TAXONOMIC STUDIES ON BRAZILIAN LEGUMES WITH FORAGE POTENTIAL - SESBANIA, LUPINUS

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St Andrews, November 1984

CERTIFICATE

I certify that REINALDO MONTEIRO has satisfied the conditions of the Ordinance and Regulations and is qualified to submit the accompanying application of Doctor of Philosophy.

Dr. PETER E. GIBBS

DECLARATION

I declare that the following thesis is a record of research carried out by me, that the thesis is my own composition, and that it has not been previously presented in application for a high degree.

Reinaldo Monteiro

ABSTRACT

The present study consists of a taxonomic revision of the New World species of *Sesbania* (Papilionoideae, Robinieae) and taxonomic studies on the unifoliolate species of *Lupinus* (Papilionoideae, Genisteae) in Brazil.

The genus *Sesbania* in the New World is here recognised as comprised of the subgenera *Sesbania* (with three native and three introduced species), *Daubentonia* (with five species) and *Agati* (one species, introduced). As part of the taxonomic revision of *Sesbania*, a survey on chromosome number and studies on pollen and seed morphology are presented.

In an outline treatment of the genus *Lupinus* in Brazil the problems associated with the ca. 16 multifoliolate species are reviewed. The unifoliolate species have been studied in detail and 13 species are recognised. A taxonomic account of the unifoliolate species with key, descriptions and illustrations and specimen citations is presented. A SEM survey of pollen grains and testa of *Lupinus*, with particular emphasis on the Brazilian unifoliolate species accompanies this study.

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1 . INTRODUCTION

The Leguminosae (or Fabaceae) is a very large and diversified family which comprises about 650 genera and 18,000 species (POLHILL, RAVEN & STIRTON, 1981). The family extends in all terrestrial habitats but much of its diversity is centred in areas of varied topography and distinct seasons (RAVEN & POLHILL, 1981). Because of their diversity and economic importance to Man, the legumes are a family of considerable interest.

Recently, POLHILL & RAVEN (1981) have provided a up-to-date synthesis of the family with many contributions from specialists who attended the "Kew International Legume Conference" (July 1978). In this work, POLHILL (1981) outlined a synopsis of the classification of the subfamily Papilionoideae as comprised of 32 tribes. Of these tribes, 440 genera and ca. 12,000 species (i.e., approximately 80 % of the whole family) are recognised.

In the present thesis, two genera placed widely apart in the tribal arrangement proposed by POLHILL (1981) are studied : Sesbania Scop., treated in the Sesbanieae or in the Robinieae, and Lupinus L. which belongs to the Genisteae. No obvious links between these two genera exist except by the fact that both are, naturally, members of the Papilionoideae. Rather, the practical reasons for this present study were based on the fact that the report of the project "Coleta, Identificação e Distribuição de Leguminosas Forrageiras Tropicais Brasileiras" (ROCHA, 1979) has shown that, among several other genera, Sesbania and Lupinus are rather poorly known in their taxonomy in the New World, particularly in Brazil. Since both genera would seem to have a potential use as either forage or green manure, mainly in the context of the agricultural exploitation of poor quality soils in Brazil, Sesbania and Lupinus were considered eminently suitable for taxonomic studies.

Sesbania was revised in Africa (GILLETT, 1963) and in Australia (BURBIDGE, 1965) but, despite its occurrence and diversity in the New World, no modern taxonomic revision has yet been provided, a gap that is filled by this thesis.

Lupinus, a genus with distinct distributions and morphological patterns in the New and Old World has recently received some attention for the latter area, where ca. 12 species are recognized (GLADSTONES, 1974; PLITMANN, 1981). However, because of the difficulties caused by nomenclatural problems and lack of extensive collection in the New World, its species (approximately 500, acc. DUNN, 1980) are less known. In the first instance, therefore, this genus is probably most amenable to taxonomic revision by way of detailed treatments of geographical sub-areas.

Originally, it was intended to include all Brazilian species of Lupinus in this taxonomic study. However, at an early stage it was discovered that D. B. DUNN* and A. M. PLANCHUELO had carried out a study of the Argentinian Lupinus species which included a number of Brazilian taxa and involved nomenclatural changes and specific limits (DUNN, pers. com.). Unfortunately, this "soon to be published" revision has still not appeared. Furthermore, DUNN

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has accumulated loans of Lupinus from temperate SE South America from many institutions so that these specimens are simply not available for study.

As a consequence, it was decided to restrict to the unifoliolate lupin species from Brazil for which at least adequate herbarium material, including types, could be obtained on loan.

2 . ECONOMIC USES

The association of Man with the Leguminosae is a very old one which has been studied by a number of authors and most recently analysed by ISELY (1982), who has summarised the ways that legumes support human cultures and suggested new techniques for broader uses and improvement of legumes for the future.

The centres of origin of the most important food legumes are correlated with the development of ancient human societies and their agricultural activities (ADAMS & PIPOLY III, 1980; GLADSTONES, 1982a; ISELY, 1982; HAWKES, 1983). Nevertheless, only very few of potentially hundreds of legume taxa have been cultivated by Man and are now known as the dominant agricultural sources among the Leguminosae. Furthermore, since plant breeding with its North Temperate dominance has placed more emphasis on cereals rather than on legumes, the legumes have been relatively neglected and our knowledge of potentially useful taxa is still in its infancy, particularly in the tropics (RACHIE et al., 1979). As a consequence, underdeveloped (tropical and subtropical) countries have not been able to acquire a full knowledge of the agricultural potential of their native legume crops.

With the growth of the world's population, agriculture can no longer be confined to the soils of natural high fertility (which can support cereals with minimum fertilising). Particularly in the tropics and subtropics farming has extended onto soils which demand heavy applications of nitrogen fertilizers. In Brazil, for example, agriculture has been extended into the areas of "cerrados" (savanna-like vegetation), which are distributed discontinuously between 4° latitude N to 24° latitude S and 42° - 65° longitude W.G., but which have their main core in central and central-eastern Brazil.

This vast area, which comprises more than 1.5 million km (ca. 2/5 of Brazil), includes one of the most important cattle ranching areas of Brazil, and also, increasingly, areas being brought into cultivation of cereals (HOMEM DE MELO, 1982; PASCHOAL, 1983). Interestingly, the climate is not a limiting factor of the "cerrado" vegetation distribution and the soils under this vegetation do not have water deficiency (CAMARGO *et al*., 1977; FERRI, 1960). These characteristics led to the preparation of climatic maps in which, based on the ecological requirements of each species, the following crops of major importance to Brazil were plotted : coffee, sugar-cane, citrus, cassava, rubber-tree, peanuts, rice, maize, soybeans and wheat (CAMARGO *et al*., 1977). The results showed that, theoretically, given improved, adapted cultivars to the different areas, the use of the "cerrado" soils with these crops is perfectly viable provided that fertilizers are added into the soil.

Despite its huge potential, expressed mainly by its area, location and topography, the "cerrados" have been little or wrongly exploited (PASCