning of the Jurassic periods i.e. between 180 m.y. to 130 m.y. BP (Pielou, 1979). Axelrod (1970, 1972) considers that they originated in the Triassic - Jurassic transition but the first recorded tri colpate pollen characteristic of nearly all of the dicots comes only from the Hauterivian to Barremian, approximately 127 m.y. BP (Raven and Axelrod, 1974). By this time such pollen is widespread over both hemispheres although seemingly not diverse. Only by Upper Albian time (113-110 m.y. BP) is there proof that diverse angiosperm floras existed (Raven and Axelrod, l.c.). Although more diversity appears in the pollen record in the Cenomanian (110-100 m.y. BP) it is not until the Turonian and Senonian (100-70 m.y. BP) that angiosperm pollen becomes more abundant than the spores of ferns and the pollen of gymnosperms, as the latter increases in diversity (Raven and Axelrod, l.c.).

The fact that pollen is widespread but not diverse near the beginning of the Cretaceous indicates that the angiosperms must have originated considerably earlier, although they were probably present in low numbers. Axelrod (1970) suggests that angiosperms evolved on Archean terrain in the uplands of the warmer parts of West Gondwanaland where climates were seasonally dry. It was a vast continent in which arid to subhumid tracts occurred in tropical latitudes, and terrain and edaphic conditions were diverse (Raven and Axelrod, 1974). Aridity is amply demonstrated in the geology of the areas concerned, and many edaphically dry sites derived from Archean crystalline baserock were found in close proximity to more mesic ones. The scattered distribution of edaphically arid sites and steep gradients of decreasing moisture have provided environmental opportunities that have encouraged the origin of taxa adapted to varying grades of drought (Axelrod, 1972).

If the/.....

If the environmental stresses that occurred in the dry interior of West Gondwanaland favoured evolution of the special features that make angiosperms i.e. closed carpels, insect-mediated pollination systems, xylem vessels, drought-resistant leaves and abundant secondary metabolites - then many of the most primitive lines might have become extinct as humid conditions spread in this area (Raven and Axelrod, 1974). As Gondwanaland broke up there was a general trend to a moister, milder climate as the ratio of sea to land surface increased and maritime climates spread to areas once far inland (Axelrod, 1972). The seasonally dry conditions in upland areas where original evolution of angiosperms is believed to have occurred, were not sites that would promote their being preserved as fossils. Some taxa that had evolved in drier areas probably then adapted to moister climates retaining some of their ancient features even though they had no 'need' of them (Axelrod, 1972).

The fixing of characters central to the success of angiosperms, (i.e. the drought resistant characters mentioned above) is envisaged in terms of their allowing new types of functional systems to develop i.e. new compromises between external and internal selective forces (Polhill, Raven and Stirton, 1981). A significant shift in the various constraints placed on existing functional plant systems would allow a whole new range of compromise along lines of least resistance. As evolution proceeded, there was a gradual accumulation of constrained, canalised and fixed features in a variety of taxa exploiting new niches. The appearance of recognisable families must have come about as multi-functional, optimal sets of constraints established around fixed features; and resistance, built up from the accumulative effect of previous adaptations, channelled the possibility of further adaptation along distinct lines.

Many of the mesophytic angiosperms now so well represented among archaic and ancient groups generally regarded as primitive, may have come into being as West Gondwanaland split (Raven and Axelrod, 1974). With the spread of more moderate climates to which they had become adapted, they migrated to other parts of the world where similar climates occurred (Raven and Axelrod, l.c.). A number of secondary mesophytic lines might have become extinct later with the spread of a dry climate over Africa and the elevation of mountains in the Tertiary. For these reasons primitive angiosperms might not be so well represented in areas where they appear to have originated (Raven and Axelrod, l.c.). This is offered as an alternative to the theory,

that/.....

that southeast Asia and northern Australasia to New Caledonia and Fiji, represent a source-origin for the angiosperms because of their greater concentration of ancient and archaic forms (Taktajan, 1969). These areas have retained moist equable climates with little change for a long time whereas Africa and South America became devastated by subsequent geological and climatic events. This suggests that the primitive angiosperms have survived in the greatest numbers in two regions where comparable habitats are ancient geologically and relatively well protected from immigration : southeast Asia and Australasia (Raven and Axelrod, 1974).

In support of the subtropical highlands being the most equable and suitable for the spread of angiosperms, Axelrod (1970, 1972) notes that in every class, the more primitive families and genera are now found in warm temperate or high altitude tropical regions whereas the more advanced taxa occur predominantly in less equable regions. Taktajan (1969) notes that forests of the subtropics and those higher on mountains within the tropics, contain more representatives of primitive families than do the tropical lowlands.

Reasons why continental areas other than West Gondwanaland are considered unsuitable for the origin of the angiosperms are given in Raven and Axelrod (1974).

West Gondwanaland is seen as being a primary area for evolution of many major families (although Laurasia is the centre of a good many others). With the opening of the South Atlantic 130 - 125 m.y. BP and the spread of more mesic climates over much of the region, it seems that a major evolutionary radiation was triggered and angiosperms became dominant in the mesic lowland record $\pm$ 110 m.y. BP. (Raven and Axelrod, l.c.). Probably a majority of families and many modern genera of seed plants had come into existence by the early Paleocene (Raven and Axelrod, l.c.). There is also an almost complete floristic continuity at family and often generic level between Africa and southeast Asia, indicating the ease of migration between the two areas into early Paleocene time. This connection appears to break down some time after 63 m.y. BP when Africa diverged from Eurasia. Down to 54 m.y. BP, Africa and South America were separated by a gap of roughly 800km, populated with volcanic islands which aided east-west dispersal of tropical taxa (Raven and Axelrod, l.c.).

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5.4. Early evolution of the Leguminosae

The time of origin of Leguminosae is unknown but fossil woods and pollen indicate the presence of Mimosoideae and Caesalpinioideae in the Maastrichtian, 70-60 m.y. BP (Raven and Polhill, 1981). The family may be considerably older but it is only known to have become large and diverse from the Eocene (54-38 m.y. BP). The tribe Caesalpinieae were almost certainly differentiated well before the close of the Cretaceous and are represented by the archaic living genera Gymnocladus and Gleditsia (Raven and Polhill, l.c.).

The Papilionoideae are believed to have arisen from early Caesalpinieae with the links being suggested most convincingly among living genera of the Sclerolobium group of the Caesalpinieae (Raven and Polhill, l.c.). Sclerolobium and Tachigalia, the two largest genera are centered in Amazonia and they appear to lie on the borderline of the Caesalpinieae and are not greatly different from early Sophoreae. Raven and Polhill (l.c.) state, "The occurrence of pollen with distinctive very coarse rope-like striations identified as Crudia, and certainly a member of Detarieae - Amherstieae (other tribal offshoots from early Caesalpinieae) in the Paleocene (-60 m.y. BP) of tropical Asia, and pollen with distinctive circular endoapertures away from the equator, like Sindora from the Maastrichtian of Siberia, Canada and Columbia, represent the oldest accepted pollen records of legumes." Connaraceae, a family mentioned earlier as having close affinities to the Leguminosae, have a West Gondwanaland pattern of origin and seem to have migrated between Africa and South America in Paleogene time, and to Asia. (Raven and Axelrod, 1974). In the Leguminosae both Mimosoideae and Caesalpinioideae have distributions like Connaraceae whereas Papilionoideae have radiated more extensively in Laurasia (Ravel and Axelrod, l.c.). "Although the family is easily dispersed and offers perplexing patterns of distribution, it may well have originated or at least undergone its primary radiation and differentiation into subfamilies in West Gondwanaland."

Raven and Polhill (1981) point out that although the legume flora of South America is exceptionally diverse, particularly in groups central to the main radiation of the family, there are relatively few endemic groups of genera and no notable concentration of the most archaic genera. The Sclerolobium group, however, is endemic to this region (Raven and Polhill, l.c.) and is of particular importance

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in that it suggests more closely than any other living group, the nature of the transition between Caesalpinieae and Papilionoideae. Among the early Papilionoideae, the Myroxylon group of the Sophoreae is endemic to Latin America and the Swartzieae are much better represented there than in Africa (Raven and Polhill, l.c.). This combination of early groups suggest strongly that Papilionoideae may have originated in South America. Raven and Polhill (l.c.) also point out that the representation of legumes in both the moist and dry forests of Africa is comparatively much richer than for many families of tropical plants. This is consistent with their postulate of Africa as a prime area for the early radiation and evolution in Leguminosae.

5.5. Evolution of the tribe Desmodieae

The base group Sophoreae (n=8 - 14) are central to the radiation of Papilionoideae and gave rise among others to the Tephrosieae (n=10 or 11) which represents a large diffuse core for the development of Old World tropical tribes (Polhill, 1981). Advanced tropical tribes such as Desmodieae (n=10, 11), Phaseoleae (n=10, 11) and Indigofereae (n=8) were originally Old World though most are now pantropical in distribution. These advanced tribes are predominantly herbaceous although the Desmodieae contain some woody genera approximating towards the Tephrosieae, from India to New Caledonia.

These advanced tropical tribes, and the Desmodieae in particular have shown trends in the following directions.

a) towards a marked thickening of the endexine and an almost complete loss of the foot layer in pollen walls.

b) the development from an intrastaminal disc nectary to flowers with an explosive release of pollen and disorientation of petals, and loss of nectar production.

c) Flowers often small and clustered along the rachis, forming a pseudoracemose inflorescence.

d) first leaves of seedlings often unifoliolate and opposite.

e) Canavanine generally present in the seeds (Polhill, 1981).

As noted by Polhill (l.c.), "The patterns of variation change significantly between seemingly older and younger parts of the subfamily and this poses problems for formal systematics."

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The Desmodieae are considered to be one of the most highly advanced tribes of the Papilionoideae (Ohashi et al, 1981). In the latest synopsis of the tribe (Ohashi et al, l.c.) 27 genera are divided into three subtribes. The relictual subtribe Bryinae consists of two genera endemic to the New World (one in Cuba to Jamaica and Hispaniola and the other in Brazil). This group is characterised by glochidiate hairs and periporate pollen. The subtribe Lespedezinae is a small, more temperate offshoot of the main tropical subtribe, and is of Sino-Himalayan origin (Ohashi et al, l.c.). It comprises 5 genera principally of east and tropical Asia, Australia and North America. The subtribe is ecologically and morphologically considerably different from the rest of the tribe and is characterised by the absence of specialised hairs and by one-ovulate ovaries.

The subtribe Desmodiinae is the largest and most diverse with 20 genera, and is dominated by the large genus Desmodium and its varying number of controversial segregates (Ohashi et al, l.c.) which for the most part are maintained in infrageneric categories (Schubert, 1980). The most archaic genera in the subtribe have the following geographical distributions. Arthroclianthus and Nephrodesmus occur in New Caledonia, Trifidacanthus in Vietnam and southern China and Dendrolobium in tropical Asia and Australia.

The bulk of genera are centered in southeast Asia to Australia, some spread to India and Madagascar and a few are widespread in the Old World tropics. Desmodium is pantropical. Ohashi (1973) examined Asiatic members of the tribe in great detail and stated that the facts clearly indicate that the primary centre of distribution as well as generic differentiation in the subtribe Desmodiinae is in the Asiatic region from India through southeast Asia and Malaysia to northeast Australia. The genus Desmodium is essentially indigenous to the tropics and subtropics and has two major centres of distribution and differentiation, southeast Asia and Mexico - Brazil (Ohashi, l.c.). The Asiatic species appear considerably distinct from the tropical American ones (Schubert, 1963) indicating some period of isolation. Desmodium in tropical America thus represents a secondary centre of radiation of the genus.

Greater isolation between Asia and America is indicated by groups with a purely tropical affinity. The relictual subtribe Bryinae clearly shows a considerable period of isolation from Asia, and the New World subgenera of Desmodium have also become differentiated

from Asian relatives. However there are examples of genera with species in Asia and America, which have a more temperate distribution in the latter, and do not appear to be as markedly differentiated from one another i.e. species of Lespedeza and Kummerowia. An interesting disjunction is also noted in Desmodium subgenus Podocarpium, one of the most advanced subgenera in which there are nine species extending from Hokkaido across China and along the southern curve of the Himalayas to Punjab, east India and Ceylon; and three species found in eastern north America from closely adjacent to Canada to above the Florida peninsula; their western limits are along a north-south line from North Dakota to eastern Texas (Isley, 1951). These are the only species of Desmodium with a temperate distribution.

5.5.1. The Asia - North America Discontinuity

These latter examples illustrate a pattern of disjunction that has long been recognised in numerous plant groups between eastern Asia and eastern North America. It is a disjunction first commented on by Linnaeus and later recognised independently by Thunberg but really brought to the attention of botanists by Asa Gray (Wood, 1972). It was Gray who advanced the hypothesis involving migration and interchange of species between Asia and America across the region of the Bering Strait (Wood, l.c.). Over the years palaeobotanists have confirmed the widespread occurrence of many genera, mainly woody ones, in Eurasia and North America in broad areas from which they are now missing (Wood, l.c.) making it clear that extant representatives are the survivors of gradual climatic change, volcanism, orogenic movements and the glaciation that followed. As opposed to the present floristic kingdoms of the world in which the division in the tropical flora is rather pronounced between neotropical and palaeo-tropical; during the Tertiary, up to the major climatic deterioration of the Oligocene ($\pm$ 31 - 32 m.y. BP) the division was more pronounced between the northern and southern hemispheres, i.e. a boreotropical kingdom versus austrotropical kingdom (Wolfe, 1975). One of the chief routes of migration of this boreotropical flora appears to have been the region of Berengia (the Bering Strait with adjacent eastern Siberia and Alaska) which for a considerable part of its history has existed as a direct land connection. Many fundamentally megathermal families and genera (those characteristic of a mean annual temperature of over 20°C) have been recorded from this region during the Eocene (Wolfe, 1975) and the overall floristic similarities indicate a direct migration route between the two areas.

Floristic/.....

Floristic similarities in the boreotropical flora continued well into the Oligocene, some 15 m.y. after the North Atlantic ceased to be of major importance as a direct migration route (Raven and Axelrod, 1974), again indicating the importance of Berengia from the Eocene onwards. Following the Oligocene however, the boreotropical vegetation became highly restricted in its distribution (Wolfe, 1975). The floristic affinities of the boreotropical flora are very clearly Indo-Malayan in present distribution thus much of the present Indo-Malayan flora can be thought of as a relict of this boreotropical flora. It is tempting to surmise on the basis of this evidence, that the forerunners of the neotropical Bryinae and Desmodium subgenera, migrated across Berengia from Asia some time in the Oligocene and have been isolated since the Neogene. The more temperate genera and Desmodium subgenus Podocarpium would have been able to cross Berengia up to the late-Miocene before conditions became significantly cooler. A word of warning though is expressed by Wolfe (l.c.), "Little is known of the historical biogeography of major herbaceous groups. A family such as Compositae appeared almost simultaneously on all continents near the Palaeogene-Neogene boundary in both tropical and extratropical regions. The patterns in such families are reflections of later Cenozoic phenomena, but at this time palaeobotany has little to contribute regarding the distributional patterns of many of these advanced families."

Long distance dispersal over large gaps by means of effective seed dispersal mechanisms has undoubtedly been responsible for a good deal of the present distribution of the Desmodieae but it is felt that this is not a realistic mechanism for explaining the pattern of discontinuity between southeast Asia and North America, a pattern shared by many other genera and families of Angiosperms.

5.5.2.   The Asia - Australasia connection

New Caledonia together with New Zealand separated from Australia $\pm$ 80 m.y. BP and had reached their present positions by the Paleocene (Raven and Axelrod, 1974). This occurred some considerable time before Australia broke away from Gondwanaland.

The flora of New Caledonia is exceedingly rich with large numbers of archaic genera and endemics, and it appears to be a surviving modified sample of the late Cretaceous austral temperate flora of

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eastern Australia (Raven and Axelrod, 1972). There is also a strong influence however of more modern floras derived from the Malaysian region. New Guinea was first elevated to form an extensive land area in the late Oligocene, as the leading edge of the Australian plate collided with the Asian plate (Raven and Axelrod, l.c.). It was then colonised into the Miocene from the adjacent rich tropical lowlands of Malaysia. From about 15 m.y. BP (Raven and Axelrod, 1974) it became possible for Asian elements to migrate into Australia and New Caledonia and across the archipelago of more recently formed island groups. This is undoubtedly the earliest date that can be considered for more or less direct migration of plants into Australasia from Asia, and many of the Desmodiinae have used this migration route.

The two most archaic genera of the Desmodieae, Arthroclianthus and Nephrodesmus (which is scarcely distinct from the former, Ohashi et al, 1981) are only found in New Caledonia. Since the tribe is of Asian origin and because these genera have no relatives elsewhere it is thought that the Arthroclianthus prototype may have arrived by long distance dispersal earlier than the Miocene where it underwent considerable radiation into 16 species; i.e. before the land bridge of New Guinea was formed.

At the other extreme many of the Desmodiinae have achieved striking disjunctions in range very recently as weeds; since the initiation of human activities on a global scale (Raven, 1972). These are species with widespread Old World or pantropical distributions.

Raven (1972) makes the following point, "It is worth noting in passing that we have very little hard evidence about the rates of evolution of particular taxa, and it is extremely dangerous to reason from a given degree of morphological divergence to a length of time thought necessary to produce that divergence."

5.5.3. The North America - South America connection

Dispersal between North and South America became possible from the early Miocene ($\pm$ 26 m.y. BP) with increasing probability until 5,7 m.y. BP when the two continents were connected by land for the first time (Raven and Axelrod, 1974). During this period Desmodium dispersed southwards from Central America and established another centre of radiation in Brazil.

Besides <u>Lespedeza</u> and the centres of radiation shown by <u>Desmodium</u> in the New World, the genera under present study have a similar pattern of distribution, i.e. widespread in the Old World tropics. <u>Alysicarpus</u> (25-30 species) and <u>Pseudarthria</u> (4-6 species) are like <u>Desmodium</u> ($\pm$ 300 species) in having the bulk of their diversity occurring in tropical and subtropical Asia and Malaysia. They are also alike in being relatively poorly represented in Africa.

7 genera of the subtribe Desmodiinae have species in Africa of which two only, are endemic; <u>Droogmansia</u> forms a single species complex of some 30 species which include perhaps a few distinct relatives (Ohashi <u>et al</u>, 1981) as well as 4 species in West Africa which show a relationship to <u>Tadehagi</u> of southern Asia to Australia. The other genus <u>Meliniella</u> comprises 1 species and is a minor segregate of <u>Alysicarpus</u> (Ohashi <u>et al</u>, l.c.).

The genera <u>Uraria</u> and <u>Pycnospora</u> are represented in Africa by widespread Old World tropical species.

Of roughly 300 species of <u>Desmodium</u> at least 28 species occur naturally in Africa south of the Sahara and more are becoming naturalised as escapes from cultivation. 21 species can be considered as indigenous and 14 endemic, 2 of which are also found in Madagascar and the Mascarene islands. The other 7 indigenous species are Asian in origin and are widespread in the Old World tropics. Two are pantropical weeds. Of the naturalised species which have often become pantropical weeds 4 are from the New World and 2 from the Old World. It should be noted that the 7 "indigenous" species originally from Asia that are widespread in the Old World tropics most probably represent species that have become naturalised since the effects of human influence.

One of the major factors preventing a satisfactory treatment of the genus <u>Desmodium</u> has been how to circumscribe it from closely allied segregates (Ohashi <u>et al</u>, 1981). It is felt by Ohashi <u>et al</u> (l.c.) that among others, genera such as <u>Pseudarthria</u> and <u>Droogmansia</u> should be included despite the differences in their fruit characteristics. They state "The genus would be diverse, but to no greater extent than for example <u>Indigofera</u>." However as far as this study is concerned, <u>Pseudarthria</u> is considered distinct from <u>Desmodium</u> on the

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basis of its different chromosome numbers, 2n=34 in <u>Pseudarthria</u> <u>hookeri</u> and 2n=22 in <u>Desmodium</u> (Goldblatt, 1981).

A further problem aggravated by the above arises out of the lack of a suitable treatment of subgeneric categories in <u>Desmodium</u>. Ohashi (1973) recognised 7 subgenera within Asian representatives and Schubert (1963) at least 3 subgenera among Mexican species. Schubert (pers. comm.) has noted that she is not in complete agreement with Ohashi's concept of subgeneric division. She also notes (Schubert, 1963) that although many subgeneric categories of <u>Desmodium</u> occur in tropical Africa there do not seem to be any groups of several to many related species in Africa. Endemics do occur but there seems to be a much lower development of the genus in Africa than in America or Asia and there are scarcely any unquestionably native species which have American relatives (Schubert, l.c.).

However, indications are that most or all of the endemic African species appear to belong to the subgenus <u>Sagotia</u> (Duchass. et Walp.) Bak. In fact the only other subgenus represented by indigenous African species is the widespread Old World tropical species <u>Desmodium</u> <u>repandum</u> which belongs to the subgenus <u>Podocarpium</u> (Benth.) Ohashi. Although it is placed in this most advanced subgenus it is considered by Ohashi (1973) to be very unusual palynologically and he places it near the base of the group allied to the more primitive subgenus <u>Dollinera</u> (Endl.) Schindl. The subgenus <u>Sagotia</u> has been divided into a number of sections and again it appears that the bulk of endemic African species can be placed in either the section <u>Nicolsonia</u> (DC.) Benth. or section <u>Heteroloma</u> Benth. This indicates that African endemics may have arisen from only a very few Asian prototypes, a barrier to dispersal from Asia being suggested by the considerable areas of aridity between them. Again it is important to remember that a number of species have found no difficulty in crossing large distances and these have become highly successful invaders. <u>D. repandum</u>, <u>D. velutinum</u>, <u>D. gangeticum</u>, <u>D. barbatum</u> and <u>D. adscendens</u> are either pantropical or widespread in the Old World tropics. In addition to the abovementioned species another five occur in the southern African region. <u>D. incanum</u> and <u>D. tortuosum</u> are naturalised introductions from the New World and three African endemic species occupy a 'tailend' distribution in our flora area, <u>D. setigerum</u> which is loosely allied to <u>D. adscendens</u> (section <u>Nicolsonia</u>), <u>D. dregeanum</u> which is allied to <u>D. barbatum</u> and <u>D. salicifolium</u> which is allied to the/.....

to the section Heteroloma. This latter section includes among others, D. velutinum and D. gangeticum.

Pseudarthria hookeri is also a widespread species of the Old World tropics and is the only species of the genus to reach southern Africa. It has very close links with Desmodium velutinum and particularly with Desmodium kingianum (an Asian species) which has similar fruit characteristics (Ohashi, 1971). Perhaps the relationship will be better understood when the unusual chromosome number of P. hookeri is examined in terms of being historically an aneuploid form of the normal 2n=22 for Desmodium. Owing to the large variation in chromosome numbers for species of the genus Pseudarthria (Goldblatt, 1981) the suggestion is made here that Pseudarthria is not a natural genus and that the species belonging to it may have different origins.

The genus Alysicarpus has at least 5 species indigenous in Africa, one endemic and 4 which are widespread in the Old World tropics. A. vaginalis is also described as a noxious weed introduced in the New World (Schubert, 1980). Including the above A. rugosus and A. glumaceus occur in southern Africa as well as the endemic species A. zeyheri.

It is therefore proposed that a very small number of Asian prototypes of the tribe reached Africa by long distance dispersal, probably across the Indian Ocean islands. These gave rise to the relatively few groups of African endemics. The species mentioned earlier which are widespread in the Old World tropics seem more likely to owe their arrival in Africa to human influence with consequent rapid spread due to efficient dispersal. It cannot be discounted though that some may have reached Africa earlier by natural means and may have given rise themselves to some of the endemics. It is felt that this may be a valid explanation in the case of Alysicarpus. It is possible also that the low level of development of the tribe in Africa may be due to the recency of its arrival.

5.6.   The Geophysical history of Africa

Down to the close of the Oligocene, humid forest clothed nearly all of Africa, except perhaps for the south and on edaphically dry sites (Raven and Axelrod, 1974). The tropical African flora was very diverse and some of its richness has survived on Madagascar which was part

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of Africa until mid or late Cretaceous times. Axelrod (1972) noted that the development and spread of dry climatic conditions probably began near the close of the Oligocene at which time considerable upwarping of the continent commenced.

At the end of the Oligocene - early Miocene (25-23 m.y. BP) the African landscape was flexed tectonically into a number of broad warps and basins. As the warping commenced, rifts developed and volcanism was initiated (Axelrod and Raven, 1978). Major uplift of the interior followed in distinct phases; at the end of the Miocene and again at the close of the Pliocene - early Pleistocene. The tendency for the earth's crust to maintain a state of near equilibrium results in the uplift or depression of continental or sub-continental landmasses. These isostatic movements along mobile belts occur between the less dense, more siliceous part resting upon a heavy, more basic and feebly plastic substratum; and they compensate for weight distribution changes that occur during quiescent periods when continued erosion of landmasses makes them lighter (du Toit, 1954). During uplift phases, long ridge-like axes were elevated, separated by relatively broad depressed basins (Axelrod and Raven, 1978). In southern Africa maximum uplift took place along a line outside the Great Escarpment while the central Karroo developed as a basin. Superimposed on this were minor upwarps and basins and the central plateau was elevated far above its former level (Axelrod and Raven, l.c.). The Plio-Pleistocene upwarps and downwarps of southern Africa are correlated with the seismicity of the Afro-Arabian rift system which continues down to the Cape (Axelrod and Raven, l.c.). With the elevation of plateaux, rivers are rejuvenated and during quiescent denudatory periods they carve back new valleys exposing new strata and different soils. Major regional differences in climate and hence in vegetation developed only following the early Miocene.

During the late Cretaceous - Paleocene, Africa was 15° south of its present position and the continent was separated from Asia by the Tethys sea. The Atlantic was much narrower and warmer and the continent reached well into the southern belt of westerlies which contributed abundant moisture to southern Africa. The highlands of East Africa and the Eurasian - Alpine axis had not yet emerged, so moisture from the Indian Ocean was not impeded. Lowered contrast between sea surface and landsurface temperatures would have resulted in a less intense and less stationary high pressure centre over the ancestral south Atlantic than that of today (Axelrod and Raven, 1978). This

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made possible the entry of Atlantic moisture across the west coast thus supplementing Indian Ocean precipitation. In the southern sub-tropics a broad monsoonal area existed with drier Savanna conditions resulting from the descending air of the subtropical high.

The following factors contributed to a trend towards increasing aridity and consequent impoverishment of the African flora.

a) The elevation of eastern Africa supplemented by the building of a volcanic field from Ethiopia southward down the rift valleys, blocking the path of Indian Ocean moisture into the continent.

b) In the mid to late Oligocene, Antarctica separated from the South Tasman Rise (Axelrod and Raven, 1978) and moved to its present position over the south pole. As the 'proto' - Benguela current began to bring colder water to the west coast of Africa, a drier season spread over the southwest of the continent.

c) The Alpine mountain building system of southern Eurasia and North Africa elevated land and the seaways retreated from the continents. Africa and Arabia had moved north and joined Iran in the mid-Miocene altering the major latitudinal system of circulation.

d) A result of this was the present great anticyclones in the lower-middle latitudes became progressively stronger, more persistent and more stable in position and dry climates increased in area. This is reflected in the abrupt appearance in the Miocene of numerous woody Leguminosae which earlier were poorly represented.

During the mid-Tertiary the change was from an ancient (Cretaceous - Paleogene) broadly latitudinal circulation with well distributed moisture over wide tracts to more restricted north-south cellular circulation systems that were increasingly intensified as colder climates developed in high latitudes, leading to the expansion of more arid climates over the lower latitudes as the thermal gradient increased.

e) As ice conditions increased towards 5 m.y. BP the Benguela current gained in strength, became colder and increased the intensity and stability of the south Atlantic anticyclone. With the Tethys blocked and the Panamanian portal closed by this time, the Canary high pressure system increased in strength and area and the subsidence of dry air during the warm season now brought increased drought to the west coast of most of tropical Africa.

f) Selection for drought resistance was intensified considerably

in the Plio-Pleistocene as the altitude of eastern Africa was increased fully 8000 ft above that of the Miocene (Raven and Axelrod, 1974) which further increased the rainshadow effect and brought greater drought and temperature extremes to the interior.

g) During the Quaternary while the great ice sheets expanded and shrank (Pilou, 1979) climates elsewhere varied enormously. These ice sheets caused worldwide changes in atmospheric circulation. In each hemisphere the belt of eastward-moving cyclones was shifted toward the equator when the icesheets expanded and back again when they retreated. Therefore areas that were dry under normal conditions experienced 'pluvial' periods of ample precipitation and similarly normal equatorial regions where rainfall is heavy, experienced dry periods. With reference to southern Africa; although the thermal equator was displaced southward as a consequence of the growth of the northern ice sheet, this did not result in a southward extension of the intertropical convergence zone. This southward movement normally is responsible in summer for most of southern Africa's rainfall from moist air flowing in from the Indian Ocean in an anticlockwise direction (van Zinderen Bakker, 1978). The reason for this was that the westerlies moved simultaneously northwards. The summer-rainfall area was not only diminished in size but also received less precipitation. This is largely due to global oceanic cooling lowering the mean evaporation rate and therefore reducing the advection of moist air to the continents. At higher latitudes conditions were entirely different during a glacial maximum, as the northward shift of the westerlies brought cyclonic rain perhaps as far inland as 24°S (van Zinderen Bakker, l.c.). This northward shift of cyclonic rain coincided with a considerable lowering of temperature as depressions of very cold polar air penetrated deeply into the subcontinent. The opposite occurred during warm interglacial periods when climatic belts moved southwards. The intertropical Convergence zone could extend its influence in the present savanna and woodland regions which received more summer rainfall. The zone of westerlies shifted south so winter rain could only reach a limited area of the south west Cape. This shift in the rainfall belts was accompanied by a considerable amelioration in temperature.

Other consequence of ice age activity were the considerable eustatic changes in the overall sea level between glacial and non glacial phases. It is estimated (Pielou 1979) that the total amplitude of sea level changes between glacial and non glacial epochs is of the order of 230m. The overall effect of the weight distribution of

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ice and water contributed much to the more recent isostatic adjustment and crustal warping of the earth's surface. The biotic effects of such a change in sea level are considerable, among others, the possible opening and closing of direct migration routes for plants and the cause of some subsequent plant disjunctions, particularly on exposed strips of what is now submerged continental shelf.

5.7. Ecology of the tribe Desmodieae in southern Africa

The African rainforest was progressively impoverished with the spread of aridity during the Miocene and notably in the Pliocene as the ice cap developed on Antarctica (after 5 m.y. BP). Savanna - type ecosystems spread rapidly at the expense of forest as drier open environments expanded, especially during the renewed warping and uplift of the late Pliocene - early Pleistocene. The climatic changes of the Quaternary had enormous influences on the vegetation. They were responsible for extinction on a wide scale (Goldblatt, 1978) and resulted in the restriction of the more mesophytic taxa to favourable sites, hence the number of relicts confined to the coastal and mountain belts of the Cape to Natal. They were also the cause of tremendous bursts of speciation in many taxa. Goldblatt (l.c.) states, "Elimination of some taxa would give opportunities for the evolution of the remaining species into vacant or newly created niches. While the fragmentation of large populations into smaller ones would promote divergence by genetic drift; with rigorous selection in harsher conditions and with amelioration of the climate later, changes would favour some taxa more than others, their populations would grow, hybridize with related taxa, and variation and speciation would continue to expand."
 The flora of the northern part of South West Africa, northern Botswana and the northern half of the Transvaal is part of a floristically rich, cosmopolitan or pantropical flora (Goldblatt, 1978) belonging to the Zambezian Domain (Werger, 1978). This is the southerly extension of the large Sudano - Zambezian region of savanna and woodland areas of tropical Africa (Brenan, 1978). Family and generic endemism is slight in this region but specific endemism is high and the Zambezian Domain is relatively richer than the rest (Brenan, l.c.). The southern portion bordering on the flora area becomes more depauperate in species. It is a tropical area of grassland and open woodland with Gramineae and woody and shrubby Leguminosae well represented. Evolution from tropical African forest and savanna elements is suggested for most of the constituents of this region, with some taxa arriving from the Asian and New World tropics by long distance dispersal or from

Asia by more or less direct migration before the formation of deserts in North Africa and Eurasia.

The presence of the endemic members of the tribe Desmodieae in Africa can most probably be ascribed to adaptive radiation from a few recent Asian migrants in the Sudano-Zambezian region of tropical Africa. It is clear that the desert regions of North Africa and Arabia have acted as a barrier to the dispersal of the tribe to Africa and argument is made here that migrants arrived by dispersal across the Indian Ocean islands or more recently by human influence. The Desmodieae have a tropical to subtropical requirement and their 'tailend' distribution in our flora area represents the southerly extension of a much wider range in tropical Africa. Members of the tribe enter the flora area in the Zambezian Domain of northern South West Africa, northern Botswana and northern Transvaal. In the latter the distribution follows a line along the lower eastern slopes and foothills of the mountains of the Soutspansberg, Drakensberg and Swaziland, southwards in Acocks Veld Type 9, the Lowveld sour bushveld. This merges into Veld Type 10, the Lowveld proper and the tribe is found occupying the plains at altitudes between 150 - 600m across the eastern foot of the Drakensberg and other mountains southwards through Swaziland and Zululand and the western foot of the Lebombo range (Acocks, 1953).

Rainfall varies from 500 - 1000mm per year falling in summer, and the climate is hot. At its southern extremity the tribe merges into the Tongoland - Pondoland region of White, 1978 (Goldblatt, 1978). Here it occupies almost exclusively the extensions of the Lowveld, Veld Type 10, into Zululand and the belt of coastal forest and thornveld Veld Type 1. Here the upper boundary is approximately 450m in the north and 300m in the south and the rainfall is between 900 - 1500mm per year. This region benefits from the South East Trades bringing moisture across the warm Agulhas Current to the coast and the northeastern interior (van Zinderen Bakker, 1983). Some species extend beyond the Pondoland region into the eastern part of the Cape Region of White, 1978 (Goldblatt, 1978). Certain species transgress this basic pattern in the following ways. Pseudarthria hookeri, Desmodium repandum, Alysicarpus zeyheri and Alysicarpus rugosus subsp. perennirufus extend into the various bush and thornveld vegetation of Acocks Veld Types 18, 19 and 20 between the major grid references of Thabazimbi and Nylstroom for P. hookeri, and Rustenberg and Pretoria for the others. These species also, to varying degrees, cut across the south eastern Transvaal and occur widely in Natal and Transkei. D. repandum

and/.....

and A. rugosus subsp. perennirufus are widespread in Natal and Transkei and extend well into the eastern Cape. A. zeyheri which is the only species of the tribe not to occupy the usual lowveld distribution occurs on the plateau of eastern and central Transvaal and northern Natal. P. hookeri occurs up in the Pietermaritzburg and Underberg grids of Natal.

The tribe therefore, with few exceptions occupies the lower, hotter and wetter areas in the eastern half of the country which is consistent with it being the 'tail-end' of a wider tropical African distribution.

Ecologically the tribe can be compared in a number of categories. Annuals which are often ruderal weeds i.e. Alysicarpus glumaceus and A. rugosus subsp. rugosus, and perennial suffrutices which may vary from subshrubs up to 3m, to small multistemmed pyrophytes in the grassland sublayer. Pseudarthria hookeri, Desmodium velutinum, and D. salicifolium usually occur as woody subshrubs. D. gangeticum, D. dregeanum and D. barbatum may do so in protected areas but usually occur as small pyrophytes due to the influence of fire. D. setigerum and Alysicarpus are grassland herbs branching from woody rootstocks. Certain species also occur where moisture is locally abundant such as depressions or swampy areas i.e. D. dregeanum and D. setigerum. D. salicifolium occurs in water on river margins or in swamp. Others are forest undergrowth species, i.e. D. adscendens var. robustum mostly of coastal dune forest and D. repandum, widespread in patches of evergreen forest away from the immediate coast up to the Drakensberg. This is different from the rest of the species which occur in open bushveld or grassland or forest margins. The tribe has an exceptionally efficient method of seed dispersal with its often articulate pods covered with hooked hairs. An example of how well they can spread is shown by D. incanum which was probably introduced on the Natal coast within this century. It now has a distribution from the eastern Cape to Tongaland. Species generally remain true with no evidence of hybridisation occurring between them. At times D. incanum can look very much like D. adscendens var. robustum where the former produces a shade form in coastal forest margins and intermingles with the latter. No intermediates were however discovered. There is also little sign of active evolution of species i.e. those showing considerable variation. One exception is the annual weeds of Alysicarpus. In A. glumaceus, Verdcourt (1971) recognises 3 subspecies and 2 varieties in the subsp. glumaceus. Although only one variety, var. glumaceus occurs in the flora area, the complex appears very variable in eastern Africa.

Indigenous members of the tribe appear to be relatively stable in southern Africa and although spread may occur into new environments this is thought to be unlikely much beyond those it occupies at present for climatic reasons. A different pattern is seen for the escapes from cultivation or naturalised introductions.

D. tortuosum or Florida Beggarweed has recently been observed in two big populations wide apart from one another along the Natal coast. Lespedeza cuneata or Japanese bush-clover is now naturalised in a number of localities in the Natal midlands. Desmodium uncinatum and D. intortum or Silverleaf and Greenleaf Desmodium, have been deliberately introduced from Central America and cultivated as pasture legumes. This introduction has been largely in the eastern Cape out of the range of the rest of the tribe, and it remains to be seen if these become naturalised. Desmodium asperum was once collected on the south coast of Natal but has not been seen again, indicating that not all species that escape are successful. Finally a large number of other species of Desmodium are being tested in agricultural stations around the country for their pasture potential.

TABLE 3.
Naturalised species of Desmodium in Africa

TOTAL = 28 species

1) African endemics
   a) D. hirtum
   b) D. appressipilum
   c) D. setigerum
   d) D. stolzii
   e) D. cordifolium
   f) D. tanganykense
   g) D. ospriostreblum
   h) D. dregeanum
   i) D. schweinfurthii
   j) D. helenae
   k) D. wittei
   l) D. fulvescens
   m) D. ramosissimum   . also
   n) D. salicifolium   Madagascar
                        and Masca-
                        renes.

2) Indigenous in Africa
   but widespread in Old
   World tropics
   (Of Asian origin)
   a) D. umbellatum
   b) D. velutinum
   c) D. heterocarpon
   d) D. repandum
   e) D. gangeticum (intro. into
                     the West
                     Indies).
   f) D. adscendens
                     pantropical
   g) D. barbatum   species.

3) Introduced into Africa
   from Asia
   a) D. laxiflorum
   b) D. triflorum
   c) D. dichotomum

4) Introduced into Africa
   of New World Origin
   (Pantropical weeds)
   a) D. incanum
   b) D. tortuosum
   c) D. procumbens
   d) D. scorpiurus

5) Many others are in cultivation
   or in experimental Research
   Stations.
   i.e. a) D. uncinatum
        b) D. intortum
        Cultivated as pasture
        legumes. From New World.

TAXONOMIC TREATMENT

In the citation of specimens examined, the names of the different herbaria referred to have been abbreviated where possible according to Holmgren, Keuken and Schofield (1981).

A   Cambridge : Arnold Arboretum, Harvard University.

B   Berlin : Botanical Garden and Botanical Museum.

BM   London : British Museum (Natural History).

BOL   Cape Town : Bolus Herbarium, University of Cape Town.

BR   Brussels : National Botanical Garden.

C   Copenhagen : Botanical Museum and Herbarium.

G   Geneva : Botanical Garden and Conservatory.

GH   Cambridge : Gray Herbarium of Harvard University.

GRA   Grahamstown : Herbarium of the Albany Museum,
         Botanical Research Unit.

J   Johannesburg : The Moss Herbarium, University of
         the Witwatersrand.

K   Kew : The Herbarium, Royal Botanic Gardens.

LINN   London : The Linnean Society of London.

LISU   Lisbon : Museum, Institute of Botany.

NBG   Cape Town : Compton Herbarium, National Botanic Gardens
         of South Africa, Kirstenbosch.

NH   Durban : Natal Herbarium, Botanical Research Unit.

NU   Pietermaritzburg : Department of Botany, University
         of Natal.

P   Paris : National Museum of Natural History,
         Institute of Phanerogams (including P-JU, Jussieu
         and P-LA, Lamarck collections).

PRE   Pretoria : Botanical Research Institute, National
         Herbarium.

PRU   Pretoria : H.G.W.J. Schweickertdt Herbarium,
         University of Pretoria.

S   Stockholm : Section for Botany, Swedish Museum of
         Natural History.

SAM   Cape Town : South African Museum Herbarium, National
         Botanic Gardens of South Africa, Kirstenbosch.

STE   Stellenbosch/.....

STE   Stellenbosch : Government Herbarium, Botanical Research
        Unit.
VENDA   Tate Vondo : Venda Herbarium.
W   Vienna : Natural History Museum.
WIND   Windhoek : South West African Herbarium.
ZULU   Empangeni : Herbarium, University of Zululand.

Desmodieae (Benth.) Hutch., Gen. Fl. Pl. 1 : 477 (1964) pro parte; Schubert and Verdc., Fl. Trop. E. Afr., Legum. - Papil. : 450 (1971); Verdc. in Kirkia, for Fl. Zamb. 9 (2) : 505 (1974); Ohashi et al in Polhill and Raven (ed.), Adv. Leg. Syst. 1 : 292 (1981).   Type genus Desmodium Desv.

Coronilleae Adans., Fam. Pl. 2 : 327 (1763) pro parte

Hedysareae DC., Prodr. 2 : 307 (1825) pro parte

Hedysareae subtribe Desmodiinae (as Desmodieae) Benth. in Benth. and Hook.f., Gen. Pl. 1(2) : 449 (1865) pro parte; Taub. in Pflanzenfam. III, 3 : 325 (1894) pro parte

Coronilleae subtribe Desmodiinae (Benth.) Schulze-Menz in H. Melchior, Engl. Syll. Pflanzenfam. 2 : 237 (1964) pro parte; Ohashi in Journ. Fac. Sci. Univ. Tokyo, sect. 3, 2 : 52 (1971)

Herbs or suffrutices, sometimes shrubs or rarely trees; roots woody, often dichotomously branched, cord-like and producing rhizomes, or more rarely taproots; leaves pinnately 3 (-9) or 1 - foliolate, petioles sulcate, foliar and foliolar pulvini present; stipellate (except Lespedeza); stipules mostly striate; inflorescence of variously contracted terminal, axillary or occasionally leaf-opposed pseudoracemes, which may be paniculately branched; flowers pedicellate, small, fasciculate, paired or rarely solitary on rhachis, usually subtended by 2 series of bracts and occasionally bracteoles; calyx 2-lobed, the upper 2 connate sepals often slightly bifid, the lower 3-toothed with the central tooth longer than the laterals or calyx almost equally 5-lobed; corolla papilionoid, exceeding the calyx; stamens mostly diadelphous with the vexillary stamen free, rarely partly monadelphous; filaments equal or alternating in length, anthers uniform; pollen tricolporate with a generally thickened endexine and thin or no foot layer; fruits transversely jointed into a number of articles or reduced to one article or less often 2-valved, opening along one suture (valves not twisting); seeds with a well developed radicular lobe, longer than the cotyledonary lobe; mostly with a rim aril; seedlings generally epigeous with the first two eophylls opposite and unifoliolate.

Plants/.....

Plants with characteristic small hooked hairs; tertiary venation $\pm$ scalariform; stipels present; flowers chasmogamous, with an explosively dehiscent pollination mechanism; standard with hardly or slightly inflexed auricles; ovary (1) - many ovulate.

subtribe Desmodiinae

Plants without hooked hairs; tertiary venation reticulate; stipels mostly absent; flowers chasmogamous, not explosively dehiscent, often mixed with cleistogamous flowers; standard with inflexed auricles more persistent than most Desmodiinae; ovary 1 - ovulate.

subtribe Lespedezinae

6.1. Desmodiinae

Desmodiinae sensu Ohashi et al in Polhill and Raven (ed.), Adv. Leg. Syst. 1 : 296 (1981)

Pseudarthrieae Hutch., Gen. Fl. Pl. 1 : 398 (1964) pro parte

Herbs, suffrutices or shrubs with small hooked hairs; leaflets (1) - 3 - (9) with tertiary venation somewhat scalariform; petiolulate, the laterals each subtended by 1 stipel, the terminal by 2; bracts striate and ciliate, inflorescence bracts each subtending a fascicle of 2-to-several flowers (rarely only one flower); floral bracts often present, similar to inflorescence bracts or depauperate, each subtending a single flower; bracteoles occasionally present; flowers explosively dehiscent with petals becoming disarrayed; standard with hardly or slightly inflexed auricles, orbicular to obovate, mostly constricted into a claw at the base; wings obliquely oblong, slightly wider dis- tally, cultrate, extended into a short claw at the base, often auricu- late near the base of the blade; keel petals joined for most of the length of the bottom of the keel and along the distal erect margin, broadly oblong, narrowing for the proximal third into a long claw, deeply pocketed with a minute peg of tissue toward the base of the lamina corresponding and closely applied to the auricle of the wing, which often adheres to the keel; ovary sessile or shortly stipitate with (1) - many ovules; stigma broadly capitate, terminal or slightly lateral.

Calyx often membranous, never glumaceous or striate, shallowly divided, usually inconspicuous in fruit; fruit mostly held away from erect; leaves (1) - 3 -(5)-foliolate:

Stipules stramineous, striate, erect or spreading but never sharply recurved or velutinous; fruit distinctly jointed, breaking up into individual articles.

Desmodium

Stipules mostly sharply recurved, dark brown adaxially, silver velutinous abaxially; fruit splitting into two valves.

Pseudarthria

Calyx glumaceous, striate, deeply divided, persistent and often partially enclosing the fruit; fruit held erect, usually consisting of a number of 'stacked' terete or subterete articles; leaves 1 - foliolate.

Alysicarpus

6.1.1. Desmodium

Desmodium Desv., J. Bot., Paris ser. 2, 1 : 122, t. 5 (1813) nom conserv.; DC., Prodr. 2 : 325 (1825); Benth. in Miq., Pl. Jungh. : 220 (1852); Harv. in Harv. and Sond., Fl. Cap. 2 : 227 (1862); Benth. in Benth. and Hook.f., Gen. Pl. 1 (2) : 519 (1865); Harv. Gen. : 82 (1868); Bak. in Oliv., Fl. Trop. Afr. 2 : 159 (1871) and in Hook.f., Fl. Br. Ind. 2 (4) : 161 (1876); Taub. in Pflanzenfam. III (3) : 327 (1894); Schindl. in Feddes Repert. Beih. 49 : 263 (1928); Hutch and Dalz., Fl. W. Trop. Afr. 1 : 417 (1928); Bak.f., Leg. Trop. Afr. : 324 (1929); Phill., Gen. ed 2 : 332 (1951); Schubert in Bull. Jard. Bot. Brux 22 : 287 (1952) and in Fl. Congo Belge 5 : 180 (1954); Hepper in Fl. W. Trop. Afr. ed 2, 1 : 582 (1958); Knaap - van Meeuwen in Reinwardtia 6 : 240 (1962); Hutch., Gen. Fl. Pl. 1 : 481 (1964); Torre in Consp. Fl. Angol. 3 : 217 (1966); Schreiber in Prodr. Fl. SW. Afr. 60 : 30 (1970); Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 451 (1971); Ohashi in Ginkgoana 1 : 87 (1973); Verdc. in Kirkia, for Fl. Zamb. 9, (2) : 506 (1974); Dyer, Gen. 1 : 263 (1975); Compton, Fl. Swazi : 272 (1976); Schubert in Ann. Mo. bot. Gdn 67 : 622 - 623 (1980); Type species : D. scorpiurus (Swartz) Desv. (Hedysarum scorpiurus Swartz).

> Hedysarum L., Sp. Pl. : 745 (1753) pro parte (name still valid for other plants.)

> Meibomia Heist. ex Fabricius, Enum. : 168 (1759), nom rejic. Adans., Fam. Pl. 2 : 509 (1763); Kuntze, Rev. Gen. 1 : 195 (1891)

> Nicolsonia DC., Prodr. 2 : 325 (1825)

> The name Desmodium was conserved over the name Meibomia by the International Botanical Congress of Vienna in 1905. (Schubert, 1950)

> Desmodium is derived from the Greek 'desmos' meaning a band or chain and 'hode' meaning, - like - ; in reference to the jointed pods' resemblance to the links of a chain.

Herbs, subshrubs or shrubs; erect, ascending or decumbent to scrambling. Leaves (1) - 3-foliolate. Stipules free or rarely connate, usually oblique; narrowly ovate to lanceolate - attenuate, often persistent, scariose, striate and ciliate. Leaflets variously shaped, thinly chartaceous /.....

chartaceous to coriaceous; the lateral leaflets smaller than the terminal one; venation either craspedodromus, eucamptodromus or partially brochidodromus.. Pseudoracemes terminal or axillary, frequently paniculately branched, variously contracted from open lax arrangements to tight spikes or heads. Calyx usually broadly campanulate, 4 - 5 lobed, the upper two often connate for some length; lateral lobes sometimes shorter than the others, usually triangular; the lower lobe more-or-less longer than the rest. Corolla commonly purple, mauve or pink and hyaline, rarely red. Androecium mostly diadelphous rarely monadelphous; anthers basifixed. Gynoecium longer than androecium, sessile or stipitate; ovary narrow oblong, usually many-ovulate; mostly puberulent; style inflexed or incurved. Fruit well exserted from an often senescent calyx; compressed, jointed, mostly indehiscent with 1 - seeded articles separating at the joints; occasionally tardily dehiscent. Seeds compressed, often flat, transversely broadly elliptic, ovate or reniform; hilum lateral, mostly distinctly rim arillate around the hilum. 2n = 22 - (20)

Key to Desmodium

1. Inflorescences of variously lax to dense, elongated axillary and terminal pseudoracemes, the terminal one often paniculately branched; calyx teeth short, triangular or lanceolate; the adaxial two usually markedly connate forming a lip:

    2. Flowers large, brick red; herb or subshrub climbing or scrambling and forming a dense undergrowth in forest; leaflets rhomboid, deep green, venation craspedodromus; inflorescences very lax; stamens partially monadelphous:

                                                  D. repandum

    2. Flowers small, variously pink, mauve or purple but never red; plants not as above, stamens always diadelphous:

        3. Plants becoming erect to semierect suffrutices or subshrubs if not burned; leaflets never obovate, lateral veins not obviously looping in the distal half of leaves; floral bracts present at the base of the pedicels; inflorescences variously contracted.

            4. Flowers uniformly deep mauve; pseudoracemes terminal only and never paniculately branched; leaflets glossy dark green with characteristic light discoloration along midrib above; widespread weeds of disturbed areas in coastal Zululand, Natal, Transkei

Eastern Cape to 1000m.

<div align="right">D. incanum</div>

4. Flowers light pink or purple, dark purple only at the tip of the keel; pseudoracemes terminal and often axillary, the terminal often paniculately branched; leaflets various, not as above.

  5. Leaves trifoliolate:

    6. Leaf venation mixed craspedodromus with principal lateral veins prominent and parallel; leaflets distinctly saliciform and characteristic; shrub growing in or near water.

<div align="right">D. salicifolium</div>

    6. Leaf venation eucamptodromus lateral veins neither prominent nor regular; stipules markedly auriculate at base on leaf opposed margin, connate at least when young, resembling a collar; introduced weed with restricted distribution.

<div align="right">D. tortuosum</div>

  5. Leaves unifoliolate:

    7. Leaflets chartaceous, ovate or cordiform with entire margins, venation eucamptodromus; stipules gradually narrowed from the base to a slender apex.

<div align="right">D. gangeticum</div>

    7. Leaflets thick, velutinous, suborbicular often with sinuate margins; venation craspedodrumus; stipules abruptly narrowed from an auriculate base to a long slender apex; northeastern Transvaal only.

<div align="right">D. velutinum</div>

3. Plants procumbent, or stoloniferous creepers; leaflets small, obovate, lateral veins obviously looping in the distal half of the leaves; floral bracts usually absent, inflorescences lax:

8. Procumbent herbs rooting from lower nodes, in open grassland to forest fringes, often drying brown or grey-green in herbarium specimens; fruit characteristic (fig. 9).

D. setigerum

8. Stoloniferous herbs of moist forest and forest edge undergrowth, often drying deep green in herbarium specimens; fruit characteristic (fig. 9).

D. adscendens

1. Inflorescences congested into dense spicate or capitate pseudoracemes, never paniculately branched but often with upper axillary and terminal inflorescences crowded together; calyx teeth long acuminate, the adaxial two not markedly connate:

9. Leaves variously 3 - 1-foliolate; inflorescence spicate, petioles obvious, often dark coloured, visibly deflexed distally, bract-eoles absent; woody herbs in mixed open woodland north and eastern Transvaal.

D. barbatum

9. Leaves 3-foliolate, conduplicate; inflorescence densely capitate, petioles not obvious; bracteoles 2 clasping calyx; woody herb often of moist grassland.

D. dregeanum

6.1.1.1. Desmodium repandum (Vahl) DC., Prodr. 2 : 334 (1825); Schindl. in Feddes Repert. Beih. 49 : 295 (1928); Schubert in Bull. Jard. Bot. Brux. 22 : 293 (1952) and in Fl. Congo Belge 5 : 193, t.14 (1954); Hepper in Fl. W. Trop. Afr. ed 2,1 : 584 (1958); White, For. Fl. N. Rhod. : 150 (1962); Laundon in Consp. Fl. Angol. 3 : 221 (1966); Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 465, fig. 65/11 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 517 (1974); Compton, Fl. Swazi. : 272 (1976). Type : Yemen, Forsskäl (C, holo. fide Schindl.; GH, photo. !)

Hedysarum repandum Vahl, Symb. Bot. 2 : 32 (1791); Poir. in Lam., Encycl. 6 (2) : 408 (1805).

Desmodium scalpe DC., Prodr. 2 : 334 (1825); Bak. in Oliv., Fl. Trop. Afr. 2 : 164 (1871); Hutch. and Dalz., Fl. W. Trop. Afr. 1 : 418 (1928); Bak.f., Leg. Trop. Afr. : 328 (1929); Robyns, Fl. Parc Nat. Alb. 1 : 327, t. 30 (1948); Brenan in Checklist Tang. Terr. : 420 (1949). Type : Mauritius (Isle de Bourbon) Commerson (P-LA, holo., GH, photo.!)

Desmodium strangulatum Wight and Arn., Prodr. Fl. Ind. 1 : 228 (1834); Harv. in Harv. and Sond., Fl. Cap. 2 : 228 (1862). Type : E. Peninsular India, Walker in Wight cat. No. 774 (K, holo. !, GH, iso.)

Desmodium caffrum Eckl. and Zeyh., Enum. : 251 (1835) non (E. Mey.) Druce which is a later illegitimate name for D. dregeanum Benth.

Perennial herb or scandent shrub 0,3 - 1,0m tall, scrambling and often forming a dense undergrowth; arising from an irregularly knotty-elongate woody rhizome extending horizontally, and also rooting at intervals at the nodes. Stems many, ascending from branches of the cord-like rhizome; terete, glabrescent, brown to red below; becoming angular and grooved, minutely uncinulate puberulent and sparsely to moderately spreading pilose with long upwardly directed pointed hairs above. Leaves trifoliolate. Stipules 6,0 - 25mm long, 2,0 - 6,0mm wide; partly reflexed and somewhat curled; oblong-lanceolate to attenuate; minutely puberulent and scarcely, long strigose; margin ciliate; striate, early stramineous. Petioles 0,8 - 11cm long; vesture similar to stem. Leaflets 1,8 - 11cm long, 1,5 - 8,5cm wide; rhombi-form, apex acute or more rarely obtuse; base cuneate; margin entire to repand/.....

to repand or sinuate, ciliate; both surfaces puberulent and moderately long strigose (more densely so on veins of the abaxial surface); veins not sunken adaxially and only major veins slightly prominent abaxially; lateral veins extend fully to the leaf margin, no looping of veins distally, deep green above with characteristic silvery discoloration in the centre spreading out along veins to perimeter; paler below; terminal leaflet symmetrical, laterals smaller and strongly assymmetrical; base oblique. Petiolules 3,0 - 4,1mm long; more densely pilose than rhachis; slightly swollen and rugose. Stipels 0,8 - 2,6mm long; linear - attenuate; four, one subtending each lateral leaflet and two, reduced, the terminal one. Pseudoracemes elongate, lax, terminal or axillary, often paniculately branched. Rhachis uncinulate puberulent and moderately to densely fulvous spreading pilose. Inflorescence bracts 3,5 - 7,0mm long, 2,0 - 3,0mm wide; cochleariform, attenuate; vesture similar to stipules; striate; early caducous; each subtending a fascicle of 3 - 5 pedicels, the median ones reduced to buds, one of which may elongate producing a flower sometime after outer two which mature first and together, rarely, one pedicel may be seen as a branch of another, showing incomplete reduction of botrys to fascicle. Floral bracts 0,2 - 1,8mm long, 0,2 - 0,5mm wide; triangular or subulate; margin ciliate; very much reduced, one subtending the base of each pedicel. Pedicels 1,2 - 3,8cm long, vesture similar to rhachis; slender and lax, curving erect. Flowers 8,0 - 14,4mm long, conspicuous; bright orange to brick red. Calyx 4,0 - 5,4mm long; puberulent and scarcely pilose, becoming more so on the teeth; striate; tube, 1,4 - 2,6mm long; teeth, four, upper tooth of two connate sepals, 2,0 - 2,6mm long, 2,0 - 2,3mm wide; ovate- attenuate, bifid for upper 0,5mm; others 2,0 - 2,8mm long, 0,8 - 1,1mm wide; oblong narrowing abruptly to an acuminate apex. Standard 8,0 - 13,5mm long, 7,0 - 14,0mm wide; orbicular, retuse, gradually narrowing to a short, sharply reflexed claw at the base; orange with two deep red dots on either side of the midline near the base. Wings 8,0 - 12,5mm long, 2,5 - 3,5mm wide, cultrate, oblong, long pocketed; apex rounded; extended into a short claw at the base. Keel blades up to 14,5mm long; longer than wings; securiform, apex truncate; base extended into a claw 1,5 - 2,5mm long; deeply long pocketed; hyaline becoming red terminally. Staminal sheath 7,0 - 12mm long, 1,5 - 2,5mm wide, oblong; vexillary stamen up to 11mm long, partially coherent to sheath. Gynoecium 7,0 - 12,5mm long; ovary 6,0 - 8,0mm long; style 1,5 - 2,5mm long, flexed erect. Fruit, stipe 2,0 - 4,5mm long; of 1 - 5 articles each 5,5 - 12,5mm long, 2,0 - 4,5mm wide; straight on the upper suture or slightly concave at the centre of
each/
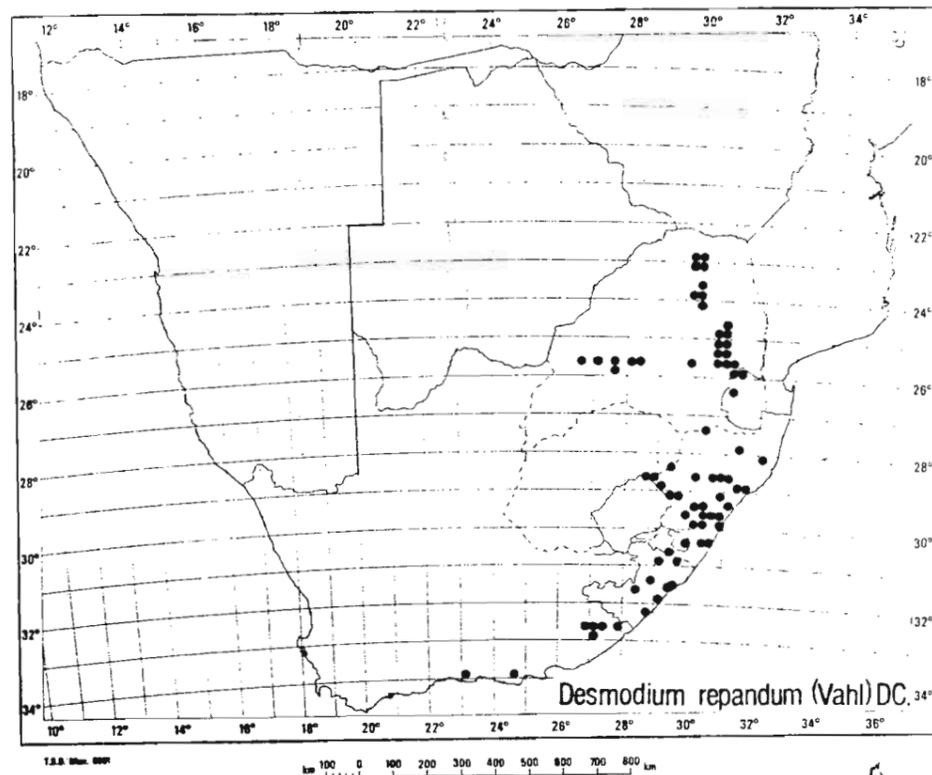
each article, curved obliquely below, deeply indented at the isthmi; densely uncinulate puberulent on surfaces, less so on sutures; style persistent. Seed 5,5 - 7,0mm long, 2,0 - 4,2mm wide; same shape as article; pericarp wall closely applied to the testa, brown.

Desmodium repandum is found in shaded areas in moist to dry evergreen mountain, riverine or other gallery forest often near paths or along streams from $\pm$ 3000m to near sea level. It occurs as a forest floor herb or scrambling subshrub in such forest patches located in the following regions and vegetation types:-

TRANSVAAL 1) in Mixed and sourish Mixed Bushveld, Acocks Veld Types 18 and 19 from Zeerust in the west to near Witbank in the east.

2) in similar bushveld or in other types of Sourveld and Sour Bushveld, Acocks Veld Types 8 and 9 from Louis Trichardt, Pietersberg and Tzaneen in the north, through between Lydenberg and Graskop, Belfast and Barberton, to western Swaziland in the south. It is not found in the lowveld.

NATAL where suitable forest patches occur from the Drakensberg to almost sea level except in the lowveld of Zululand and in coastal dune forest.

TRANSKEI and EASTERN CAPE to the coastal southern Cape at Knysna.

Flowering occurs from August to June although most commonly from January to May.

TRANSVAAL.-2229 (Waterpoort): 10 miles N. of Wyllies Poort (-DD), A.O.D. Mogg J 36211 (J). 2230 (Messina): Hanglip, 20 miles NE. of Louis Trichardt (-CC), J. Gerstner 6005 (PRE); Entabeni (-CC), A.A. Obermeyer sub TRV 30371 (PRE). 2329 (Pietersberg): Louis Trichardt (-BB), Miss Blenkinson J 14446 (J); Dr. Breyer subTRV 19552 (PRE); Grobbelaars Farm, Louis Trichardt (-BB), C. Letty 248 (PRE); Hanglipbos (-BB), A.E. van Wyk 915 (PRE, PUC); Zoutspansberg Mtns. Louis Trichardt Distr. (-BB), R.G.N. Young PRE 55596 (PRE); R.G.N. Young 55607 (PRE); Pietersberg Distr. (-CD), R.A. Dyer 3153 (PRE); Houtbosch (-DD), R. Schlechter 4742 (BOL, PRE). 2330 (Tzaneen): Elim (-AA), A.A. Obermeyer sub TRV 30325 (PRE); Westfalia Estate (-CA), J.J. Bos 1230 (PRE, STE); Farm Deelkraal, Mooketsi Valley (-CA), de Winter and Killick 8922 (PRE); Duiwelskloof (-CA), E.E. Galpin 10090 (PRE); Spelonken (-CA), H. Junod 46 (PRE); Duiwelskloof (-CA), J.C. Scheepers 248 (PRE, PRU); Politsi, Letaba Distr. (-CC), R.D. Bayliss 2757 (NBG, PRE); De Hoek Forest Station (-CC),

Mrs./....

Desmodium repandum (Vahl) DC.

Mrs. Eliovson J 26989 (J); Franschhoek, Magoebaskloof (-CC), W.J. Hanekom 2299 (PRE); Slopes below Magoebaskloof Hotel (-CC), O.A. Leistner 648 (PRE); Woodbush Reserve (-CC), C. Letty 460 (PRE); Newagatha (-CC), I. McCallum sn. (PRE); Woodbush village (-CC), C.J. Swierstra PRE 55605 (PRE); Woodbush (-CC), H. Wager sub TRV 22988 (PRE). 2430 (Pilgrim's Rest): Mamotswiri (-AA), H. Junod 182 (PRE); The Downs (-AA), H. Junod 4357 (PRE); Marieskop (DB), Fitzsimons and van Dam sub TRV 26257 (PRE); H.P. van der Schijff 4332 (PRE, PRU); H.P. van der Schijff 4941 (PRE, PRU); G. van Son sub TRV 30688 (PRE); Mt. Sheba Forest Nature Res. (-DC), K.H. Cooper 204 (PRE); Pilgrim's Rest (-DC), Forrester and Gooyer 187 (PRE); Orighstad dam Nature Res. (-DC), N. Jacobsen 2671 (PRE); G.K. Theron 3612 (PRE, PRU); Pilgrim's Rest Distr. (-DD), L. Collins sub TRV 9895 (PRE); Kowyns Pass, Graskop Distr. (-DD), E.E. Galpin 14457 (BOL, PRE); Bonnet, Pilgrim's Rest Dist. (-DD), R.G. Strey 3725 (PRE). 2526 (Zeerust): Rietfontein betw. Swartruggens and Lichtenburg (-DA), D.J. Botha 2583 (PUC). 2527 (Rustenburg): 'Rainhill' farm nr. Rustenburg (-CA), L.E. Codd 1076 (PRE); Rustenburg Kloof (-CA), E.N. Prosser 5862 (PRE), Tierkloof, Rustenburg (-CA), F. Venter 697 (PRE); Jacksonstuin, 6 miles E. of Hartebeespoortdam (-DA), A.O.D. Mogg 33984 (J); D.V. van Vuuren 88 (PRE); Castle Gorge, Magaliesberg (-DA), L.L. Vorster 15 (PRE); Kromme Kloof, Krugersdorp Distr. (-DC), J. Phillips J 35347 (J). 2528 (Pretoria): Rooival (-CA), I.C. Verdoorn PRE 58467 (PRE); Pienaars Poort (-CB), L.R. Vogt PRE 55600 (PRE). 2529 (Witbank): Leeusklip Waterfall, Belfast Distr. (-DB), R.G. Strey 4103 (PRE). 2530 (Lydenburg): Lydenburg to Dullstroom (AB/AC), I.B. Pole Evans 4549 (PRE); Maritzbos (-BA), G.L. Mohle 268 (PRE); Langverwag, Sabie (-BB), W.J. Louw 2730 (PUC, STE); Bridal Veil Falls (-BB), S. Morgan 70 (PRE); Lydenburg (-BB), P.J. Muller 2352 (PRE); Wonderkloof Nature Res. (-BC), D. Elan Puttick 16 (PRE); Witklip (-BD), J.P. Kluge 467 (PRE, PRU); Schagen (-BD), L.C.C. Liebenberg 2947 (PRE); Berlin, Godwan River (-DA), G.J. Hofmeyer PRE 55621 (PRE); Devils Kantoor, Kaapse Hoop (-DB), I.B. Pole Evans 970 (PRE). 2531 (Komatipoort): Uitkyk (-CA), C.H. Stirton 1753A (PRE); C.H. Stirton 1753 B (PRE); Barberton (-CC), E.E. Galpin 1287 (PRE); R. Pott 5335 (PRE); Twello Farm, 9,7km E.S.E. of Barberton (-CC), P. van der Merwe 312 (PRE); Barberton (-CC), Miss Williams sub TRV 7622 (PRE).

O.F.S. - 2828 (Bethlehem): Golden Gate National Park (-DA), E. Thorpe NH 29880 (NH), Sungubala, Drakensberg (-DB), Stone 39 (NU).

SWAZILAND.-2531 (Komatipoort): Nr. Havelock Mine (-CC), Codd and

Muller 325 (PRE); O.B. Miller 4279 (PRE); Peak Timbers Estate, Piggs Peak Distr. (CC/CD), D.K. Fisher SAM 66046 (SAM). 2631 (Mbabane): Ukutula Forest (-AC), R.H. Compton 25615 (PRE, SAM); Sheba's Veil (-AC), R.H. Compton 27287 (NBG, PRE); Hill N. of Mbabane (-AC), R.H. Compton 28692 (NBG, PRE); B. Dlamini NBG 49172 (NBG); B. Dlamini PRE 55645 (PRE); 4km E. of Mbabane (-AC), E. Kemp 1153 (PRE)

NATAL.-2730 (Vryheid): Donkerhoek (-AD), N.J. Devenish 819 (NH, PRE); Naauwhoek (-AD), N.J. Devenish 1647 (NU); Pongola Mtns. to Kafir Drift (-AD), J. Thode A317 (NH, PRE). 2731 (Louwsburg): Ceza Forest (-CD), Hilliard and Burtt 3310 (NU); Ngome Forest (-CD), G. Nichols 477 (NH); 35km from Nongoma to Vryheid (-CD), B. Schrire 399 (NH). 2828 (Bethlehem): The Cavern, Drakensberg (-DB), D.M. Gemmell BLFU 5349; M. Henderson 53 (BLFU); P. L'Ange 86 (NU). 2829 (Harrismith): Boschfontein nr. Brakwalstasie (-AD), M.L. Jacobs 1757 (PRE); Cathedral Peak (-CC), E. Esterhuysen 12875 (BOL, PRE); D.J.B. Killick 1667 (PRE). 2830 (Dundee): Kafir Drift (-CA), J. Thode STE 3802 (STE); Qudeni, rd. to Tissiman's Farm, Nkandla Distr. (-DA), O.M. Hilliard 1365 (NH,NU); Turnoff at foot of Qudeni (-DB), D. Edwards 1312 (NU, PRE), Qudeni (-DB), J. Gerstner 626 (PRE). 2831 (Nkandla): Nkandla Forest Res. (-CA), H.J.T. Venter 3485 (ZULU), Entumeni (-CD), J. Gerstner 3845 (NH); Eshowe (-CD), J.G. Lawn 72 (NH); C.E. Moss J15784 (J); Dlinza Forest (-CD), J.H. Ross 1994 (NH, PRE); Eshowe (-CD), B. Schrire 335 (NH); Ngoye Forest Res. (-DC), E.J. Moll 5421 (NH); H.J.T. Venter 2424 (PRE, ZULU). 2832 (Mtubatuba): Hluhluwe Game Reserve (-AA), E.D. Guy 34 (NU, PRE); C.J. Ward 2155 (NU). 2929 (Underberg: Nr. Champagne Castle Hotel (-AB), J.P.H. Acocks 10118 (NH); Cathkin Park (-AB), E.E. Galpin 11858 (BOL, PRE); B. & C. Howlett 16 (NH, NU, PRE); B. & C. Howlett 106 (NH, PRE); Cathkin Peak Ravine (-AB), R.G. Strey 7843 (NH); Giants Castle Game Reserve (-AB), W.R. Trauseld 375 (PRE); Ntabamhlope (-BA), O. West 1089 (PRE); Deepdale (-DB), M.S. Evans 112 (NH). 2930 (Pietermaritzburg): Farm Ehlatini, Karkloof (-AD), E.J. Moll 3439 (NH, NU); Rd. to Lilani (-BB), O.M. Hilliard 1951 (NU); Sunnyside, beyond Town Bush Valley (-CB), Dohse and Lindahl 198 (NH, PRE); Kettlefontein nr. P.M. Burg (-CB), N.U.C. Students 29 (NH); Town Hill (-CB), J. Randles 10 (NU); P.M. Burg (-CB), Stanton 70 (NU); Town Hill (-CB), J. Thode STE 6443 (STE); Nr. Murchison (-CB), J.M. Wood 3103 (NH); Byrne (-CC), E.E. Galpin 11933 (PRE); Deepdene nr. Richmond (-CD), J. Sanderson 870 (NH); Table Mtn. (-DA), D.J.B. Killick 144 (NU, PRE); Inanda (-DB), J.M. Wood 508 (BOL, SAM); Hillcrest (-DD), J. Kalf 35 (NU); Kloof (-DD), J.H. Ross NU 25769 (NU)./.....

(NU). 2931 (Stanger): Eisdumbini (-AC), J.M. Wood 5350 (PRE). 3029 (Kokstad): Zuurberg, nr. Kokstad (-DA), W. Tyson 1165 (BOL); W. Tyson 1525 (PRE, SAM). 3030 (Port Shepstone): Farm Friedenau, Dumisa (-AD), H. Rudatis 334 (PRE); Ifafa, Umgayeflat (-BC), H. Rudatis 115 (STE); Umgayi (-BC), C.J. Ward 5498 (NU)

TRANSKEI.- 3029 (Kokstad): Mt. Malowe nr. Clydesdale (-BD), W. Tyson 1439 (SAM, STE); W. Tyson 2114 (BOL); Insizwa (-CC), R.G. Strey 10752 (NH, NU, PRE); Magusheni (-DC), W. Tyson 2816 (SAM). 3127 (Lady Frere): Tsomo River (BC/DA/DC), H. Bowker sn. (GRA). 3128 (Umtata): Tsitsa Falls (-BD), C.E. Moss J 18018 (J.); Baziya (-CB), R. Baur 114 (BOL,GRA). 3129 (Port St. Johns): Isinuka R. (-CB), E.E. Galpin 11444 (PRE); Forest betw. Ngqeleni and Umtata R. mouth (-CC), G.J. Lewis SAM 68720 (SAM); Nr. Port St. Johns (-DA), H. Bolus STE 24837 (STE); H.G. Flanagan PRE 55637 (PRE); Port St. Johns (-DA), E.E. Galpin 3479 (BOL); C. Howlett 26 (PRE); G.J. Lewis SAM 61374 (SAM); C.E. Moss 3300 (PRE); Ntafufu (-DA), R.G. Strey 8530 (NH, PRE); Port St. Johns (-DA), G.C. Theron 1600 (PRE); H.A. Wager PRE 55633 (PRE). 3228 (Butterworth); Dwessa Forest Nature Res. (-BD), E.J. van Jaarsveld 3800 (NBG)

CAPE.-3226 (Fort Beaufort): Hogsback (-DB), M.H. Giffen 837 (PRE); Slopes of Amatola Mtns, below Hogsback (-CA), G.J. Lewis SAM 68719 (SAM). 3227 (Stutterheim): Kologha (-CB), J.P.H. Acocks 9648 (PRE); Stutterheim Forest (-CB), H. Bokelmann NBG 67393 (NBG); Waterfall Kloof nr. Stutterheim (-CB), E.E. Galpin 6303 (PRE); Kologha Forest (-CB), M.J. Wells 2880 (GRA, NH, PRE); Pirie Forest, nr. K.W. town (-CC), C.E. Moss J 14213 (J); Pirie bush (-CC), S. Schonland 845 (GRA, PRE); Pirie, K.W. town Distr. (-CC), J.R. Sim 4057 (GRA, PRE); Mngquesha nr. K.W. town (-CC), W. Tyson 3151 (PRE); nr. Komgha, along the Gwenkala stream (-DB); H.G. Flanagan 515 (BOL, GRA, NBG, NU, PRE, SAM). 3323 (Willowmore); Deepwalls Forest Stn. (-CC), C.M. Schonken 15 (STE). 3324 (Steytlerville): Blaauwkrantz Pass, Zitzikamma (-DC), Fourcade 233 (BOL, GRA)

In the latest Asian revision of Desmodium by Ohashi (1973), D. repandum is placed in the most advanced subgenus Podocarpium because it is characterised by monadelphous androecia and long-stipitate pods consisting of indehiscent, approximately shallowly obtriangular segments. However the androecium of D. repandum cannot be considered to be truly monadelphous, the vexillary stamen being coherent (not fused) for only part of its length. The pollen grains (Ohashi, l.c.)/.....

l.c.) are also quite distinct from those of all other species of the subgenus Podocarpium especially in the shape of the grains, colpi and thickness of exine. Ohashi (l.c.) also notes that D. repandum is similar in several vegetative characters to some members of the more primitive subgenus Dollinera.

From observations on the degree of contraction of the pseudoraceme in D. repandum it appears that this also shows a less derived situation. Occasionally one pedicel may be seen to branch off another above the fascicle indicating incomplete reduction of the botrys. A number of pedicels also occur in the fascicle, three or four of which may flower with one or two reduced buds inbetween. The fascicle in all the other species has been reduced to two pedicels with or without one enclosed, median bud.

D. repandum is a widespread species of tropical and subtropical Africa, Madagascar, Mascarene Is., India and S.E. Asia to Malesia.

6.1.1.2 <u>Desmodium incanum</u> DC., Prodr. 2 : 332 (1825); Bak. in Oliv., Fl. Trop. Afr. 2 : 163 (1871); Hutch. and Dalz. in Fl. W. Trop. Afr. 1 (2) : 418 (1928); Nicolson in Taxon 27 (4) : 365-370 (1978). Type illustration : Plumier, ed. Burman, Pl. Amer. : 140, t. 149, fig. 1 (1757) - <u>Hedysarum folii's ternatis; ovatis, floribus spicatus</u>(!)

<u>Hedysarum racemosum</u> Aubl., Hist. Pl. Guian. 2 : 774 (1775). Type : as for species. First legitimate name but epithet unavailable in <u>Desmodium</u>.

<u>Hedysarum frutescens</u> sensu Jacq., Hort. Vindob. 3 : 47, t. 89 (1776). Misidentified by Jacquin with <u>H. frutescens</u> L.

<u>Hedysarum incanum</u> Swartz, Prodr. Veg. Ind. Occ. : 107 (1788) reprint 1962, and Fl. Ind. Occ. 3 : 1264 (1806) non Thunb. (1784). Type : as for species. Illegitimate renaming of <u>H. racemosum</u> Aubl.

<u>Hedysarum canum</u> J.F. Gmel., in L., Syst. Nat., ed 13, 2 (2) : 1124 (1791), non Lunan (1814). Type : as for species. Super-fluous renaming of <u>H. racemosum</u> Aubl.

<u>Desmodium canum</u> (J.F. Gmel.) Schinz and Thell., in Schellenb., Schinz and Thell., Mem. Soc. Neuchatel. Sci. Nat. 5 : 371 (1913) and Feddes Repert. 12 : 428 (1913); Schubert in Fl. Congo Belge 5 : 184 (1954); Hepper in Fl. W. Trop. Afr., ed. 2, 1 : 584 (1958); Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 456 (1971). Treated as a new name with priority from publication because of the illegitimate 'basionym', it is a superfluous renaming of <u>D. incanum</u> DC.

<u>Desmodium frutescens</u> sensu Schindl., Feddes Repert. 21 : 9 (1925); Bak.f., Leg. Trop. Afr. : 328 (1929). Intended as a new combin-ation of <u>H. frutescens</u> sensu Jacq.

Perennial, spreading to ascending or erect, multistemmed herb or becoming a wiry or stout subshrub 0,2 - 1,5m high, arising from a large, dichotamously branching woody rootstock. <u>Stems</u> woody below, glabrous, prostrate ones often rooting at nodes; young stems puberulent and thickly pilose with long ascending tapering hairs, terete to angular; striate. <u>Leaves</u> trifoliolate. <u>Stipules</u> 3,0 - 8,0mm long, 1,5 - 3,0mm wide; erect, oblique, stem-clasping; partially connate

along/.....

along leaf-opposed margins at least when young; ovate-attenuate; abaxially, appressed ascending pilose; margin ciliate; striate; early stramineous; persistent. Petioles 0,8 - 3,2cm long, sulcate; puberulent and long, spreading pilose; red-streaked. Leaflets 1,5 - 10cm long, 1,5 - 5,5cm wide; shape very variable; oval, oblong, elliptic or ovate-lanceolate, apex acute or obtuse, base rounded; adaxially scattered puberulent and sparsely pilose, vesture denser along the veins, abaxially densely pilose; major veins sunken above and prominent below, reticulation prominent on the lower surface, lateral veins turn upwards and diminish apically before the margin, no looping distally; margin slightly revolute, ciliate; lustrous dark green above usually with characteristic paler streak along midrib, paler blue-green below; subcoriaceous; terminal leaflet symmetrical; lateral leaflets often asymmetrical, base oblique, smaller. Petiolules 1,5 - 3,5mm long, vesture similar to petiole, more stiffly pilose, slightly swollen; rugose. Stipels 1,0 - 3,5mm long, four, one subtending each lateral leaflet and two the terminal one; subulate to linear - attenuate; vesture similar to stipules. Pseudoracemes elongate, $\pm$ 6,0 - 10cm, relatively densely flowered, terminal. Rhachis ridged and grooved, slightly angular, densely puberulent and scattered pilose. Inflorescence bracts 2,4 - 4,1mm long, 0,5 - 1,8mm wide; lanceolate - acuminate; margin ciliate; striate; each subtending a fascicle of two pedicels and a median, reduced bud. Floral bracts 1,0 - 2,0mm long to 0,6mm wide, ovate-lanceolate to subulate; three, one subtending each lateral pedicel and one slightly higher at the junction of the reduced rhachilla and pedicel of the median bud. This pedicel frequently elongates producing another flower sometime after the outer two. Pedicels 4,0 - 10mm long, ascending from 45° to axis; densely uncinulate puberulent with abundant erect bulbous-based, glandular-tipped hairs and longer tapering hairs scattered distally, some occasionally bearing one caducous bracteole near the calyx up to 1mm long. Flowers 6,0 - 7,5mm long; variously magenta, mauve to hyaline. Calyx 2,4 - 3,0mm long; minutely puberulent with scattered glandular hairs and longer tapering hairs becoming denser on the teeth; tube, 1,0 - 1,2mm long; cupulate; teeth, 1,0 - 1,6mm long; four, subequal, triangular to lanceolate; upper tooth of 2 connate sepals, 1,8 - 2,1mm broad, bifid for upper 0,2 - 0,3mm; others 1,0 - 1,3mm broad. Standard 6,0 - 7,0mm long, 5,0 - 7,0mm wide, obovate to orbicular, retuse, extending into a short claw; bright mauve with two yellow patches on either side of the midline near the base. Wings 4,0 - 6,2mm long 1,5 - 2,0mm wide; cultrate, oblong, apex rounded, extended into a short claw at the base; mauve above becoming hyaline below;

Desmodium incanum DC.
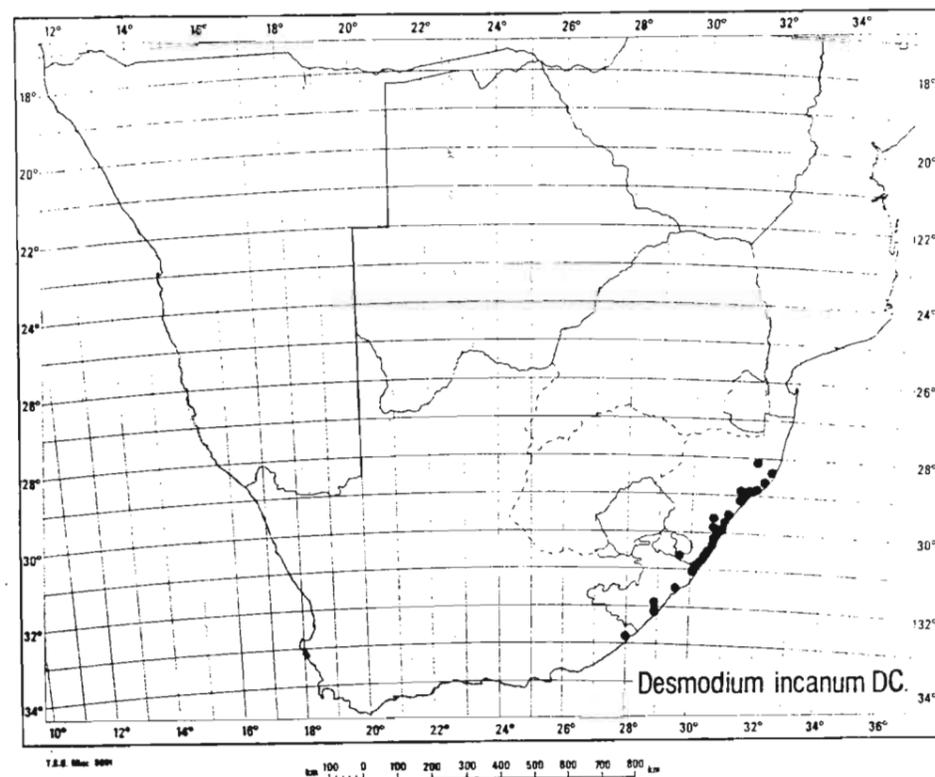
equal in length to the keel. Keel blades 4,0 - 6,2mm long, 1,8 - 2,0mm wide, elliptic, cleaver shaped, proximally forming a small peg of tissue closely applied to the wings; apex obtuse to acute; extended into a short claw at the base; magenta distally becoming hyaline below. Staminal sheath 5,5mm long; vexillary stamen 4,8 - 5,5mm long, free. Gynoecium 4,5 - 5,0mm long; ovary 3,3 - 3,5m long, puberulent and densely pilose; style 1.1 - 1.3mm long; flexed 45° in distal 1,0mm. Fruit, stipe 1,5 - 2,5mm long; of 4 to 8 articles; each article 3,5 - 5,0mm long, 2,0 - 3,5mm wide; essentially straight above, indented about two thirds their width at the isthmi below; densely fulvous, long uncinulate puberulent and short pilose; style persistent; articles reticulate on surface, bordered by a raised rim, indehiscent. Seed 1,0 - 3,0mm long, 0,5 - 2,0mm wide; reniform; khaki to brown.

D. incanum is found along the coast and hinterland up to 1400m in Natal and in coastal Transkei just into the Eastern Cape.

The plant is a weed in disturbed grassland, woodland and forest edges, along streams, paths and roadsides and often occurs in lawns. It is also found taking hold in moist natural grassland.

NATAL.-2831 (Nkandla): 4 km from Hluhluwe G. Res. to Hlabisa (-BB), B. Schrire 392 (NH); Eshowe (-CD), S.M. Johnson 369 (NBG);nr. Eshowe station (-CD), J.G. Lawn 32 (NH); J.G. Lawn 752 (NH); 20 miles from Gingindhlovu (-DC), F.M. Getliffe 113 (NU); Ngoye (-DC), B.J. Huntley 686 (NU); Ngoye Forest Reserve (-DC), E.J. Moll 5410 (NH); ± 5km from Melmoth/Eshowe turnoff from N2 (-DC), B. Schrire 332 (NH); Ngoya (-DC), H.J.T. Venter 7 (ZULU); H.J.T. Venter 300 (BLFU); H.J.T. Venter 2273 (ZULU); Eshowe Hill, 7.7km E. of Eshowe (-DC), M.J. Wells 4266 (PRE); University of Zululand Campus (-DD), J.P. Mtombeni 26 (ZULU); Port Durnford (-DD), B. Schrire 340 (NH). 2832 (Mtubatuba): St. Lucia (-AD), B. Schrire 350 (NH); Mbonambi (-CA), A. Balsinhas 2804 (PRE). 2930 (Pieter-maritzburg) : Nagal Dam (-DA), M.J. Wells 1429 (NU); Shongweni Dam (-DC), B. Schrire 281 (NH); Mariann Hill Mission (-DD), B. Fisher 590 (NH,NU); Isipingo (-DD), H.M.L. Forbes STE 13501 (STE); Mrs. Gillett 1203 (BOL,NH); Hillcrest (-DD), J. Kalf 38 (NU); Durban Airport (-DD), S.A.R. PRE 55639 (PRE); Pigeon Valley, Durban (-DD), B. Schrire 671 (NH); Umlaas River (-DD), C.H. Stirton 508 (PRE); Isipingo North (-DD), C.J. Ward 584 (NU, PRE). 2931 (Stanger) : 8 km S. of bridge over Tugela R. (-AB), N. Grobbelaar 1807/....·

1807 (PRE); Amtikulu estuary, Mtunzini (-BA), R.G. Strey 7394 (NH, PRE); Hawaan Forest (-CA), Ross and Moll 2267 (NH, PRE); 8km from Tongaat to New Hanover (-CA), B. Schrire 262 (NH); 1.5 miles N. of Umhlanga Rocks Hotel (-CA), R. Watmough 486 (PRE); S. of Tongaat R on main Rd. N. of Durban (-CA), M.J. Wells 4263 (NH); Burman Bush (-CC), O. Bourquin 253 (NU); Berea, Durban (-CC), H.M.L. Forbes 35 (NH, PRE); H.M.L. Forbes 605 (NH); Beachwood (-CC), W. Lawson 307 (NU); Durban (-CC), F.A. Rogers 15050 (SAM); F. A. Rogers 15061 (J); Durban North (-CC), B. Schrire 263 (NH); Berea (-CC), R.G. Strey 4559 (NH, PRE); Causeway to Salisbury Island, Durban Bay (-CC), C.J. Ward 6263 (NU); Durban Flat (-CC), J.M. Wood 644 (BOL, SAM); J.M. Wood 3134 (NH); J.M. Wood sn (GRA). 3029 (Kokstad) : Weza, Ingeli Slopes (-DA), R.G. Strey 6354 (NH, PRE). 3030 (Port Shepstone) : Ellingham 6 miles inland from Umkomaas (-BA), J.H. Ross 78 (NU); Illovo Beach (-BB), E.E. Galpin 9743 (PRE); Amanzimtoti R., nr. Civic Centre (-BB), B. Schrire 279 (NH); Umdoni Park (-BC), Jarman and Guy 71 (NU); 18km from Scottborough to Port Shepstone (-BC), B. Schrire 276 (NH); Scottborough (-BC), B. Schrire 278 (NH); Port Shepstone (-CB), J.P.H. Acocks 10888 (PRE); The Valleys, Port Shepstone Distr. (-CB), W.F. Barker 61388 (NBG); 1.5 miles SE. of Mehlomnyana (-CB), L.E. Codd 9362 (NH, PRE); The Valleys, Port Shepstone Distr. (-CB), B. Martin 191 (NBG); Blackwood, Umtentwini (-CB), G.W. Miller PRE 55638 (PRE); 20km from Umtentwini to Highflats (-CB), B. Schrire 264 (NH); B. Schrire 265 (NH); 10km from Umtentwini to Highflats (-CB), B. Schrire 266 (NH); Oribi Gorge (-CB), B. Schrire 282 (NH); Roadside near Umtentwini (-CB), B. Schrire 717 (NH); Paddock Distr. (-CC), J. Sidey 3876 (PRE); Margate (-CD), J.W. Morris 190 (NU); Palm Beach (-CD), B. Schrire 291 (NH); Southbroom (-CD), B. Schrire 293 (NH); Umzumbe (-DA), N. Grobbelaar 1337 (PRU); 3km N. of Umzumbe (-DA), B. Schrire 272 (NH); 2km from Hibberdene to Port Shepstone (-DA), B. Schrire 275 (NH). 3130 (Port Edward): Port Edward (-AA), R. Crawford 368 (PRE); N. Grobbelaar 127 (PRE, PRU); N. Grobbelaar 284 (PRE, PRU); B. Schrire 288 (NH).

TRANSKEI.-3128 (Umtata): Kloof betw. Mqanduli and Coffee Bay nr. Kwaaiman Post Office (-DD), G.J. Lewis SAM 61554 (SAM). 3129 (Port St. Johns): Port St. Johns (-DA), E.E. Galpin 11019 (PRE); J. Hutchinson 1759 (BOL); F.M. Leighton 3083 (BOL,PRE); C.E. Moss 3298 (J, PRE); H.B. Rycroft 2601 (NBG); H. Wager sub TRV 24101 (PRE); 1 mile from Needles Hotel on Umtata rd. (-DA), M.J. Wells 3375 (GRA , PRE). 3228 (Butterworth): The Haven (-BB), J.L. Gordon-Gray 94 (NU); J.L. Gordon-Gray 97 (NU); Haga Haga (-CC), R Clark 464

(PRE, PRU); <u>R.P. Ellis 2616a</u> (PRE).

A spreading herb to woody subshrub up to 1m (if protected from fire); the leaf shape can vary if in deep shade, to superficially resemble <u>D. adscendens</u> a forest floor herb in coastal dune forest. Confusion may only occur on the forest margin and the partially connate stipules, deep mauve flowers or characteristic fruit of <u>D. incanum</u> will help to distinguish between them. <u>D. incanum</u> is otherwise readily recognised by its shiny dark green leaves with light discoloration along the midrib.

Flowering occurs from September to June.

<u>D. incanum</u> is tropical American in origin but is widely scattered throughout tropical Africa where it has been introduced. It is most likely to have entered the flora area along the Natal coast. The Zulu name 'isinama' describes the fruit which readily catches and sticks to clothing. Allen and Allen (1981) refer to the plant as Kaimi clover or creeping beggarweed and it is favoured as a forage in Hawaii and Florida for its tolerance to acid soils and wet warm climate.

6.1.1.3. <u>Desmodium tortuosum</u> (Swartz) DC., Prodr. 2 : 332 (1825); Schubert in Fl. Congo Belge 5 : 202 (1954); Hepper in Fl. W. Trop. Afr. ed 2, 1 : 585 (1958); Lind and Tallentire, Fl. Pl. Uganda : 82 fig. 32 (1962); Laundon in Consp. Fl. Angol. 3 : 223 (1966); Schubert in Fl. Trop. E. Afr., Legum. - Papil : 474 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 526 (1974). Type : Jamaica, <u>Swartz</u> (S, lecto., GH, photo. !)

<u>Hedysarum tortuosum</u> Swartz, Prodr. Veg. Ind. Occ. : 107 (1788) reprint 1962 and Fl. Ind. Occ. 3 : 1271 (1806)

<u>Desmodium spirale</u> sensu Bak. in Oliv., Fl. Trop. Afr. 2 : 160 (1871); Bak.f., Leg. Trop. Afr. : 331 (1929), non (Swartz) DC.

The <u>Swartz</u> specimen has been chosen as the type in preference to the Sloan illustration, : 116 fig. 9(1696), following the precept in the Guide for the Determination of Types, ICBN 75. (1978), 4b; 'Other things being equal, a specimen should be given preference over pre Linnaean or other cited descriptions or illustrations when lecto types of species or infraspecific taxa are designated, provided that the choice is in accordance with Rec. 7B. (Schubert pers. comm., 1983)

Perennial erect herb or subshrub up to 1,0m tall branching from near the base and arising from a woody rootstock. <u>Stems</u> woody below, terete, lenticular; becoming grooved, reddish to green, striate above and minutely puberulent with scattered, upwardly directed, tapering hairs. <u>Leaves</u> trifoliolate. <u>Stipules</u> 0,3 - 12,5mm long, 1,0 - 7,0mm wide; obliquely ovate, long attenuate; extended into large lobes near base on leaf-opposed margin; fused at the base on this margin when young, appearing like a collar; minutely puberulent abaxially; margin ciliate; striate, becoming early red then stramineous, stem markedly red above and below stipules. <u>Petiole</u> 0,5 - 5,0cm long, pubescent as stem. <u>Rhachis</u> 0,3 - 2,0cm. similar. <u>Leaflets</u> 1,0 - 8,0cm long, 0,5 - 3,0cm wide; elliptic or ovate in upper half, cuneiform below; apex obtuse or rounded, base cuneate; margin entire, ciliate; both surfaces sparsely strigose with variously sized tapering hairs and minutely puberulent; terminal leaflet symmetrical, laterals smaller and mostly asymmetrical; veins pallid, conspicuous but not sunken adaxially, major veins prominent below, commissures scarcely so; lateral veins turn upwards and diminish apically inside margin, not looping distally. <u>Petiolules</u> 2,0 - 3,6mm long, more densely hairy/.....

hairy than petiole or rhachis, swollen, rugose. Stipels 3,5 - 5,5mm long, lanceolate - attenuate, striate; four, one subtending each lateral leaflet and two the terminal one. Pseudoracemes elongate to $\pm$ 60cm; terminal and axillary, lax, many flowered, often paniculately branched. Rhachis striate, moderately to densely uncinulate puberulent and pilose with short bulbous-based, erect glandular hairs. Inflorescence bracts 3,0 - 6,5mm long, 0,5 - 1,5mm wide; narrowly ovate - attenuate, glandular - pilose and scarcely strigose on the abaxial surface; margin ciliate, each subtending two pedicels and a median reduced bud; early caducous. Floral bracts 2,0 - 2,6mm long, to 0,5mm wide; linear - attenuate; margin ciliate; 3, one subtending each lateral pedicel and one slightly higher at the junction of the reduced rhachilla and pedicel of the median bud. Pedicels 0,5 - 1,7cm long, ascending from 30° to axis, puberulent and densely glandular pubescent with erect bulbous-based, glandular-tipped hairs. Flowers 4,5 - 6,5mm long, pink tinged with green. Calyx 3,5 - 4,8mm long, puberulent, glandular - pubescent and with longer tapering hairs becoming denser on the teeth; tube 0,9 - 1,3mm long; teeth four, the upper tooth of 2 connate sepals, 1,4 - 1,8mm long, 1,0 - 1,2mm wide at the base, bifid for upper 0,4mm; ovate - lanceolate; lower tooth 2,0 - 3,6mm long, to 1,0mm wide, long-attenuate; laterals 1,6 - 2,0mm long, lanceolate. Standard 4,0 - 6,0mm long, 2,5 - 4,5mm wide; obovate, retuse, gradually narrowing into a short claw at the base, pink with two yellow-green marks on either side of the midline towards the base; keeled. Wings 4,0 - 6,0mm long, 1,5 - 2,0mm wide; cultrate, wider in the distil half; apex rounded; extended at the base into a short claw, slightly auriculate at the base; deep pink becoming green below. Keel blades 4,8 - 6,0mm long, to 2,2mm wide, hatchet shaped, apex truncate, narrowing proximally and forming a peg of tissue closely applied to the wings; extended to the base as a long claw; pinkish to hyaline, usually longer than wings. Staminal sheath 3,8 - 4,2mm long, to 1,0mm wide, vexillary stamen up to 4,0mm long, free. Gynoecium 4,6 - 5,1mm long; ovary to 3,5mm long, densely glandular - pilose; style flexed 45° in distal 1,2mm, slightly thickened at point of flexure. Fruit 1,0 - 3,2cm long, stipe 0,5 - 2,0mm long; of 3 - 7 articles, strongly constricted inbetween to the central axis, articles 3,0 - 6,0mm long, 3,0 - 4,5mm wide, mostly orbicular to elliptic, margins occasionally revolute thus appearing rhomboidal, minutely puberulent and glandular, reticulate. Seeds to 3,0mm long and 2,0mm wide, compressed - ellipsoid or slightly wider at one end; brown, green or yellow.

D. tortuosum/....

Desmodium tortuosum (Swartz) DC.
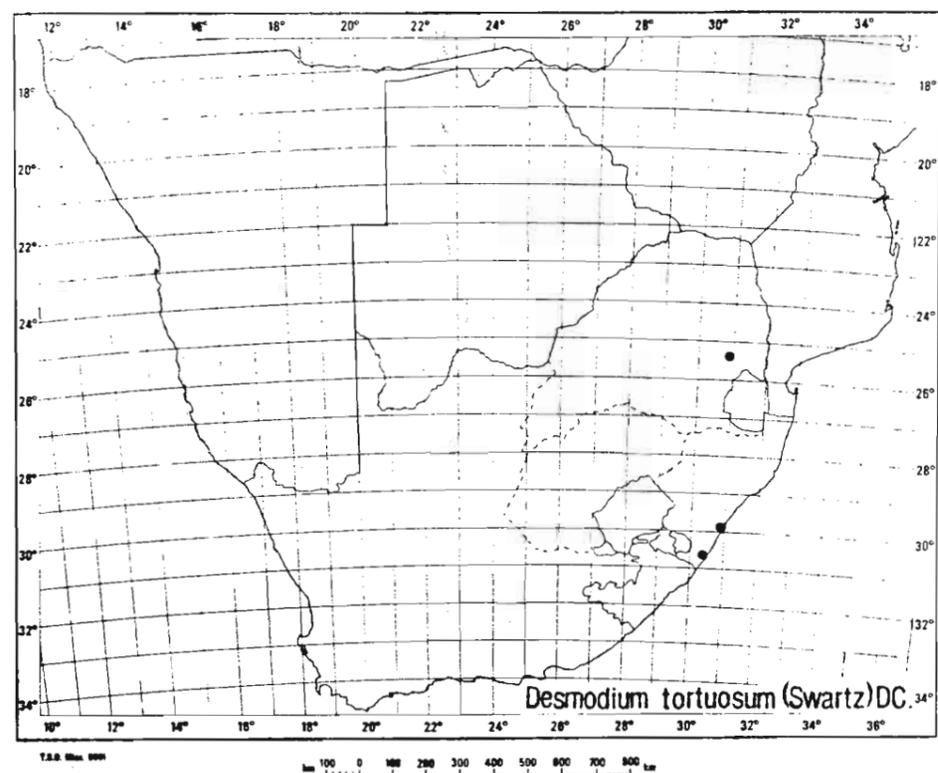
D. tortuosum is an escape from cultivation which has now become natural-
ised in disturbed grassy areas or along roadsides in Nelspruit in
the Transvaal and in the Durban and Port Shepstone districts of Natal.

The plant is an herbaceous suffrutex or small shrub to $\pm$ 1m. Flowering
from December to May.

TRANSVAAL.-2528 (Pretoria): Pretoria (-CA), A.O.D. Mogg Govt Herb
10071 (PRE). 2530 (Lydenburg): Nelspruit (-BD), J. Rabie 273 (PRE).

NATAL.-2930 (Pietermaritzburg): Queensborough (-DD), T.A. Coleman
1103 (NH). 3030 (Port Shepstone): Batstone's Drift, bridge over
Umzimkulu R. (-CB), G.R. Nichols 433 (NH).

D. tortuosum is known as Florida beggar weed in the south eastern
United States (Schubert, 1971) and is cultivated commercially as
a green manure. It is now naturalised throughout the Old World tropics
coming originally from tropical and subtropical America.

The populations in Durban and Port Shepstone are large and well estab-
lished.

6.1.1.4. Desmodium salicifolium (Poir.) DC., Prodr. 2 : 337 (1825).

Type : Herb. de L'Inde de M. Poivre (P - Ju 15552, holo., GH, Photo.!, A-GH, Microfiche (IDC 2606. 1144 : 11,3)

Hedysarum salicifolium Poir. in Lam., Encycl. 6(2) : 422 (1805)

Desmodium paleaceum Guill. and Perr. in Fl. Sen. 1 : 209 (1823)
Type : Senegal, Perrottet 246 (P, holo., W. ? iso.)

Desmodium grande E. Mey., Comm. : 124 (1836).
Type : South Africa, Durban (Port Natal),
Drege (B. holo. , W, iso., K, ? iso.!)

var. salicifolium
Schubert in Bull. Jard. Bot. Brux. 22 : 294 (1952);
Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 470,
fig.65/1 (1971); Verdc. in Kirkia, for Fl. Zamb. 9,
2 : 523 (1974)

Hedysarum salicifolium Poir. in Lam., Encycl. 6 (2) : 422 (1805)

Desmodium salicifolium (Poir.) DC., Prodr. 2 : 337 (1825); Bak.f.,
Leg. Trop. Afr. : 330 (1929); Schubert in Bull. Jard. Bot. Brux.
22 : 294 (1952) and in Fl. Congo Belge 5 : 198, Pl. XV (1954);
Hepper in Fl. W. Trop. Afr., ed 2, 1 : 584 (1958); White, For.
Fl. N. Rhod. : 150 (1962); Laundon in Consp. Fl. Angol. 3 :
224, fig. 20A (1966); Schubert in Fl. Trop. E. Afr., Legum.-
Papil.: 469, fig. 65/1 (1971); Verdc. in Kirkia, for Fl. Zamb.
9, 2 : 522 (1974)

Desmodium paleaceum Guill. and Perr. in Fl. Sen. 1 : 209 (1832);
Bak. in Oliv. Fl. Trop. Afr.2 : 166 (1871); Hutch. and Dalz.
Fl. W. Trop. Afr. 1 : 418 (1928)

Desmodium grande E. Mey., Comm. : 124 (1836); Harv. in Harv.
and Sond. Fl. Cap. 2 : 228 (1862)

Perennial, spreading to erect suffrutex, subshrub or shrub to 2.5m
arising from a basal rootstock producing many long slender, woody,
cord-like roots with an extensive fibrous root system, and thicker
rhizomes. Stems single to many; rhizomes creeping, producing erect

leafy/.....

leafy shoots and rooting at and between nodes; erect stems thick, branching frequently, often at right angles, becoming cord-like above and similar to rhizomes; glabrous, terete; reddish to brown, wrinkled or striate below; becoming angular, grooved, minutely puberulent and moderately soft spreading pilose with long ascending tapering hairs above; maroon on upper surface, green below. <u>Leaves</u> trifoliolate. <u>Stipules</u> 5,0 - 16mm long, 2,5 - 5,5mm wide; ovate - lanceolate, atten-uate; oblique, auricled at the base on leaf-opposed margin; abaxially puberulent and pilose only towards the base; margin ciliate; becoming early, partly or fully reflexed, brown and somewhat curled; striate, persistent. <u>Petioles</u> 0,7 - 6,0cm long; moderately to densely puberulent and appressed long pilose; robust; adaxial channel wide, appearing flattened above. <u>Rhachis</u> 0,6 - 2,0cm long, similar but more deeply sulcate. <u>Leaflets</u> 3,0 - 17,5cm long, 1,0 - 6,5cm wide; oblong - elliptic, ovate - lanceolate to lanceolate or broadly ovate, saliciform; apex acute or acuminate and mucronulate, or rounded and obtuse; base rounded or slightly sub-cordate; margin entire to repand, slightly revolute; scattered puberulent and sparsely pilose; shiny dark green above, moderately appressed soft pilose on veins or throughout; paler beneath; sub-coriaceous; adaxially with regularly arranged, conspicuously sunken lateral veins giving leaf a ribbed appearance; major veins and chief commisures prominent abaxially; lateral veins most frequently terminating at the margin; not looping distally; terminal leaflet usually symmetrical, laterals smaller often asymmetri-cal; base oblique. <u>Petiolules</u> 2,5 - 5,0mm long; more densely pilose than rhachis. <u>Stipels</u> 4,0 - 8,5mm long, 1,0 - 2,0mm wide; lanceolate - attenuate, much curled; similar to stipules; four, one subtending each lateral leaflet and two the terminal one. <u>Pseudoracemes</u> elongate, 9,0 - 20 (30)cm long, many, relatively densely flowered, terminal and axillary, the terminal often laxly branched. <u>Rhachis</u> angular, minutely uncinulate puberulent, abundantly mixed with longer hooked hairs, and moderately spreading pilose. <u>Inflorescence bracts</u> 3,0 - 10mm long, 0,7 - 2,0mm wide; erect; ovate to lanceolate, attenuate; abaxially glabrous to minutely puberulent and pilose towards the base; margin ciliate; striate; early stramineous, each subtending a fascicle of 2 pedicels, no median bud present. <u>Floral bracts</u> 0,6 - 2,4mm long; subulate or ovate to lanceolate, attenuate; puberulous, two, one subtending each pedicel. <u>Pedicels</u> 2,5 - 6,5mm long ascending from 45° to axis, becoming reflexed later on; densely minute uncinulate puberulent with or without scattered longer hairs intermixed. <u>Flowers</u> 5,5 - 8,0mm long, pink to magenta or purple. <u>Calyx</u> 3,0 - 4,0mm long; densely minute puberulent and scattered pilose becoming denser on the teeth/.....

Desmodium salicifolium
(Poir.) DC. var. salicifolium
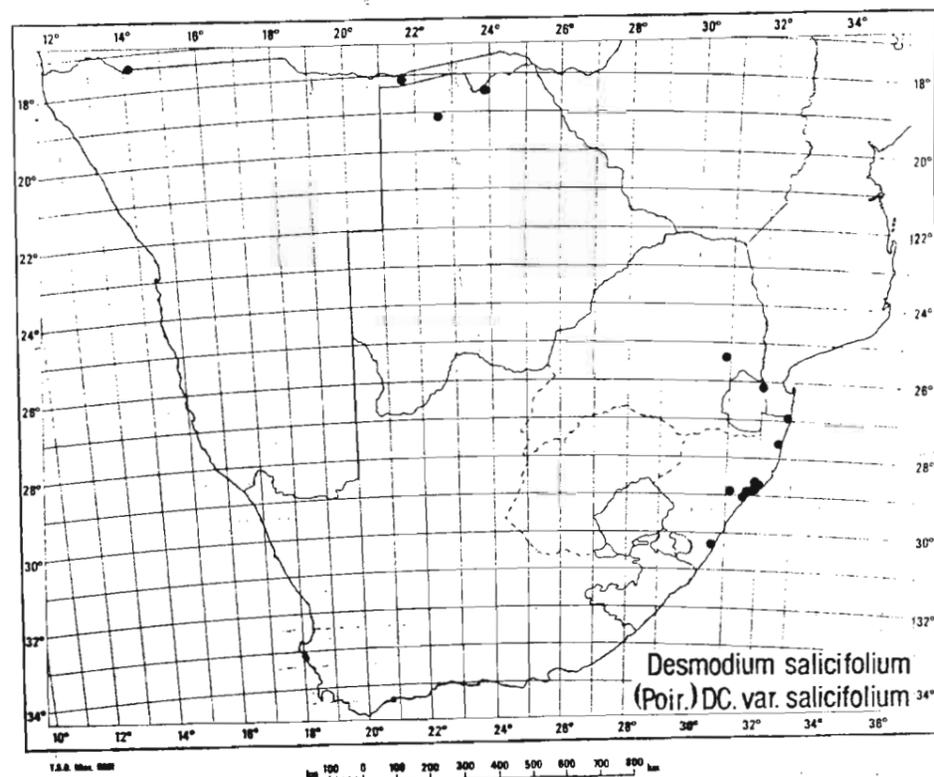
the teeth; <u>tube</u>, 1,0 - 1,4mm long; <u>teeth</u>, four, upper tooth of 2 connate sepals, 2,0 - 2,6mm long, 1,8 - 2,0mm wide; broadly ovate tapering to a point; bifid for upper 0,2mm; others 1,5 - 2,2mm long, up to 1,0mm broad, ovate - attenuate or lanceolate. <u>Standard</u> 5,0 - 7,0mm long, up to 7,0mm broad; orbicular; apex retuse; base constricted into a short claw, rose-pink to magenta; 2 hyaline folds present above the claw on either side of the midline; two darker patches present above each fold and darker down the midline between the folds. <u>Wings</u> 5,0 - 6,5mm long, 1,4 - 3,0mm wide, cultrate, broader distally, apex obtuse, auricled proximally, extended into a short claw at the base; deep pink to magenta in the distal half becoming hyaline below. <u>Keel blades</u> 5,0 - 6,5mm long, 1,0 - 2,0mm wide; elliptic; apex acute to obtuse; auricled at the base forming a minute peg of tissue closely applied to wings; hyaline. <u>Staminal sheath</u> 4,0 - 5,0mm long, 1,5 - 2,0mm wide; vexillary stamen up to 4,2mm long, free. <u>Gynoecium</u> 4,5 - 5,0mm long; <u>ovary</u> 3,0 - 3,5mm long, densely appressed pilose; <u>style</u> ± 1,8mm long, flexed to 60° in distal 1,0 - 1,2mm. <u>Fruit</u> 2,0 - 4,5cm long; stipe absent or up to 2,5mm long; of 2 - 7 articles, each 4,5 - 8,0mm long, 2,5 - 3,5mm wide; rectangular or oblong, not or slightly constricted at the isthmi; densely puberulent and scattered pilose; marginal rim thickened; vein reticulation raised when mature; apex of last article rounded, style persistent. <u>Seeds</u> 2,5 - 4,0mm long, 1,5 - 2,0mm wide; ellipsoid - oblong; khaki to brown or maroon.

<u>D. salicifolium</u> occurs from northern South West Africa, Caprivi and northern Botswana and from Mozambique coming into Komatipoort and Nelspruit in the Transvaal, eastern Swaziland and southward along coastal Natal, 0 - 1000m.

The plant is a suffrutex or shrub of wet places, principally along river margins or in swamp forest. Often in wet clayey soil. Flowering from August to May.

SWA.-1714 (Ruacana Falls). Ruacana Falls (-AC), <u>T.J. Kotze 51</u> (WIND); <u>H.B. Rycroft 2420</u> (NBG). 1821 (Andara) : Popa Falls, W. Caprivi strip (-BA), <u>Müller and Giess</u> (PRE, WIND); <u>K.L. Tinley 1487</u> (WIND)

BOTSWANA.-1823 (Siameisso) : Kwando River (-BD), <u>P.A. Smith 2331</u> (PRE). 1922 (Nokoneng) : Moshupatsila Island (-BA), <u>P.A. Smith 693</u> (PRE)

TRANSVAAL.-2530 (Lydenburg) : Lowveld Botanic Garden (-BD), E. Buitendag 1155 (NBG, PRE); E.J. van Jaarsveld 678 (NBG, PRE)

SWAZILAND.-2632 (Bela Vista) : Blue Jay Ranch, Black Umbuluzi R. (-AA), J. Culverwell 1235 (PRE)

NATAL.-2732 (Ubombo) : Kosi Lakes (-BB), Moll and Nel 5610 (NH, PRE); Sodwana Bay (-DA), A. Balsinhas 3223a (PRE); B. Schrire 385 (NH); J. Vahrmeijer 667 (NH,PRE); Vahrmeijer and Tölken 859 (PRE). 2831 (Nkandla) : Fort Yolland (-CC), Wylie sub Wood 8990 (NH); Enseleni R. below Inzeze lake (-DB), C.J. Ward 5560 (NH,NU); 'Twinstreams', Mtunzini (-DC), Hilliard and Burtt 6852 (NU); Ngoye (-DC), Wylie sub Wood 10335 (GRA, PRE, SAM, STE). 2832 (Mtubatuba) : Richards Bay (-CC), H.J.T. Venter 4993 (ZULU); H.J.T. Venter 5489 (PRE, ZULU). 2931 (Stanger) : Gingindhlovu (-BA), Haygarth sub Wood 10161 (BOL, PRE). 3030 (Port Shepstone) : Inyangwine (-BC), J.M. Wood 3010 (NH, SAM)

D. salicifolium var. salicifolium occurs widely in tropical Africa, Madagascar and the Mascarene Islands.

6.1.1.5. Desmodium velutinum (Willd.) DC., Prodr. 2 : 328 (1825);
Schubert in Bull. Jard. Bot. Brux. 22 : 294 (1952) and in Fl. Congo
Belge 5 : 194 (1954); Hepper in Fl. W. Trop. Afr., ed. 2,1 : 584
(1958); White, For. Fl. N. Rhod. : 150 (1962); Schubert in J. Arn.
Arb. 44 : 292 (1963); Laundon in Consp. Fl. Angol. 3 : 219 (1966);
Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 466, fig. 65/7 (1971);
Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 518 (1974). Type : Herb. Willden-
ow 13763 (B, holo., GH, photo. !)

Hedysarum velutinum Willd. in L., Sp. Pl. ed 4, 3 (2) : 1174
(1802)

Hedysarum lasiocarpum Beauv., Fl. Oware and Benin 1 : 32 t.
18 (1805) Type : Nigeria, Palisot de Beauvois (G. holo., A,
photo.)

Desmodium lasiocarpum (Beauv.) DC., Prodr. 2 : 328 (1825), Bak.
in Oliv. Fl. Trop. Afr. 2 : 162 (1871); Hutch. and Dalz., Fl.
W. Trop. Afr. 1 : 418 (1928); Bak.f., Leg. Trop. Afr. : 326 (1929)

Perennial, erect to suberect, single or multistemmed herb or subshrub
up to 3,0m arising from a large woody dichotomously branching rootstock.
Stems branching sparsely below, with corky light brown streaks where
epidermis is broken; maroon, glabrescent becoming conspicuously grooved;
densely fulvo-puberulent and scattered pilose above. Leaves trifolio-
late. Stipules 5,0 - 8,5mm long, 1,0 - 4,0mm wide at the base; ovate,
long attenuate; lobed at the base on either side, soon narrowing
to a long caudate tip; abaxially densely pilose with long tapering
fulvous or white hairs; margin ciliate; striate, stramineous. Petioles
0,2 - 2,2cm long, sulcate; densely fulvous-pilose with long tapering
hairs. Leaflets 2,5 - 15,5cm long, 1,5 - 10,5cm wide; ovate to elliptic
or orbicular; apex bluntly acute to very rounded, apiculate; base
broadly cuneate, truncate or subcordate, thick, mostly soft velvety
on both surfaces; densely fulvous uncinulate puberulent and scattered
pilose, scabrous, rugose; fulvo-velutinous below; margin repand to
sinuate, densely short ciliate; veins pallid; primary, lateral and
commissural reticulation prominent abaxially; lateral veins extended
fully to the margin, not looping distally. Petiolules 1,5 - 3,5mm
long, more stiffly pilose than petiole, rugose. Stipels 1,5 - 3,8mm
long, up to 1mm wide, ovate - long attenuate, similar to stipules;
paired. Pseudoracemes elongate to 20 (30)cm, numerous, narrow, very
densely flowered, terminal and extensively axillary, the terminals
mostly|.....

Desmodium velutinum
(Willd.) DC.
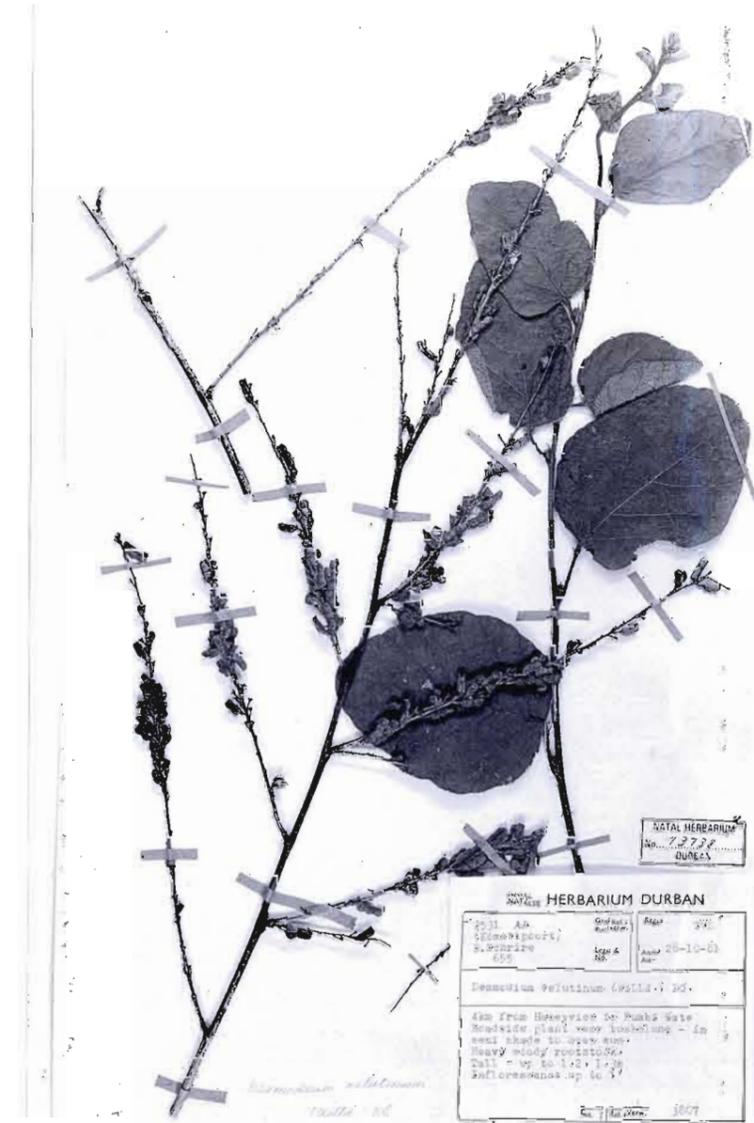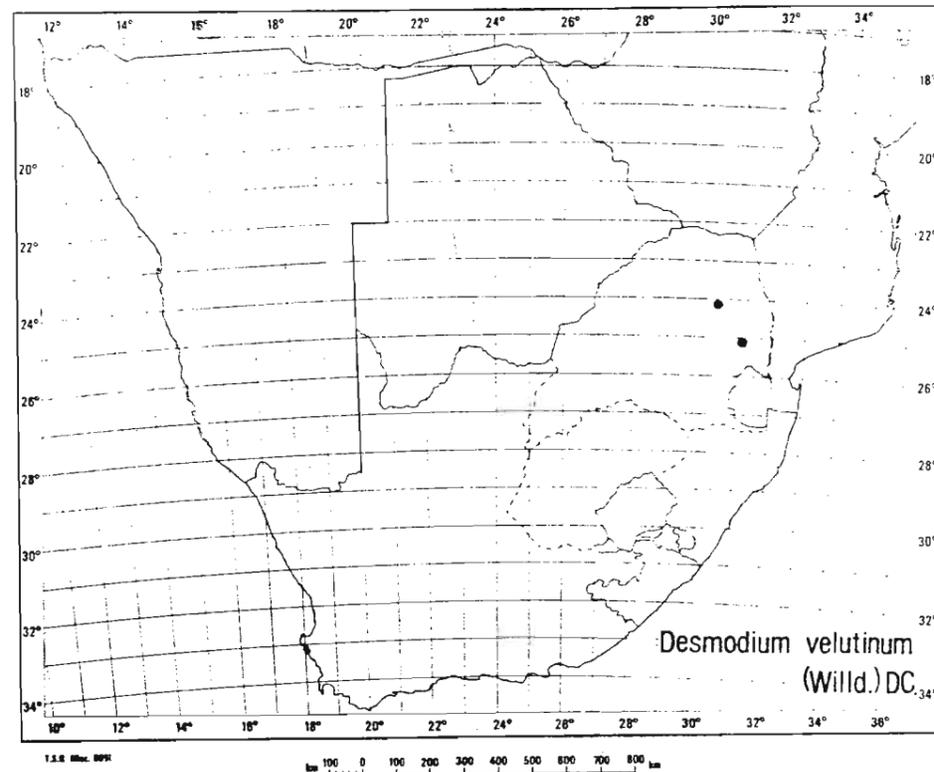
mostly laxly branched. Rhachis vesture fulvous, densely long and short uncinulate puberulent and scattered pilose; angular, ridged. Inflorescence bracts 2,5 - 3,4mm long, 0,5 - 1,0mm wide; ovate to lanceolate, long attenuate, abaxially puberulent and densely long fulvous pilose; margin ciliate; striate, early caducous, each subtending a fascicle of 2 (rarely three) pedicels and a median reduced bud which may elongate later to produce the third pedicel. Floral bracts 1,0 - 2,2mm long 0,2 - 0,6mm wide; linear-attenuate; one subtending each pedicel and one the base of the median bud. Pedicels 1,0 - 3,0mm long, abundantly puberulent intermixed with straight tapering hairs; rarely a small bracteole maybe present on the distal half of the pedicel. Flowers 6,5 - 7,5mm long variously deep to light pink turning blue to lilac after tripping. Calyx 3,0 - 3,6mm long, densely fulvous puberulent and long appressed pilose, particularly on teeth; tube, 1,0 - 1,5mm long; teeth, four, upper tooth of 2 connate sepals; 1,0mm long, up to 2mm broad, broadly triangular, apex rounded to acute; bifid for upper 0,1 - 0,2mm; laterals 1,0 - 1,2mm long, to 1mm broad, triangular; lower, 1,8 - 2,2mm long, 1,0mm broad, lanceolate-attenuate. Standard 4,2 - 7,0mm long, 4,0 - 7,5mm wide, obovate to orbicular, apex retuse, base narrowed to a short claw, pink flushed with two darker areas on either side of the midline near the base; two folds occur beneath these on the slightly reflexed claw. Wings 4,5 - 6,2mm long, up to 3,0mm wide, cultrate, appearing oblong but wider distally; apex rounded, auriculate proximally, extended into a short claw at the base; purple. Keel blades 4,5 - 6,5mm long, cleaver-shaped, deeply pocketed, auricled at base of blade above claw, produced abaxially as a minute peg of tissue closely applied to the wings; longer than wings; light pink distally becoming hyaline. Staminal sheath 4,0 - 5,2mm long, vexillary stamen 4,0 - 4,8mm long, free. Gynoecium 4,8 - 5,8mm long; ovary 3,8 - 4,2mm long, puberulent and densely pilose; style 1,5mm long, flexed 60° at the base. Fruit 1,0 - 2,4cm long, stipe absent or up to 1,5mm long; of 2 - 7 articles, each 2,5 - 4,0mm long, 2,5 - 3,5mm wide; densely uncinulate puberulent with longer hairs intermixed. Seeds to 2,5mm long, 1,8mm wide; ellipsoid - reniform, green to brown.

D. velutinum is only known from the north-eastern lowveld of Transvaal from near Leydsdorp in the north to the southern Kruger National Park; to 750m.

The plant occurs as a small shrub or suffrutex in wooded and open grassland, woodland or on forest margins.

TRANSVAAL./.....

TRANSVAAL.-2430 (Pilgrim's Rest) : Shiluvane (-AB), H. Junod sub
   TRV 5279 (PRE). 2531 (Komatipoort) : 4km from Hazeyview to Numbi
   Gate (-AA), B. Schrire 655 (NH); Numbi, Kruger National Park
   (-AA), H.P. van der Schijff 2659 (PRE)

D. velutinum is widespread throughout the Old World tropics from
Africa and Madagascar to India, S.E. Asia and Malesia.

6.1.1.6. Desmodium gangeticum (L.) DC., Prodr. 2 : 327 (1825); Wight and Arn., Prodr. Fl. Ind. 1 : 225 - 226 (1834); Bak. in Oliv., Fl. Trop. Afr. 2 : 161 (1871); Hutch, and Dalz., Fl. W. Trop. Afr. 1 : 418 (1928); Bak.f.,Leg. Trop. Afr. : 327 (1929); Brenan in Checklist Tang. Terr. : 420 (1949); Schubert in Fl. Congo Belge 5 : 196 (1954); Hepper in Fl. W. Trop. Afr. ed 2, 1 (2) : 584 (1958); White, For. Fl. N. Rhod. : 150 (1962); Laundon in Consp. Fl. Angol. 3 : 219 (1966); Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 465, fig. 65/10 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, (2) : 520 (1974). Type : Herb. Linnaeus 921.13 (LINN, holo., A photo.)

Hedysarum gangeticum L., Sp. Pl. : 746 (1753)

H. maculatum L., Sp. Pl. : 746 (1753). Type : Herb Linnaeus 921.14 (LINN holo., A photo.)*

Desmodium natalitium Sond., in Linnaea 23 : 32 (1850) : Harv. in Harv. and Sond., Fl. Cap. 2 : 229 (1862); Schindl. in Feddes Repert. 49 : 285 (1928). Type : Port Natal, Gueinzius 203 (Herb. Sond.)

Desmodium gangeticum (L.) DC. var. maculatum (L.) Bak., in Hook.f. Fl. Brit. Ind. 2 : 168 (1876); Hepper in Fl. W. Trop. Afr. ed 2, 1 (2) : 584 (1958); Laundon in Consp. Fl. Angol. 3 : 220 (1966)

* Note: the epithets gangeticum and maculatum are equally old and they were combined under the name Desmodium gangeticum by Wight and Arn., Prodr. Fl. Ind. 1 : 225 - 226 (1834).

Perennial spreading herb or woody subshrub up to 50cm tall, arising from a thick woody rootstock much divided below into long cord-like roots. Stems many, either arising as branches from the top of the rootstock or as short rhizomes from the side, producing erect shoots and subsidiary root systems close to the parent; prostrate to erect; terete below becoming angular grooved and striate above; uncinulate puberulent and abundantly pilose with upward directed tapering hairs. Leaves unifoliolate. Stipules 4,0 - 10mm long, 1,0 - 2,0mm wide, erect; slightly oblique, ovate - long attenuate; abaxially minutely puberulent and stiffly pilose; margin ciliate; striate; early stramin-eous, persistent. Petioles 0,4 - 2,0cm long; adaxial channel wide, appearing flattened above, trigonous, puberulent throughout and moder-

moderately/.....


Desmodium natalitium Sond.

moderately to densely pilose. Leaflets 2,0 - 8,0cm long, 1,6 - 3,6cm wide; ovate - lanceolate, ovate or orbicular to cordiform; apex acute to rounded, base cordate; minutely puberulent throughout with long tapering hairs along midrib, and scattered on surface above, abundantly long pilose beneath; margin ciliate; major veins conspicuously sunken abaxially, giving a ribbed appearance, veins prominent below, inter-connecting commissures also abaxially prominent; lateral veins extend very nearly or to margin, but usually turn upwards and diminish apically just before; not looping distally; subcoriaceous; dark green above, paler below; generally asymmetrical. Petiolules 2,0 - 2,5mm long, more stiffly pilose than petiole, slightly swollen, rugose. Stipels 3,5 - 4,5mm long; paired, setaceous. Pseudoracemes elongate, relatively densely flowered, terminal and axillary, rarely paniculately branched. Rhachis less densely pubescent than stem, scarcely pilose. Inflor-escence bracts 1,4 - 7,0mm long, 0,4 - 1,0mm wide; linear to lanceolate - attenuate; vesture similar to stipules; striate; each subtending a fascicle of 2 pedicels and a median reduced bud. Floral bracts 0,5 - 2,0mm long, 0,2 - 0,8mm wide; lanceolate-attenuate; three, one subtending each pedicel and one at the base of the median bud. Pedicels 3,5 - 5,5mm long, curving erect, densely puberulent; streaked with red; Flowers 5,0 - 6,0mm long; variously pink, magenta to purple. Calyx 2,0 - 2,3mm long; minutely puberulent, with scattered gland tipped hairs and long tapering hairs becoming denser on the teeth; tube, 0,9 - 1,1mm long; teeth, four, subequal, triangular to subulate; upper tooth of two connate sepals; 1,2mm long, 1,2mm broad, others 1,2mm long, 0,8mm broad. Standard 5,0 - 5,5mm long, 5,5 - 6,0mm wide; broadly obovate, retuse, extended into a short claw with two small folds directly above; pink with two light coloured spots ringed with purple on either side of the midline above the folds. Wings 4,0 - 5,2mm long, up to 2mm wide; cultrate, broader above, apex rounded; extended into a short claw at the base; deep magenta becoming hyaline towards the base. Keel blades 4,5 - 5,6mm long, 1,0- 1,8mm wide; falcate, auriculate midway forming a peg of tissue closely applied to the wing; apex obtuse, base extended into a short claw hyaline. Staminal sheath 4,5 - 5,0mm long, 1,5mm wide, vexillary stamen to 4,5mm long, free. Gynoecium 4,0 - 4,5mm long; ovary 3,5 - 4,0mm long; puberulent and densely long pilose; style flexed 60° in distal 1,0 - 1,2mm. Fruit stipe to 1,0mm long; of 3 to 7 articles often curving upwards, each article to 2,5mm long, 3,0mm wide, essentially straight along upper suture, slightly indented at isthmi, lower suture curved, more deeply indented; puberulent on surfaces and scattered pilose on sutures; style persistent. Seed 1,8 - 2,2mm long, 1,5
1,5 - 1,8mm/.....
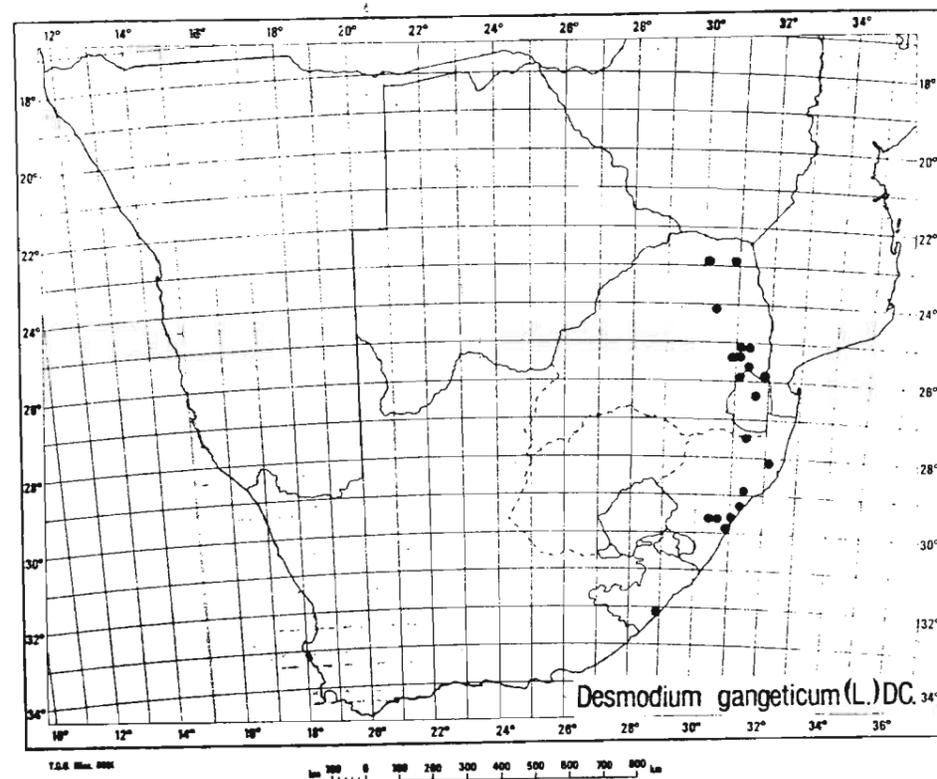
- 1,8mm wide; reniform, light khaki brown.

D. gangeticum occurs in Transvaal from the Zoutspansberg in the north, through the lowveld to between Barberton and Nelspruit and Swaziland in the south. In Natal this distribution continues through northern Natal to Zululand and is then mainly coastal southwards into the Transkei, 0-1200m.

The plant is a spreading suffrutex to erect subshrub occurring in wooded grassland, bushveld or thicket or in open grassland. It readily becomes a weed in semi-disturbed areas i.e. old lands or roadsides. Flowering from August to March.

TRANSVAAL.-2230 (Messina): Entabeni, Zoutspansberg (-CC), A.A. Obermeyer sub TRV 29363 (PRE); Baiandbai, Zoutspansberg Dist. (-DD), H. Lang sub TRV 32297 (PRE). 2430 (Pilgrim's Rest): Shiluyane (-AB), H. Junod 5270 (PRE). 2530 (Lydenburg): Lowveld Botanic Garden, Nelspruit (- BD), E. Buitendag 209 (NBG, PRE); E. Buitendag 271 (PRE); Brondal Park (-BD), D.D. van der Merwe PRE 58466 (PRE). 2531 (Komatipoort): Kruger Park, Numbi (-AA), H.P. van der Schijff 965 (PRE, PUC); H.P. van der Schijff 1132 (PRE); Pretoriuskop, Kruger Park (-AB), H.P. van der Schijff 1325 (PRE); White River (-AC), F.A. Rogers 23564 (NH); F.A. Rogers sub TRV 20707 (PRE); Betw. Komati R. Drift and Crocodile R. Drift (-BD), H. Bolus 7731 (BOL); Louws Creek (-CB), H. Wager sub TRV 22462 (PRE); Barberton (-CC), R. Pott 5334 (PRE)

SWAZILAND.-2631 (Mbabane): Mafutseni Ranch, about 9 miles from Manzini on rd. to Stegi (-BC), B. Clarke 269 (PRU)

NATAL.-2731 (Louwsberg): Craigadam Farm, Itala Nature Reserve (AD/CB), D.J. McDonald 118 (NU, PRE). 2831 (Nkandla): Eshowe (-CD), J. Gerstner 2936 (NH). 2832 (Mtubatuba): Mansiya, Hluhluwe Game Res. (-AA), P. Hitchins 391 (PRE); Hluhuwe Game Res. (-AA), C.J. Ward 2406 (NH, PRE). 2930 (Pietermaritzburg): Alexandra Park, P.M.burg (-CB), A.R. Fairall 13 (NBG); Alexandra Park, P.M.burg (-CB), B.S. Fisher 752 (NH); Scottsville (-CB), J.W. Morris 175 (NU); Cato Ridge (-DA), B. Schrire (NH); Cato Manor (-DD), B. Schrire 883 (NH). 2931 (Stanger): Groutville (-AD), E.J. Moll 2471 (PRE); Nr. Phoenix (-CA), R. Schlechter 3129 (BOL,GRA,PRE); J.M. Wood 4936 (BOL,PRE,SAM); Umhlanga R. (-CA), J.M. Wood 4936 (GRA)

TRANSKEI/.....

Desmodium gangeticum (L.) DC.

TRANSKEI.-3228 (Butterworth): The Haven (-BB), <u>J.L. Gordon-Gray 1047</u>
(NU)

This species is widespread throughout the Old World tropics and has
been introduced into America. Allen and Allen (1981) note that <u>D.</u>
<u>gangeticum</u> is used as a pioneer plant to control erosion of denuded
areas. Roots of <u>D. gangeticum</u> also yield a lectone and seven alkaloids.
One of these, Hordenine has been used in experimental medicine as
a sympathomimetic and another, bufotenine is an hallucinogen.

6.1.1.7. <u>Desmodium setigerum</u> (E. Mey.) Benth. ex Harv., in Harv.
and Sond. Fl. Cap. 2 : 229 (1862); Milne - Redh. in Kew Bull.: 417
(1937); Schubert in Fl. Congo Belge 5 : 187, fig. 11E (1954); Hepper
in Fl. W. Trop. Afr. ed. 2,1 : 585 (1958); Laundon in Consp. Fl.
Angol. 3 : 222 (1966); Schubert in Fl. Trop. E. Afr., Legum. - Papil.
: 460, fig. 65/5 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 513
(1974). Type: South Africa, Transkei, Umzimvubu River, <u>Drege (446)</u>
(W, ? iso. , K, ? iso. !). Lectosyntype : Port Natal, <u>Sanderson</u> (K,
!)

    Misinterpretation of types (Schubert, 1971) has led to confusion
between two separate species, <u>Desmodium setigerum</u> (E. Mey.)
Benth. ex Harv. and <u>Desmodium hirtum</u> Guill. and Perr. The follow-
ing are the references in which the latter refers to <u>D. setigerum</u>
and it is usually described in the literature as <u>D. hirtum</u> sensu
Bak. since it was here that the misinterpretation began.

    <u>D. hirtum</u> Guill. and Perr. described in Fl. Sen. : 209 (1832);
Bak. in Oliv., Fl. Trop. Afr. 2 : 163 (1871) pro parte; J.M. Wood
Natal Plants, 3 : 14, t. 212 (1902); Schindl. in Fedde Rep.
Beih. 49 : 279 (1928); Hutch. and Dalz., Fl. W. Trop. Afr. 1
: 418 (1928); Bak.f., Leg. Trop. Afr. : 329 (1929) pro parte;
Compton, Fl. Swazi. : 272 (1976). Type : Senegal, <u>Perrottet
247</u> (BM, isosyn.!, GH, photo. !)

    <u>Nicolsonia setigera</u> E. Mey., Comm. 1 : 124 (1836)

Perennial herb with scandent to procumbent aerial stems to 1,5m long,
rooting at the lower nodes, arising from a much dichotomously bran-
hed, slender, often twisted woody rootstock. Long slender roots
may become distally thickened some way from parent, and give rise
to new shoot systems. <u>Stems</u> prostrate, many branched, terete, glabres-
cent, lenticulate, fissured where epidermis is broken; or ascending
becoming puberulent and densely patent white to yellowish pilose
above, subangular, faintly ridged, red (particularly on upper surface
if prostrate) to green. <u>Leaves</u> trifoliolate. <u>Stipules</u> 3,5 - 16,0mm
long, 1,8 - 3,0mm wide; obliquely ovate-long attenuate; erect; abaxially
minutely puberulent or essentially glabrous; margin ciliate; striate,
soon becoming stramineous; persistent. <u>Petioles</u> 7,0 - 19mm long;
trigonous, sulcate but adaxial channel wide. sparsely strigose and
densely pilose as stem. <u>Leaflets</u> 1,0 - 4,2cm long, 0,7 - 2,4cm wide;
obovate or elliptic to sub-orbicular; apex retuse or apiculate, rounded
to truncate; base rounded to cuneate; adaxially moderately pilose,

                                     more/.....

more so along veins, or glabrous, abaxially puberulent and more densely pilose; venation either inconspicuous adaxially or with median and lateral veins slightly sunken, reticulate venation prominent abaxially, lateral veins turn upwards and diminish apically inside margin, conspicuous looping between ends of lateral veins distally; leaflets symmetrical, laterals smaller, often more elliptic. Petiolules 1,6 - 2,2mm long, swollen, densely appressed pilose. Stipels 0,5 - 6,0mm long, 0,2 - 0,6mm wide, setaceous; four, one subtending each lateral leaflet and two the terminal one; sparsely pilose. Pseudoracemes open, lax, terminal or axillary, often paniculately branched. Rhachis terete to angular; uncinulate puberulent, sparsely pilose below becoming covered with bulbous-based glandular-tipped hairs above; striate. Inflorescence bracts 2,0 - 6,6mm long, 1,5 - 3,0mm wide, cochleariform, broadly ovate, apex long attenuate; slightly auricled and flared at the base; abaxially puberulent and sparsely pilose, margin ciliate; striate; early caducous; each subtending a fascicle of 2 pedicels and occasionally a median reduced rhachilla with terminal bud. Floral bracts usually absent, if present, depauperate, 1,3 - 2,0mm long, 0,5 - 1,5mm wide; broadly to narrowly ovate, apex acuminate; similar to inflorescence bracts; early caducous, often found as remains, clasping the proximal part of the pedicel. Pedicels 4,0 - 14mm long at right angles to axis, uncinulate puberulent with scattered bulbous-based, erect, glandular-tipped hairs; rarely with a minute bracteole. Flowers 4,8 - 5,2mm long, variously violet, magenta, pink to white, turning blue after tripping. Calyx 2,0 - 3,5mm long, minutely puberulent and becoming long pilose on the teeth; tube 0,8 - 1,1mm long; teeth four, upper tooth of 2 connate sepals 1,5 - 1,8mm long, 1,2 - 1,4mm wide at the base, bifid for upper 0,7 - 0,9mm; others 1,5 - 2,4mm long, up to 1,0mm wide; lanceolate-attenuate. Standard 3,0 - 5,0mm long, up to 5,0mm wide; orbicular to obovate, retuse, gradually tapering to a slight reflexed claw at the base; strongly keeled, light pink to magenta with two darker purple spots streaked with yellow just above 2 folds on either side of the midline near the base. Wings 3,5 - 4,5mm long, 1,5 - 2,0mm wide; cultrate, wider in the distal half, apex rounded, extended into a short claw at the base, auriculate just above the claw, deep violet in the upper half becoming hyaline towards the base. Keel blades 4,6 - 5,2mm long, up to 2,0mm wide; hatchet shaped, apex truncate, auricled at the base forming a peg of tissue on the outside closely applied to the wing; extended into a long claw; hyaline, longer than wings. Staminal sheath 3,0 - 3,6mm long, 1,0 - 1,2mm wide, vexillary stamen up to 3,5mm long, free. Gynoecium 3,4 - 4,2mm long; ovary 2,1 - 2,4mm long, densely

pilose/.....
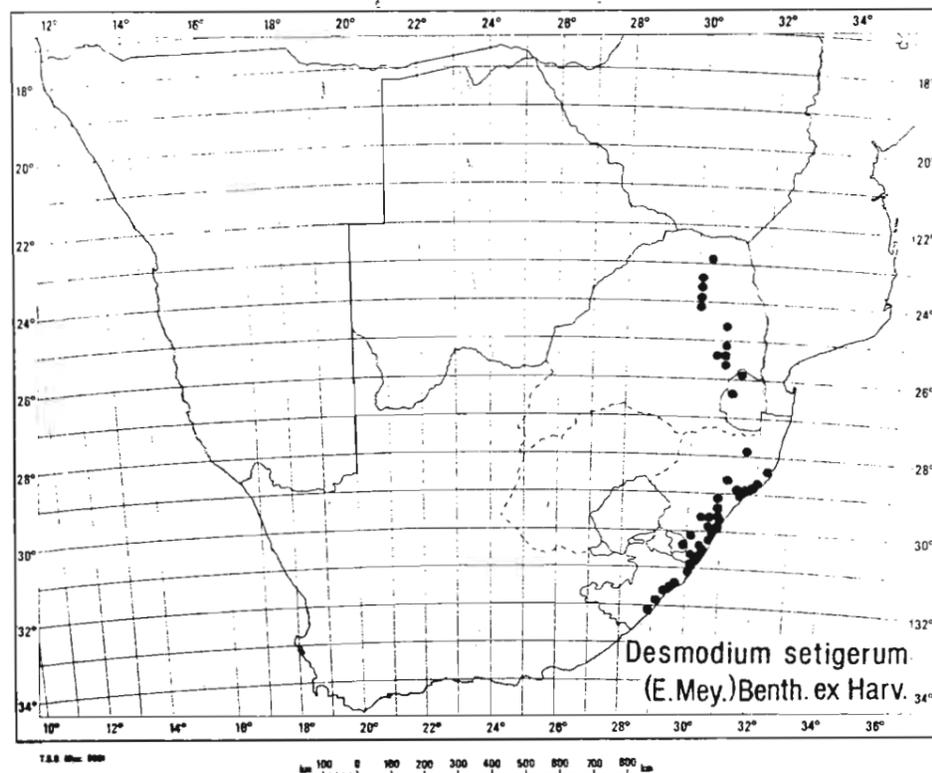
pilose; style 1,2mm long, flexed 90° at base. Fruit 0,5 - 1,5cm long; of up to 6 articles, shortly stipitate or basal 1 or 2 articles aborted; upper suture slightly, the lower deeply, indented at the isthmi; articles obtusely curved below; 1,5 - 3,0mm long, 1,5 - 2,0mm wide; puberulent, reticulate, surrounded by a conspicuous rim; style persistent often twisted; indehiscent. Seed 1,5 - 2,3mm long, 1,0 - 1,6mm wide; compressed, reniform, yellow-brown to dark castaneous

D. setigerum occurs in the Transvaal from Zoutpansberg and Tzaneen in the north, through between Lydenberg and Sabie to western Swaziland in the south. In Natal it is found from sea level to 2000m except in the lowveld of Zululand and it extends to coastal Transkei.

The plant is a low prostrate or semi erect suffrutex of open grassland in damp sites occurring occasionally on streambanks, forest margins or on drier rocky hillsides. It is also found in semi-disturbed vegetation of roadsides. Flowering is from December to May i.e. it is a later summer-flowering species.

TRANSVAAL.-2230 (Messina) : Tate Vondo (-CD), E. Netshiungani sn (VENDA). 2330 (Tzaneen) : Letaba R. (-AC), H.A. Junod 5265 (PRE); Westfalia estate, nr. Duiwelskloof (-CA), J.J. Bos 1253 (PRE, STE); Duiwelskloof (-CA), J.C. Scheepers 581 (PRE, PRU); J.C. Scheepers Alk. Surv. 1485 (PRE); Westfalia estates, Letaba (-CA), Scheepers and Haasbroek Alk. Sur. 1140 (PRE); De Hoek Forest Station (-CC), B. Clarke 371 (PRE, PRU). 2430 (Pilgrim's Rest) : The Downs, Zoutspansberg (-AA), H.A. Junod 4382 (PRE); Nr. Reitz's Grave, Mariepskop (-DB), H.P. van der Schijff 5066 (PRE, PRU); H.P. van der Schijff 5976 (PRE, PRU); Mariepskop (-DB), H.P. van der Schijff 6437 (PRE, PRU). 2530 (Lydenburg) : Langverwag, Sabie (--BB), W.J. Louw 2165 (PUC, STE); 3 miles W. of Sabie (-BB), R.G. Strey 2996 (NH, PRE); Tweefontein Experimental area, Sabie distr. (-BB), V. Wager C45 (PRE); Poverty Creek, Elands Hoek (-BC), G. Thorncroft Gov. Herb. 11261 (PRE); Witklip (-BD), J.P. Kluge 483 (PRE, PRU); Kaapse Hoop (-DB), L.C.C. Liebenberg 2551 (PRE)

SWAZILAND.-2531 (Komatipoort) : Piggs Peak (-CD), R.H. Compton 30608 (NBG, PRE). 2631 (Mbabane) : Betw. Bremersdorp and Mbabane, Dalriach (-AC), H. Bolus 11827 (BOL, PRE); Nr. Mbabane (-AC), L.E. Codd 6412 (PRE); Little Usutu, Mbabane distr. (-AC), R.H. Compton 25075 (NBG); Hill NE of Mbabane (-AC), B. Dlamini NBG 49174 (NBG); Mbabane (-AC), F.A. Rogers 11606 (J)

Desmodium setigerum
(E.Mey.)Benth. ex Harv.

NATAL.-2731 (Louwsburg) : 25km from Nongoma to Vryheid (-DC), B. Schrire 396 (NH). 2831 (Nkandla) : Nkandla forest (-CA), O.M. Hilliard 2639 (NU); Eshowe (-CD), J. Gerstner NH 28779 (NH); Signpost for Kanyile nr. Eshowe (-CD), N. Grobbelaar 2324 (PRU); Eshowe (-CD), J.G. Lawn 169 (NH); J.G. Lawn 217 (NH); 'Twinstreams' Mtunzini (-DC), Bourquin and Lawson 1168 (NH, PRE); Ngoye Forest Reserve (-DC), B.J. Huntley 195 (NH, PRE); E.J. Moll 5406 (NH); Ngoye Mtn, Ubisana Valley (-DC), H.J.T. Venter 832 (ZULU); H.J.T. Venter 2289 (BLFU); 'Hamewith' Mtunzini (-DD), A.O.D. Mogg 4399 (PRE); A.O.D. Mogg 4891 (PRE); University of Zululand campus (-DD), J.P. Mtombeni 40 (ZULU). 2832 (Mtubatuba) : Dukuduku (-AC), R.G. Strey 5486 (NH, PRE); Richards Bay (-CC), H.J.T. Venter 4996 (ZULU). 2930 (Pietermaritzburg) : 12 miles from Kranskop on Mapumulo/Kranskop rd. (-BB), J.H. Ross 208 (NU); Noodsberg (-BD), O.M. Hilliard (NU); Town Hill (-CB), E.D. Ahrens 23 (NU); R.J. Allsopp 1024 (NH, NU); P.M.burg (-CB), W.F. Barker 5155 (NBG); Sunnyside beyond Town Bush Valley, P.M.burg (-CB), Dohse and Lindahl 94 (NH, PRE); Cedara (-CB), G.A. Gill NH 22592 (NH); P.M.Burg (-CB), C.E. Moss 3298 (J); Town Bush Valley (-CB), J.H. Ross 723 (BLFU, NH, NU); Chase Valley (-CB), J.H. Ross NU 25765 (NU); Inchanga (-DA), O. Bourquin 122 (NU); F. Frith 121 (J); Table Mtn (-DA), A.P.D.McClean 183 (PRE); Inchanga (-DA), J.M. Wood 9788 (NBG); Inanda (-DB), J.M. Wood 93 (BOL, SAM); J.M. Wood 790 (BOL); Shongweni (-DC), J.H. Ross 775 (NU); Inchanga/Hammarsdale turnoff on N2 (-DC), B. Schrire 273 (NH); B. Schrire 274 (NH); Merebank West (-DD), H. Baijnath 185 (NU, PRE); Manora (-DD), T.A. Coleman 65 (NH, PRE); Krantzkloof (-DD), W. Haygarth STE 9446 (STE);Everton Eskotene (-DD), O.M. Hilliard 134 (NU); Congella (-DD), E.P. Phillips PRE 55667 (PRE); Merebank East (-DD), C.J. Ward 5381 (NH, PRE); Sarnia Beacon Hill (-DD), C.J. Ward 7601 (NU); Kloof (-DD), Williams 8 (NU). 2931 (Stanger) : Amatikulu Institution Hospital (-BA), J.H. Ross 1679 (NH, NU, PRE); Durban (-CC), Jenkins 7068 (PRE); A. Rehmann 8699 (BOL); Beach Terminus (-CC), J. Thode STE 3803 (STE); Berea, Durban (-CC), J.M. Wood NH 6414 (NH). 3030 (Port Shepstone) : Ixopo (-AA) H.M. Otto 124 (PRE); R. Schlechter 3354 (PRE); R. Schlechter 6668 (BOL); Hlokozi, Alexandra Cty. (-AD), H. Rudatis STE 2339 (STE); Isipingo beach (-BB), C.J. Ward 733 (NU, PRE); 4km beyond Scottburgh to Port Shepstone (-BD), B. Schrire 882 (NH); 2km along Oribi Gorge turnoff from Izingolweni rd. (-CA), B. Schrire 283 (NH); 10km from Umtentwini to Highflats (CA), B. Schrire 267 (NH); Suurberg (-CC), L.E. Codd 9339 (GRA, PRE); 2 miles from St. Michaels-on-sea (-CD), H.B. Nicholson 1200 (PRE);

Uvongo/

Uvongo (-CD), R.G. Strey 9618 (NH, NU, PRE); R.G. Strey 10937 (NH, PRE); Hibberdene (-DA), N. Grobbelaar 66 (PRE, PRU)

TRANSKEI.-3029 (Kokstad) : Umzimkulu, Clydesdale (-BD), W. Tyson 1438 (SAM, STE); W. Tyson 2782 (PRE, SAM). 3129 (Port St. Johns) : Magwe Falls (-BC), E.E. Galpin 11024 (PRE); Magwe Waterfall, Lusikisiki (-BC), N. Grobbelaar 78 (PRE, PRU); Umgazi, Pondoland (-CB), H. Bolus 8884 (BOL); Isinuka, nr. Port St. Johns (-CB), H.G. Flanagan 2608 (PRE, SAM); 73,2km from Umtata to Port St. Johns (-CB), N. Grobbelaar 2312 (PRU); Coffee Bay (-CC), G.J. Lewis SAM 61553 (SAM); Port St. Johns (-DA), R.D.A. Bayliss 4667 (NBG); Bolus 8883 (BOL)

D. setigerum is widespread throughout tropical Africa.

6.1.1.8. <u>Desmodium adscendens</u> (Swartz) DC., Prodr. 2 : 332 (1825);
Bak. in Oliv., Fl. Trop. Afr. 2 : 162 (1871); Hutch. and Dalz., Fl.
W. Trop. Afr. 1 (2) : 418 (1928); Bak.f., Leg. Trop. Afr. : 330 (1929);
Brenan in Checklist Tang. Terr. : 419 (1949); Laundon in Consp. Fl.
Angol. 3 : 222 fig. 20 A1 (1966).   Type : West Indies, <u>Swartz</u> (S,
holo., GH, photo. !)

    <u>Hedysarum adscendens</u> Swartz, Prodr. Veg. Ind. Occ. : 106 (1788)
reprint 1962, and Fl. Ind. Occ. 3 : 1263 (1806)

<u>var. robustum</u> Schubert in Bull. Jard. Bot. Brux. 22 : 290 (1952)
and in Fl. Congo Belge 5 : 190 (1954); Hepper in Fl. W. Trop. Afr.
ed 2, 1 : (1958); Schubert in Fl. Trop. E. Afr., Legum. - Papil.
: 461 fig. 65/13 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 514
(1974). Type : Congo, Kivu, Mokoto Lakes, <u>Ghesquiere 4994</u> (BR, holo.)

Perennial creeping and spreading herb, to 1.2m long, 30cm high; arising
from a slender woody rhizome, at or just below ground level, rooting
at the nodes. <u>Roots</u> woody, short, dividing to form long, finely branched
slender fibrous roots. <u>Stems</u> rhizome prostrate, branching obliquely
at ground level, ascending finally as tufts of leaf-bearing shoots
or producing numerous erect shoot branches along its length. Rhizome
slender, terete; glabrescent, lenticulate; finely ridged; leaf-
bearing shoots, moderately to densely upward directed or spreading
pilose, scattered uncinulate puberulent; striate, ridged or angular.
<u>Leaves</u> trifoliolate. <u>Stipules</u> 5,0 - 10mm long, 1,5 - 3,0mm wide;
erect, obliquely ovate - lanceolate with long attenuate apex and
slightly auriculate base; abaxially puberulent and appressed pilose;
margin ciliate; striate, early stramineous; persistent. <u>Petioles</u>
1,0 - 3,0cm long, adaxial channel wide, appearing flattened above,
trigonous; vesture similar to stems but less dense. <u>Leaflets</u>
1,3 - 4,4cm long, 0,7 - 3,2cm wide; obovate or obovate - cuneiform;
apex obtuse to rounded, minutely apiculate or retuse; base cuneate;
adaxially glabrous to sparsely strigose and puberulent with primary
and rarely lateral veins only, slightly sunken; abaxially sparse
to dense soft pilose with primary and lateral veins only, prominent;
Lateral veins turn upwards and diminish apically inside margin; conspic-
uously looping between ends of lateral veins distally, characteristic
silver discolouration around perimeter and at base of upper surface,
leaflets symmetrical, laterals smaller. <u>Petiolules</u> 1,8 - 2,4mm long;
more densely hairy than rhachis; slightly swollen and rugose. <u>Stipels</u>
0,6 - 2,5mm long; linear - attenuate; four, one subtending each lateral
leaflet/.....

Desmodium
adscendens (Swartz) DC.
var. robustum Schubert
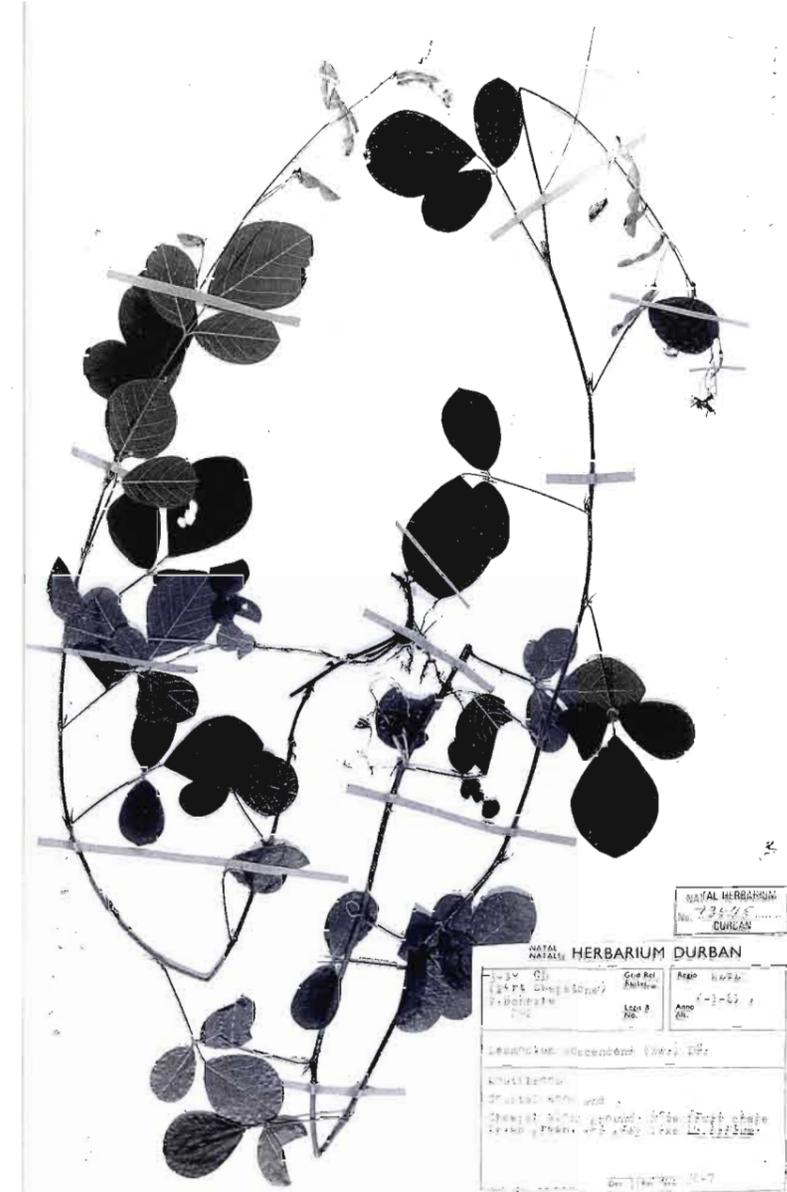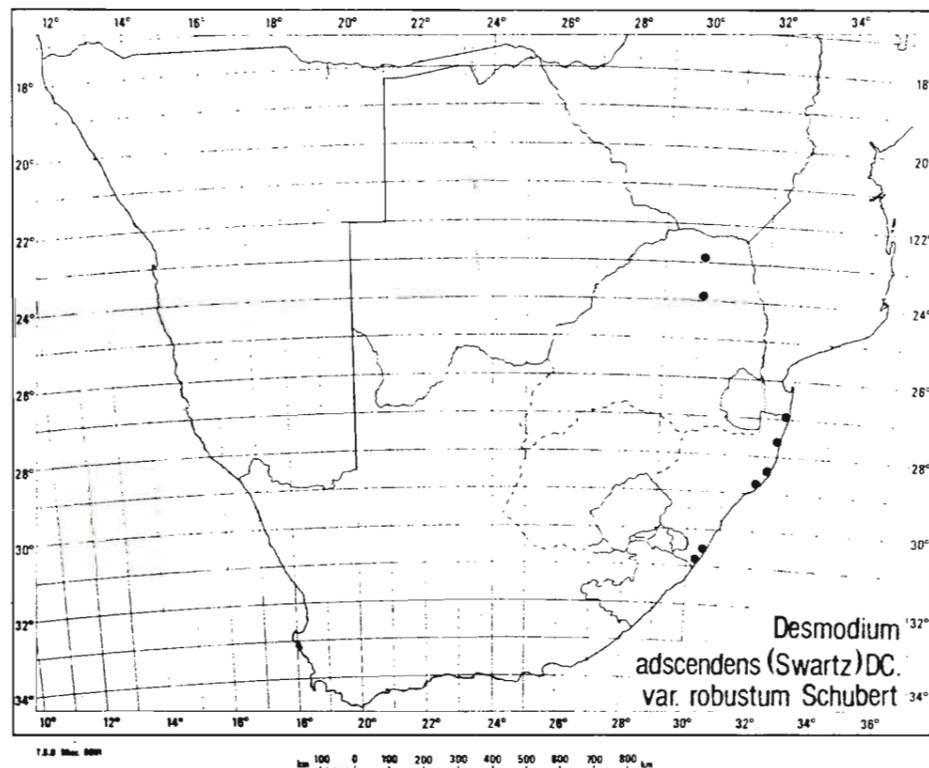
leaflet and two the terminal one. Pseudoracemes open, lax, terminal or axillary, not paniculately branched. Rhachis uncinulate puberulent, and sparsely to abundantly strigose with scattered erect bulbous-based glandular hairs. Inflorescence bracts 3,0 - 5,0mm long, 1,0 - 2,5mm wide; cochleariform, oblique with long attenuate apex; abaxially moderately to densely pilose; early caducous; each subtending a fascicle of two pedicels; median panicle branch reduced to tuft of hairs. Floral bracts absent or if rarely present, depauperate. Pedicels 0,5 - 1,7cm long; ascending from 30° to axis, densely uncinulate puberulent with numerous erect, bulbous-based, gland-tipped multicellular hairs. Flowers 5,0 - 6,0mm long, variously white magenta or purple. Calyx 2,0 - 3,0mm long; minutely puberulent becoming pilose on the teeth; tube, 1,4 - 1,6mm long; teeth, four, upper tooth of two connate sepals, 1,2 - 1,4mm long, 1.6mm wide, bifid for upper 0,5mm; others 1,0 - 1,2mm long, 0,5 - 0,7mm wide; lanceolate. Standard 4,0 - 6,0mm long, 3,5 - 7.0mm wide; obovate to orbicular, gradually tapering to a short slightly reflexed claw; apex retuse; white flushed pink with two purple dots streaked with yellow on either side of the midline near the base. Wings 4,2 - 4,6mm long, 1,8 - 2,3mm wide; cultrate, broader above, auricled proximally; apex rounded, extended into a short claw at the base; mauve in the upper distal half, hyaline below. Keel blades 4,0 - 5,0mm long, 1,0 - 1,6mm wide, longer than wings; securiform; apex truncate; narrowing midway to a peg of tissue, closely applied to the wing auricle, extended into a long claw at the base; deeply long pocketed; hyaline. Staminal sheath 3,5 - 4,2mm long, 1,0mm wide; vexillary stamen 3,8 - 4,0mm long, free. Gynoecium 4,5 - 5,1mm long; ovary 2,0 - 2,5mm long; puberulent and strigose; style flexed 60° in distal 1,2mm. Fruit stipe 0,5 - 2,0mm long; of 1 - 5 articles each 3,5 - 5,5mm long, 2,5 - 3.0mm wide, straight on the upper suture, or slightly indented, curved obliquely below, constricted to less than half their width at the isthmi; densely brown uncinulate puberulent throughout; style persistent. Seed 2,5 - 5,0mm long, 1.5 - 2.7mm wide, reniform to oblong elliptic; light brown.

D. adscendens var. robustum is found in the Zoutspansberg and Woodbush areas of the Northern Transvaal and entering from Mozambique along the Natal coast to the Transkei border.

The plant is a straggling herb or undershrub of shaded mesic forest floors i.e. in coastal dune or swamp forest. Flowering from November to March.

TRANSVAAL.-2230 (Messina) : Witvlag, about 16 miles E. of Lake Funduzi
(-CC), J.B. Gillett 3156 (BOL, PRE, STE).   2330 (Tzaneen) : Woodbush
(-CC), J. Hutchinson 2245 (BOL, PRE)

NATAL.-2632 (Bela Vista) : Malangeni, E. of Maputa (-DD), A.J. Martin
061 (NU); Kosi, Sihadla River crossing (-DD), Moll and Strey 3896
(NH, PRE); 6 miles from Kosi Bay on Maputa rd. (-DD), Ross and
Moll 1841 (NH, PRE); Dumanini stream, W. of Kosi Lake (-DD), K.L.
Tinley 343 (PRE), River nr. Maputa store (-DD), J. Vahrmeijer 541
(PRE); Nr. Maputa (-DD), P. Vorster 2623 (PRE).   2732 (Ubombo) :
4km before Sodwana Bay (-DA), B. Schrire 386 (NH).   2832 (Mtubatuba)
: Dukuduku East (-AD), E.J. Moll 2720 (NU, PRE); Umhlatuzi Lake
area (-CC), H.J.T. Venter 5283 (BLFU); H.J.T. Venter 5291 (PRE,
ZULU).   3030 (Port Shepstone) : Izotsha (-CD), B. Schrire 268;
Palm Beach (-CD), B. Schrire 290 (NH); Southbroom (-CD), B. Schrire
292 (NH); Izotsha (-CD), B. Schrire 297 (NH); St. Michaels-on-sea
(-CD), R.G. Strey 7151 (NH, NU, PRE); Bendigo Nature Reserve, South-
port (-DA), G.R. Nichols 423 (NH)

var. robustum is widespread in tropical Africa but the species is
pantropical from America, Africa, Asia and Malesia.

On forest margins along the coast this species may be confused with
the shade form of D. incanum (see under that species).   Schubert
(1971) records that D. adscendens is an excellent food for stock.

6.1.1.9. <u>Desmodium dregeanum</u> Benth. in Miq., Pl. Jungh. : 222 in adnot. (1852); Harv. in Harv. and Sond., Fl. Cap. 2 : 228 (1862); Bak. in Oliv., Fl. Trop. Afr. 2 : 165 (1871); Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 476 fig. 65/3 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 528 (1974). Type : South Africa, Transkei, stream in vicinity of Umsimkaba (Omsamcaba) River, <u>Drege</u> (B, holo. ✝, GH, iso. !, K, ? iso !). Based on <u>Nicolsonia caffra</u> E. Mey.

<u>Nicolsonia caffra</u> E. Mey., Comm. : 123 (1836)

<u>Desmodium caffrum</u> (E. Mey.) Druce, Rep. Bot. Soc. Exch. Club Br. Isl. 4 : 619 (1917); Schindl. in Feddes Repert. 23 : 360 (1927); Bak.f., Leg. Trop. Afr. : 331 (1929), Brenan in Checklist Tang. Terr. : 419 (1949); Laundon in Consp. Fl. Angol. 3 : 225 (1966) <u>non</u> Eckl. and Zeyh. (1836) <u>nom. illegit.</u> D. caffrum Eckl. and Zeyh. is a later homonym of <u>D. repandum</u> (Vahl) DC.

Perennial, prostrate to decumbent and erect, multistemmed herb or single-stemmed, branching, erect, subshrub, 0,6 - 1,2m long or high arising from a dichotomously branching woody rootstock. <u>Stems</u> woody below; terete becoming variously grooved, striate, angular above; purplish-brown glabrescent below; puberulent and densely appressed silky pilose with slender upwardly directed hairs on younger stems. <u>Leaves</u> trifoliolate, conduplicate. <u>Stipules</u> 5,0 - 9,0mm long 1,0 - 2,2mm wide; erect, oblique; lanceolate - attenuate, clasping base of pulvinus; abaxially scarcely minute puberulent; margin ciliate; striate, early stramineous, persistent. <u>Petioles</u> 3,0 - 15mm long, sulcate; vesture similar to stem. <u>Leaflets</u> 0,5 - 3,5cm long, 0,3 - 1,4cm wide; obovate to obovate - elliptic or elliptic; apex rounded, mucronulate; base cuneate to rounded; glabrous or scarcely appressed pilose above, abundantly long appressed silky pilose and puberulent beneath; primary vein only, conspicuously sunken adaxially, primary and lateral veins prominent below, reticulation sometimes slightly raised on both surfaces; lateral veins turn upwards and diminish apically inside margin, looping occurs distally, between ends of lateral veins; leaflets symmetrical, laterals smaller. <u>Petiolules</u> 0,9 - 2,0mm long, more densely pilose than petiole or rhachis. <u>Stipels</u> 0,5 - 2,5mm long, linear - attenuate; four, one subtending each lateral leaflet and two (often reduced) the terminal one. <u>Pseudoracemes</u> tightly congested, contracted into a densely flowered head or spike-like florescence, 1 - 3 (6)cm long; terminal from leafy shoots or occasionally axillary, rarely paniculately branched but often appearing

so due/......
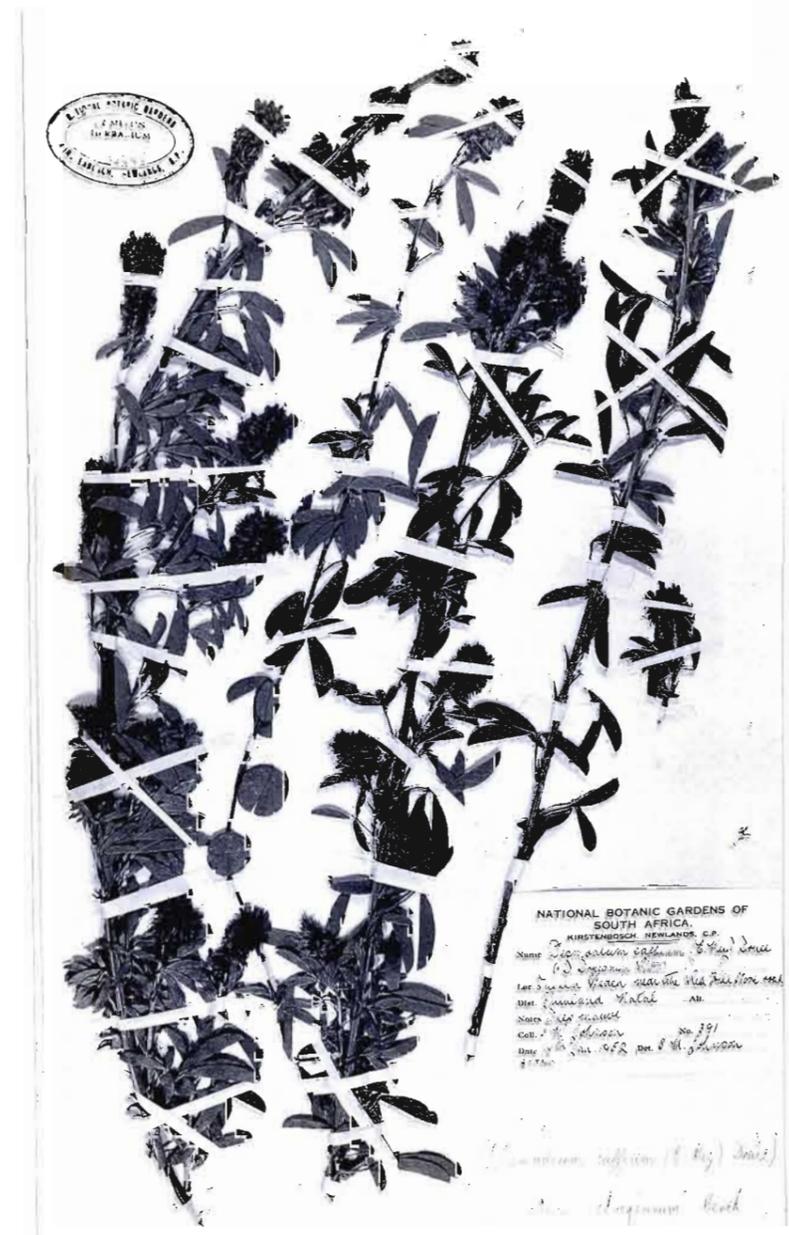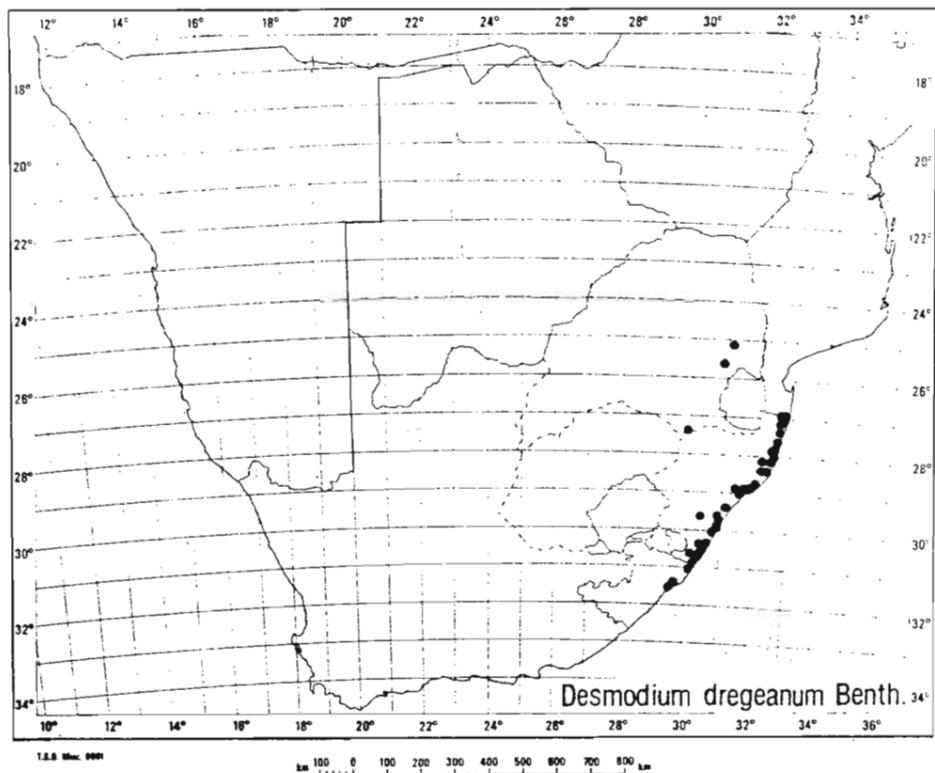
so due to secondary aggregation of terminal inflorescences. Rhachis densely silky pilose with white or golden hairs and puberulent beneath. Inflorescence bracts 3,0 - 6,5mm long, 1,0 to 2,4mm wide; ovate - acuminate, long attenuate; abaxially silky pilose and sparsely puberulent, margin ciliate, striate, stramineous; each subtending a fascicle of 2 pedicels, the median branch reduced to a patch of hairs. Floral bracts 0,5 - 2,7mm long, 0,3 - 0,5mm wide; lanceolate to linear - attenuate; two, one subtending each pedicel. Pedicels 2,5 - 5,1mm long becoming reflexed just below the calyx after anthesis; sulcate; silky pilose with scattered upwardly directed white hairs and puberulent. Flowers 5,0 - 6,5mm long, variously purple and magenta quickly discolouring to blue after tripping. Calyx 3,0 - 4,8mm long; densely silky pilose with white and golden hairs; tube 1,5mm long; teeth, five subequal; 2,5 - 3,4mm long, ovate - lanceolate to attenuate; upper two sepals connate for half their length forming an upper lip 1,6 - 1,8mm wide; others up to 1mm wide. Standard 4,5 - 7,5mm long, 2,0 - 5,5mm wide; obovate; apex rounded and slightly retuse; extended into a claw 0,5mm long at the base; 2 small hyaline folds on either side of the midline above the claw; purple with two darker patches above each fold. Wings 3,0 - 5,0mm long, 1,0 - 2,0mm wide, cultrate, oblong; apex obtuse; extended into a short claw at the base; auriculate proximally. Keel blades 3,5 - 7,0mm long, 1,0 - 2,5mm wide, dolabriform (hatchet-shaped); truncate above, narrowing midway to a small auricle produced as a peg of tissue closely applied to the wings, extended at the base into a claw 1,5 - 2,5mm long. Staminal sheath 3,5 - 5,5mm long, 2,0mm wide, vexillary stamen to 5,0mm long, free. Gynoecium 5,5 - 6,1mm long; ovary, up to 2,6mm long; style thickened at point of upward flexure, flexed erect in distal 1,5 - 1,8mm; stigma small, globose. Fruit sessile or substipitate, stipe 0,5 - 1,0mm long; of 3 to 5 articles, each 2,0 - 3,5mm long, 2,0 - 3,0mm wide; upper suture essentially straight, the lower curved; silky pilose throughout and densely puberulent; reticulate, articles not strongly constricted inbetween, indehiscent. Seed 1,6 - 2,0mm long, 1,0 - 1,5mm wide, rectangular - ellipsoid to reniform; yellow-brown, khaki to castaneous.

D. dregeanum is predominantly a low altitude plant entering the flora area from coastal Mozambique to the coast of northern Transkei. It does however occur in the Lydenberg - Barberton and Volksrust regions of Transvaal and the hinterland of Natal from 0 - 1800m.

The plant is an erect or straggling herb in open grassland most often in moist or marshy areas in sandy soils. It can become a woody subshrub

to/.....

Desmodium dregeanum Benth.

to - 1m if protected from fire and it readily takes to semidisturbed grasslands, roadsides or forest margins. Flowering may occur the whole year round.

TRANSVAAL.-2530 (Lydenburg) : Betw. Barberton and Kaapse Hoop (-DB), N. Grobbelaar 1104 (PRE, PRU); Kaapse Hoop (-DB), F.A. Rogers 18410 (PRE). 2531 (Komatipoort) : W. of Pretoriuskop camp (-AA), H.P. van der Schijff 2023 (PRE).

NATAL.-2632 (Bela Vista) : 5½ miles from Sihangwane Store on Maputa rd. (-DC), Ross and Moll 1830 (NH, PRE); Near Maputa Store (-DD), Strey and Moll 3873 (NH, PRE). 2729 (Volksrust) : Volksrust (-BD), J.L. Sidey 3976 (NH, PRE). 2732 (Ubombo) : Manzengwenya, just E. of Vasi swamp (-BA), E.J. Moll 4767 (NH, PRE); Lake Nhlange (-BB), O. Bourquin 357 (NU); Vasi Swamp (-BB), Stephen van Graan and Schwabe 1197 (PRE); Nyaneni, Lake Sibayi (-BC), Vahrmeijer and Hardy 1627 (a) (PRE); Sordwana Bay (-CD), Vahrmeijer and Tölken 828 (PRE); 95km from Mkuze to Sordwana Bay (-DA), B. Schrire 382 (NH); Mpangazi (-DA), R.G. Strey 4971 (NH, NU, PRE); St. Lucia, Park just S. of Sengwana Point (-DC), C.J. Ward 7696 (NH, NU, PRE). 2830 (Dundee) : Culvers, Weenen (-CC), F.A. Rogers 28284 (GRA, STE). 2831 (Nkandla) : Signpost to Kanyile, nr. Eshowe (-CD), N. Grobbelaar 2329 (PRU); Eshowe (-CD), J.G. Lawn 3 (NH); Valley beyond Lutu Mission Church, Eshowe (-CD), J.G. Lawn 2031 (NH); 'Twinstreams', Mtunzini (-DC), O. Bourquin and W.J. Lawson 1171 (NH, PRE); Ngoye Forest Reserve (-DC), C.H. Stirton 462 (PRE); Ubisana Valley, Ngoye Mtn (-DC), H.J.T. Venter 570 (NH); H.J.T. Venter 634 (NH); H.J.T. Venter 729 (ZULU); University of Zululand Campus (-DD), A. Eicker sn. (ZULU); Uqubu Lake (-DD), H.J.T. Venter 3303 (ZULU). 2832 (Mtubatuba) : Hluhluwe Game Reserve (-AA), D. Edwards 3250 (NU, PRE); C.J. Ward 1874 (NH, NU); C.J. Ward 1875 (NH, PRE); Charters Creek (-AB), W.F. Barker 10012 (NBG); Nyalazi Station Forest (-AB), D.N.S. Tomlinson 2/115 (NH); Palm Ridge Farm, Hlabisa (-AC), E.R. Harrison 244 (NH,PRE); St. Lucia (-AD), J.P. Dutton 47 (NH); Airport, St. Lucia (-AD), N. Grobbelaar 1821 (PRE,PRU); St. Lucia (-AD), B. Schrire 356 (NH); St. Lucia Estuary (-AD), C.J. Ward 4361 (NH, PRE); Lake St. Lucia, eastern shores (-BA), R.H. Taylor 85 (NU); 1 mile W. of Richards Bay (-CC), N. Grobbelaar 649 (PRE,PRU); Richards Bay (-CC), J.G. Lawn 1807 (NH); S. of Lake Umzingazi,near Richards Bay (-CC), T.B. Oatley 26 (PRE);Richards Bay (-CC),W.G. Rump sn.(NU); C.H. Stirton 536 (PRE); Umhlatuzi Lake

bluff (-CC), H.J.T. Venter 4547 (BLFU). 2930 (Pietermaritzburg) : Town Hill, P.M.burg (-CB), R.J. Allsopp 969 (NU); R.J. Allsopp 1017 (NH); Inanda (-DB), J.M. Wood 817 (BOL, SAM); Everton (-DD), T.A. Coleman 13 (NH, PRE); Fields Hill (-DD), M.S. Evans 181 (NH); Everton, Eskotene (-DD), O.M. Hilliard 1336 (NU); Hillcrest (-DD), J. Kalf 36 (NU); Monteseel, Inchanga (-DD), W.J. Lawson 479 (NH); Forest Hills, Kloof (-DD), W.J. Lawson 704 (NH); Gillitts (-DD), J.M. Macgregor 64 (NU); Durban Westville University Campus (-DD), B. Schrire 855 (NH); Merebank East (-DD), C.J. Ward 5389 (NH, NU, PRE); Steinbank Nature Reserve (-DD), C.J. Ward 6375 (NH, NU, PRE); Sarnia Beacon Hill (-DD), C.J. Ward 7598 (NU, PRE); Clairmont near Durban (-DD), J.M. Wood 209 (BOL, SAM); Near Pinetown (-DD), J.M. Wood 5591 (PRE). 2931 (Stanger) : Chakaskraal (-AC), J. Thode STE 3805 (STE); Tugela Beach, near Red Hill Store rd. (-BA), S.M. Johnson 391 (NBG); Durban (-CC), Jenkins sub TRV 7072 (PRE); Durban Flats (-CC), W. Keit NH 11142 (NH); Durban (-CC), F.A. Rogers 1259 (PRE); F.A. Rogers 15059 (J); Wentworth (-CC), C.J. Ward 6509 (NH, NU); Durban Flats (-CC), J.M. Wood 3129 (NH); Sydenham (-CC), J.M. Wood 11845 (PRE); Durban Flats (-CC), J.M. Wood NH 163 (NH). 3030 (Port Shepstone) : Farm Friedenau, Umgaye-flat, Alexandra Cty. (-AD), H. Rudatis 68 (STE); H. Rudatis 288 (PRE); Umkomaas (-BB), R.L. Shuter 59 (NU); Amanzimtoti (-BB), E. Wilson 35 (NU); Scottburgh Golf course (-BC), A.A. Mauve 4099 (PRE); Umzinto (-BC), E. Schelpe 51 (BOL); 3km from Scottburgh to Port Shepstone (-BC), B. Schrire 277 (NH); B. Schrire 881 (NH); Oribi Flats, river valleys (-CA), A. McClean 496 (NH); Baboon Castle, Oribi Gorge (-CB), A. McClean 439 (NH); 1km from trading store, Gibraltar Rock to Oribi Gorge (-CB), B. Schrire 284 (NH); Roadside near Umtentwini on N2 (-CB), B. Schrire 716 (NH); Port Shepstone (-CB), G. Weeks 82 (J); Munster (-CC), D.M. Gemmel BLFU 6050 (BLFU); $\pm$ 8 miles from Port Edward on Izingolweni rd. (-CC), F. Getliffe NU 27810 (NU); Betw. Port Edward and Izingolweni (-CC), O.M. Hilliard 1134 (NU); Paddock (-CC), J.L. Parkhouse NBG 16886 (NBG); J.L. Sidey 4186 (PRE); Near Southbroom turning (-CD), J.P.H. Acocks 10899 (PRE); Uvongo (-CD), N. Grobbelaar 999 (PRE, PRU); L.C.C. Liebenberg 8048 (PRE); Shelly Beach (-CD), A.O.D. Mogg 11921 (PRE); A.O.D. Mogg 12700 (PRE); Uvongo (-CD), A.O.D. Mogg 13455 (PRE); Margate (-CD), J.W. Morris 195 (NU); St. Michaels-on-sea (-CD), H.B. Nicholson 105 (NH); Wichmann's Farm near St. Michaels-on-Sea (-CD), J.H. Ross 1822 (NH, PRE); Margate (-CD), W.G. Rump NH 21063 (NH); W.G. Rump sn. (NU); 'Skyline' Farm on rd. from Izingolweni to Port Edward (-CD), B. Schrire

287 (NH); Palm Beach (-CD), B. Schrire 289 (NH): Southbroom (-CD), B. Schrire 294 (NH); Izotsha (-CD), B. Schrire 296 (NH); Uvongo (-CD), R.G. Strey 4887 (NH, PRE); Hibberdene (-DA), N. Grobbelaar 59 (PRU). 3130 (Port Edward) : Port Edward (-AA), N. Grobbelaar 279 (PRE, PRU); B. Schrire 285 (NH); B. Schrire 286 (NH);

TRANSKEI.-3129 (Port St. Johns) : Magwa Falls (-BC), L.E. Codd 9312 (PRE); E.E. Galpin 11005 (PRE); Fraser Falls, Lusikisiki (-BC), O.M. Hilliard 1095 (NU); F.M. Leighton (BOL); Near St. Johns R. (-DA), Bolus 8882 (BOL); Westgate, Port St. Johns (-DA), Comins 1956 (GRA, PRE); Port St. Johns (-DA), A. Denley J30699 (J); H.G. Flanagan 2574 (NH, PRE, SAM); Noxolweni Forest, Port St. Johns (-DA), A.O.D. Mogg 13072 (PRE); Port St. Johns (-DA), C.E. Moss J3299 (J). 3130 (Port Edward) Sea View, Port Edward - Bizana Rd. (-AA), C.J. Ward 222 (NU). 3228 (Butterworth) : The Haven (-BB), J.L. Gordon-Gray 1308 (NU).

D. dregeanum is an endemic African species occurring widely in eastern and southern Africa.

6.1.1.10. <u>Desmodium barbatum</u> (L.) Benth. in Miq., Pl. Jungh. : 224 (1852); Schubert in Fl. Trop. E. Afr., Legum. - Papil.; 477 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 530 (1974). Type: Jamaica?, <u>Herb. Linnaeus 921 . 48</u> (LINN, holo., A-GH, Microfiche (IDC-Linn. 504 : III, 3) !)

<u>Hedysarum barbatum</u> L., Syst. Nat. ed. 10,2 : 1170 (1759)

var. <u>dimorphum</u> (Welw. ex Bak.) Schubert in Bull. Jard. Bot. Brux. 22 : 298 (1952); and in Fl. Congo Belge 5 : 205 (1954); Hepper in Fl. W. Trop. Afr. ed 2, 1 : 564 (1958); Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 478 (1971); Verdc. in Kirkia, for Fl. Zamb. 9, 2 : 531 (1974). Type : Angola, Cuanza Norte. Golungo Alto, 2400ft., <u>Welwitsch 2165</u> (LISU, lecto., K, BM, isolecto.!) Syntype Malawi, Manganya alt. 3000ft. <u>Kirk</u> (K).

<u>Desmodium dimorphum</u> Welw. ex Bak. in Oliv., Fl. Trop. Afr. 2 : 161 (1871); Hutch. and Dalz.,Fl. W. Trop. Afr. 1 (2) : 417 (1928); Bak.f.,Leg. Trop. Afr. : 332 (1929)

<u>Nicolsonia barbata</u> (L.) DC. var. <u>dimorpha</u> (Welw. ex Bak.) Schindl. in Feddes Repert. 23 : 359 (1927)

<u>Desmodium barbatum</u> (L.) Benth. subsp. <u>dimorphum</u> (Welw. ex Bak.) Laundon in Consp. Fl. Angol. 3 : 225, t 20/A2 (1966)

Perennial spreading to erect multi-stemmed suffrutex or subshrub to 90cm tall arising from a woody dichotomously branching rootstock. <u>Stems</u> angular, shallowly grooved or terete; glabrous below becoming densely silky pilose with appressed to spreading long white to greyish, occasionally ferruginous, upwardly directed hairs. <u>Leaves</u> 1 - 3 foliolate. <u>Stipules</u> 3,5 - 9,5mm long, to 3,0mm wide at the base; ovate, lanceolate to deltoid, attenuate, often slightly auricled at the base; base oblique; closely applied to the stem becoming concave above petiole; abaxially minutely puberulent and abundantly spreading silky pilose; margin ciliate; striate, persistent, stramineous. <u>Petioles</u> 0,6 - 2,0cm long flattened above, vesture similar to stems. <u>Leaflets</u> 0,5 - 6,5cm long, 0,4 - 3,5cm wide; elliptic, elliptic - oblong or obovate, orbicular or oval, rarely ovate; apex obtuse, shortly mucronulate or retuse; base rounded, cuneate or occasionally subcordate; adaxially essentially glabrous or sparsely puberulent and scattered appressed pilose, abaxially puberulent and moderately

to/.....

NASIONALE HERBARIUM, PRETORIA.
NATIONAL HERBARIUM, PRETORIA.
Kruger National Park.
Transvaal
Desmodium dimorphum Welw.

to densely spreading silky pilose, particularly along veins; primary vein only, sunken and conspicuous adaxially, major veins and reticulation prominent below; lateral veins turn upwards and diminish apically before margin, looping between ends of lateral veins distally; margin ciliate; leaflets symmetrical (reversably conduplicate). Petiolules 1,5 - 4,0mm long. Stipels 1,5 - 4,0mm long, up to 1,0mm wide; narrow lanceolate - attenuate; four, one subtending each lateral leaflet (if present), and two the terminal one. Pseudoracemes very compact, or slightly less so with restricted elongation of the rhachis, capitate or spicate; 1,0 - 4,0 (6,0)cm long, densely flowered, unbranched; axillary and terminal. Rhachis terete, densely minute puberulent and sparsely to abundantly patent silky pilose. Inflorescence bracts 2,5 - 6,0mm long, 1,5 - 3,5mm wide; ovate - acuminate, somewhat cochleariform, abaxially minutely puberulent with scattered erect glandular tipped hairs and variable ascending white pilose; margin ciliate; stramineous, striate, persistent, each subtending a fascicle of 2 pedicels, no median bud. Floral bracts when present, 1,0 - 1,5mm long, subulate and often falcate, one subtending each pedicel, usually absent. Pedicels 4,0 - 10mm long, densely minute puberulent with scattered longer uncinulate hairs and abundant erect bulbous-based, glandular tipped multicellular hairs; initially held to 45° from axis, becoming arcuately reflexed later, conspicuous, with flowers deflexed at ends of pedicels. Flowers 6,0 - 7,0mm long, variously pink, lilac or purple turning blue after tripping. Calyx 4,0 - 6,0mm long subequally 5 toothed, densely minute puberulent becoming silky pilose on the teeth; tube 1,2 - 1,6mm long; teeth 3,0 - 4,2mm long, the upper two partly connate, up to 2,2mm wide at the base and bifid for upper 2,0 - 3,0mm, ovate lanceolate, acuminate; others 0,6 - 1,0mm wide, the lower often shorter and more narrowly attenuate. Standard 4,5 - 7,0mm long, 4,0 - 6,0mm wide, obovate to sub-orbicular, tapering to a short slightly reflexed claw at the base; apex retuse, two barely perceptible folds on either side of the midline above the claw merging into two deep pink spots; hyaline flushed with pink. Wings 3,5 - 5,5mm long, 1,5 - 3,0mm wide; cultrate, broadly oblong becoming wider distally; apex rounded, auriculate at the base, extended into a short claw, deep pink. Keel blades up to 5,5mm long and 2,2mm wide, slightly longer than wings; broadly elliptic, securiform, apex almost truncate, long pocketed, forming a small peg of tissue to the outside near the base where closely applied to the wing, extended at the base into a long claw; hyaline becoming pink in the distal half. Staminal sheath 4,0 - 4,6mm long, to 1,6mm wide; vexillary stamen 3,6 - 4,0mm long, free. Gynoecium up to 5,5mm long; ovary

2,2/.....
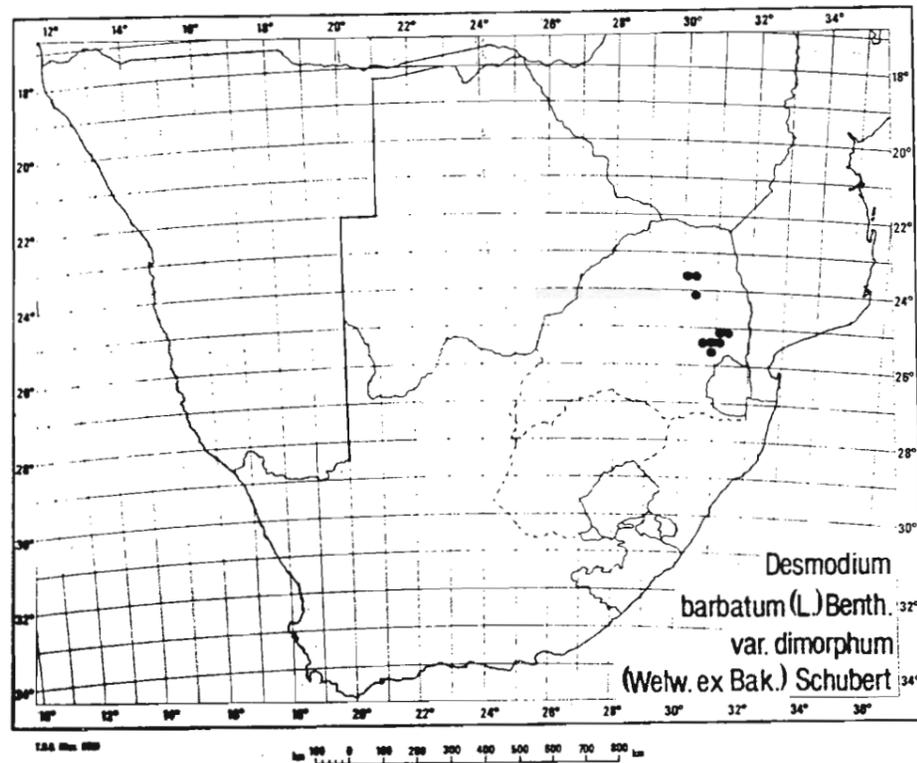
2,2 - 2,7mm long, abundantly appressed pilose; style to 2,8mm long, flexed 90° in distal 1,2mm. Fruit 0,5 - 1,6cm long, of 3 - 6 articles; each 2,0 - 3,0mm long, 1,5 - 2,5mm wide, oblong with upper margin straight and lower curved; constricted between articles; puberulent with scattered longer hairs; dehiscent; reticulate, rim prominent. Seeds 1,7 - 2,1mm long, to 1,5mm wide, squarish, reniform to elliptic - reniform, khaki to brown.

D. barbatum var. dimorphum is found in the Transvaal from the Letaba district near Tzaneen south to Lydenberg, Barberton and Nelspruit. 100 - 1000m.

The plant is a spreading suffrutex to erect subshrub $\pm$ 1m high in the grassland component of open woodland. Flowering from February to June.

TRANSVAAL.-2330 (Tzaneen) : Duiwelskloof (-CA), J.C. Scheepers 241 (PRE, PRU); Mojadjeskraal (-CB), Krige 139 (J). 2430 (Pilgrim's Rest) : Shiluvane (AB), H. Junod sub TRV 5267 (PRE); H. Junod sub TRV 5284 (PRE). 2530 (Lydenburg) : Wonderkloof Nature Reserve (-BC), J.P. Kluge 1222 (PRE); Nelspruit (-BD), H.G. Breyer sub TRV 17848 (PRE); Alkmaar (-BD), L.C.C. Liebenberg 2374 (PRE); Schagen (-BD), L.C.C. Liebenberg 2897 (PRE); Kaapse Hoop (-DB), F.A. Rogers 20835 (PRE). 2531 (Komatipoort) : 9 miles NW. of Pretoriuskop on Numbe drive (-AA), Codd and de Winter 5144 (PRE); Bushman's Rock Hotel (-AA), B. Schrire 661 (NH); C.H. Stirton 8685 (NH); Pretoriuskop (-AB), H.P. van der Schijff 2419 (PRE); Plaston (-AC), W.E. Holt 207 (PRE)

D. barbatum is a pantropical polymorphic species. Both varieties are widespread in central, eastern and southern Africa. The plant is considered by Allen and Allen (1981) to be a good wild forage on acid and calcium deficient soils in Brazil and northern Argentina.

var. argyreum (Welw. ex Bak.) Schubert in Bull. Jard. Bot. Brux. 22 : 298 (1952); and in Fl. Congo Belge 5 : 205 (1954); Schubert in Fl. Trop. E. Afr., Legum. - Papil. : 479 (1971); Verdc. in Kjrkia, for Fl. Zamb. 9, 2 : 531 (1974). Type : Angola, Huila, Welwitsch 2162 (LISU holo., BM, iso. !)

Desmodium dimorphum Welw. ex Bak. var. argyreum Welw. ex Bak. in Oliv.,/.....

Desmodium
barbatum (L.) Benth.
var. dimorphum
(Welw. ex Bak.) Schubert

Desmodium barbatum (L.)Benth. var. argyreum (Welw. ex Bak.)

in Oliv., Fl. Trop. Afr. 2 : 161 (1871); Bak.f., Leg. Trop. Afr. : 332 (1929)

Nicolsonia barbata (L.) DC. var argyrae (Welw. ex Bak.) Schindl. in Feddes Repert.23 : 359 (1927)

Desmodium barbatum (L.) Benth. subsp. dimorphum sensu Laundon in Consp. Fl. Angol. 3 : 225 (1966) proparte

Erect plants with stems silvery-white or fulvous, appressed silky-pilose; leaves almost all 1-foliolate; leaflets densely silvery-silky beneath; inflorescence often a panicle of pseudoracemes.

SOUTH WEST AFRICA.-1820 (Tarikara) : Fumbe (-AA), Merxmüller and Giess 1862 (WIND)

D. barbatum var. argyreum has been recorded from South West Africa in woodland or grassland, 1000 - 2000m.

Schubert (1971) however, states that although this variety is quite distinguishable from var. dimorphum in the extreme, there are many plants which form a line of transition.
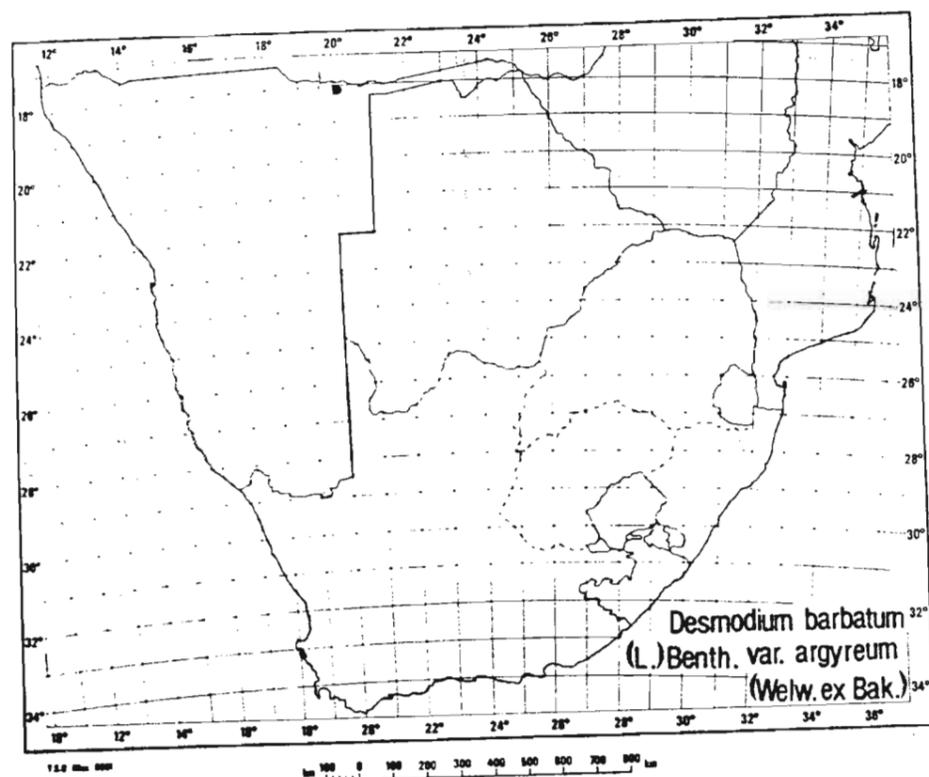
Pseudarthria Wight and Arn., Prodr. Fl. Ind., 1 : 209 (1834); Benth. in Benth. and Hook.f., Gen. Pl. 1 (2) : 521 (1865); Bak. in Oliv., Fl. Trop. Afr. 2 : 167 (1871) and in Hook.f., Fl. Br. Ind. 2 (4) : 153 (1876); Taub. in Pflanzenfam. III (3) : 329 (1894); Schindl. in Feddes Repert. Beih. 2 (1914); Hutch. and Dalz., Fl. W. Trop. Afr. 1 : 386 (1928); Bak.f., Leg. Trop. Afr. : 338 (1929); Burtt Davy, Fl. Pl. Tvl. 2 : 381 (1934); Phill., Gen. ed 2 : 419 (1951); J. Leonard in Fl. Congo Belge 5 : 234 (1954); Hepper in Fl. W. Trop. Afr. ed 2, 1 : 585 (1958); White., For. Fl. N. Rhod. : 161 (1962); Hutch., Gen. Fl. Pl. 1 : 399 (1964); Torre in Consp. Fl. Angol. 3 : 231 (1966); Verdc. in Kew Bull. 24 : 64 (1970), Fl. Trop. E. Afr., Legum. - Papil. : 483 (1971), and in Kirkia, for Fl. Zamb. 9, (2) : 534 (1974); Dyer, Gen. 1 : 264 (1975). Type species : P. viscida (L.) Wight and Arn. (Hedysarum viscidum L.)

Hedysarum L., Sp. Pl. : 745 (1753) pro parte

Desmodium Desv. in DC., Prodr. 2 : 325 (1825) pro parte

Anarthrosyne E. Mey., Comm. : 124 (1835); Harv. in Harv. and Sond., Fl. Cap. 2 : 229 (1862) pro parte; Harv., Gen.: 82 (1868)

The name Pseudarthria is derived from the Greek 'pseudo' meaning false and 'arthron' or joint; the constriction between the seeds gives the pod the impression of being falsely jointed.

Perennial, erect, woody herbs or subshrubs. Stems one to many, strongly ribbed and densely grey to fulvous tomentose. Leaves pinnately 3 - foliolate (sometimes abnormally 5 - foliolate). Stipules persistent, scarious, free, lanceolate - acuminate, striate, sharply recurved, densely tomentose abaxially; dark brown, glabrous adaxially. Leaflets characteristic, thick, soft, velvety, rugose, appearing viscid - scabrous, stipellate. Pseudoracemes elongate, laxly many-branched densely flowered, terminal and axillary; bracts narrow; bracteoles present, early caducous. Calyx 5 - lobed, the upper two sepals partly connate forming a lip. Corolla small, pink; standard without appen- dages. Style filiform curving upwards distally. Fruit a linear oblong or slightly falcate compressed pod, the sutures often sinuate between the seeds; dehiscing into 2 non twisting reticulate valves. Seeds subreniform, compressed; almost without an aril; funicle elong- ated. 2n = 26

6.1.2.1. **Pseudarthria hookeri** Wight and Arn., Prodr. Fl. Ind. 1 :
209 (1834); Bak. in Oliv., Fl. Trop. Afr. 2 : 168 (1871); Schindl.
in Feddes Repert. Beih. 2 : 11 (1914); Hutch. and Dalz., Fl. W. Trop.
Afr. 1 : 386 (1928); Bak. f., Leg. Trop. Afr. : 339 (1929); Robyns,
Fl. Parc Nat. Alb. 1 : 313 (1948); Brenan in Checklist Tang. Terr.
: 436 (1949); J. Leonard in Fl. Congo Belge 5 : 235, fig. 15/A-B
(1954); Hepper in Fl. W. Trop. Afr. ed 2, 1 : 586 (1958); White,
For. Fl. N. Rhod. 161 (1962); Torre in Consp. Fl. Angol. 3 : 232
(1966); Verdc. in Kew Bull. 24 : 65 (1970); in Fl. Trop. E. Afr.,
Legum. - Papil. : 484, fig. 69/1-9 (1971); and in Kirkia, for Fl.
Zamb. 9,(2) : 534 (1974). Type : Mauritius, cultivated from Zanzibar
material, Telfair (K, ? holo. !)

> **Anarthrosyne** robusta E. Mey., Comm. 1 : 125 (1836); in Harv.
> and Sond., Fl. Cap. 2 : 229 (1862)
> Type : Transkei, Umgazana, Drege 452

var. hookeri

> Verdc. in Kew Bull. 24 : 65 (1970), in Fl. Trop. E. Afr.,
> Legum. - Papil. 484, fig. 69/1-9 (1971) and in Kirkia, for
> Fl. Zamb., 9, 2 : 535 (1974)

Perennial, erect to suberect woody herb or subshrub 0,3 - 3,0m tall
arising from a thick rhizomatous, branching woody rootstock. Stems
single or a few, sparsely branched below, woody with corky light
brown streaks where epidermis is broken, otherwise greyish-brown,
canescent; becoming strongly ribbed above, densely tomentose with
spreading white or yellow hairs particularly along the ribs; often
maroon on the undersurface of stem if not erect. Leaves trifoliolate
(abnormally subpalmately 4 - 5 foliolate). Stipules 5,0 - 12,5mm
long, 1,5 - 5,0mm wide, lanceolate-attenuate; strongly recurved almost
immediately; abaxially densely white tomentose and puberulent, adaxially
glabrous, striate, dark brown; margin ciliate; persistent. Petiole
1,0 - 7,0cm long, sulcate; densely tomentose adaxially less densely
so abaxially. Rhachis 0,2 - 3,0cm long, similar but more deeply
sulcate. Leaflets 2,5 - 16,5cm long, 1,3 - 10cm wide; ovate - lanceo-
late to ovate or cuneiform - obovate; apex obtuse to acute, mucronulate;
base rounded to cuneate; thick, soft, velvety; margin repand to sinuate;
adaxially rugose, scabrous due to dense uncinulate puberulence; sparsely
pilose, denser along veins, abaxially scattered pilose to dense grey-
white tomentose, veins pallid, major veins and reticulation particular-
ly prominent, lateral veins extended fully to the margin, not looping
distally/.....
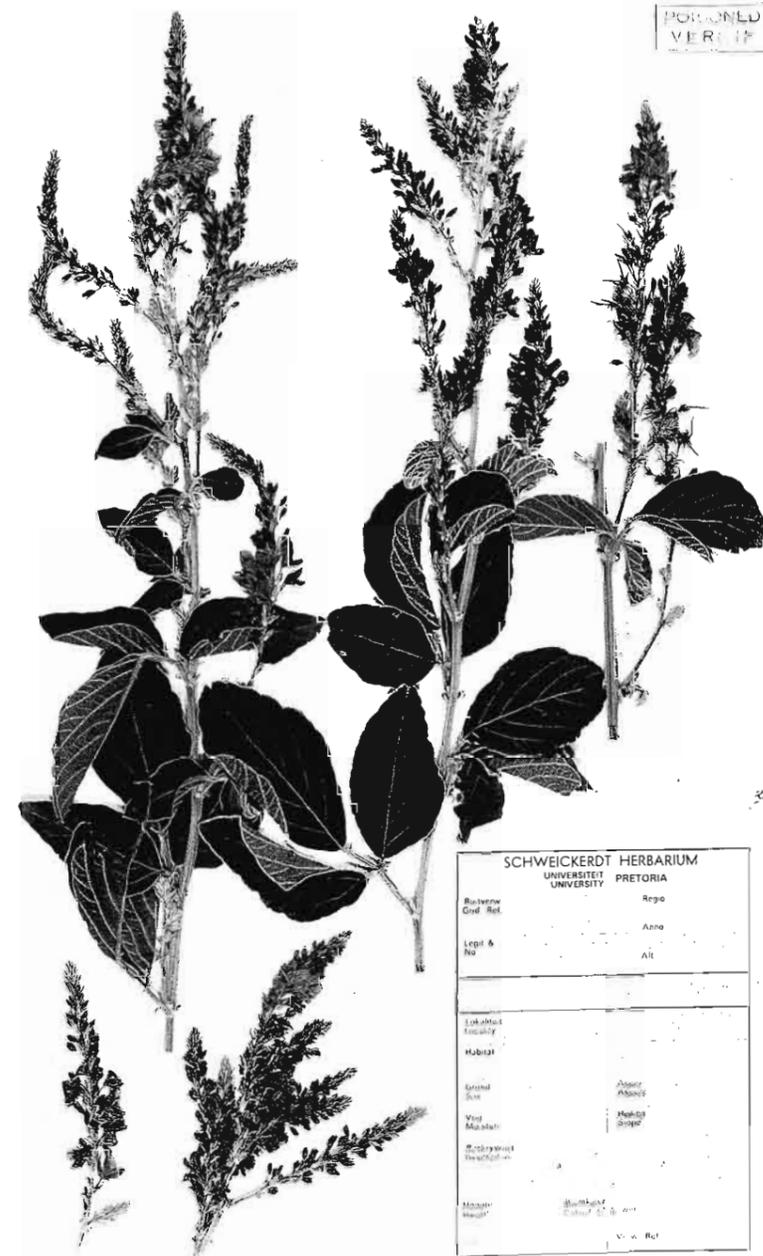
distally, terminal leaflet symmetrical, laterals smaller, the base
often oblique. Petiolules 0,2 - 1,0cm long, slightly swollen, very
densely tomentose. Stipels 0,5 - 7,0mm long 0,2 - 1,0mm wide, lanceo-
late to setaceous; 4 (5 - 6), one, subtending each lateral leaflet
(either one or both occasionally paired) and two the terminal one,
bases enlarged, obvious. Pseudoracemes elongate, to $\pm$ 35cm, laxly
many-branched, densely flowered, terminal and axillary at the distal
ends of branches, showy. Rhachis densely puberulent and patent pilose
with upwardly directed tapering hairs, often flattened and deeply
grooved. Peduncles similar but terete, to 10cm long. Inflorescence
bracts 3,0 - 10mm long, 0,6 - 2,0mm wide; narrow lanceolate-attenuate;
recurved in the upper half; similar to stipules; each subtending
a fascicle of two pedicels and a median reduced bud. Floral bracts
1,0 - 4,0mm long, 0,1 - 0,3mm wide; linear - attenuate, often falcate;
3, one subtending each pedicel and one, reduced at base of medium
bud. Pedicels 3,0 - 8,5mm long, densely uncinulate puberulent and
moderately pilose distally, erect becoming reflexed later. Bracteoles
0,5 - 1,5mm long, variously paired, single or absent, on distal half
of pedicel. Flowers 7,0 - 9,5mm long, pink. Calyx 5,0 - 5,7mm long;
puberulent and scattered pilose; tube, 1,9 - 2,2mm long; teeth four,
3,2 - 3,5mm long subequal, lanceolate-attenuate; upper-tooth of two
connate sepals, bifid for upper 0,5 - 1,0mm; 2,0 - 2,2mm wide; others
1,5 - 1,7mm wide. Standard 6,5 - 10mm long, 4,0 - 9,5mm wide; orbic-
ular; apex retuse, abruptly constricted into a short claw at the
base; pink to reddish-purple with two hyaline patches outlined in
purple on either side of the midline towards the base. Wings 8,0
- 9,5mm long, 2,8 - 3,0mm wide, cultrate, oblong, apex rounded, extended
to a short claw at the base, longer than keel, pink. Keel blades
7,0 - 8,5mm long, 2,0 - 2,5mm wide, oblong, subfalcate, apex rounded;
extended into a claw 3,0 - 3,5mm long; closely applied to wings;
light pink to hyaline. Staminal sheath 4,5 - 7,0mm long, 1,0 - 1,2mm
wide, vexillary stamen to 7,0mm long. Gynoecium 5,0 - 8,5mm long;
ovary, 3,5 - 5,5mm long, densely appressed tomentose; style, 3,0mm
long, flexed 45° in distal 1,5mm. Fruit 1,2 - 3,8cm long, 3,0 -
5,0mm wide, linear oblong or slightly falcate, apex rounded; stipe
to 1,5mm long; densely puberulent to tomentellous and scattered pilose;
not articulate; one-celled, dehiscing along abaxial suture, the sutures
often sinuate between seeds; 3 - 12 seeded, style persistent. Seeds
1,8 - 2,4mm long, 1,2 - 1,5mm wide, 0,8mm thick; reniform or oblong
- ovoid, smooth, brown to khaki.

Pseudarthria hookeri occurs in the Transvaal from Louis Trichardt
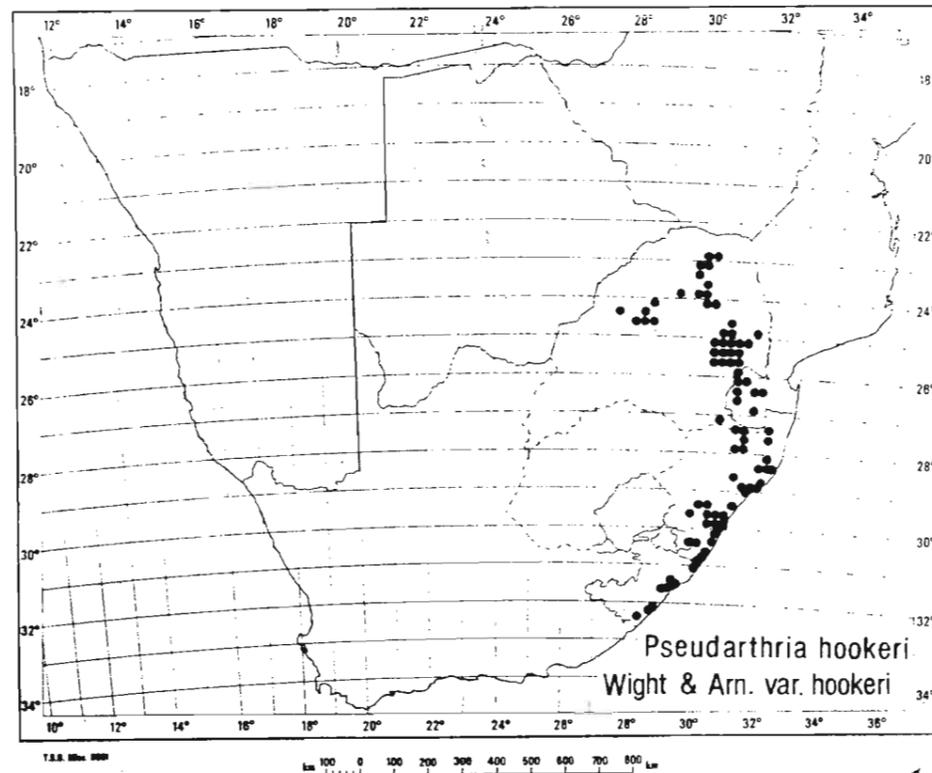
and Tzaneen; between Lydenburg and Skukuza, and between Middleburg and Komatipoort; to Swaziland and Piet Retief in the south. The range also extends southwest from Pietersburg through Nylstroom to Thabazimbi in the Waterberg mountains. In Natal the range extends southwards through northern Natal and Zululand to the coast and midlands up to Pietermaritzburg, Richmond, Ixopo and Harding. Further south the range becomes restricted to coastal Transkei to the Eastern Cape border.

VENDA.- 2230 (Messina) : Sibasa, N. Tvl (-CD), Gerstner 6216 (BOL); Tate Vondo Forestry Res. Sibasa distr. (-CD), G. Hemm 555 (J, PRE, VENDA); Dzimauli, Venda (-CD), A.E. van Wyk 4044 (PRE)

TRANSVAAL.- 2329 (Pietersburg): Louis Trichardt (-BB), E.C. Koker 5 (PRE); Soekmekaar (-BD), R.D. Bayliss 1145 (PRE); Pietersburg (-CD), R.A. Dyer 3152 (PRE); Around Houtbosch, Pietersburg distr. (-DD), H. Bolus 10949 (BOL, PRE); Rd. to Ebenezer dam from Haenertsburg (-DD), R. Crawford 434 (PRE); Houtbosch (-DD), A. Rehmann 6281 (BOL). 2339 (Tzaneen) : Elim, Zoutspansberg (-AA), A.A. Obermeyer 484 (PRE); Elim (-AA), R. Schlechter 4551 (BOL, GRA); R. Schlechter sub TRV 2220 (PRE); Westfalia Estate, near Duiwelskloof (-CA), J.J. Bos 1300 (PRE, STE); Duiwelskloof, Fairy Glen (-CA), J.C. Scheepers 106 (PRE, PRU); J.C. Scheepers 320 (PRE); Duiwelskloof - Tzaneen rd. 30 miles N. of overhead railway bridge (-CA), J. Stephan 298 (PRE); Magoebaskloof (-CC), N. Grobbelaar 448 (PRE, PRU); Tzaneen (-CC), B. Maguire 689 (J); Newagatha (-CC), I. McCallum PRE 55668 (PRE). 2427 (Thabazimbi) : Foot of Krantzberg Mtn. on rd. from Thabazimbi to Rankins Pass (-BC), L.E. Codd 5918 (PRE); Mr. Erasmus' Farm near Kranzberg (-BC), G. van Son sub TRV 30436 (PRE). 2428 (Nylstroom) : Tarentaalpas, Waterberg; 20,2 miles from Vaalwater in direction of Naboomspruit (-AD), B. Clarke 47 (PRE, PRU); Farm Louwskraal (-BA), D.C. Biggs 197 (PRE); 40km. Nylstroom to Vaalwater (-CA), J. Stephan 581 (PRE); Olifantspruit, in Poort 6 miles N.E. of Nylstroom (-CB), J.E. Repton 3482 (PRE); Tweefontein (-CD), R. Schlechter sub TRV 13151 (PRE); Naboomspruit (-DA), D.P. Murray 690 (PRE). 2430 (Pilgrim's Rest) : The Downs, Zoutspansberg distr. (-AA), H.A. Junod 4381 (PRE); Malopetsi R. valley between foot of Wolkberg and George's Valley (-AA), A. Meeuse 9884 (PRE); Selati Estates, The Downs (-AA), J. Vahrmeijer 2403 (PRE); Shiluvane (-AB), H.A. Junod 2369 (PRE); Makhujwi R. (-BA), Dr. Breyer sub TRV 18387 (PRE); Perdeskoenwaterval (-DB), D.J. Botha 1335 (PRE, PUC); Hebron, Pilgrim's/.....

Pseudarthria hookeri
Wight & Arn. var. hookeri

Pilgrim's Rest distr. (-DB), R.G. Strey 3322 (PRE); Solique turnoff, Pine plantation, Mariepskop distr. (-DB), H.P. van der Schijff 4577 (PRE, PRU); Ohrigstad Dam Nature Res. (-DC), N. Jacobsen 2255 (PRE); Pilgrim's Rest (-DD), L. Collins sub TRV 9892 (PRE); Graskop (-DD), E.E. Galpin 14386 (PRE); E.E. Galpin Bol 32275 (BOL); Macmac (-DD), C. Mudd PRE 55678 (PRE). 2431 (Acornhoek) : Nr. Skukuza, Kruger National Park (-DC), E. Cholmondeley PRE 55672 (PRE). 2530 (Lydenburg) : Nr. Lydenburg, farm Zwagershoek (-AB), A.A. Obermeyer 319 (PRE); 23km from Machadodorp on rd. to Nelspruit (-AD), L.A. Coetzer 211 (BLFU, PRU); Schoemanskloof (-AD), J.C. Smuts 255 (PRE); J.C. Smuts 301 (PRE); 9 miles W. of Sabie (-BA), S. Eliovsen J 27186 (J); Tweefontein Experimental area Sabie distr. (-BA), V. Wager c30 (PRE); Sabie at Henry Glynn's Store (-BB), J. Burtt Davy 1546a (PRE); Sabie Valley (-BB), E.E. Galpin 13727 (PRE); E.E. Galpin Bol 32274 (BOL); Vertroosting Nature Res. 12km. S. of Sabie (-BB), P.J. Muller 2475 (PRE); Between Sabie and Graskop (-BB), Wedermann and Oberdieck 2116 (PRE); Wonder-kloof Nature Res. (-BC), D. Elan-Puttick 255 (PRE); Nelspruit (-BD), Dr. Breyer PRE 55685 (PRE); Dr. Breyer sub TRV 17844 (PRE); Witklip (-BD), J.P. Kluge 410 (PRE, PRU); 3 miles S. of Nelspruit (-BD), L.C. Leach 12109 (PRE); Nelspruit (-BD), L.C.C. Liebenberg 2379 (PRE); Nelspruit (-BD), van Elden 1 (PRE); Nelspruit airport (-BD), M.J. Wells 4270 (NH); Between Waterval Boven and Waterval Onder (-CB), L.L. Britten 4753 (GRA, PRE); Waterval Boven (-CB), J. Burtt Davy 1451 (PRE); Waterval Onder (-CB), Miss Harding sub TRV 5181 (PRE); Waterval Onder (-CB), Jenkins PRE 55702 (PRE); Waterval Onder (-CB), S.A. Morgan 67 (PRE); Waterval Boven (-CB), C.E. Moss 18448 (J); Waterval Boven (-CB), F.A. Rogers STE 13602 (STE); Mashonamini, Airlie, Belfast distr. (-DA), E.J. Cross 86 (NBG); Berlin, Godwane R. (-DA), Davison 91 (PRE); Godwane R. (-DA), Jenkins PRE 55703 (PRE); Starvation Creek Nature Res. (-DA), J.P. Kluge 1183 (PRE); Elands Hoek (-DA), I.B. Pole-Evans H. 17030 (PRE); Langverwag, Sabie (-DB), W.J. Louws 2134 (PUC, STE). 2531 (Komatipoort) : $\pm$ 5km from Hazeyview to Whiteriver (-AA), B. Schrire 663 (NH); Numbi, Kruger Park (-AA), H.P. van der Schijff 722 (PRE); 4 miles W. of Pretoriuskop (-AB), L.E. Codd 6015 (PRE); Roadside near Pretoriuskop (-AB), I.C. Verdoorn 2442 (PRE); Nyamazane Bantu Trust (-AC), E. Buitendag 498 (NBG, PRE); Plaston (-AC), W.E. Holt 42 (NH); W.E. Holt 192 (NH, PRE); W.E. Holt 207 (NH); Karino, Nyamazane (-AC), J. Theron 2351 (PUC); Mtns. overlooking de Kaap valley, Nelspruit distr. (-CA), C. Letty 441 (PRE); Mtn. pass between Nelspruit and Malelane (-CA), P.J. Robbertse 102 (PRU),

Eerste/.....

Eerste geluk No. 16 (-CA), C.H. Stirton 1751 B (PRE); Barberton
(-CC), E.E. Galpin 776 (GRA, NH, SAM); Highland Creek, Barberton
(-CC), E.E. Galpin 778 (PRE); Barberton (-CC), W.E. Holt 42 (PRE);
Barberton (-CC), F.A. Rogers 24054 (PRE); Berea, Barberton (-CC),
G. Thorncroft 402 (PRE); G. Thorncroft sub TRV 2849 (PRE); Barberton
(-CC), G. van Dam PRE 55684 (PRE); Endahwin, Zeist Farm (-CC),
E. v.d. Merwe 106 (PRE); Barberton (-CC), E. Williamson 269 (PRE).
 2730 (Vryheid) : Mooihoek, Piet Retief distr. (-BA), N.J. Devenish
629 (PRE)

SWAZILAND.-2631 (Mbabane) : Nr. Komati R. on rd. Mbabane to Piggs
Peak (-AA), Codd and Muller 329 (PRE); Hawane Falls (-AA), R.H.
Compton 27393 (NBG, PRE); 3 miles SE. of Komati R., Mbabane distr.
(-AA), J.H. Schlieben 9478 (PRE); Endingeni (-AB), Barrett 532
(PRE); Umbeluzi Valley, Mbabane distr. (-AC), R.H. Compton 24876
(NBG); R.H. Compton 31263 (NBG, PRE); Between Bremmersdorp and
McNabs on the road to Lebombo (-BC), J. Burtt Davy 2923 (PRE);
Isateki Beacon, Stegi distr. (-BD), R.H. Compton 26606 (NBG, PRE);
Malkerns Research Stn. (-CA), J.M. Watson 3 (PRE); Kubuta Estate
(-DC), I. Pierce 6 (PRE)

NATAL.-2731 (Louwsburg) : Itala Nature Res., 3 - 4 miles S. of Itala
R. (-AC), Brown and Shapiro 464 (PRE); Louwsburg (-CB), W. van
Rooyen 6 (NU); 'Leeunek', Emyati (-CC), J. Thode STE 3456 (STE);
35km from Nongoma to Vryheid (-CD), B. Schrire 400 (NH); 25km
from Ngome to Vryheid (-DC), B. Schrire 397 (NH). 2732 (Ubombo)
: Nr. Gwalaweni forest (-AC), R.G. Strey 4686 (NH, PRE); Gwalaweni
forest (-AC), A.E. van Wyk 2568 (PRE); 1.5 miles before Ubombo
on Mkuzi - Ubombo rd. (-CA), J.H. Ross 271 (NU). 2831 (Nkandla)
: Umfolozi Game Reserve (-BD), H.J. Schlieben 10183 (PRE); Nr.
Nkandla (-CA), J.P.H. Acocks 12717 (PRE); Eshowe (-CD), J.G. Lawn
305 (NH); Ngoye Forest Reserve (-DC), B.J. Huntley 209 (NH, NU,
PRE); Ubisana Valley, Ngoye Mtn. (-DC), H.J.T. Venter 870 (BLFU);
Ngoye Forest Reserve (-DC), H.J.T. Venter 2300 (ZULU); Ngoye,
Umhlatuzi Bridge (-DD), H.J.T. Venter 744 (ZULU). 2832 (Mtubatuba)
: Hluhluwe Game Reserve (-AA), P. Hitchins 737 (NH, PRE); E.J.
Moll 5265 (NH, PRE); C.J. Ward 2069 (NU, PRE); C.J. Ward 2510
(NH, PRE); Palm Ridge Farm, Hlabisa distr. (-AC), E.R. Harrison
450 (NH, PRE); Dukuduku West (-AC), E.J. Moll 2744 (NH, NU, PRE);
Forestry/Army rd. to Umfolozi R. to St. Lucia channel (-AD), E.S.
Pooley and F. Joubert 2013 (E, K, MO, NU); Richards Bay (-CC),
H.J.T. Venter 5212 (PRU, ZULU). 2929 (Underberg) : N. side of
Kumba/.....

Kumba Mt. Polela distr. (-DB), J.P.H. Acocks 22136 (PRE). 2930 (Pietermaritzburg) : Shafton, Howick (-AC), Mrs. H. Hutton 50 (GRA); Albert Falls (-AD), D.M. Collins 88 (NH, NU); Karkloof (-AD), Dimock Brown 356 (PRE); Pietermaritzburg (-CB), R.W. Adlam SAM 15562 (SAM); Town Hill, Pietermaritzburg (-CB), E.D. Ahrens 13 (NBG); Pietermaritzburg (-CB), R.J. Allsopp 800 (NU); Town Hill, Pietermaritzburg (-CB), M.A. Boulle 8 (NU); Mandeston (-CB), Edwards 6 (NU); Town Bush Valley, Pietermaritzburg (-CB), J.H. Ross 771 (BLFU); Pietermaritzburg (-CB), W.G. Rump NH 20403 (NH); Winterskloof Station (-CB), C.A. Smith PRE 55688 (PRE); Pietermaritzburg (-CB), J. Thode STE 6367 (STE); Boughton, Pieter-maritzburg distr. (-CB), M.J. Wells NU 34142 (NU); Richmond (-CD), J. Wade NU 52896 (NU); Inchanga (-DA), O. Bourquin 127 (NU); F. Frith 141 (J); Table Mountain (-DA), D.J.B. Killick 74 (PRE); Nagle Dam (-DA), J.M. Lovell PRE 55698 (PRE); Table Mountain (-DA), A.P.D. McClean 147 (PRE); Nagle Dam (-DA), M.J. Wells 1111 (NU, PRE); Inanda (-DB), J.M. Wood 802 (PRE); Bothas Hill (-DC), A.P.D. McClean 129 (PRE); Shongweni Dam (-DC), J.W. Morris 786 (NH, NU, PRE); Shongweni (-DC), J.H. Ross 780 (NU); Manors (-DD), T.A. Coleman 66 (NH); Pinetown (-DD) Dohse and Lindahl 104 (NH, PRE); Krantzkloof (-DD), W. Haygarth STE 214 (STE); Gillitts (BD), O.M. Hilliard 1325 (NH, NU); J.M. Macgregor 55 (NU); Umlaas Filters (-DD), B.D. Schrire 484 (NH); Sarnia Beacon Hill (-DD), C.J. Ward 7591 (PRE); Northdene, nr. Durban (-DD); J.M. Wood 802 (BOL); J.M. Wood 1036 (BOL, SAM); Palmiet (-DD), J.M. Wood 7402 (PRE); Durban (-DD), J.M. Wood 9992 (NH); Pinetown (-DD), J.M. Wood NH 1491 (NH). 2931 (Stanger) : 25 miles Tongaat to Wartburg (-AC), E.J. Moll 1527 (NH, NU, PRE); Tugela Beach rd., 1st Red Hill (-AB/BA), S.M. Johnson 368 (NBG); Durban (-CC), Jenkins sub TRV 7077 (PRE); J.M. Wood 802 (SAM). 3030 (Port Shepstone) : 10km from Highflats on rd. to Umzinto (-AC), B. Schrire 872 (NH); Ellingham, 6 miles inland of Umkomaas (-BA), J.H. Ross 85 (NU); Amanzimtoti (-BB), E. Wilson 20 (NU); Park Rynie (-BC), Indian collector NH 17731, sub TRV 34012 (NH, PRE), Ifafa, Umgaye flat; H. Rudatis 392 (STE); Vernon Crookes Nature Reserve (-BC), B.D. Schrire 857 (NH); B.D. Schrire 859 (NH); Port Shepstone (-CB), Dimock Brown 482 (PRE); Uvongo, Nordens Farm (-CB), R.G. Strey 9721 (NH, PRE); Southbroom (-CD), B.D. Schrire 295 (NH). 3130 (Port Edward) : Port Edward (-AA), H.B. Nicholson 236 (NH)

TRANSKEI.-3029 (Kokstad) : Clydesdale (-BD), W. Tyson 1440 (PRE, SAM, STE); W. Tyson 2046 (SAM). 3129 (Port St. Johns) : Mlengana betw./....

betw. Umtata and Port St. Johns (-CA), H.G. Flanagan 2534 (PRE, SAM); Isinuka (-CB), Bolus 8885 (BOL); 73,2km from Umtata on rd. to Port St. Johns (-CB), N. Grobbelaar 2310 (PRU); West Gate, Port St. Johns (-DA), D.M. Comins 1948 (GRA, PRE); Nr. Port St. Johns (-DA), H.G. Flanagan 2571 (PRE). 3228 (Butterworth) : Kentani distr. and at Cats Pass (-AD), A. Pegler 697 (BOL, PRE); The Haven (-BB), J.L. Gordon-Gray 1372 (NU); Msendo Halt, between Mpozolo school and Mendu, Willowvale distr. (-BB), R. Wood 156 (NU)

This species is found most frequently as a suffrutex or subshrub up to 3m in mixed woodland or bushveld, along forest margins, in open grassland or as a ruderal along roadsides or in other disturbed areas; from 0 - 2000m. It is also occasionally associated with streambanks, vleis or swampy areas. Flowering occurs between November and May.

P. hookeri var. hookeri occurs widely in tropical and southern Africa, Madagascar, Mauritius and Reunion.

6.1.3. Alysicarpus

Alysicarpus Desv., J. Bot., ser. 2, 1 : 120 t.4.f.8. (1813) nom.
conserv.; DC., Prodr. 2 : 352 (1825); Harv. in Harv. and Sond., Fl.
Cap. 2 : 230 (1862); Benth. in Benth. and Hook.f., Gen. Pl. 1 (2)
: 522 (1865); Harv., Gen. : 82 (1868); Bak. in Oliv., Fl. Trop.
Afr. 2 : 169 (1871) and in Hook.f., Fl. Br. Ind. 2 (4) : 157 (1876);
Hutch. and Dalz., Fl. W. Trop. Afr. 1 : 418 (1928); Bak.f., Leg.
Trop. Afr. : 341 (1929); Burtt Davy., Fl. Pl. Tvl. 2 : 427 (1934);
Phill., Gen. ed 2 : 419 (1951); J. Leonard in Bull. Jard. Bot. Brux.
24 : 84 (1954) and in Fl. Congo Belge 5 : 223 (1954); Hepper in Fl.
W. Trop. Afr. ed 2, 1 : 586 (1958); Hutch., Gen. Fl. Pl. 1 : 482
(1964); Torre in Consp. Fl. Angol. 3 : 234 (1966); Schreiber in Prodr.
Fl. SW. Afr. 60 : 13 (1970); Verdc., Fl. Trop. E. Afr., Legum. -
Papil. : 491 (1971) and in Kirkia, for Fl. Zamb. 9, (2) : 544 (1974);
Dyer, Gen. 1 : 264 (1975); Compton, Fl. Swazi. : 273 (1976); Dillon
in Ann. Mo. Bot. Gdn. 67 : 548-549 (1980). Type species : A. bupleuri-
folius (L.) DC. (Hedysarum bupleurifolium L.)

Hedysarum L, Sp. Pl. : 745 (1753) pro parte

Fabricia Scop., Introd : 307 (1777); Kuntze, Rev. Gen. Pl.
1 : 181 (1891); Taub. in Pflanzenfam. III, 3 : 329 (1894)

Annual or perennial, erect to decumbent herbs and suffrutices. Stems
one to many, often freely branching, slender, flexous and finely
grooved, with many short internodes. Leaves 1 - foliolate, very
rarely 3 - foliolate. Stipules conspicuous, persistent, scarious,
free or connate, erect, acuminate and striate. Petiole sulcate,
winged. Leaflets characteristic with usually marked reticulate vena-
tion; bluish to grey-green, subcoriaceous, stipellate. Pseudoracemes
usually elongate, spike-like, mostly terminal and leaf-opposed, rarely
paniculately branched; rhachis often densely flowered, flowers in
pairs; bracts in two series, bracteoles absent. Calyx glumaceous,
persistent, striate, appearing 4 - lobed, the lobes subequal, the
upper slightly bifid representing 2 partly fused sepals. Corolla
small, pink to purple or orange - apricot, standard with 2 conspicuous
appendages present as small longitudinal folds near the base. Style
filiform, curving upwards distally, often incrassated at point of
flexure with erect part thicker than the rest. Fruit usually held
near erect, linear-oblong, mostly constricted between several indehi-
scent articles; articles subcylindrical or rounded often with raised
reticulation./.....

reticulation. <u>Seeds</u> subglobose, hilum minute. 2n = 16.

<u>Alysicarpus</u> Neck., Elem. Bot. 3 : 15 (1790), according to ICBN Art. 20 is not to be treated as a generic name unless it has been published as such by a subsequent author. In Stafleu (1967) the following appears, "Since Necker designated this category as 'species', the monomial names (which are in many cases the generic names of previous authors) are to be regarded as unitary designations of species and hence to be regarded as not validly published." The name <u>Alysicarpus</u> Desv. has been conserved according to the dicta in Jeffrey, <u>Biological Nomenclature</u>, ed 2 : 64 - 65 (1977).

<u>Alysicarpus</u> gets its name from the Greek, 'halysis' which means chain and 'karpos' meaning fruit, the pods are moniliform with the joints in chain formation.

Key to Alysicarpus

Fruit with straight margins, not constricted between articles; calyx lobes narrow, sharply acuminate, not at all overlapping at the base.

<u>A. vaginalis</u>

Fruit moniliform, strongly constricted between articles; calyx lobes lanceolate to ovate - lanceolate, slightly to conspicuously overlapping at the base.

Articles smooth; leaves coriaceous with very prominent reticulate venation.

<u>A. zeyheri</u>

Articles with obvious, transverse ridge sculpturing; leaves subcoriaceous with reticulate venation only slightly prominent:

Calyx lobes 0,8 - 1,5mm wide, slightly overlapping and imbricate initially, not so in fruit; sepals with white cilia.

<u>A. glumaceus</u>

Calyx lobes 1,5 - 2,5mm wide, conspicuously overlapping, imbricate, rounded or subcordate at the base; sepals with white or brown cilia; inflorescence often short, compact; fruit only partially exserted from calyx.

6.1.3.1. **Alysicarpus vaginalis** (L.) DC., Prodr. 2 : 353 (1825);
Bak. in Oliv., Fl. Trop. Afr. 2 : 170 (1871) pro parte; Hutch. and
Dalz. Fl. W. Trop. Afr. 1 : 419 (1928) pro parte; Bak.f., Leg. Trop.
Afr.: 342 (1929) pro parte; Robyns, Fl. Parc Nat. Alb. 1 : 331 (1948);
J. Leonard in Bull. Jard. Bot. Brux. 24 : 84 (1954) and in Fl. Congo
Belge 5 : 224, fig 13/A (1954); Hepper in Fl. W. Trop. Afr. ed 2,
1 : 587 (1958); Torre in Consp. Fl. Angol. 3 : 234 (1966); Verdc.,
Fl. Trop. E. Afr. Legum. - Papil. : 493, fig 71/A (1971) and in Kirkia,
for Fl. Zamb. 9, (2) : 546 (1974); Compton, Fl. Swazi. : 273 (1976).
Type : Ceylon, Hermann (BM-HERM, 1 : 27, 59, syn.)

Hedysarum vaginale L., Sp. Pl. : 746 (1753)

var. vaginalis

Verdc. in Kew Bull. 24 : 67 (1970); Fl. Trop. E. Afr., Legum. - Papil.
: 493, fig 71/A (1971); in Kew Bull. 27 : 443 (1972); and in Kirkia,
for Fl. Zamb., 9 (2) : 546 (1974)

Perennial, spreading, decumbent to erect multistemmed herb 10 to
60cm tall, up to 1,0m wide; arising from a long dichotomously branching,
often knotty, woody taproot much divided near the top giving rise
to the stems. Stems woody at the base remaining slender, flexuous;
conspicuously fine grooved; glabrous or sparsely to densely minute
puberulent; freely branching, with many short internodes. Leaves
unifoliolate. Stipules 8 - 15mm long, 1,6 - 2,6mm wide, lanceolate,
acuminate; glabrescent, scarious, striate; oblique, extended at the
base along leaf-opposed margins and fused for lower 2 - 3mm; margin
not ciliate. Petiole 3 - 15mm long; glabrous, sulcate, conspicuously
grooved. Leaflets 5 - 50mm long, 3 - 20mm wide, ovate to narrowly
lanceolate or oblong, elliptic or obovate; apex acute, retuse or
mucronulate; base subcordate or truncate to rounded; sparsely minute
puberulent with a few long tapering hairs or glabrous above, and
moderately puberulent, scattered strigose particularly along the
veins below; margin ciliate, entire; reticulation prominent on both
surfaces, major veins turning upwards and diminishing well before
the margin, lateral veins looping distally; dark green above, paler
below. Petiolules 1,0 - 2,0mm long, glabrous to sparsely pilose;
rugose. Stipels 0,8 - 1,2mm long, 0,2 - 0,4mm wide, paired; obliquely
ovate or subulate, similar to stipules. Pseudoracemes elongate to
compact; unbranched, spike-like, usually densely flowered, internodes
shorter than flowers; terminal and leaf-opposed. Rhachis 2,0 - 13cm
long, shiny glabrous to moderately minute puberulent; finely grooved;
terete to slightly angular. Inflorescence bracts 4,0 - 8,5mm long,
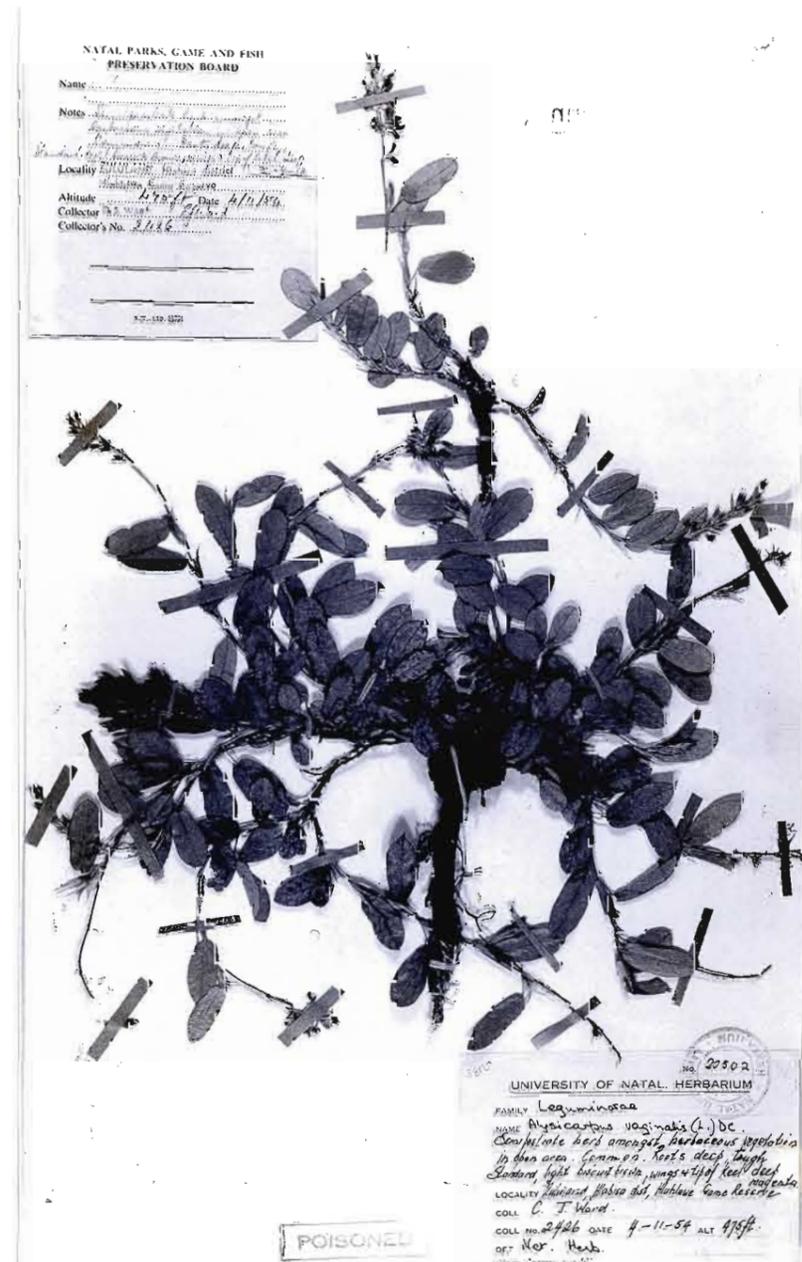
1,5 - 2,5mm wide, ovate - lanceolate to lanceolate - attenuate; glabrous, scarious, striate; margin ciliate; early caducous, each subtending a fascicle of two pedicels. Floral bracts 2,5 - 3,5mm long, 0,6 - 1,5mm wide; trullate (trowel-shaped) to rhomboid, one at the base of each pedicel. Pedicels 5 - 20mm long. Flowers 6,0 - 7,5mm long, variously orange, apricot to maroon-purple, turning blue-violet after tripping. Calyx 4,5 - 6,5mm long, minutely puberulent below, with larger uncinulate hairs on the teeth, scattered bulbous-based glandular hairs also becoming denser on the teeth and stiffly ascending pilose with tapering hairs particularly on the teeth; tube 1,6 - 2,5mm long, narrow; teeth 5, subequal; upper two 2,5 - 3,2mm long, 1,4 - 1,6mm wide at the base, partially connate and bifid for upper 1,6 - 2,0mm; others to 4,0mm long and 1,0mm wide; ovate - lanceolate or lanceolate-acuminate, markedly striate; glumaceous; persistent; margin ciliate; sepals valvate, conspicuously narrow and characteristic of the species. Standard 4,0 - 6,5mm long, 3,5 - 5,5mm wide, orbicular to obovate; apex retuse, narrowing to a short, sharply reflexed claw at the base; two conspicuous folds present at the base, above the claw, each extended on either side of the midline into the hyaline base of the lamina; abaxially pink-buff or pale orange; adaxially apricot flushed with maroon-purple, particularly around two hyaline patches just above the folds. Wings 5,5 - 6,5mm long, up to 1,8mm wide; cultrate, slightly wider distally, apex rounded; auriculate and extended into a short claw at the base; deep maroon-purple becoming orange and hyaline near the claw. Keel blades up to 6,5mm long and 1,5mm wide, broadly oblong, narrowing for the proximal third into a long claw; deeply pocketed with a minute peg of tissue toward the base applied very closely, often adhering to the wings; maroon-purple along upper rim and apically, becoming hyaline below. Staminal sheath 4,5 - 6,0mm long, 1,0mm wide; vexillary stamen free, to 5,5mm long. Gynoecium 4,5 - 5,5mm long; ovary 2,2 - 2,8mm long; densely minute puberulent and stiff ascending pilose at the junction of ovary and style; style 4,0 - 5,0mm long flexed to near erect in distal 1,6mm; distal part of style incrassated. Fruit 0,5 - 2,5cm long, not constricted between articles; well exserted from calyx; articles 4 - 7, subcylindrical, 2,5 - 3,0mm long, 1,5 - 3,0mm wide; reticulation prominent; densely puberulent with isolated longer hairs. Seed 1,6 - 2,0mm long, up to 1,5mm wide, 1,0mm thick; ellipsoidal, smooth, khaki to green or yellow.

Alysicarpus vaginalis occurs in the Transvaal lowveld through Swaziland and Tongaland to the Zululand coast. It occurs as a semi-prostrate
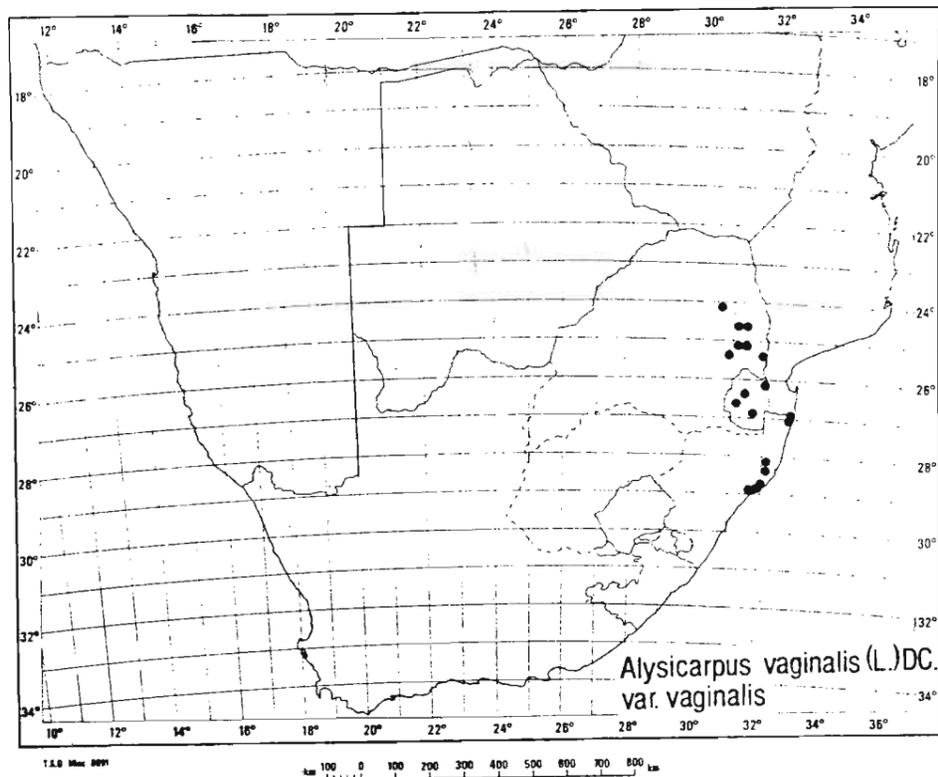
or decumbent trailing herb in the herbaceous vegetation of open areas in bushveld or in grassland up to 800m. More commonly, it becomes a weed of disturbed sandy or rocky soils in these areas i.e. in alluvia, old lands or along roadsides. It flowers nearly all year round, from July to May.

TRANSVAAL.-2430 (Pilgrim's Rest) : Farm Buffelshoek, Selati Distr. (-BA), Hall and Sons PRE 55715 (PRE). 2431 (Acornhoek) : 26km from Bosbokrand on the rd. to Klaserie (-CA), L.A. Coetzer 135 (PRE); Albatros, Manyeleti Game Res. (-CB), G.J. Bredenkamp 1865 (PRE). 2530 (Lydenburg) : Nelspruit (-BD), Dr. Breyer sub TRV 17056 (PRE); Dr. Breyer sub TRV 17857 (PRE); Lowveld Botanic Gardens, Nelspruit (-BD), E. Buitendag 302 (NBG, PRE); Schagen (-BD), L.C.C. Liebenberg 3293 (PRE); Nelspruit (-BD), S.R. Reachmoor PRE 11854 (PRE); F.A. Rogers 25092 (J). 2531 (Komatipoort) : 6 miles N. of Pretoriuskep on rd. to Skukusa (-AA), Codd and de Winter 4964 (PRE); Shabeni, Kruger Park (-AA), H.P. van der Schijff 1396 (PRE); nr. Pretoriuskop, Kruger Park (-AB), Codd and de Winter 4884; H.P. van der Schijff 437 (PRE); P. van Wyk 4712 (PRE); Komatipoort (-BD), Moss and Rogers 517 (J); Moss and Rogers 602 (J)

SWAZILAND.-2631 (Mbabane) : About 7 miles from Manzini on rd. to Mbabane (-AD), B. Clarke 262 (PRE, PRU); Ntendezi, Mankaiana Distr. (-CA), R.H. Compton 28348 (NBG, PRE); Kubuta Estate, 'Htatikulu' Distr. (-DC), Purce PRE 55727 (PRE). 2632 (Bela Vista) : Ndzindza Nature Res., Umbuluzi Gorge (-AA), J. Culverwell 1325 (PRE)

NATAL.-2632 (Bela Vista) : Kosi Estuary (-DD), Vahrmeijer and Tölken 905 (NH, PRE). 2732 (Ubombo) : Umbhanga Neck, Tongaland (-BB), O. Bourquin 371 (NU). 2831 (Nkandla) : Ngoya Mtn. - Ubisana valley (-DC), H.J.T. Venter 774 (ZULU); Mtunzini, Parks Board Reserve (-DD), B. Schrire 1411 (NH). 2832 (Mtubatuba) : Hluhluwe Game Reserve (-AA), O. Bourquin 650 (PRE); C.J. Ward 1796 (NH, NU, PRE); C.J. Ward 2426 (NH, NU, PRE); Gates of camping area, St. Lucia Estuary (-AC), B. Clarke 523 (PRU); Umhlatuzi Lake bluff (-CC), H.J.T. Venter 4593 (BLFU, PRE); Dhangezwa Trig. Beacon, Richards Bay Sanctuary (-CC), C.J. Ward 8805 (PRE)

Alysicarpus vaginalis is widespread throughout the Old World tropics and has been introduced into America where it is reported to have no economic importance except as a noxious weed (Schubert, 1980). However in Africa, Schubert(l.c.) quotes a report that various species including/.....

Alysicarpus vaginalis (L.)DC.
var. vaginalis

including A. vaginalis are used locally as, "a fodder for all kinds
of domestic stock, used fresh, but preferably cut after fruiting
and stored as hay; regarded as an excellent fodder for horses, but
it is said to cause mucous diarrhoea if given in excess in the young
and immature state during the rains." Known also as Alyce clover,
Allen and Allen (1981) state that it is considered as a good cover
crop in Malaysia to prevent erosion on clay soils of rubber plant-
ations. It is readily distinguished from other species of Alysicarpus
by its narrow calyx lobes which never overlap at the base, and its
distinctive pod.

6.1.3.2 *Alysicarpus zeyheri* Harv. in Harv. and Sond., Fl. Cap. 2
: 230 (1862); Bak. in Oliv., Fl. Trop. Afr. 2 : 170 (1871); Hutch.
and Dalz., Fl. Trop. W. Afr. 1 : 419 (1928); Bak.f., Leg. Trop. Afr.
: 343 (1929); Robyns, Fl. Parc Nat. Alb. 1 : 332 (1948); J. Leonard
in Fl. Congo Belge 5 : 228, fig. 13/C (1954); Hepper in Fl. W. Trop.
Afr. ed. 2. 1 : 587 (1958); Torre in Consp. Fl. Angol. 3 : 235 (1966);
Verdc., Fl. Trop. E. Afr., Legum. - Papil. : 494, fig. 71/C (1971)
and in Kirkia, for Fl. Zamb. 9, (2) : 549 (1974). Type : South Africa,
Transvaal, Aapies R., Burke and Zeyher (K , syn. ! , PRE, isosyn.
!)

Although quoted as Burke and Zeyher in Fl. Cap. these are in fact
two simultaneous collections and as such are therefore syntypes (Article
7.7, ICBN, 1978)

Perennial, erect to somewhat spreading multistemmed herb 10 - 80cm
tall; arising from a long woody taproot often knotty and much divided
near the top giving rise to the stems. Stems woody at the base either
aerial, remaining slender, flexuous, conspicuously fine grooved,
often compressed or angular; moderately to densely minute puberulent
and scattered pilose; or rhizomatous giving rise to erect aerial
stems. Leaves unifoliolate. Stipules 6 - 25mm long, 2,5 - 4,2mm
wide; lanceolate - attenuate; glabrous or minutely puberulent; scarious,
striate; oblique, extended at the base along leaf-opposed margins;
margin ciliate. Petiole 1,5 - 8,5mm long, channel slightly winged
distally; minutely puberulent and scattered pilose below. Leaflets
8 - 80mm long, 2 - 18mm wide; mostly ovate to lanceolate, sometimes
linear or elliptic to orbicular; apex acute to rounded, mucronulate;
base rounded, truncate or slightly cordate; adaxially glabrous or
minutely puberulent along veins; abaxially moderately puberulent
and isolated pilose; margin with occasional appressed cilia, entire;
reticulation particularly prominent on both surfaces; major veins
turning upwards and diminishing well before the margin; lateral veins
looping distally; thick textured, green to grey-green. Petiolules
1,0 - 2,0mm long, pilose, rugose. Stipels 1,6 - 2,4mm long to 0,6mm
wide, paired; subulate, similar to stipules. Pseudoracemes terminal,
leaf-opposed or axillary; spike-like, unbranched; relatively densely
flowered; internodes shorter than flowers. Rhachis 2,5 - 35cm long,
angular; densely puberulent. Inflorescence bracts 5,0 - 14mm long,
2,0 - 5,0mm wide; elliptic to ovate-rhomboid; apex attenuate; asymme-
trical; moderately puberulent; glumaceous, striate; green often purple
distally; margin ciliate; early caducous, each subtending a fascicle
of 2/.....

Alysicarpus zeyheri Harv.
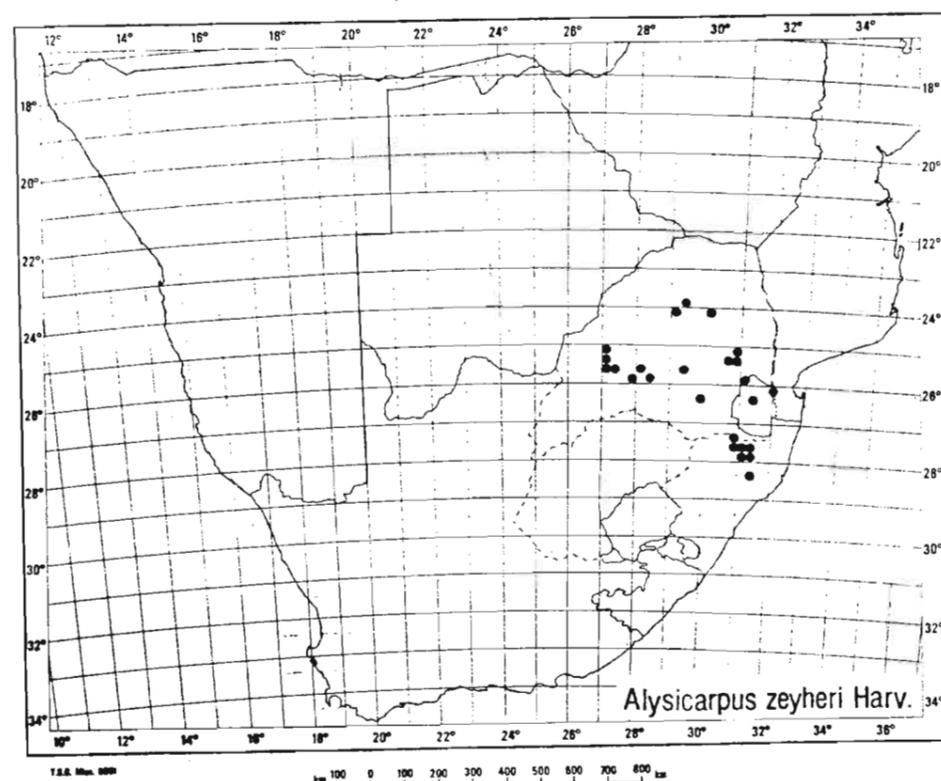
of 2 pedicels. Floral bracts 2,0 - 8,0mm long to 1,8mm wide, linear, one at the base of each pedicel on either side of the inflorescence bract. Pedicels 1,0 - 5,0mm long, densely pubescent and glandular haired. Flowers 8,0 - 9,5mm long variously cream, apricot, pink-buff flushed red to magenta. Calyx 7,0 - 9,0mm long; tube to 2,0mm long, narrow, densely puberulent, glandular haired; teeth 5,5 - 7,0mm long, four; upper tooth of two connate sepals, to 2,6mm wide; bifid for upper 1,0mm; lower to 2,0mm wide, keeled, laterals 1,0 - 1,5mm wide; ovate - lanceolate, acuminate; densely puberulent and scattered with long brown hairs; margins conspicuously ciliate; glumaceous, striate, persistent; splayed out in open flower; lobes imbricate at the base in fruit. Standard 6,5 - 8,5mm long, 5,5 - 8,5mm wide; broadly orbicular to obovate; apex retuse; narrowing to a short (not markedly reflexed) claw at the base; two conspicuous folds present at the base above the claw, each extended on either side of the midline into the hyaline base of the lamina; salmon-pink, pink-buff or apricot often flushed reddish or light magenta, two yellow streaks on either side of midline towards the base just above folds. Wings 7,5 - 9,5mm long, to 2,0mm wide; broadly cultrate, slightly wider distally, apex rounded; auriculate near base, and extended into a short claw; magenta, becoming hyaline near the claw. Keel blades to 9,0mm long and 2,0mm wide distally; magenta or reddish along upper rim and apically, hyaline below. Staminal sheath to 7,5mm long, vexillary stamen partly connate; to 7,0mm long. Gynoecium 7,0 - 8,5mm long; ovary to 3,2mm; style to 5,5mm long flexed to 45° in distal 2,0mm. Fruit 0,7 - 1,5cm long, well exserted from calyx, moniliform; articles 2 - 6; 2,5 - 3,0mm long, to 2,8mm wide; oblong-elliptic to sub-orbicular; smooth; densely puberulous. Seeds 1,5 - 2,0mm long, 1,2 - 1,5mm wide, to 1,0mm thick; oblong; pale yellow - brown.

Alysicarpus zeyheri occurs in the Transvaal and northern Natal at altitudes between 900 and 2400m. It is found from Pietersburg south-wards to Pretoria and from Pretoria westwards to Zeerust in mixed and sourish mixed bushveld. East of Pretoria it occurs in the mountain sourveld and lowveld sourbushveld from Lydenburg, Nelspruit and Barber-ton down through Swaziland; and also in the sandy highveld, Piet Retief sourveld and related veld types from near Middleburg through Ermelo to Louwsburg and Mahlabathini in the south.

TRANSVAAL.-2329 (Pietersburg) ; Pietersburg (-CD), H. Bolus 11074 (BOL)/.....

(BOL); Pietersburg Nature Res. (-CD), Bredenkamp and van Vuuren 139 (PRE). 2429 (Zebediela) : Percy Fife Nature Res. (-AA), B.J. Huntley 1502 (PRE); 2430 (Pilgrim's Rest) : The Downs, Pietersburg Div. (-AA); F.A. Rogers 21921 (PRE). 2526 (Zeerust) : Zeerust (-CA), R. Leendertz sub TRV 11298 (PRE). 2527 (Rustenburg) : Buffelskloof Farm, Pilanesberg (-AA), G. Germishuizen 551 (PRE); Houwater, on Houwater Farm (-AC), G. Germishuizen 654 (PRE); Tierkloof on Baviaanskrans Farm, Rustenburg Distr. (-CA), G. Germishuizen 388 (PRE); Rustenburg (-CA), R. Leendertz sub TRV 9754 (PRE); C.E. Moss 13214 (J); Farm Waagfontein, 20km. from Rustenburg on rd. to Pretoria (-CB), L.A. Coetzer 103 (PRE); Scheerpoort, Brits Distr. (-DD); D. van Vuuren 531 (NH). 2528 (Pretoria) : Aapies R. (-AA), Burke PRE 9323 (PRE); Zeyher SAM 32864 (SAM); Nr. Pretoria, Skinners Court (-CA), J. Burtt Davy 804 (PRE); Pretoria (-CA), R. Leendertz 399 (BOL, J, PRE); Wonderboom Res. (-CA), J.E. Repton 2767 (PRE); 14 miles from Pretoria on Hartebeespoort Dam rd. (-CA), H.P. van der Schijff 5291 (PRE (split collection), PRU); Silverton, Pretoria (-CB), C.E. Moss 8490 (J); 1,9 miles from Tygerpoort to Rayton (-CD), B. Clarke 131 (PRU). 2529 (Witbank) : Middelburg, Mapochsdrift (-CB), C.J. du Plessis 1136 (PRE, PRU); Buffelsvlei, Middelburg (-CD), H. Rudatis 131 (STE). 2530 (Lydenburg) : 2.2km from Lydenburg on rd. to Dullstroom (-BB), B. Schrire 668 (NH); Wonderkloof Nature Res. (-BC), D. Elan-Puttick 246 (PRE); Nelspruit (-BD), Dr. Breyer PRE 55731 (PRE); Dr. Breyer PRE 55733 (PRE); Nr. Nelspruit (-BD), L.C.C. Liebenberg 2788 (PRE). 2531 (Komatipoort), Plains around Barberton (-CC), E.E. Galpin 1158 (GRA, NH, PRE, SAM); Barberton (-CC), R. Pott 5345 (PRE). 2629 (Bethal) : Breten, Ermelo Distr. (-BD), M. Steyn 995 (NBG). 2730 (Vryheid) : Commondale Stn (-BD), J.P.H. Acocks 13160 (PRE)

SWAZILAND.-2631 (Mbabane) : Hill near 'Loch May' nr. Bremersdorp (-AD), H. Bolus 11829 (BOL, PRE). 2632 (Bela Vista) : Blue Jay Ranch, 3 miles s. of w. entrance to Umbuluzi Gorge (-AA), J. Culverwell 1183 (PRE)

NATAL.-2730 (Vryheid) : Warmbaths (-DB), R. Leendertz sub TRV 5985 (PRE). 2731 (Louwsburg) : 18km. from Nkongolane on rd. to Louwsburg (-CA), C.N. Buthelezi 150 (NH); 21km from Louwsburg on rd. to Nongoma (-CB), B. Schrire 1120 (NH); Nr. Gluckstadt Mission (-CC), R.G. Strey 9115 (NH, PRE); Gweloberg, Ngome (-CD), L.C.C Liebenberg 5312 (NH). 2831 (Nkandla) : Zondela, Mahlabatini Distr. (-AD), J. Gerstner NH 33781 (NH)

It is an erect to spreading herb of open areas in bushveld or in grassland in sandy, rocky or gravel soils, and often occurs in grazed, seasonally burned grassland, along roadsides or railway lines and in old lands. It flowers from October through to April.

Watt and Breyer-Brandwijk (1962) report A. zeyheri as a South African remedy for impotence while Allen and Allen (1981) quote a reference in which the species has been used as a snake-bite remedy in some African communities. It is readily distinguished from other species of Alysicarpus on leaf characteristics and by its distinctive pod.

6.1.3.3. _Alysicarpus rugosus_ (Willd.) DC., Prodr. 2 : 353 (1825);
Bak. in Oliv., Fl. Trop. Afr. 2 : 171 (1871) pro parte; J. Leonard
in Bull. Jard. Bot. Brux. 24 : 92, fig. 12 (1954) and in Fl. Congo
Belge 5 : 229 (1954); Hepper in Fl. W. Trop. Afr. ed 2, 1 : 587 (1958);
Lind and Tallentire, Fl. Pl. Uganda : 82 (1962); Torre in Consp.
Fl. Angol. 3 : 236 (1966); Schreiber, in Prodr. Fl. SW. Afr. 60 :
14 (1970); Verdc., Fl. Trop. E. Afr., Legum. - Papil. : 495 (1971)
and in Kirkia, for Fl. Zamb. 9, (2) : 550 (1974); Compton, Fl. Swazi.
: 273 (1976). Type: Guinea, _Isert_ in Herb. Willdenow (B, holo.)

Hedysarum rugosum Willd. in L., Sp. Pl. ed. 4, 3 (2) :
1172 (1802)

Alysicarpus violaceus (Forssk.) Schindl. in Feddes Repert.
21 : 13 (1925), pro parte; Hutch. and Dalz., Fl. W. Trop.
Afr. 1 : 419 (1928), pro parte, non _Hedysarum violaceum_
Forssk. nec _H. violaceum_ L.

Erect, prostrate or ascending robust annual to 1,5m tall or multi-
stemmed suffruticose perennial herb 0,2 to 1,0m tall or wide; arising
from a long dichotomously branching woody taproot producing many
horizontal, cord-like roots and much divided near the top giving
rise to the stems. _Stems_ woody at the base (occasionally also so
in the annual), robust and erect or slender and flexuous; conspicuously
fine grooved; glabrous or sparsely to densely minute puberulent,
often pilose; freely branching, with many short internodes. _Leaves_
unifoliolate, rarely mixed with trifoliolate. _Stipules_ 5 - 30mm long,
1,0 - 4,0mm wide; lanceolate - attenuate; glabrescent or minutely
puberulent; scarious, striate, oblique, extended at the base along
leaf-opposed margins, sometimes fused partially along this margin;
margin ciliate near apex. _Petiole_ 0,2 - 1,6cm long, minutely puberulent
also with scattered glandular hairs and isolated long tapering hairs;
winged on either side of adaxial channel. _Leaflets_ 0,6 - 11cm long,
0,2 - 2,1cm wide; exceedingly variable in shape, nearly orbicular
to ovate, ovate - lanceolate, linear - attenuate or oblong, rarely
obovate, apex acute less often rounded, mucronulate; base subcordate,
truncate to rounded; adaxially glabrous or minute puberulent, occasion-
ally sparsely pilose; abaxially more densely hairy than above particu-
larly along veins; margin with appressed cilia, entire; reticulation
prominent on both surfaces, more so below; major veins turning upwards
and diminishing well before margin; lateral veins looping distally;
deep blue-green above, and paler light green along midrib. Petiolules

1,0/.......

1,0 - 2,0mm sparsely pilose, rugose. Stipels 0,7 - 1,2mm long, paired, subulate, similar to stipules. Pseudoracemes axillary, terminal or leaf-opposed, unbranched, elongate or compact, spike-like, lax or mostly densely flowered, internodes shorter than flowers. Rhachis 3,0 - 20 (30)cm long; angular, finely grooved, densely uncinulate puberulent. Inflorescence bracts 4,0 - 10,0mm long, 2,0 - 3,0mm wide; elliptic to ovate - rhomboid; apex attenuate; glabrous to puberulent particularly near the apex; glumaceous, striate, green becoming purple distally; margin ciliate, early caducous; each subtending a fascicle of two pedicels. Floral bracts lacking (have been reported occasionally, linear 1,0 - 2,5mm long). Pedicels 2,0 - 6,5mm long, vesture of dense glandular hairs. Flowers 6,0 - 7,5mm long variously pink-buff, magenta to purple turning blue-violet after tripping. Calyx 6,0 - 7,2mm long; tube 1,2 - 1,5mm long, narrow, puberulent and densely glandular haired; teeth 5,5 - 6,0mm long, four, the upper of two connate sepals 2,0 - 2,2mm wide, bifid for upper 0,5 - 2,0mm; lower 1,8 - 2,0mm wide, laterals to 1,5mm wide; ovate-lanceolate to lanceolate-acuminate; scattered glandular hairy and puberulent, lower sepal with dark tapering hairs along middle, margin ciliate; markedly striate, glumaceous, persistent; splayed out in flower, lobes imbricate at base in fruit. Standard 6,0 - 7,5mm long, 6,0 - 8,0mm wide, broadly orbicular to obovate, apex retuse; narrowing to a short (not markedly reflexed) claw at the base; two conspicuous folds present above the claw, each extended on either side of the midline into the hyaline base of the lamina; salmon-pink, pink-buff to light reddish-purple, two darker flushes on either side of the midrib in the middle towards the base above the folds. Wings 6,0 - 7,5mm long, to 2,0mm wide; broadly cultrate, rounded at the apex; auriculate near the base and extended into a short claw; magenta becoming hyaline near the claw. Keel blades 5,5 - 6,5mm long, to 1,8mm wide distally, magenta along upper rim and apically (above staminal column), hyaline below. Staminal sheath 4,0 - 5,5mm long, vexillary stamen partly connate, to 4,5mm long. Gynoecium 5,0 - 6,0mm long; ovary 2,0 - 3,1mm long; style to 3,1mm long, flexed to near erect in distal 1,5mm. Fruit 0,5 - 1,5cm long, partially exserted from calyx; moniliform; articles 3 - 6, trans-versely elliptic, 1,0 - 2,0mm long, 1,8 - 3,0mm wide, strongly rugose; puberulent; style persistent, hooked. Seeds to 1,8mm long, squarish, compressed brown to khaki.
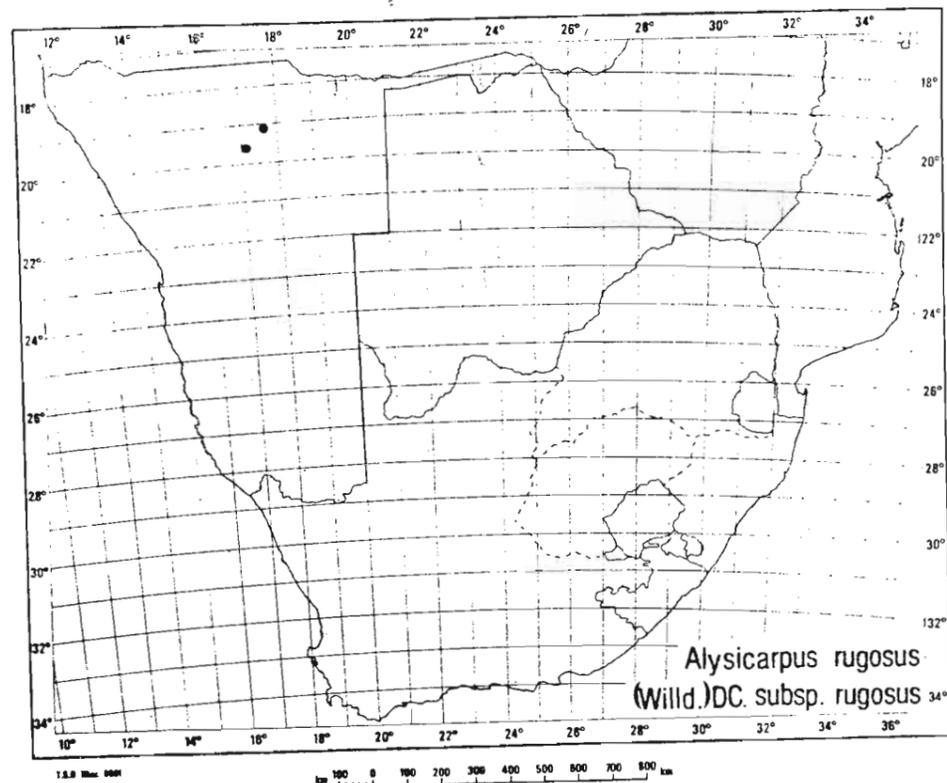
Key to subspecies/.......

Erect annual; calyx lobes with white cilia, S.W.A. only.

....subsp. rugosus

Decumbent, spreading perennial, with many flexuous stems; calyx lobes with brown to orange cilia.

....subsp. perennirufus

subsp. rugosus
J. Leonard in Bull. Jard. Bot. Brux.24 : 92, fig 12 (1954) and in Fl. Congo Belge 5 : 229 (1954)

SOUTH WEST AFRICA.-1917 (Tsumeb) : Grootfontein, rd. Tsumeb-Bobas, Omaramba (-BA), K. Dinter 7628 (BOL, PRE, WIND); Farm Kumkauas (GR 552) (-CA), H. Merxmüller and Giess 30098 (WIND)

subsp. rugosus is only recorded in the Flora area from the Grootfontein district in South West Africa. A specimen Liebenberg 2789 from Barberton in the Transvaal may be subsp. rugosus but it is too underdeveloped to say with any certainty. It is an erect annual in open areas in thornveld savanna or in swamps.

subsp. perennirufus J. Leonard in Bull. Jard. Bot. Brux. 24 : 95 (1954) and in Fl. Congo Belge 5 : 230, fig. 13/D (1954); Torre in Consp. Fl. Angol. 3 : 236 (1966); Verdc., Fl. Trop. E. Afr., Legum. - Papil. : 496 fig. 71/D (1971) and in Kirkia, for Fl. Zamb. 9, (2) : 552 (1974). Type: Congo,Kivu, Rutshuru, Lebrun 9021 (BR, holo., K, iso. !)

Alysicarpus wallichi Wight and Arn., Prodr. Fl. Ind. 1 : 234 (1834); Harv. in Harv. and Sond., Fl. Cap. 2 : 230 (1862)

A. glaber E. Mey., Comm. : 125 (1836). Type : Transkei; between Umzimvubu and Umzikaba R's, Drege (K, iso. ?)

A. violaceus (Forssk.) Schindl., Feddes Repert. 21 : 13 (1925) pro parte; Hutch. and Dalz., Fl. W. Trop. Afr. 1 : 419 (1928) pro parte, non Hedysarum violaceum Forssk. nec H. violaceum L.

Verdc. (1971) notes that intermediates occur between the two subsp. in the flora area of Tropical East Africa. He notes rare examples have been found in the Transvaal.

Alysicarpus rugosus (Willd.)DC. subsp. rugosus

Alysicarpus
rugosus (Willd.) DC.
subsp. perennirufus J. Léonard
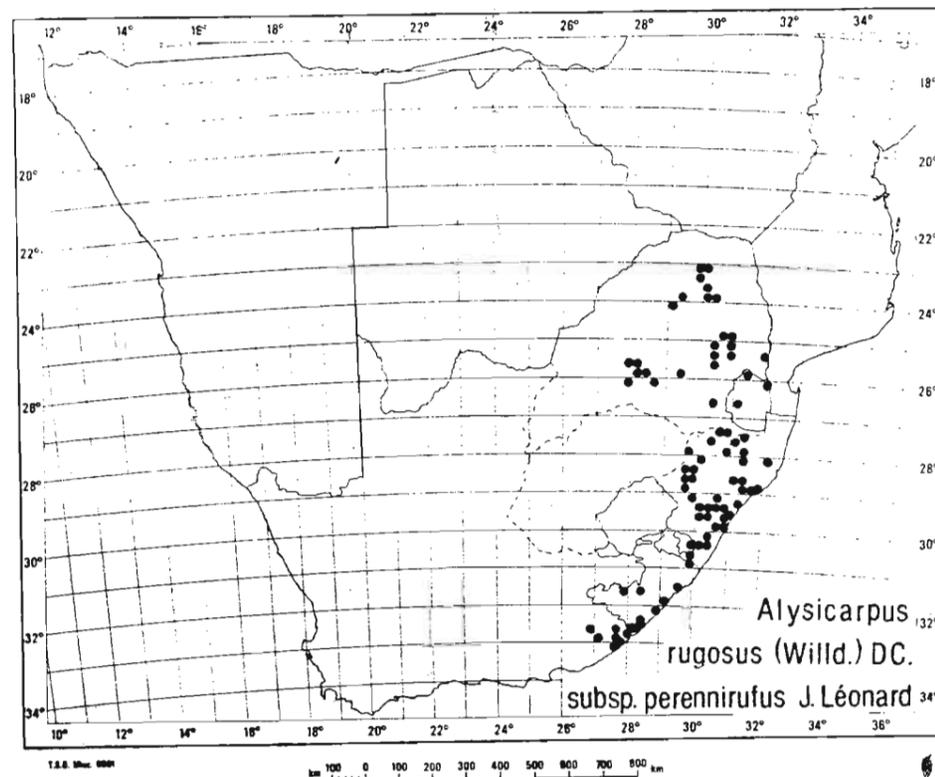
subsp. _perennirufus_ J. Leonard is widespread in the eastern half of the Flora area, from the Transvaal, Swaziland, Natal to the Eastern Cape. In Transvaal it occurs from Louis Trichardt and Tzaneen in the north through Pietersburg and Potgietersrust to Lydenburg and Komatipoort and Swaziland in the south. Westwards it occurs from Belfast and Ermelo through Pretoria to Rustenburg with a slight extension into the higher altitude Bankenveld north of Johannesburg and Potchefstroom. The distribution in Natal is chiefly northern Natal from Newcastle to Pongola (an extension of the range in the southeast Transvaal) through the midlands to the coast. It does not occur further west of a line extending from Bergville, Estcourt and Richmond i.e. into the uplands nor does it occur further north than Hluhluwe in Zululand. Along the coast and adjacent interior, particularly where there are projections inland of valley bushveld, the distribution continues down to East London and inland to Harding, Umtata, Engcoba and the Fort Beaufort District.

TRANSVAAL.-2329 (Pietersburg) : Louis Trichardt (-BB), Dr. Breyer sub TRV 20903 (PRE); Zoekmekaar (-BD), Moss and Rogers 993 (J); Pietersburg Nature Reserve (-CD), Bredenkamp and van Vuuren 293 (PRE). 2330 (Tzaneen) : Valdezia (-AA), A.A. Obermeyer 1144 (PRE); Duiwelskloof, Letaba District (-CA), J.C. Scheepers 176 (PRE, PRU); Tzaneen, below dam wall (-CC), C.H. Stirton 5757 (PRE); Letaba landgoed, Tzaneen (-CD); N. Grobbelaar 323 (PRE, PRU). 2429 (Zebedeïla) : Potgietersrust (-AA), F.A. Rogers 301 (GRA). 2430 (Pilgrim's Rest) : Ohrigstad Nature Reserve (-DC), N. Jacobsen 1588 (PRE); Pilgrim's Rest (-DD), F.A. Rogers 18294 (J). 2527 (Rustenburg) : Hartebeespoort, C.E. Moss 383 (J). 2528 (Pretoria) : Skinners Court, Pretoria (-CA), J. Burtt Davy 811 (PRE); Erf 33, Les Marais, Pretoria (-CA), W.J. Hanekom 1913 (PRE); Reservoir, Pretoria (-CA), A. Leeman 23 (PRE); Pretoria (-CA), R. Leendertz 407 (PRE, SAM); New Muckleneuk, Pretoria (-CA), A.A. Obermeyer 148 (PRE); Wonderboompoort, Pretoria (-CA), Rehmann 4612 (BOL); Wonderboom Reserve (-CA), J.E. Repton 2785 (PRE); Pretoria, bottom of du Toit Street (-CA), C.A. Smith 1451 (PRE); Onderstepoort (-CA), Dr. Theiler PRE 55709 (PRE); Pretoria (-CA), H.P. van der Schijff 5290 (PRE, PRU); 14 miles from Pretoria on Hartebeespoort dam rd. (-CA), H.P. van der Schijff 5291 (PRE); Waterkloof ravine (-CC), A.O.D. Mogg 15604 (PRE); Fountains Valley, Pretoria (-CC), Obermeyer and van Nouhuys sub TRV 27805 (PRE); Fountains Valley, Pretoria (-CC), J.E. Repton 87 (PRE); J.E. Repton 838 (PRE); Waterkloof (-CC), I.C. Verdoorn 135 (PRE); Pretoria, Garsfontein (-CD)/.....

(-CD), L.C.C. Liebenberg 8721 (PRE); Faerie Glen (-CD), S.A.G.P./ S.A.A.B. 1/113 (PRE, PRU). 2529 (Witbank) : Middelburg (-CD), F.A. Rogers 24860 (PRE). 2530 (Lydenburg) : Lydenburg (-AB), F. Wilms 5873 (PRE); Schoemanskloof, between Nelspruit and Machadadorp (-AD), N. Grobbelaar 2, (PRE, PRU); Somerset Farm, Schoemanskloof (-AD), Smuts and Gillett 2214 (PRE); Schoemanskloof, W. end. (-AD), R.G.N. Young A331 (PRE); 2,2km from Lydenburg on road to Dullstroom (-BB), B. Schrire 667 (NH); Schagen (-BD), L.C.C. Liebenberg 3298 (PRE); Machadodorp (-CB), E.E. Galpin 12975 (BOL, PRE); Waterval Boven (-CE), F.A. Rogers 10931 (PRE); F.A. Rogers 14394 (J, PRE). 2627 (Potchefstroom) : Randburgrif, near D.F. Malan rd. (-BB), L.C.C. Liebenburg 8482 (PRE); Little Falls (-BB), M. Pelletier J 30510 (J). 2628 (Johannesburg) : 18 miles S. of Bronkhorstspruit on Delmas rd. (-BA), B. de Winter 7692 (PRE). 2630 (Carolina) : Spitskop, Ermelo distr. (-CB), R. Pott 5073 and sub TRV 15081 (PRE); Athole Pasture Research Stn., Ermelo distr. (-CB), J.H. Preller 139 (PRE)

SWAZILAND.-2531 (Komatipoort) : Piggs Peak (-CD), Dr. Penny Col. Herb. 2388 (PRE). 2631 (Mbabane) : About 7 miles from Manzini on rd. to Mbabane (-AD), B. Clarke 263 (PRU PRE); near Mankaiana (-CA), R.H. Compton 28332 (PRE). 2632 (Bela Vista) : Nzindza Nature Reserve, Umbuluzi Gorge (-AA), J. Culverwell 1196 (PRE)

NATAL.-2729 (Volksrust) : 6km from Newcastle on road to Memel (-DC), C.N. Buthelezi 252 (NH). 2730 (Vryheid) : 'Mooihoek', Piet Retief distr. (-BC), N.J. Devenish 929 (PRE); Paulpietersburg (-BD), C.N. Buthelezi 218 (NH); Dumbe Mtn. Paulpietersburg (-BD), E.E. Galpin 9729 (PRE); Paulpietersburg (-BD), B. Schrire 1320 (NH); Utrecht (-CB), A. Wahl PRE 55723 sub TRV 15525 (PRE); Rd. from Vryheid to Gluckstadt (-DD), B. Schrire 403 (NH). 2731 (Louwsburg) : Itala Nature Reserve (-AD), C.N. Buthelezi 168 (NH); 11km from Nkongolane on rd. to Louwsburg (-CA), C.N. Buthelezi 142 (NH); 12km from Ngome Forest on rd. to Vryheid (-CD), C.N. Buthelezi 114 (NH); Gweloberg, Ngome (-CD), L.C.C. Liebenberg 5308 (NH); 11km W. of Ngome on rd. to Vryheid (-CD), A.A. Mauve 5298 (NH); Rd. between Ngome and Vryheid, Ngotshe Distr. (-CD), K.L. Tinley 751 (NU). 2829 (Harrismith) : Farm "Excelsior", at foot of van Reenens Pass (-BC), M.L. Jacobsz 768 (PRE); M.L. Jacobsz 805 (PRE); Elandslaagte, Kliprivier Distr. (-BD), N.E. Shirley 304 (NU); Spionkop area (-DA), E.A. van Rensburg 2 (NU), Colenso (-BD), P.B. Dixon 21 (NU); Ladysmith (-DB), F.A. Rogers sub TRV 5165 (PRE)/.....

(PRE); Grantleigh (-DC), <u>K.F. King 57</u> (PRE); <u>K.F. King 64</u> (PRE).
2830 (Dundee) : Dundee (-AA), <u>N.E. Shirley NU 32878</u> (NU); Dundee
(-AA), <u>D. Gordon Truscott 7a</u> (PRE). 2831 (Nkandla) : Mahlabatini
(-AB), <u>J. Gerstner 4209</u> (NH); Nkandla Forest Reserve (-CA), <u>H.J.T.</u>
<u>Venter 3436</u> (ZULU); Melmoth (-CB), <u>H.M.L. Forbes 738</u> (NH); Mfulazane
near Melmoth (-CB), <u>A.O.D. Mogg 6143</u> (PRE); Eshowe (-CD), <u>J.G.</u>
<u>Lawn 1120</u> (NH); N. of Umlalazi R., Eshowe (-CD), <u>J.G. Lawn 1908</u>
(NH); Hlinza Forest, Eshowe dist. (-CD), <u>R.G. Strey 4808</u> (NH);
Hamewith, Mtunzini distr. (-DC), <u>A.O.D. Mogg 5960</u> (NH, PRE); Univ.
of Zululand, Ngoye (-DD), <u>H.J.T. Venter 1699</u> (NH, PRE); Empangeni
(-DD), <u>H.J.T. Venter 1969</u> (PRE). 2832 (Mtubatuba) : Godeni, Hluhlwe
Game Reserve (-AA), <u>P.M. Hitchins 866</u> (PRE); Hluhluwe Game Reserve
(-AA), <u>C.J. Ward 1512</u> (NH, PRE). 2929 (Underberg) : Estcourt
(-BB), <u>Acocks 9872</u> (NH, PRE). 2930 (Pietermaritzburg) : Howick
(-AC), <u>E.J. Moll 1057</u> (NU, PRE); Outside Howick on Karkloof rd.
(-AC), <u>B. Schrire 270</u> (NH); Albert Falls (-AD), <u>D.M. Comins 436</u>
(NU); Impolweni (-AD), <u>W.G. Rump NH 20290</u> (NH); <u>W.G. Rump NH 20328</u>
(NH); 8 miles from Greytown on Muden rd. (-BA), <u>O.M. Hilliard</u>
<u>1943</u> (NU); Greytown (-BA), <u>J. Wylie NH 28026</u> (NH, PRE); 20km from
Greytown to P.M.burg (-BC), <u>C.H. Stirton 5190</u> (PRE); 2 miles W.
of Noodsberg (-BD); <u>E.J. Moll 1505</u> (NH, NU, PRE); Midmar Dam
(-CA), <u>B. Schrire 269</u> (NH); Richmond rd. near P.M.burg (-CB),
<u>W.F. Barker 4382</u> (NBG); Scottsville, P.M.burg (-CB), <u>O. Bourquin</u>
<u>103</u> (NU); Cedara Agricultural College (-CB), <u>Coetzee NH 35014</u>
(NH); Ukilinga hill behind Exp. farm. P.M.burg (-CB), <u>N. Cuthbert</u>
<u>NU 52685</u> (NU); Town Hill, P.M.burg (-CB), <u>B.S. Fisher 743</u> (NH,
NU); P.M.burg. (-CB), <u>M.S. Frankish 66</u> (NU); Bisley (-CB), <u>E.J.</u>
<u>Moll 1686</u> (NU, PRE); Inanda (-DB), <u>J.M. Wood 274</u> (NH); Key Ridge
(-DC), <u>C.H. Stirton 5076</u> (PRE); <u>C.H. Stirton 10516</u> (NH); Gillitts
(-DD), <u>O.M. Hilliard 1848</u> (NU); Gillitts (-DD), <u>R. Schlechter</u>
<u>3221</u> (BOL, PRE). 2931 (Stanger) : Mvoti R. mouth (-AD), <u>E.J.</u>
<u>Moll 2595</u> (NU, PRE); Umhlanga (-CA), <u>J.M. Wood 6091</u> (BOL); Nr.
Phoenix (-CA), <u>R. Schlechter 3121</u> (PRE); 3029 (Kokstad) : 'Rooival',
Harding (-DB), <u>O.M. Hilliard 1259</u> (NU); 'Bedford', Harding (-DB),
<u>Fay Lennox NU 28057</u> (NU). 3030 (Port Shepstone) : McDonald, Dumisa,
Alexandra Cty. (-AB), <u>H. Rudatis 1365</u> (STE); <u>H. Rudatis 1729</u> (PRE);
10km from Highflats to Umzinto (-AC), <u>B. Schrire 271</u> (NH); B.
<u>Schrire 874</u> (NH); Allerton (-DA), <u>A.O.D. Mogg 6603</u> (PRE)

TRANSKEI.-3029 (Kokstad) : Clydesdale (-BD), <u>W. Tyson 1196</u> (PRE,
SAM); <u>W. Tyson 1441</u> (SAM, STE); <u>W. Tyson 2002</u> (BOL, NBG, PRE);
86,5km from Lusikisiki to Port Edward (-DD), <u>N. Grobbelaar 2320</u>
(PRU)/.....

(PRU). 3127 (Lady Frere) : Nr. Engcoba, Mgwali R. (-DB), H.G. Flanagan 2802 (PRE). 3128 (Umtata) : Baziya (-CB), R. Baur 572 (SAM). 3129 (Port St. Johns) : Coffee Bay (-CC), W. Tyson 23 (GRA, NH, PRE); West Gate, Port St. Johns (-DA), E.E. Galpin 3408 (BOL, PRE). 3228 (Butterworth) : Columba, Kentani distr. (-AD) A. Pegler 163 (PRE); The Haven (-BB), J.L. Gordon-Gray 1128 (NU); Nytura Garden enclosure, Kentani distr. (-CB), A. Pegler 1459 (PRE); Nr. Kei mouth (-CB), H.B. Flanagan 416 (GRA, PRE, SAM)

CISKEI.-3226 (Fort Beaufort) : Hogsback (-DB), M.H. Giffen 1070 (PRE); M.H. Giffen 1096 (PRE). 3227 (Stutterheim) : Pirie (-CC), T.R. Sim 19436 (PRE)

CAPE.-3227 (Stutterheim) : 'Stockton Farm', Kei rd. (-DA), D.M. Comins 1779 (GRA, PRE); Kabousie (-DA), H. Hutton 1031 (GRA, NBG); Kei rd. (-DA), G.A. Ranger 302 (PRE); Berlin (-DC), W.F. Barker 2742 (BOL, NBG). 3228 (Butterworth) : 1km along turnoff to Morgans Bay from rd. betw. Komgha and Haga Haga (-CA), B. Clarke 470 (PRE, PRU); Haga Haga (-CC), R.P. Ellis 2616b (PRE); Kwenqura R. mouth (-CC), E.E. Galpin 5779 (PRE). 3327 (Peddie). East London (-BB), G. Rattray 616 (GRA); East London, beach (-BB), T.R. Sim 20175 (NU, PRE); East London (-BB), Thode STE 6662 (STE)

6.1.3.4. Alysicarpus glumaceus (Vahl) DC., Prodr. 2 : 353 (1825);
Robyns, Fl. Parc Nat. Alb. 1 : 332 (1948) pro parte; J. Leonard,
in Bull. Jard. Bot. Brux. 24 :98, fig.13 (1954) and in Fl. Congo
Belge 5 : 231, fig.13/E (1954); Hepper in Fl. W. Trop. Afr. ed 2,1
: 587 (1958); Lind and Tallentire, Fl. Pl. Uganda : 82 (1962); Torre,
in Consp. Fl. Angol. 3 : 236 (1966); Verdc., Fl. Trop. E. Afr., Legum.
- Papil. : 497, fig.71/E (1971) and in Kirkia, for Fl. Zamb. 9,
(2) : 553 (1974). Type : Yemen, Surdūd, Forsskål (C, holo.)

Hedysarum violaceum Forssk., Fl. Aegypt. - Arab. : 136 (1775)
non L., nom illegit. Type as for Alysicarpus glumaceus

H. glumaceum Vahl, Symb. Bot. 2, Add. et Corrig. : 106 (1791)

Alysicarpus violaceus (Forssk.) Schindl. in Feddes Repert.
21 : 13 (1925) pro parte; Bak.f., Leg. Trop. Afr. : 342 (1929)
pro parte

subsp. glumaceus var. glumaceus

Verdc. in Kew Bull. 24 : 68 (1970); Fl. Trop. E. Afr., Legum. - Papil
: 497, fig.71/E (1971); and in Kirkia, for Fl. Zamb. 9, (2) : 553
(1974)

Note. Only the typical taxon is found in the Flora area.

Annual, erect or occasionally procumbent herb 0,1 - 1,0 (1,5)m tall;
arising from a slender taproot. Stem single but branching freely
above, becoming woody below; with many short internodes; slender,
conspicuously fine grooved; minutely puberulent becoming glabrous
later, strigose with long appressed tapering hairs usually along
a narrow longitudinal line. Leaves unifoliolate. Stipules 5 - 16mm
long, 1,5 - 2,6mm wide; obliquely ovate - lanceolate, attenuate;
glabrous or sparsely minute puberulent, scarious, striate; extended
at the base along leaf-opposed margins and fused for lower 1,0 -
2,0mm; margin sparsely ciliate. Petiole 1,5 - 6,0mm long, sulcate;
puberulent and with scattered tapering hairs in adaxial channel.
Leaflets 0,6 - 10,0 (12,5)cm long, 0,2 - 1,1 (1,6)cm wide; oblong,
linear or linear-lanceolate; apex acute, mucronulate; base subcordate
to rounded; minutely puberulent with isolated longer hairs on both
surfaces and densely strigose with appressed tapering hairs along
the midribs and margin, margin revolute; major veins prominent adaxially
turning upwards and diminishing well before the margin; lateral veins
looping/.....
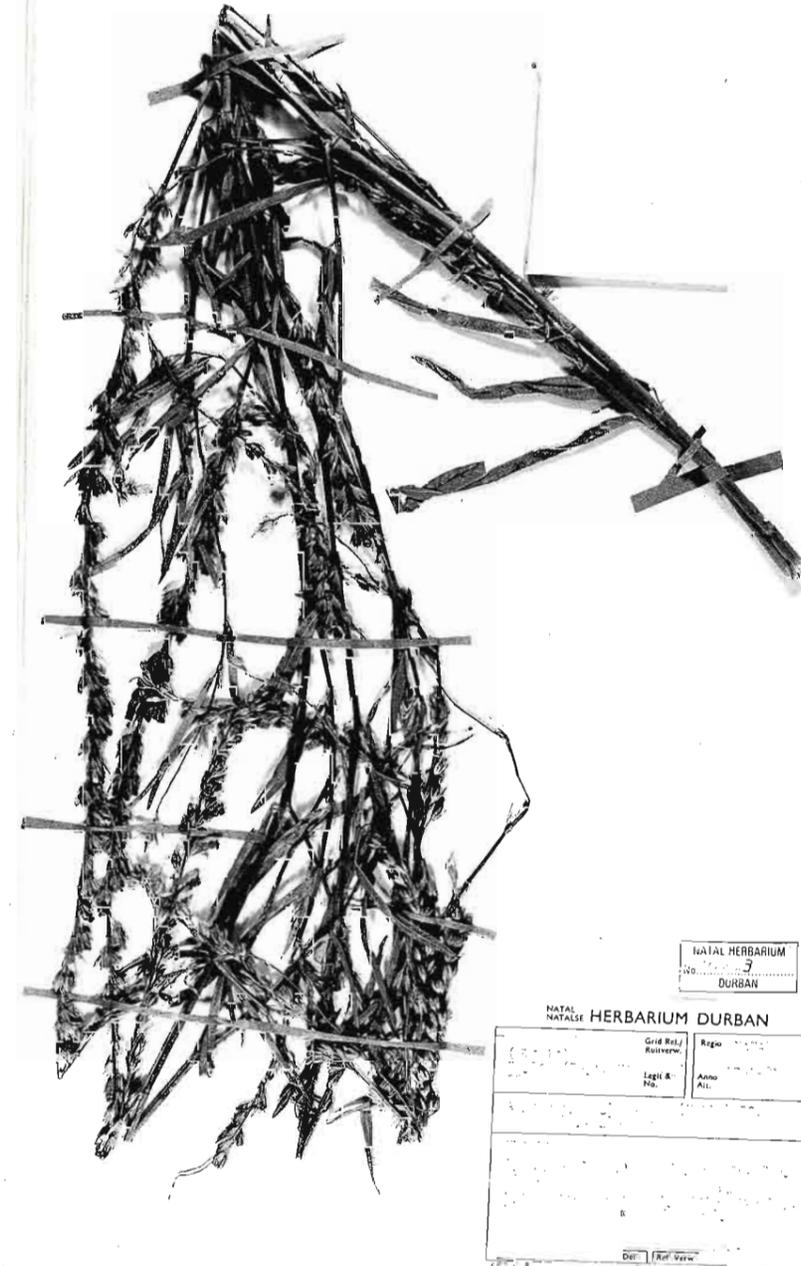
looping distally, reticulation more prominent below. Petiolules 0,6 - 1,8mm long, slightly swollen, rugose; puberulent with scattered long tapering hairs. Stipels 0,8 - 1,6mm long, 0,1 - 0,4mm wide, paired; lanceolate or subulate, similar to stipules. Pseudoracemes elongate, unbranched, spike-like; usually densely flowered, internodes shorter than flowers; terminal and leaf-opposed. Rhachis 3,0 - 30cm long, angular, flattened or deeply channelled; striate; densely puberulent and scattered glandular pilose. Inflorescence bracts 4,0 - 6,5mm long to 2,0mm wide, trullate to rhomboid, acuminate; abaxially minutely puberulent with scattered longer hooked hairs, sparsely pilose and with scattered glandular tipped hairs; margin ciliate; striate, scarious; each subtending a fascicle of two pedicels. Floral bracts 1,0 - 2,5mm long, 0,2 - 0,4mm wide, narrowly elliptic - obovate to linear, similar to inflorescence bracts; one subtending each pedicel. Pedicels 1,5 - 5,0mm long, densely puberulent and glandular haired, the hairs becoming sparser with age. Flowers 6,0 - 7,5mm long, variously salmon, apricot to orange-red or purple with a gold-buff. Calyx up to 8,0mm long, abundantly minute puberulent mixed with larger hooked hairs and densely covered with erect multicellular glandular hairs, sparsely pilose at base of sepals and along keel of lower sepal; margin ciliate; tube 1,0 - 1,5mm long, narrow; teeth 5,5 - 7,5mm long, four, upper tooth of 2 connate sepals up to 6,5mm long, 2,2mm broad at the base, bifid for upper 1,0mm; lower tooth to 7,5mm long, up to 2,2mm broad, strongly keeled; laterals up to 6,8mm long, 1,0 - 1,2mm wide, ovate-lanceolate to lanceolate, acuminate; striate, glumaceous, persistent, sepals hardly overlapping. Standard 5,0 - 6,5mm long, 4,0 - 6,5mm wide, orbicular to obovate; apex retuse, gradually tapering to a not markedly reflexed claw at the base; two conspicuous folds present at the base of the petal above the claw, each extended on either side of the midline into a yellow patch above; abaxially pink-buff; adaxially apricot with gold-buff flushed with reddish-purple towards the base and around the yellow patches. Wings 5,0 - 6,5mm long, 1,0 - 2,5mm wide; cultrate becoming wider distally; auriculate near the base; apex rounded, extended into a short claw at the base; orange below becoming reddish-purple above, tinged with purple on the rim. Keel blades up to 6,5mm long, 2,0mm wide; broadly oblong widening distally and narrowing for the proximal third into a long claw; apex more or less truncate; long pocketed with a minute peg of tissue toward the base on the outer surface, applied closely to the wings; hyaline flushed with purple distally, purple rimmed. Staminal sheath 3,5 - 4,3mm long, up to 1,5mm wide; vexillary stamen free, up to 4,0mm long. Gynoecium 4,5 - 5,0mm long; ovary up to 2,2mm long/·····
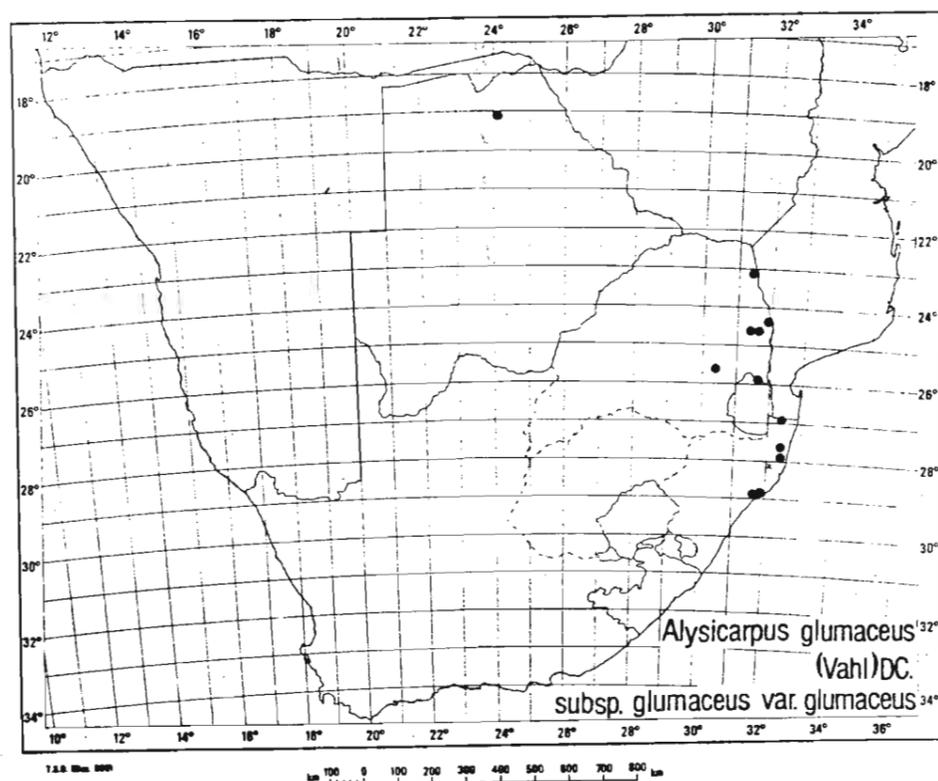
2,2mm long, abundantly minute puberulent; <u>style</u> to 4,5mm long, flexed 45° and incrassated in distal 1,0mm. <u>Fruit</u> 0,8 - 2,5cm long, erect, moniliform; articles 2 - 7; 1,5 - 3mmlong, 2,0 - 3,0mm wide; transversly elliptic to sub-quadrate, strongly rugose; densely puberulent. <u>Seeds</u> 1,8 - 2,2mm long, up to 1,8mm wide, rounded-rhomboid or ellipsoid, compressed; reddish-brown to khaki, smooth.

<u>Alysicarpus glumaceus</u> is found in the hot lowlands of northern Botswana, Transvaal, Swaziland and Natal. In South Africa it occurs from Phalaborwa in the north through Satara and between Louws Creek and Komatipoort, to eastern Swaziland; and in Tongaland and coastal Zululand south to Eshowe.

BOTSWANA.-1924 (Joverega) : Mababe depression (-AA), <u>P.A. Smith 2443</u> (PRE)

TRANSVAAL.-2331 (Phalaborwa) : Phalaborwa, betw. Shingwidzi and Bububu rivers (-AB), <u>W.P.D. Gertenbach 7021</u> (PRE). 2431 (Acornhoek) : Kruger Park, Satara (-BD), <u>B.J. Coetzee 6063</u> (PRE); Hermitage, Manyeleti Game Res. (-CB), <u>G.J. Bredenkamp 1737</u> (PRE); <u>G.J. Bredenkamp 1739</u> (PRE); Buffelshoek, Manyeleti Game Res. (-DA), <u>G.J. Bredenkamp 1847</u> (PRE). 2530 (Lydenburg) : Louws Creek (-CB), <u>G. van Dam 21137</u> (PRE)

SWAZILAND.-2531 (Komatipoort) : Tshaneni (-DC), <u>Barrett 348</u> (PRE)

NATAL.-2632 (Bela Vista) : Ndumu Game Res., edge of Pongola floodplain (-CD), <u>E.S. Pooley 726</u> (NH, NU). 2732 (Ubombo) : Ubombo (-CB), <u>Taylor 55</u> (NH); False Bay (-CD), <u>J. Gerstner 6844</u> (PRE). 2831 (Nkandla) : $\pm$ 16km from Eshowe to N2 (-DC), <u>B. Schrire 909</u> (NH); Umhlatuzana Hills (-DD), <u>H.J.T. Venter 3765</u> (ZULU). 2832 (Mtubatuba) : Hluhluwe Game Reserve (-AA), <u>C.J. Ward 1891</u> (NH, NU)

This species occurs as an erect annual herb of open places in bushveld or in grassland, and is often associated with moisture i.e. floodplains, depressions, saline marshes or near streams. It is also a weed in old lands or along roadsides. Flowering takes place from November to June.

Allen and Allen (1981) report that this is also known as Alyce clover and like <u>A. vaginalis</u> is said to be cultivated as a summer graze for domestic animals. Watt and Breyer - Brandwijk (1962) state that

A. glumaceus/.....

Alysicarpus glumaceus
(Vahl)DC.
subsp. glumaceus var. glumaceus

A. glumaceus is used by Africans in East Africa as a remedy for thrush and veld sores. In Arabia and India the herb is used as an external application to swollen feet.

6.2. Lespedezinae

Lespedezinae (Hutch.) B.G. Schubert, stat. nov. in Polhill and Raven (ed.), Adv. Leg. Syst. 1 : 300 (1981)

Tribe Lespedezeae Hutch., Gen. Fl. Pl. 1 : 486 (1964)

Herbs or subshrubs without hooked hairs; leaflets 3, with tertiary venation reticulate; stipels mostly absent; flowers not explosively dehiscent, some sometimes cleistogamous, standard with inflexed auricles more persistent than most Desmodiinae and keel petals not as tightly interlocking with wings; ovary 1 - ovulate.

6.2.1. Lespedeza

Lespedeza Michx., Fl. Bor. Amer. 2 : 70 (1803); Hutch., Gen. Fl. Pl. 1 : 487 (1964); Clewell in Rhodora 68 : 365 (1966). Type species L. procumbens Michx.

Hedysarum L., Sp. Pl. 2 : 745 (1753) pro parte

The name Lespedeza is derived from Vincento Manuel de Céspedes, governor of the Florida colony from 1784 - 1790 and patron of the botanist Michaux. The current spelling of the genus name presumably resulted from illegibility or a printer's error (Allen and Allen 1981).

Perennial herbs from woody rhizomes bearing 1 - many virgate, aerial stems, usually branched. Leaves 3 - foliolate. Stipules persistent. Leaflets nearly equal in shape, often mucronate, the terminal often longer than laterals. Stipels mostly absent. Inflorescences axillary fascicles. Flowers borne in pairs, each pair subtended by two series of bracts, the second series usually paired. Bracteoles, 2, at the base of the calyx. Chasmogamous flowers showy. Calyx campanulate, persistent in fruit, the lobes subequal, the upper 2 being more connate than the others. Stamens diadelphous, anthers uniform. Style long, filamentous, persistent in fruit. Fruit ovate to orbicular, sometimes asymmetrical, laterally compressed, reticulate, mostly indehiscent. Cleistogamous flowers few, inconspicuous and intermixed with petaliferous; about one tenth the size of the others. Corolla greatly reduced. Style short, persistent in fruit, the distal half sharply recurved and nearly touching the proximal half. Fruit tending to be more orbicular and slightly shorter than those of chagmogamous flowers./....

flowers. <u>Seed</u>, one. One species only, naturalised in Natal.

6.2.1.1. <u>Lespedeza cuneata</u> (Du Mont.) G. Don, Gen. Syst. 2 : 307 (1832), Wilbur in N.C. Agr. Expt. Sta. Tech. Bul. 151 : 185 (1963). Type : Japan, Nagasaki, <u>Oldham 328</u> (K, iso ? !)

<u>Hedysarum sericeum</u> Thunb., Fl. Jap. 287 (1784) nom illegit.

<u>Anthyllis cuneata</u> Du Mont., Bot. Cult. ed. 2. 6 : 100 (1811)

<u>Lespedeza sericea</u> (Thunb.) Miq. in Ann. Mus. Lugd. Bat. 3 : 49 (1867) non Benth.

Perennial erect to spreading, herb or subshrub to 80cm tall, arising from the thickened top of a dichotomously branching, cord like, woody rootstock with extensive fibrous root system. <u>Stems</u> single to many; woody below; terete, becoming conspicuously ridged and densely clothed with stiff spreading tapered hairs, striate with vesture prominent on ridges. <u>Branches</u> many, suberect, virgate, densely leaved. <u>Leaves</u> trifoliolate. <u>Stipules</u> 0,4 - 7,0mm long, triangular to subulate, attenuate; abaxially with scattered stiff hairs, adaxially glabrous; erect or recurving later; striate, early stramineous, persistent. <u>Petioles</u> 1,0 - 11,0mm long, flattened above, trigonous; strigose, more densely so abaxially. <u>Rhachides</u> 0,4 - 2,5mm long, more deeply channelled than petiole. <u>Leaflets</u> 0,5 - 32mm long, 1,5 - 10,5mm wide; narrowly obovate to cuneiform, apex obtuse, rounded to truncate, occasionally retuse, mucronate; base cuneate to acute, unequal in lateral leaflets; essentially glabrous with isolated appressed tapering hairs adaxially, densely strigose to sub-sericeous particularly along the midvein below; margin ciliate; dull green above with lateral veins parallel, conspicuous, looping at the margin, silvery-grey below; conduplicate. <u>Petiolules</u> 0,3 - 1,0mm long, swollen, densely covered with appressed tapering hairs. <u>Stipels</u> none. <u>Inflorescence</u> axillary fascicles of 2 or 1 flowers borne on pedicels at the end of a single reduced rhachis. <u>Rhachis</u> 0,2 - 1,5mm long, densely covered with spreading tapered hairs. <u>Inflorescence bracts</u> 0,2 - 0,3mm long, ovate to lanceolate - acuminate; margin ciliate; scale-like, caducous; subtending the pedicels. <u>Floral bracts</u> up to 0,5mm long, ovate to subulate; paired, one pair at the base of a pedicel, the other pair attached higher up on the other pedicel if present. <u>Pedicels</u> 0,8 - 2.4mm long, erect, vesture similar to rhachis. <u>Bracteoles</u> 0,6 - 2,5mm long, 0,2 - 0,4mm wide; ovate to subulate, paired, one on either side of the calyx base. <u>Flowers</u> 6,8 - 8,0mm long, white with mauve markings. <u>Calyx</u> 4,5 - 5,1mm long, densely covered with spreading

appressed/.....
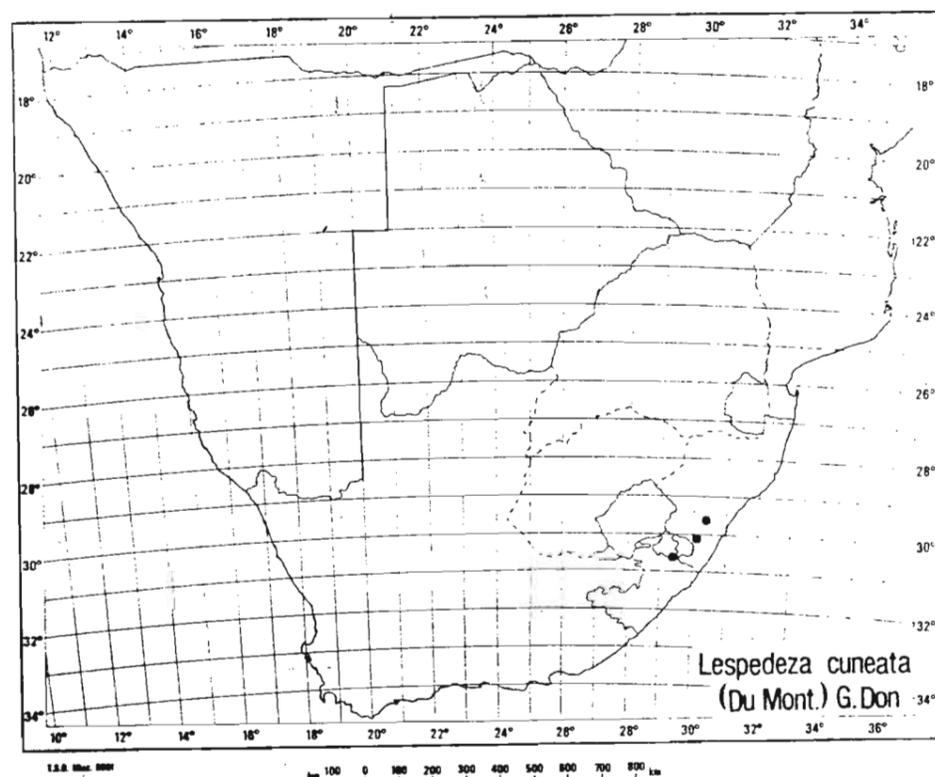
appressed tapering hairs; <u>tube</u> up to 2,1mm long; <u>teeth</u> 5, lanceolate-attenuate; the upper two to 3,2mm long, 0,8 - 1,0mm broad at the base, partially connate, bifid for upper 2,0mm, others up to 3,8mm long, 0,7mm wide; striate, margins ciliate. <u>Standard</u> 6,0 - 7,5mm long, 3,5 - 4,5mm wide; broadly elliptic; apex rounded, apiculate, base extended into a short claw to 1,0mm long, auricled at the base on either side above the claw; sharply reflexed from about 1,0mm above the base; cream to hyaline with two purple markings on either side of the midline above the point of reflexion. <u>Wings</u> 5,5 - 7,0mm long, 0,5 - 1,7mm wide; cultrate, broader above; apex rounded, base extended into a slender claw to 1,5mm long, slightly auriculate at the base where closely applied to keel, hyaline, shorter than keel. <u>Keel blades</u> 6,5 - 7,5mm long, 1,0 - 2,4mm wide, cleaver shaped, falcate; apex rounded, narrowing abruptly to a slender claw up to 2,0mm long at the base, slightly auriculate above the claw, long pocketed, hyaline. <u>Staminal sheath</u> up to 5,5mm long, vexillary stamen to 6,6mm long, free; filaments equal, anthers fixed near the base dorsally. <u>Gynoecium</u> up to 6,5mm long; <u>ovary</u> 1,0 - 1,2mm long; <u>style</u> 5,5 - 6,0mm long, flexed to near erect in distal 3,0mm. <u>Fruit</u> 2,5 - 3,5mm long, 1,8 - 2,2mm wide, orbicular to broadly obovate, compressed; scattered with strong appressed tapering hairs; surface reticulate, bordered by a conspicuous rim, style persistent; of one article only. <u>Seed</u> 1,7 - 2,0mm long, 1,2 - 1,5mm wide; subreniform to obovate, light khaki to brown.

L. cuneata is an escape from cultivation now naturalised in the Natal midlands in the Kokstad, Ixopo and Pietermaritzburg districts.

The plant occurs in old lands, along roadsides or old railway lines. It is an herbaceous suffrutex to - 80cm high, flowering from February to April.

NATAL.-2930 (Pietermaritzburg) : Worldsview, Pietermaritzburg (-CB), O.M. Hilliard 3888 (NU); B.D. Schrire 1368 (NH). 3029 (Kokstad) : Kokstad (-CB), Edwards 12 (NH). 3030 (Port Shepstone) : Ixopo (-AA), Tainton sn (NU)

L. cuneata is native to eastern Asia but is widely cultivated in the United States. Known as Japanese bush-clover it is the most widespread and familiar of all the species and widely employed to control erosion on roadside banks and similar areas (Wilbur, 1963). It is also held in high esteem as a forage, hay and protein supplement to stockfeed (Allen and Allen) 1981).

Lespedeza cuneata (Du Mont.) G.Don

CHAPTER 7

DISCUSSION AND CONCLUSIONS

This study was undertaken with the objective of producing a taxonomic revision of the tribe Desmodieae for the Flora of Southern Africa, and 16 species belonging to 4 genera in two subtribes are described and their distributions discussed. By considering only 4 genera out of 27 worldwide however, as well as only 10 species of Desmodium ($\pm$ 300 spp. in all) it is difficult to present a unified concept of the tribe. With this aim the following conclusions are drawn from evidence provided in chapter 5.

i) The origin of the angiosperms goes back further than is commonly accepted, since by the early Cretaceous it appears that angiosperm pollen, although not diverse, is already widespread over both hemispheres.

ii) West Gondwanaland (Africa and South America) is seen as being a primary area for the evolution of many major families of flowering plants including the Leguminosae - Papilionoideae.

iii) The Sophoreae are central to the radiation of the Papilionoideae and they gave rise to among others, the Tephrosieae which represent a large diffuse core for the development of more advanced Old World tribes.

iv) With a basic chromosome number n = 11 or 10, the Tephrosieae possess some of the features later canalised and fixed in the more derived Old World tropical tribes, i.e. intrastaminal disc nectaries or alternatively explosive release of pollen; pseudoracemose inflorescences; seedlings with eophylls usually unifoliolate and opposite; the presence of canavanine in seeds and the presence of pulvinate, imparipinnate leaves with opposite leaflets.

v) The Desmodieae is one of the most advanced tropical Old World tribes and superimposed on the Tephrosieae pattern, other features have become central or fixed in most of the tribe i.e. leaves typically (1) - 3 - foliolate; the presence of stipels; a characteristic uncinate pubescence; explosive release of pollen with a loss of nectaries; marked thickening

of the/.....

of the endexine with loss of the foot layer in pollen and
a predominantly herbaceous habit.

Many of these features may be present individually in other tribes
indicating either direct relationships or that they have arisen
separately on a number of occasions within the subfamily, but
no other tribe has the same combination of characters.

The tribe forms a relatively coherent and natural grouping of
taxa and is believed to have originated in the southeast Asian
tropics. Interesting new evidence (Hsü, 1983) shows that the
derived and more temperate subtribe Lespedezinae was already repres-
ented by the genus Lespedeza in the Paleocene pollen assemblages
of central China. Leaves of Lespedeza were again found from late
Eocene deposits and Desmodium from Miocene deposits in central
China. Since Lespedeza can be traced back to near the beginning
of the Tertiary, and that central China is a subtropical to temperate
region only subsequently colonised from the tropics; there is
a strong liklihood that the tribe Desmodieae already existed before
the close of the Cretaceous and is not principally a Neogene-derived
group as has been thought up to now. This also argues for a consid-
erably older origin for the Papilionoideae as the Desmodieae is
still considered to be one of the most advanced tribes in the
subfamily.

From southeast Asia the tribe became dispersed in a number of
ways.

i) To North America, where evidence presented by Hsü (1983)
suggests that contrary to the opinion expressed in chapter
5, Berengia was only formed in the Miocene and could not
have been a migration route for plants before then. In
fact no effective barriers existed before the mid-Eocene
to extensive migration of floras between southeast Asia
and North America via central and western Asia and Europe.
The two theories for how the tribe migrated to North America
therefore are 1) via Berengia in the Miocene with progressive
isolation of these elements as they were pushed southwards
into tropical America by spreading cooler conditions or
2) by direct migration across Asia and Europe in a Tethyan
boreotropical flora. Truly tropical elements of the tribe
in America show a considerably longer period of isolation
from their Asian relatives than do more temperate members.

The subtribe Bryinae and forerunners of the New World subgenera of <u>Desmodium</u> are tropical relics of what was once perhaps a widespread boreotropical flora that extended from North America to Asia. It is thought unlikely that these could have crossed via Berengia as there is little proof that purely tropical elements were able to take this path in the Miocene.

The temperate herbaceous species of <u>Desmodium</u> subgenus <u>Podocarpium</u>, <u>Lespedeza</u> and <u>Kummerowia</u> however, which are often the most advanced in the tribe, show relatively close affinities to Asian species and it is considered quite possible that these migrated into North America via Berengia from the Miocene.

<u>Desmodium</u> and to a far lesser extent <u>Lespedeza</u>, have radiated out to form a large subsidiary development of the tribe in the New World.

ii) To New Caledonia where two of the most archaic woody genera of the tribe survive with no obvious relatives elsewhere. They are closely related to one another and have radiated out considerably on the island. Although originally a Gondwanaland isolate, New Caledonia broke away and arrived in its present position during the Cretaceous. It is suggested that the <u>Arthroclianthus</u> prototype may have arrived in New Caledonia by long distance dispersal from the Asian boreotropical flora before many of the intervening islands and New Guinea were formed. This distribution may also indicate that closer links existed between New Caledonia and the boreotropical flora of Asia during the late Cretaceous - early Paleocene.

iii) To Australasia and South America via Malesia and central America respectively by direct migration of modern representatives in the last 10-15 m.y.

iv) To Africa, to a very limited extent owing firstly to the barrier of the Tethys sea from the Palaeocene to the Miocene and from the Miocene onwards due to the arid barrier of the Middle East. Africa is a minor centre for the tribe with only two endemic genera one of which is a minor segregate of <u>Alysicarpus</u>/.....

of _Alysicarpus_. _Droogmansia_ however, has formed a complex of some 30 species some of which bear a relationship to an Asian genus, and the group may be derived from an early Asian migrant. _Desmodium_ is represented by some 14 endemic species most or all of which belong only to two sections of one subgenus i.e. the sections _Nicolsonia_ and _Heteroloma_ of the subgenus _Sagotia_. These endemics can be considered to have arisen from a very few progenitors. Many other taxa do occur in Africa but these are often widespread Old World tropical species originating in Asia. The forerunners of the African endemics of _Desmodium_ and _Alysicarpus_ are considered here to be some of these widespread Asian species that arrived since the Miocene either by long distance migration across the Indian Ocean islands and Madagascar or even more recently due to the influence of man. The fact that there is such a minor development of the tribe, particularly _Desmodium_, in Africa indicates the probable recency of its arrival on the continent. In addition the successful methods of seed dispersal in Desmodieae make it highly possible that many taxa worldwide, have attained their present distribution over the last three to four thousand years because of man's influence. It is interesting to note that many of the _Desmodium_ endemics are closely related to pantropical species i.e. _D. dregeanum_ is closely related to the widespread _D. barbatum_ and _D. setigerum_ to _D. adscendens_. Tropical American species of _Desmodium_ have only been introduced extremely recently into Africa and some have become widely naturalised as escapes from cultivation.

Species of the tribe Desmodieae are relatively stable with no evidence of hybridization in southern Africa; and only the annual species of _Alysicarpus_ are variable enough to infer that active speciation is taking place. These are ruderal weeds.

Many introduced species and escapes from cultivation are now becoming naturalised in southern Africa, i.e. _D. incanum_, _D. tortuosum_ (or Florida Beggarweed) and _Lespedeza cuneata_. Other species _D. intortum_ and _D. uncinatum_ are being widely cultivated as pasture legumes and although these have not shown signs of spreading they may yet become naturalised. Many additional species of _Desmodium_ are being tested in agricultural stations for their pasture potential.

The following morphological trends in the tribe provide clues to relationships and also the possible direction of evolutionary development within the taxa occurring in southern Africa.

1) Perennials in most taxa to annuals in two species of Alysicarpus.

2) A characteristic desmodioid-type root nodule is found in the tribe but they do occur commonly in a number of other tribes as well.

3) Woody shrubs or subshrubs in section Heteroloma of Desmodium to herbs in section Nicolsonia of Desmodium (in D. adscendens and D. setigerum), Alysicarpus and Lespedeza.

4) Leaves trifoliolate to unifoliolate in 3 Desmodium spp. (one in section Nicolsonia) and in Alysicarpus.

5) A tendency for stipules to become fused at least when young on the leaf-opposed margins in the New World subgenera of Desmodium and in Alysicarpus.

6) Leaf size becomes reduced from section Heteroloma, through section Nicolsonia to Alysicarpus and Lespedeza. Leaf shape is characteristic of each group (including subgenus Podocarpium of Desmodium).

7) Lateral leaflets asymmetrical to symmetrical in section Nicolsonia and Lespedeza.

8) Stipels in the Desmodiinae, are lost in Lespedezinae.

9) Uncinate puberulence in Desmodiinae, is lost in Lespedezinae.

10) Trend towards reversibly conduplicate leaves in section Nicolsonia (D. dregeanum and D. barbatum) and in Lespedeza.

11) Leaf venation patterns from craspedodromus and eucamptodromus in section Heteroloma to brochidodromus in section Nicolsonia in Alysicarpus and Lespedeza.

12) Tertiary venation scalariform in Desmodiinae, reticulate in Lespedezinae.

13) Anticlinal walls of epidermal cells of the abaxial leaf surface are irregular in section Heteroloma, markedly undulate in section Nicolsonia (sunken in D. dregeanum and D. barbatum; distinctly raised in D. adscendens and D. setigerum) and pentagonal to hexagonal in Alysicarpus.

14) Stomata occur abaxially only in the leaves of most members of section Heteroloma and D. adscendens of section Nicolsonia, and on both surfaces in D. salicifolium (section Heteroloma), D. barbatum and D. dregeanum (section Nicolsonia) and in Alysicarpus and Lespedeza.

15) Papillate domes occurring on the outer periclinal walls of leaf cells are irregular and not well developed in most members of section Heteroloma but are increasingly better developed in D. gangeticum (section Heteroloma), section Nicolsonia and Alysicarpus.

16) In inflorescences a trend occurs in reduction of the pseudoraceme from the occasional incompletely reduced botrys to a fascicle with 3-5 pedicels each subtended by floral bracts in D. repandum, to true fascicles often with a reduced median bud between two pedicels, each subtended by floral bracts in section Heteroloma; to loss of median buds and/or loss of floral bracts in section Nicolsonia and Alysicarpus.

17) A trend is also seen towards contraction of the pseudoraceme from elongate and laxly to densely flowered in subgenus Podocarpium and section Heteroloma, to densely short capitate in D. dregeanum and D. barbatum of section Nicolsonia. The inflorescences of the two subdivisions of section Nicolsonia are considerably different with very lax, few flowered inflorescences with long pedicels in D. adscendens and D. setigerum and short, contracted, densely flowered heads, with short pedicels in D. dregeanum and D. barbatum. In Lespedeza contraction of pseudoracemes continues much further into few flowered axillary fascicles.

18) A trend is also found from laxly branched terminal pseudoracemes in Pseudarthria and section Heteroloma to unbranched in section Nicolsonia and Alysicarpus.

19) Pseudoracemes are terminal and axillary in Pseudarthria

and section Heteroloma becoming additionally leaf-opposed in Alysicarpus.

20) A reduction in flower size is noted from subgenus Podocarpium to section Heteroloma, section Nicolsonia and Lespedeza.

21) Explosive method of tripping in Desmodiinae with loss of nectaries, not in Lespedezinae.

22) A trend in calyces from relatively small campanulate or cupulate, scarious and insignificant when dry; 4 lobed with upper two sepals markedly connate and forming a lip; teeth triangular or ovate - lanceolate in section Heteroloma and subgenus Podocarpium becoming larger in Pseudarthria and in section Nicolsonia with a more conspicuous pubescence. In D. dregeanum and D. barbatum of section Nicolsonia the calyx is almost double the size of the calyx of section Heteroloma and subequally 5-toothed, the upper two not markedly connate and teeth narrowly lanceolate and acuminate; the lower tooth tending to become longer and more keeled for support in Alysicarpus where calyces are double the size again of those of section Nicolsonia (except for A. vaginalis). In Alysicarpus calyces taper narrowly to the base, are conspicuous, glumaceous, striate and strongly ciliate along the margins; generally 4-lobed but splayed out in flower (a very different adaptation to Desmodium). In Lespedeza the calyx is 5-lobed with no connate sepals, also densely hairy with a ciliate margin.

23) An increase in flower complexity from Desmodium to Alysicarpus with a greater development of interlocking transvenal wrinkles between wing and keel petals and better developed appendages on the standard of the latter.

24) A move from chasmogamous flowers to a mixture of chasmogamous and cleistogamous flowers in Lespedezinae indicating a trend towards selfcompatibility in breeding systems.

25) The staminal column with the vexillary stamen most often free but partly coherent in some Alysicarpus and in subgenus Podocarpium (D. repandum).

26) Stamens alternating in length in Desmodiinae, equal in Lesped-
ezinae.

27) Pollen grains increasing in size from 25 - 40 μm in <u>Desmodium</u>
to 70 μm in <u>Alysicarpus</u>.

28) A considerable thickening of the endexine in pollen with
a reduction of the foot layer in <u>Desmodium</u> to complete loss
of the foot layer in <u>Alysicarpus</u>.

29) Trends in pollen are also seen towards a very dense, short
collumellar layer and from perforate fine reticulate or
rugulate tecta in many <u>Desmodium</u> spp. to thick and entire
tecta in <u>Alysicarpus</u>.   <u>D. repandum</u> has a unique type of
pollen very different from the other species even in the
subgenus <u>Podocarpium</u>.

30) In the gynoecium there is a reduction in ovary size from
the subgenus <u>Podocarpium</u> to <u>Pseudarthria</u> ($\pm$ 5,5mm) to section
<u>Heteroloma</u> ($\pm$ 3,0 - 4,0mm) to section <u>Nicolsonia</u> (2,0 -
2,7mm) and <u>Alysicarpus</u> (2,0 - 3,0mm) to <u>Lespedeza</u> (1,0 -
1,2mm).

31) This is associated with increasing style length. In section
<u>Heteroloma</u> styles are from 1,0 - 2,0mm long flexed from
45° to erect almost immediately distal to the ovary. In
section <u>Nicolsonia</u> (<u>D. dregeanum</u> and <u>D. barbatum</u>), <u>Alysicarpus</u>
and <u>Lespedeza</u> styles are from 3,0 - 6,0mm long flexed only
at their distal ends.

32) A trend towards elaboration of the style with varying degrees
of thickening in the distal part or the presence of hairs
is noted in some <u>Desmodium</u> spp. and in <u>Alysicarpus</u>.

33) The style is solid in <u>Pseudarthria</u> (the only species tested)
and the stigma is capitate, wet papillate and protected
by an impermeable pellicle until tripped, in all species.

34) A trend is noticed in the pods from an open 2-valved pod
in <u>Pseudarthria</u> to a distinctly jointed loment with easily
separating articles either partially dehiscent to indehiscent
in most <u>Desmodium</u> and <u>Alysicarpus</u>.

35) Pericarp free from seed in nearly all species to adnate to the seed in D. repandum (subgenus Podocarpium).

36) Few seeded pods in Desmodiinae to 1 seeded pods in Lespedezinae.

37) Increasing incorporation of the calyx for use in fruit dispersal, from slightly in most Desmodium spp.; more so in section Nicolsonia (D. dregeanum and D. barbatum) and Pseudarthria, to a large extent in Alysicarpus and Lespedeza.

38) A persistent style is present in all species aiding fruit dispersal.

39) Seeds are small and hard with an aril reduced to a dry rim in all species.

40) All seedlings are phaneroepigeal with foliar cotyledons and two opposite unifoliolate eophylls.

41) A trend from n=11 in Desmodium with aneuploid reduction to n=8 in Alysicarpus and n=10 in Lespedeza.

Considering the general trends in the Papilionoideae outined by Polhill (1983), the following conclusions arise out of the above.

a) Lespedeza is a derived temperate offshoot of the tribe and collectively contains the most 'advanced' characters shown by the genera represented in southern Africa.

b) Alysicarpus is a tropical genus also significantly more derived than Desmodium and although it represents a completely independent lineage from Lespedeza, it shares a number of common 'advanced' characters.

c) In Desmodium the section Nicolsonia is considerably more derived than the section Heteroloma and is often intermediate between the latter and Alysicarpus - Lespedeza with respect to these 'advanced' characters.

d) Although the section Nicolsonia is a natural assemblage quite distinct from section Heteroloma it comprises two clear and often/.....

and often widely different groups; D. adscendens - D. setigerum and D. dregeanum - D. barbatum. The latter pair are the most highly derived members of the genus in southern Africa.

e) D. repandum which has tentatively been placed in the most advanced subgenus of Desmodium by Ohashi (1973), is considerably different from the other species in southern Africa and although it has some notably advanced characters such as partly monadelphous stamens and seeds with an adnate pericarp, its overall position seems to indicate a less derived status.

A point worth noting is that the more primitive (or less derived) a taxon appears to be, the less coherence will be found between its individual functional systems; i.e. there is a relatively greater amount of autonomy available for independent evolution within each system. Only in the more derived taxa which carry a significant amount of previous 'burden' will there tend to be a much tighter linkage between functional systems with less opportunity for any single system to develop independently of the others.

In this case if D. repandum represents a relatively less derived species this could explain why it displays such an odd combination of 'primitive' and 'advanced' characters.

The following ecological trends are noted in the tribe in southern Africa.

Rootstocks in perennial species are of two types related to habitat preference; large vertical woody rootstocks associated with rhizomes and a stylopodium, giving rise to many aerial stems by regeneration, in a typical savanna or open grassland ecosystem; or horizontal frequently branching rootstocks associated with forest floors or muddy streambanks where ability to spread quickly is more adaptive. Simple daucate roots are found in the two species which have become successful ruderals.

Interesting silvery discolouration patterns were found on the adaxial leaf surface of the shade growing species, D. repandum and D. adscendens, a feature that has been noted in other legumes growing under similar conditions. A tentative suggestion is made that there might

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be some association with leaf miner deception.   Adaxial leaf midline discolouration is also found in D. incanum and A. rugosus.

The common occurrence of multicellular glandular hairs on the inflorescence rhachis, pedicels, bracts and calyces of many species is thought to be associated with defence by secreting deterrents which protect the inflorescence and young buds from predators.   This is considered to be particularly adaptive in protecting Desmodieae pseudoracemes which have a protracted flowering period.

Pseudoracemose inflorescences allow for a very much more protracted flowering period, with the lower flowers opening first followed by others at daily intervals progressively up the inflorescence.   With individual pseudoracemes coming into flower at different times on the same plant, together with their flowering period often being extended by the intermediate buds in a fascicle elongating and flowering sometime after the others have finished; a more or less continuous flowering period of many months can be achieved.   This period is generally longest in Desmodium and shortest in Pseudarthria and Lespedeza.

Two possible strategies can be employed in a continuous-type flowering regime; either a repeatable pollen presentation where flowers have a relatively long life span and valvular, pump or brush tripping mechanisms; or a once only pollen presentation where a few flowers open for one day only and have an explosive tripping mechanism after which petals become disorientated or caducous.   The latter strategy is adopted in the Desmodieae which offers pollen as a major reward rather than nectar as in the former strategy.

In the Desmodiinae distinct trends towards

   i)   smaller flowers

  ii)   calyces adapted to supporting the floral parts (i.e. a wider upper lip and longer often keeled lower tooth)

 iii)   elaborate interconnections between standard, wings and keel petals (the latter tightly folded over the staminal column and maintaining it under tension)

  iv)   connate stamens affording greater precision by directing pollen release

v) pollen with a marked thickening of the endexine associated with loss of the foot layer

vi) elaboration of the style with distal thickening or hairs

are all associated with adaptations towards the explosive-type tripping mechanism.

The mechanism is a highly derived feature in Papilionoideae and the staminal column and stigma which are held under tension emerge eruptively from the keel as the petal configuration is disturbed, and pollen is expelled as an upwardly directed cloud.

Flowers are adapted exclusively to pollination by bees and are either tripped relatively early in the day or they self-trip as heat and environmental disturbance increases later on. Tripping is effected by the bee digging its head into the base of the standard and moving it backward releasing the base of the wing petals. With the bee's forelegs lodging in the wing petal sculpturing patterns and hindlegs scrabbling for a hold, the keel is rapidly opened and pollen is showered on the bee's under-surface.

Although pollinated only by bees, a wide range of species from numerous genera are able to operate the tripping mechanism. A number of ecological adaptations are therefore found to limit the type of bee to a relatively narrow spectrum of most 'suitable' pollinators.

i) Flowers are small therefore larger bees are excluded, e.g. Xylocopa (except perhaps for D. repandum)

ii) Rewards are hidden and the tripping mechanism is sophisticated, so only skilled bees will show the ability to learn to use them. Handling is a function of experience and the mechanism promotes skill-selection because inefficiency is energetically expensive.

iii) The continuous flowering regime provides a dependable and predictable source of food and gradually allows the establishment of a regular pattern of visitation.

iv) Resources are also often spread over considerable distances, and scattered 'clumped' populations are the general demographic pattern/.....

pattern noted in the tribe owing to the common occurrence of vegetative reproduction.

v) Combining iii) and iv) only certain bees that have sufficient energy resources (and conversely high energy demands) are able to fly the distances between populations where they can expect a regular supply of food.

vi) A corollary of this is that Desmodieae rewards are energy rich (large quantities of pollen), so a further linkage is developed between high energy rewarding plants and high energy demanding pollinators, i.e. flowers with a small energy reward cannot be used.

vii) Owing to any one population only being able to offer a limited food supply that is replenished each day; suitable bees will have to visit several sites in succession often following a set route, before they satisfy their demands.

viii) The memorised 'search image' which bees develop of each specific site enable them to follow a set sequence of visits and this phenomenon of traplining ensures that cross pollination will occur between different populations.

ix) Enhancing the process of traplining is a distinct periodicity in flowering i.e. flowers open at the same time each day and are only available from dawn to 11.00am. This increases the precision of site-fidelity since bees often return to the same site at the same time of day.

x) Different bees will also limit foraging to specific diurnal peaks i.e. a pollen resource is partitioned. This was observed in P. hookeri and is most likely a response to bee competition.

xi) Hovering although energetically expensive may be another way of maximising gains per unit time. This was noted only in Apis, one of the most highly advanced social bees. The relation-ship between advanced social and semi-social bees and skill and high energy demands is a function of the division of labour in these species which enables greater selection for more efficient food gathering.

Owing to the tremendous importance of a balance between energy return for energy expenditure it is easy to see why it is adaptively significant for visited flowers to become immediately unattractive in a population. Loss of attraction by means of the staminal column immediately blocking the nectar guide; overall rapid colour changes in the flower to a dull blue, petals becoming disorientated or caducous or resupination of the flower are all means of avoiding revisits by pollinators.

In these ways true pollinators are restricted to a relatively narrow band of highly advanced social or semi-social bees. Occasional visits may be made by many other bees but these won't constitute true pollinating visits.

To build up a relationship between plant and pollinator the flower must be visited regularly, and this develops around attraction devices and energy yielding rewards offered by the flower. If this leads to a succession of visits to a flower of the same species, this sense of purposefulness, in which pollen must incidentally be transferred from flower to flower so that effective cross-fertilisation can occur, constitutes a true pollinating visit.

Attractants take several forms.

 i) Pollen odour which is easily detected after pollen is placed in an airtight vial (very pungent with a smell reminiscent of cucumber in D. incanum). The perianth appears to be odourless in a similar test and this is reinforced by the lack of osmophores found when petals were stained with neutral red. Although anthers stain deeply, a word of warning has been expressed by van Wyk (pers. comm.) that any part of the flower where the cuticle has been broken will tend to take up dye, i.e. staining does not necessarily prove on its own that anthers actively produce odours. Pollen odour is most likely the first and major attractant, and it is also the means of communicating the food source from scouts to the hive. Osmophores in petals are probably absent from most Desmodieae but they are known to be common in many other legumes, particularly yellow flowered species (Stirton, pers. comm.)

 ii) Visual cues such as size, shape and colour reinforce and make easier the recognition of flowers that have proved rewarding and this promotes floral constancy. The bee's eye is able

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to utilise the polarised light of day to sense a vastly expanded range of colours as well as various intensities of light owing to the fact that light strikes each of the many facets differently. Only on heavily overcast days or when the sun is directly overhead at midday in the tropics, is bee navigation affected because of poor light contrast.

Different patterns on flowers are therefore recognised with ease. Most Desmodieae flowers have a visual background colour of pink, mauve, magenta, purple or white (red only in D. repandum) and in addition ultraviolet light absorption patterns are superimposed which provide additional contrasts. Colour can thus act as a long distance attractant especially if flowers are aggregated in inflorescences. The 'clumped' nature of populations enhance this. Colour can also act as a close orientation cue once the bee has arrived at the flower. Two clearly marked regions of different colour often reinforced by ultraviolet light absorption patterns are nearly always present at the base of the standard where the bee needs to place its head to activate the tripping mechanism. These are the nectar guides in most papilionoids and it is suggested here that bees learn to associate these guides as the key to activating the tripping mechanism regardless of whether it is valvular, pump, brush or explosive. The tips of the wings and keel are also strongly ultraviolet light absorbent as well as darkly coloured. This provides the orientation to the standard.

The reward to bees is pollen which is a convenient, nutritious food source and is produced in large quantities directed all over the underneath of the bee. Even after grooming and storage in particular areas, sufficient pollen is left on the body to be transferred to other flowers. Pollen is a high quality food source but the relative slowness of digesting the large quantities needed for nutrition as well as the fact that more than half the caloric value is in the indigestible exine, means that bees will generally have to supplement pollen by collecting nectar from other plants in the environment.

In Desmodieae anther dehiscence can occur up to 12 hours before anthesis, a feature not uncommon in the Papilionoideae. Since pollen is protected in the keel and the stigma is protected by the pellicle which prevents selfing, it may be advantageous for pollen to be liber-

liberated/.....

ated early in order to be dry enough to fly out in a cloud when the flower is tripped. It may also have something to do with the chemical changes necessary for odour production. It may also just be a remnant of a protandrous situation which is commonly found in many other Leguminosae.

The stigma in Desmodieae is wet and papillate but is covered by a protective dry and impermeable pellicle while untripped. On tripping the pellicle is ruptured and pollen, both self and other is able to rehydrate in the stigmatic fluid. It is here that the importance of the tripping mechanism is understood because it allows the opportunity for a newly ruptured stigma to spring up and perhaps collect non-self pollen first, from contact with the bee's body. Self-pollen is also likely to be present and will also germinate. Inhibitory reactions must be present slowing down self pollen growth in stigmas/styles of flowers with repeatable presentation mechanisms where the pellicle is broken on the first tripping. They must also occur in Desmodieae giving foreign pollen an edge. The site for any inhibitory reaction is likely to be in the style as growth proceeds from the stigma. As the pollen tube grows through the specialised transmitting tissue of the style, fluid is secreted to promote pollen tube growth. Work quoted in the text has shown that stylar fluid can have a different chemical composition to stigmatic fluid and those components present in the former but not the latter, may play a role in inhibiting self-pollen growth.

Important aspects have emerged from a study of bee foraging strategies.

  i) Pollen must be efficiently harvested and the optimal strategy is one that yields the greatest net energy and nutrient gains per unit time. Bees are extremely well adapted for carrying large amounts of pollen, i.e. up to half their body weight in specific areas of the body and they also have a hoarding instinct (particularly in Apis) to continue collecting while conditions are favourable.

 ii) Bees as a group are generalist feeders bringing back many different kinds of pollen to their hives, but as individuals they carry relatively pure loads.

iii) This is due mainly to a sense of site-fidelity developed by the individual as a memorised 'search image' once a good food

source/.....

source is located; traplining is an extension of this idea.

iv)   Scouts constantly track new food rewards, for example by the process of majoring-minoring in Bombus which is discussed in chapter 4.

v)   Information on distance, direction and type of food may be communicated to the hive by elaborate dances in Apis, or may be marked by zigzag flights, scent trails, different buzz tones etc., in other bees.

A consideration of the reproductive strategies in the tribe led to the following conclusions.

i)   The Desmodieae are predominantly self-compatible which is part of an overall trend towards self-compatibility in more herbaceous legume groups.

ii)   There is greater selection for this type of breeding system because many tropical herbaceous groups inhabit unstable habitats such as open semi-disturbed areas or fire-prone savannas subject to marked seasonal fluctuations in climate.

iii) In P. hookeri it is estimated that cross pollination occurs in between 5-20% of flowers in the average population. This was determined from the percentage increase in seed produced by completely selfed inflorescences over normal outcrossing ones; and equating this conversely to a percentage decrease in seed produced by outcrossing.

iv)   The rest of the flowers self-trip and are self fertilised.

v)   The tripping device retains the opportunity for cross fertilisation because the stigmatic pellicle is only ruptured after tripping.

vi)   Even when visited by bees, a large number of flowers are geitonogamously selfed because bees are saturated with 'own' pollen.

vii) The characteristic demographic in P. hookeri and in a number

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of other Desmodieae, is the 'clumped' nature of populations where numbers of individuals occur in dense patches. This is due partly to an efficient means of vegetative reproduction producing rhizomes and reproductive roots as well as to seed fall in the vicinity. Since such a high proportion of seed produced is selfed and because many of the individuals in a clump are genetically identical propagules, this further reduces the chance that pollen transferred between individuals will be different. The major opportunity for crossing must therefore lie between different populations. The first few flowers that are tripped in one population by each traplining bee arriving from another population, will have the chance of receiving 'different' pollen. After a while in one population each bee becomes saturated in 'own' pollen.

vii) Selfing is advantageous firstly by increasing the number of seed set (see P. hookeri experiment) and hence increasing colonising ability and secondly by contributing two gametes instead of one to the self-fertilised zygote. This presumably provides new individuals with all the genetic qualities that have adapted the parent to that environment. This increase in the success of fertilisation however, occurs at the expense of the qualitative superiority of progeny arising from cross-fertilisation.

ix) A certain level of crossing is therefore maintained and even a small amount of crossing generates new variability and provides the stimulus of heterosis or hybrid vigour. A relatively high proportion of heterozygosity will also be retained in a predominantly autogamous situation if the heterozygotes have a selective advantage over homozygotes. Such persistent genic heterozygosity is well reported (see chapter 4) and is promoted as the fitness of self-derived plants decreases due to raised levels of stress or competition. Overall selection of mating patterns can thus be viewed as effecting a compromise in individual selection between the advantages of selfing and those of outcrossing.

x) The particular ecological niche of P. hookeri illustrates this point. P. hookeri is a K-strategist occupying a particular successional stage in the grassland component of bushveld savanna or open woodland. It belongs to a grassland precursorial

stage/.....

stage to woodland regeneration associated often with <u>Cymbopogon</u> spp. It is a fire controlled succession which at one end, if burned too much, reduces the chances of <u>P. hookeri</u> survival and favours shorter <u>Themeda</u> or <u>Aristida</u> - type grassland; and at the other, if not burned enough, <u>P. hookeri</u> eventually becomes shaded out by regenerating woodland. Most Desmodieae are well adapted to this type of fire controlled succession with their perennial woody rootstocks giving rise to many aerial stems, and their effective methods of vegetative repro- duction. The crux of this balance between selfing and crossing which is integral to the particular breeding systems of Desmod- ieae, is the ephemeral nature of the successional sere in which they grow. Considering <u>P. hookeri</u>, the area best suited for its growth is constantly changing due to the push-pull effects of a fire controlled sere; the effects of forest and grassland dynamics and the semi-disturbance factor caused by man and grazing animals. <u>P. hookeri</u> can thus be considered as an habitually colonising species consisting of an extended gene pool within which alternative phenotypes are selected in alternating residential and colonising episodes. It is this that maintains both a high level of heterozygous advantage as well as a predominantly autogamous breeding system producing large quantities of seed.

This production of large quantities of seed with strong seed coats enforcing dormancy ensures a long term staggered germin- ation as seed coats gradually break down. This is the optimal strategy to maximise seedling survival in an uncertain environ- ment.

xi) Despite this strategy, <u>P. hookeri</u> and many other Desmodieae are not weeds in the true sense of colonising new open habitats. They are tied to a relatively specific seral stage in succession which is a saturated environment. They do often occur in various degrees of disturbance such as old cultivated lands, roadsides etc. where vegetation is regenerating, but not in open or waste sites. Certain species already mentioned however, are true ruderals.

The great diversity in the morphology of fruit types in the tribe is a response to strong and varying selection pressures due to para- sitism (compartments protecting neighbouring seeds from being attacked)

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and seed dispersal (indehiscent, easily separating articles covered with hooked hairs and a persistent style to facilitate wider dispersal). Desmodieae fruit are predominantly adapted to exozoochorous dispersal of seed by mammals and there is an increasing trend in using the calyx to aid dispersal especially in Alysicarpus and Lespedeza. Pseudarthria has been subjected to significantly different selection pressures as far as fruit type is concerned, although exozoochorous dispersal is still important. The two valved, open, easily detached pods with seeds remaining relatively firmly attached, are very well adapted to wind dispersal or carriage by water.

In P. hookeri the advantage of the pod transferring up to 6 seeds together ensures that if a pod arrives in a suitable spot, a number of plants may be able to develop together. Seed is held over in open pods until the environment is more suitable for dispersal and germination, with the onset of winds and the summer rains.

Seed is generally small in most Desmodieae although it is largest in D. repandum, D. adscendens and D. salicifolium which are those species noted in the beginning as having horizontal rootstocks. Larger seed size may be necessary in forest conditions to better enable establishment of seedlings. The funicle often remains attached to P. hookeri seeds where it can also aid in dispersal. The rim aril is considered to be too hard and dry to provide any attraction to ants for dispersal.

Seedlings are associated with two rest periods during development, one when cotyledons are still enclosed by envelopments and only the root and hypocotyl are exserted and second after the seedling is erect and has produced foliar cotyledons. This provides time for establishment before further growth in an uncertain environment.

Finally, it is considered that Pseudarthria hookeri is better maintained as separate from Desmodium (as opposed to the suggestion of Polhill in Ohashi et al, 1983) for the following reasons.

1) P. hookeri is easily recognisable and should never be confused with Desmodium.

2) Although it superficially resembles Desmodium a recent chromosome count (Spies pers. comm.) has determined that P. hookeri has 2n=26 compared with Desmodium, 2n=22. This latest check on

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the chromosome number in P. hookeri refutes a previous count of 2n=34 (see chapter 4) and allies it for the first time to another count of 2n=26 in Pseudarthria fagifolia. A tentative suggestion is made that an aneuploid increase has occurred in Pseudarthria from the basic x=11 in the tribe, compared with the aneuploid decrease noted in Alysicarpus and Lespedeza.

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Appendix

Specimens quoted in the taxonomy section

Desmodium

ACOCKS 9648 (PRE); 10118 (NH); 10888 (PRE); 10899 (PRE); 13332 (PRE)

AHRENS 23 (NU)

ALLSOPP 969 (NU); 999 (NH, NU, PRE); 1017 (NH); 1024 (NH, NU)

BAIJNATH 185 (NU, PRE)

BALSINHAS 2804 (PRE); 3223a (PRE)

BARKER 5155 (NBG); 6138 (NBG); 10012 (NBG)

BAUR 114 (BOL, GRA)

BAYLISS 2757 (NBG, PRE); 4667 (NBG)

BLENKINSON J 14446 (J)

BOKELMANN NBG 67393 (NBG)

BOLUS 7731 (BOL); 8882 (BOL); 8883 (BOL); 8884 (BOL); 11827 (BOL, PRE); STE 24837 (STE)

BOS 1230 (PRE, STE); 1253 (PRE, STE)

BOTHA 2583 (PUC)

BOURQUIN 122 (NU); 253 (NU); 357 (NU)

BOURQUIN & LAWSON 1168 (NH, PRE); 1171 (NH, PRE)

BOWKER (GRA)

BREYER sub TRV 17848 (PRE); sub TRV 19552 (PRE)

BUITENDAG 209 (NBG, PRE); 271 (PRE); 1155 (NBG, PRE)

CLARKE 269 (PRU); 371 (PRE, PRU); 373 (PRE, PRU); 464 (PRE, PRU)

CODD 1076 (PRE); 6412 (PRE); 9312 (PRE); 9339 (GRA, PRE); 9362 (NH,PRE)

CODD & DE WINTER 5144 (PRE)

CODD & MULLER 325 (PRE)

COLEMAN 13 (NH, PRE); 65 (NH, PRE); 1103 (NH)

COLLINS sub TRV 9895 (PRE)

COMINS 1956 (GRA, PRE)

COMPTON 25075 (NBG); 25615 (PRE, SAM); 27287 (NBG, PRE); 28692 (NBG, PRE); 30608 (NBG, PRE)

COOPER 204 (PRE)

CRAWFORD 368 (PRE)

CULVERWELL 1235 (PRE)

DENLEY J 30699 (J)

DEVENISH 1647 (NU); 819 (NH, PRE)

DE WINTER & KILLICK 8922 (PRE)

DLAMINI NBG 49174 (NBG); NBG 49172 (NBG); PRE 55645 (PRE)

DOHSE & LINDAHL 94 (NH, PRE); 98 (NH, PRE)

DUTTON 47 (NH)

DYER 3153 (PRE)

EDWARDS D. 1312 (NU, PRE); 3250 (NU, PRE)

EICKER sn (ZULU)

ELAN-PUTTICK 16 (PRE)

ELIOVSON J 26989 (J)

ELLIS 2616a (PRE)

ESTERHUYSEN 12875 (BOL, PRE)

EVANS 112 (NH); 181 (NH)

FAIRALL 13 (NBG)

FISHER B.S. 590 (NH, NU); 752 (NH)

FISHER D.K SAM 66046 (SAM)

FITZSIMONS & VAN DAM sub TRV 26257 (PRE)

FLANAGAN 515 (BOL, GRA, NBG, NU, PRE, SAM); 1441 (SAM); 2574 (NH,
           PRE, SAM); 2608 (PRE, SAM); PRE 55637 (PRE)

FORBES 35 (NH, PRE); 605 (NH); STE 13501 (STE)

FORRESTER & GOOYEN 187 (PRE)

FOURCADE 233 (BOL, GRA)

FRITH 121 (J)

GALPIN 1287 (PRE); 3479 (BOL); 6303 (PRE); 9743 (PRE); 10090 (PRE);
        11005 (PRE); 11019 (PRE); 11024 (PRE); 11444 (PRE); 14457
        (BOL, PRE); 11858 (BOL, PRE); 11933 (PRE); BOL 32273 (BOL)

GEMMELL BLFU 5349 (BLFU); BLFU 6050 (BLFU)

GERSTNER 626 (PRE); 2936 (NH); 3845 (NH); 6005 (PRE); NH 28779 (NH)

GETLIFFE 113 (NU); NU 27810 (NU)

GIFFEN 837 (PRE)

GILL NH 22592 (NH)

GILLETT MRS. 1203 (BOL, NH)

GILLETT J.B. 3156 (BOL, PRE, STE)

GORDON-GRAY 94 (NU); 97 (NU); 1047 (NU); 1308 (NU)

GROBBELAAR 59 (PRU); 66 (PRE, PRU); 78 (PRE, PRU); 127
(PRE, PRU); 279 (PRE, PRU); 284 (PRE, PRU); 343 (PRE,
PRU); 649 (PRE, PRU); 999 (PRE, PRU); 1104 (PRE, PRU);
1337 (PRU); 1807 (PRU); 1821 (PRE, PRU); 2312 (PRU);
2324 (PRU); 2329 (PRU)

GUY 34 (NU, PRE)

HANEKOM 229 (PRE)

HARRISON 244 (NH, PRE)

HAYGARTH SUB WOOD 1061 (BOL, PRE)

HAYGARTH W. STE 9446 (STE)

HENDERSON 53 (BLFU)

HILLIARD 1095 (NU); 1134 (NU); 1227 (NU); 1336 (NU); 1344 (NU);
1365 (NH, NU); 1951 (NU); 2639 (NU);

HILLIARD & BURTT 3310 (NU); 6852 (NU)

HITCHINS 391 (PRE)

HOFMEYER PRE 55621 (PRE)

HOLT 207 (PRE)

HOWLETT 16 (NH, NU, PRE); 26 (PRE); 106 (NH, PRE)

HUNTLEY 195 (NH, PRE); 686 (NU)

HUTCHINSON 1759 (BOL); 2245 (BOL, PRE)

JACOBS 1757 (PRE)

JACOBSEN 2671 (PRE)

JARMAN & GUY 71 (NU)

JENKINS 7068 (PRE); sub TRV 7072 (PRE)

JOHNSON 369 (NBG); 391 (NBG)

JUNOD 46 (PRE); 182 (PRE); 4357 (PRE); 4382 (PRE); 5265 (PRE);
5267 (PRE); 5270 (PRE); sub TRV 5279 (PRE); sub TRV 5284
(PRE)

KALF 35 (NU); 36 (NU); 38 (NU)

KEIT NH 11142 (NH)

KEMP 1153 (PRE)

KILLICK 144 (NU, PRE); 1667 (PRE)

KLUGE 467 (PRE, PRU); 483 (PRE, PRU); 1222 (PRE)

KOTZE 51 (WIND)

KRIGE 139 (J)

LANG   sub TRV 32297 (PRE)

L'ANGE   86 (NU)

LAWN   3 (NH); 32 (NH); 72 (NH); 169 (NH); 217 (NH); 752 (NH);
              1807 (NH); 2031 (NH)

LAWSON   307 (NU); 479 (NH); 704 (NH)

LEIGHTON   2993 (BOL); 3083 (BOL, PRE)

LEISTNER   648 (PRE)

LETTY   248 (PRE); 460 (PRE)

LEWIS   SAM 61374 (SAM); SAM 61553 (SAM); 61554 (SAM); SAM 68719
              (SAM); SAM 69720 (SAM)

LIEBENBERG   2374 (PRE); 2551 (PRE); 2897 (PRE); 2947 (PRE); 8048
              (PRE)

LOUW   2165 (PUC, STE); 2730 (PUC, STE)

MACGREGOR   64 (NU)

MARTIN A.J.   061 (NU)

MARTIN B.   191 (NBG)

MAUVE   4099 (PRE)

McCLEAN   183 (PRE); 439 (NH); 496 (NH)

McDONALD   118 (E, K, NU, PRE)

MEDLEY WOOD   93 (BOL, SAM); NH 163 (NH); 209 (BOL, SAM); 508 (BOL,
              SAM); 644 (BOL, SAM); 790 (BOL); 817 (BOL, SAM); 3010
              (NH, SAM); 3103 (NH); 3129 (NH); 3134 (NH); 4936 (BOL,
              PRE, SAM); 4936 (GRA); 5350 (PRE); 5591 (PRE); NH 6416
              (NH); 9788 (NBG); 11845 (PRE)

MERXMULLER & GIESS 1862 (WIND)

MILLER   PRE 55638 (PRE)

MILLER O.B.   4279 (PRE)

MOGG   4399 (PRE); 4891 (PRE); 11921 (PRE); 12700 (PRE); 13072
              (PRE); 13455 (PRE); 33984 (J); J 36211 (J)

MOHLE   268 (PRE)

MOLL   1013 (PRE); 2471 (PRE); 2720 (NU, PRE); 3439 (NU, NH);
              4767 (NH, PRE); 5406 (NH); 5410 (NH); 5421 (NH)

MOLL & NEL   5610 (NH, PRE)

MOLL & STREY 3896 (NH, PRE)

MORGAN   70 (PRE)

MORRIS   175 (NU); 190 (NU); 195 (NU)

MOSS   3298 (J); 3298 (J, PRE); J 3299 (J); 3300 (PRE); J 14213
              (J); J 15784 (J); J 18018 (J)

MTOMBENI   26 (ZULU); 40 (ZULU)

MULLER   2352 (PRE)

MULLER & GIESS 544 (PRE, WIND)

NETSHIUNGANI (VENDA)

NICHOLAS   423 (NH); 433 (NH); 477 (NH)

NICHOLSON   105 (NH); 1200 (PRE)

OATLEY   26 (PRE)

OBERMEYER   sub TRV 29363 (PRE); sub TRV 30325 (PRE); sub TRV 30371
            (PRE)

OTTO   124 (PRE)

PARKHOUSE   NBG 16886 (NBG)

PEGLER   163 (PRE)

PHILLIPS E.P   PRE 55667 (PRE)

PHILLIPS J.   J 35347 (J)

POLE-EVANS 970 (PRE); 4549 (PRE)

POTT   5334 (PRE); 5335 (PRE)

PROSSER   1840 (PRE)

RANDLES   10 (NU)

REHMANN   8699 (BOL)

REPTON   5862 (PRE)

ROGERS   1259 (PRE); 11606 (J); 15059 (J); 15060 (SAM); 15061
            (J); 18410 (PRE); sub TRV 20707 (PRE); 23564 (NH); 26050
            (PRE); 28284 (GRA, STE)

ROSS   78 (NU); 208 (NU); 723 (BLFU, NH, NU); 775 (NU); 1679
            (NH, NU, PRE); 1822 (NH, PRE); 1994 (NH, PRE); NU 25765
            (NU); NU 25769 (NU)

ROSS & MOLL 1830 (NH, PRE); 1841 (NH, PRE); 2267 (NH, PRE)

RUDATIS   68 (STE); 115 (STE); 288 (PRE); 334 (PRE); STE 2089 (STE);
            STE 2339 (STE)

RUMP   NH 21063 (NH); 14-7-1929 (NU); Feb. 1931 (NU)

RYCROFT   2420 (NBG); 2601 (NBG)

SANDERSON   870 (NH)

S.A.R.   PRE 55639 (PRE)

SCHEEPERS   241 (PRE, PRU); 248 (PRE, PRU); 581, (PRE, PRU);

SCHEEPERS & HAASBROEK Alkaloid survey SKF no. 1140 (PRE)

SCHELPE   51 (BOL)

SCHLECHTER 3129 (BOL, GRA, PRE); 3354 (PRE); 4742 (PRE); 6668 (BOL);
            12100 (SAM); 12105 (SAM); 12275 (BOL, SAM)

SCHONKEN   15 (STE)

SCHONLAND   845 (GRA, PRE)

SCHRIRE	153 (NH); 262 (NH); 263 (NH); 264 (NH); 265 (NH); 266 (NH); 267 (NH); 268 (NH); 272 (NH); 273 (NH); 274 (NH); 275 (NH); 276 (NH); 277 (NH); 278 (NH); 283 (NH); 284 (NH); 285 (NH); 286 (NH); 287 (NH); 288 (NH); 289 (NH); 290 (NH); 291 (NH); 292 (NH); 293 (NH); 294 (NH); 296 (NH); 297 (NH); 332 (NH); 335 (NH); 340 (NH); 350 (NH); 356 (NH); 382 (NH); 385 (NH); 386 (NH); 392 (NH); 396 (NH); 339 (NH); 655 (NH); 661 (NH); 671 (NH); 716 (NH); 717 (NH); 855 (NH); 881 (NH); 882 (NH); 883 (NH).
SHUTER	59 (NU)
SIDEY	3876 (PRE), 3976 (NH, PRE); 4186 (PRE)
SIM	4057 (GRA, PRE)
SMITH	693 (PRE); 2331 (PRE)
STANTON	70 (NU)
STEPHEN, van GRAAN & SCHWABE	1197 (PRE)
STIRTON	39 (NU); 462 (PRE); 508 (PRE); 536 (PRE); 1753a (PRE); 1753b (PRE); 5362 (PRE); 8685 (NH)
STREY	2996 (NH, PRE); 3725 (PRE); 3873 (NH, PRE); 4103 (PRE); 4559 (NH, PRE); 4887 (NH, PRE); 4971 (NH, NU, PRE); 5486 (NH, PRE); 6354 (NH, PRE); 7151 (NH, NU, PRE); 7394 (NH, PRE); 7439 (K, NH, NU, PRE); 7843 (NH); 8530 (NH, PRE); 9618 (NH, NU, PRE); 10752 (NH, NU, PRE); 10937 (NH, PRE)
SWIERSTRA	PRE 55605 (PRE)
TAYLOR H.C.	4430 (STE)
TAYLOR R.H.	85 (NU)
THERON	1600 (PRE); 3612 (PRE, PRU)
THODE	A317 (NH, PRE); STE 3802 (STE); STE 3803 (STE); STE 3805 (STE); STE 6443 (STE)
THORNCROFT	893 (NH); Gov. Herb. 11361 (PRE)
THORPE	NH 29880 (NH)
TINLEY	343 (PRE); 1487 (WINO)
TOMLINSON	2/115 (NH)
TRAUSELD	375 (PRE)
TYSON	1165 (BOL); 1438 (SAM, STE); 1439 (SAM, STE); 1525 (PRE, SAM); 2144 (BOL); 2782 (PRE, SAM); 2816 (SAM); 3151 (PRE)
VAHRMEIJER	541 (PRE); 667 (NH, PRE)
VAHRMEIJER & HARDY	1627 (A) (PRE)
VAHRMEIJER & TOLKEN	8282 (PRE); 859 (PRE)

VAN DER MERWE D.D. PRE 58466 (PRE)

VAN DER MERWE P. 312 (PRE)

VAN DER SCHIJFF 965 (PRE, PUC); 1132 (PRE); 1325 (PRE); 2023 (PRE); 2419 (PRE); 2659 (PRE); 4332 (PRE, PRU); 4941 (PRE, PRU); 5066 (PRE, PRU); 5976 (PRE, PRU); 6437 (PRE, PRU)

VAN JAARSVELD 12 (NBG); 678 (NBG, PRE); 3800 (NBG);

VAN SON sub TRV 30688 (PRE)

VAN VUUREN 88 (PRE)

VAN WYK 915 (PRE, PUC)

VENTER F. 697 (PRE)

VENTER H.J.T. 7 (ZULU); 300 (BLFU); 570 (NH); 634 (NH); 729 (ZULU); 832 (ZULU); 2273 (ZULU); 2289 (BLFU); 2424 (PRE, ZULU); 3303 (ZULU); 3304 (ZULU); 3485 (ZULU); 4547 (BLFU); 4993 (PRE, ZULU); 4996 (ZULU); 5283 (BLFU); 5291 (PRE, ZULU); 5489 (PRE, ZULU)

VERDOORN PRE 58467 (PRE)

VOGT PRE 55600 (PRE)

VORSTER L.L. 15 (PRU)

VORSTER P. 2623 (PRE)

WAGER H.A. sub TRV 22462 (PRE); sub TRV 22988 (PRE); sub TRV 24101 (PRE); PRE 55633 (PRE)

WAGER V. C45 (PRE)

WARD 222 (NU); 584 (NU, PRE); 733 (NU, PRE); 1874 (NH, NU); 1875 (NH, PRE); 2155 (NU); 2406 (NH, PRE); 4361 (NH, PRE); 5381 (NH, PRE); 5389 (NH, NU, PRE); 5498 (NU); 5560 (NH, NU); 6263 (NU); 6375 (NH, NU, PRE); 6509 (NH, NU); (NU, PRE); 7601 (NU); 7696 (NH, NU

WATMOUGH 486 (PRE)

WEEKS 82 (J)

WELLS 1429 (NU); 2880 (GRA, NH, PRE); 3375 (GRA, PRE); 4263 (NH); 4266 (PRE)

WEST 1089 (PRE)

WILLIAMS 8 (NU)

WILLIAMS MISS sub TRV 7622 (PRE)

WILSON 35 (NU)

WYLIE SUB WOOD 8990 (NH); 10335 (GRA, PRE, SAM, STE)

YOUNG PRE 55596 (PRE); PRE 55607 (PRE)

ZEYHER 358 (SAM)

Pseudarthria hookeri

ACOCKS	1217 (PRE); 232136 (PRE)
ADLAM	SAM 15562 (SAM)
AHRENS	13 (NBG)
ALLSOP	800 (NU)

BARRETT	532 (PRE)
BAYLISS	1145 (PRE)
BIGGS	197 (PRE)
BOLUS	8885 (BOL); 10949 (BOL, PRE)
BOS	1300 (PRE, STE)
BOTHA	1335 (PRE, PUC)
BOULLE	8 (NU)
BOURQUIN	127 (NU)
BREYER	sub TRV 17844 (PRE); sub TRV 18387 (PRE); PRE 55685 (PRE)
BRITTEN	4753 (GRA, PRE)
BROWN & SHAPIRO	464 (PRE)
BUITENDAG	498 (NBG, PRE)
BURTT DAVY	1451 (PRE); 1546a (PRE); 2923 (PRE)

CHOLMONDELY	PRE 55672 (PRE)
CLARKE	47 (PRE, PRU)
CODD	5918 (PRE); 6015 (PRE)
CODD & MULLER	329 (PRE)
COETZER	211 (BLFU, PRU)
COLEMAN	66 (NH)
COLLINS	sub TRV 9892 (PRE)
COMINS	88 (NH, NU); 1948 (GRA, PRE)
COMPTON	24876 (NBG); 26606 (NBG, PRE); 27393 (NBG, PRE); 27393 (NBG, PRE); 31263 (NBG, PRE)
CRAWFORD	434 (PRE)
CROSS	86 (NBG)

DAVISON	91 (PRE)
DEVENISH	629 (PRE)
DIMOCK BROWN	356 (PRE); 482 (PRE)
DOHSE & LINDAHL	104 (NH, PRE)
DYER	3152 (PRE)

ELIOVSEN	J 27186 (J)
EDWARDS	6 (NU)
ELAN-PUTTICK	255 (PRE)

FLANAGAN	2534 (PRE, SAM); 2571 (PRE)
FRITH	141 (J)

GALPIN	776 (GRA, NH, SAM); 778 (PRE); 13727 (PRE); 14386 (PRE); BOL 32274 (BOL); BOL 32275 (BOL)
GERSTNER	6216 (BOL)
GORDON-GRAY	1372 (NU)
GROBBELAAR	448 (PRE, PRU); 2310 (PRU)

HARDING	sub TRV 5181 (PRE)
HARRISON	450 (NH, PRE)
HAYGARTH	STE 214 (STE)
HEMM	(VENDA, J, PRE)
HILLIARD	1325 (NH, NU)
HITCHINS	737 (NH, PRE)
HOLT	42 (PRE); 42 (NH); 192 (NH, PRE); 207 (NH)
HUNTLEY	209 (NH, NU, PRE)
HUTTON	50 (GRA)

INDIAN COLLECTOR	NH 17731 (NH); sub TRV 34012 (PRE)

JACOBSEN	2255 (PRE)
JENKINS	sub TRV 7077 (PRE); PRE 55702 (PRE); PRE 55703 (PRE)
JOHNSON	368 (NBG)
JUNOD	2369 (PRE); 4381 (PRE)

KILLICK	74 (PRE)
KLUGE	410 (PRE, PRU); 1183 (PRE)

LAWN	305 (NH)
LEACH	12109 (PRE)
LETTY	441 (PRE)
LIEBENBERG	2379 (PRE)
LOUW	2134 (PUC, STE)
LOVELL	PRE 55698 (PRE)

MACGREGOR	55 (NU)
MAGUIRE	689 (J)
McCALLUM	PRE 55668 (PRE)
McCLEAN	129 (PRE); 147 (PRE)
MEDLEY WOOD	802 (SAM); 802 (BOL); 802 (PRE); 1036 (BOL, SAM); NH 1491 (NH); 7402 (PRE); 9992 (NH)
MEEUSE	9884 (PRE)
MOLL	1527 (NH, NU, PRE); 2744 (NH, NU, PRE); 5265 (NH, PRE)
MORGAN	67 (PRE)
MORRIS	786 (NH, NU, PRE)
MOSS	18448 (J)
MUDD	PRE 55678 (PRE)
MULLER	2475 (PRE)
MURRAY	690 (PRE)
NICHOLSON	236 (NH)
OBERMEYER	319 (PRE); 484 (PRE)
PEGLER	697 (BOL, PRE)
PIERCE	6 (PRE)
POLE-EVANS	H. 17030 (PRE)
POOLEY & JOUBERT	2013 (E, K, NU, MO)
REHMANN	6281 (BOL)
REPTON	3482 (PRE)
ROBBERTSE	102 (PRU)
ROGERS	STE 13602 (STE); 24054 (PRE)
ROSS	85 (NU); 271 (NU); 771 (BLFU); 780 (NU)
RUDATIS	392 (STE)
RUMP	NH 20403 (NH)
SCHEEPERS	106 (PRE, PRU); 320 (PRE, PRU)
SCHLECHTER	4551 (BOL, GRA); sub TRV 2220 (PRE); sub TRV 13151 (PRE)
SCHLIEBEN	9478 (PRE); 10183 (PRE)
SCHRIRE	295 (NH); 397 (NH); 400 (NH); 484 (NH); 663 (NH); 857 (NH); 859 (NH); 872 (NH)
SMITH	PRE 55688 (PRE)
SMUTS	255 (PRE); 301 (PRE)
STEPHAN	298 (PRE): 581 (PRE)

STIRTON	1751b (PRE)
STREY	3322 (PRE); 4686 (NH, PRE); 9721 (NH, PRE)
THERON	2351 (PUC)
THODE	STE 3456 (STE); STE 6367 (STE)
THORNCROFT	402 (PRE); sub TRV 2849 (PRE)
TYSON	1440 (PRE, SAM, STE); 2046 (SAM)
VENTER	744 (ZULU); 870 (BLFU); 2300 (ZULU); 5212 (PRU, ZULU)
VERDOORN	2442 (PRE)
VAHRMEIJER	2403 (PRE)
VAN DAM	PRE 55684 (PRE)
VAN DER MERWE	106 (PRE)
VAN DER SCHIJFF	722 (PRE); 4577 (PRE, PRU)
VAN ELDEN	1 (PRE)
VAN ROOYEN	6 (NU)
VAN SON	sub TRV 30436 (PRE)
VAN WYK A.E.	2568 (PRU); 4044 (PRE)
WADE	NU 52896 (NU)
WAGER	C.30 (PRE)
WARD	2069 (NU, PRE); 2510 (NH, PRE); 7591 (PRE)
WATSON	3 (PRE)
WELLS	1111 (NU, PRE); 4270 (NH); NU 34142 (NU)
WERDERMANN & OBERDIECK	2116 (PRE)
WILLIAMSON	269 (PRE)
WILSON	20 (NU)
WOOD	156 (NU)

Alysicarpus

ACOCKS	9872 (NH, PRE); 13160 (PRE)
BARKER	2742 (BOL, NBG); 4282 (NBG)
BARRETT	348 (PRE)
BAUR	572 (SAM)
BOLUS	11074 (BOL); 11829 (BOL, PRE)
BOURQUIN	103 (NU); 371 (NU); 650 (PRE)
BREDENKAMP	1737 (PRE); 1739 (PRE); 1847 (PRE); 1865 (PRE)
BREDENKAMP & VAN VUUREN	139 (PRE); 293 (PRE)
BREYER	sub TRV 17056 (PRE); sub TRV 17857 (PRE); sub TRV 20903 (PRE); PRE 55731 (PRE); PRE 55733 (PRE)
BUITENDAG	302 (NBG, PRE)
BURKE	PRE 9323 (PRE)
BURTT DAVY	804 (PRE); 811 (PRE)
BUTHELEZI	114 (NH); 142 (NH); 150 (NH); 168 (NH); 218 (NH); 252 (NH)
CLARKE	131 (PRU); 262 (PRE, PRU); 263 (PRE, PRU); 470 (PRE, PRU); 523 (PRU)
CODD & DE WINTER	4884 (PRE); 4964 (PRE)
COETZEE B.J.	6063 (PRE)
COETZEE	NH 35014 (NH)
COETZER	103 (PRE); 135 (PRE)
COMPTON	28332 (PRE); 28348 (NBG, PRE)
COMINS	436 (NU); 1779 (GRA, PRE)
CULVERWELL	1183 (PRE); 1196 (PRE); 1325 (PRE)
CUTHBERT	NU 52685 (NU)
DEVENISH	929 (PRE)
DE WINTER	7692 (PRE)
DINTER	7628 (BOL, PRE, WIND)
DIXON	21 (NU)
DU PLESSIS	1136 (PRE, PRU)
ELAN-PUTTICK	246 (PRE)
ELLIS	2616b (PRE)

FISHER	743 (NH, NU)
FLANAGAN	416 (GRA, PRE, SAM); 2802 (NH, PRE)
FORBES	738 (NH)
FRANKISH	66 (NU)

GALPIN	1158 (GRA, NH, PRE, SAM); 3408 (BOL, PRE); 5779 (PRE); 9729 (PRE); 12975 (BOL, PRE)
GERMISHUIZEN	388 (PRE); 551 (PRE); 654 (PRE)
GERSTNER	4209 (NH); 6844 (PRE); NH 33781 (NH)
GERTENBACH	7021 (PRE)
GIFFEN	1070 (PRE); 1096 (PRE)
GORDON-GRAY	1128 (NU)
GORDON TRUSCOTT	7a (PRE)
GROBBELAAR	2 (PRE, PRU); 5 (PRU); 323 (PRE, PRU); 2320 (PRU)

HALL & SONS	PRE 55715 (PRE)
HANEKOM	1913 (PRE)
HILLIARD	1259 (NU); 1848 (NU); 1943 (NU)
HITCHINS	866 (PRE)
HUNTLEY	1502 (PRE)
HUTTON	1031 (GRA, NBG)

JACOBSEN	1588 (PRE)
JACOBSZ	768 (PRE); 805 (PRE)

KING	57 (PRE); 64 (PRE)

LAWN	1120 (NH); 1908 (NH)
LEEMAN	23 (PRE)
LEENDERTZ	399 (BOL, J, PRE); 407 (PRE, SAM); sub TRV 5985 (PRE); sub TRV 8754 (PRE); sub TRV 11298 (PRE)
LENNOX	NU 28057 (NU)
LIEBENBERG	2788 (PRE); 2789 (PRE); 3293 (PRE); 3298 (PRE); 5308 (NH); 5312 (NH); 8482 (PRE); 87231 (PRE)

MAUVE	5298 (NH)
MEDLEY WOOD	274 (NH); 6091 (BOL)
MERXMULLER & GIESS	1862 (WIND); 30098 (WIND)
MOGG	5960 (NH, PRE); 6143 (PRE); 6603 (PRE); 15064 (PRE)
MOLL	1057 (NU, PRE); 1505 (NH, NU, PRE); 1686 (NU, PRE); 2595 (NU, PRE)
MOSS	383 (J); 3490 (J); 13214 (J)
MOSS & ROGERS	517 (J); 602 (J); 993 (J)

OBERMEYER	148 (PRE); 1144 (PRE)
OBERMEYER & VAN NOUHUYS	sub TRV 27805 (PRE)

PEGLER	163 (PRE); 1459 (PRE)
PELLETIER	J 30510 (J)
PENNY	Col. Herb. 2388 (PRE)
POOLEY	726 (E, K, NH, NU)
POTT	5073 (PRE); sub TRV 15081 (PRE); 5345 (PRE)
PRELLER	139 (PRE)
PURCE	PRE 55727 (PRE)

RANGER	302 (PRE)
RATTRAY	616 (GRA)
REACHMOOR	pre 11854 (PRE)
REHMANN	461 (BOL)
REPTON	87 (PRE); 838 (PRE); 2767 (PRE); 2785 (PRE)
ROGERS	301 (GRA); sub TRV 5165 (PRE); 10931 (PRE); 14394 (J, PRE); 18294 (J); 21921 (PRE); 24860 (PRE); 25092 (J)
RUDATIS	131 (STE); 1365 (STE); 1729 (PRE)
RUMP	NH 20290 (NH); NH 20328 (NH)

SCHEEPERS	176 (PRE, PRU)
SCHLECHTER	3121 (PRE); 3221 (BOL, PRE)
SCHRIRE	269 (NH); 270 (NH); 271 (NH); 403 (NH); 667 (NH); 874 (NH); 909 (NH); 1120 (NH); 1320 (NH)
SHIRLEY	304 (NU); NU 32878 (NU)
SIM	19436 (PRE); 20175 (PRE, NU)
SMITH	1451 (PRE) 2443 (PRE)
SMUTS & GILLETT	2214 (PRE)
STEYN	995 (NBG)
STIRTON	5076 (PRE); 5190 (PRE); 5757 (PRE); 10516 (NH)
STREY	4808 (NH); 9115 (NH, PRE)

TAYLOR	55 (NH)
THEILER	PRE 55709 (PRE)
THODE	STE 6662 (STE)
TINLEY	751 (NU)
TYSON	23 (GRA, NH, PRE); 1441 (SAM, STE); 1196 (PRE, SAM); 2002 (BOL, NBG, PRE)

VAHRMEIJER & TOLKEN 905 (NH, PRE)

VAN DAM   21137 (PRE)

VAN DER SCHIJFF 437 (PRE); 1396 (PRE); 5290 (PRE, PRU); 5291 (PRE,
                 PRU); 5291 (PRE)

VAN RENSBURG   2 (NU)

VAN VUUREN   531 (NH)

VAN WYK   4712 (PRE)

VENTER   774 (ZULU); 1699 (NH, PRE); 1969 (ZULU); 3436 (ZULU);
                 3765 (ZULU); 4593 (BLFU, PRE)

VERDOORN   135 (PRE)

WAHL   sub TRV 15525 (PRE); PRE 55723 (PRE)

WARD   1512 (NH, PRE); 1796 (NH, NU, PRE); 1891 (NH, NU)
                 2426 (NH, NU, PRE); 8805 (PRE)

WILMS   5873 (PRE)

WYLIE   NH 28026 (NH)

YOUNG   A331 (PRE)

ZEYHER   SAM 32864 (SAM)

SAGP/SAAB 1/113 (PRE, PRU)

Lespedeza

EDWARDS   12 (NH)

HILLIARD   3888 (NH, PRE)

SCHRIRE   1368 (NH)

TAINTON   s.n. (NU)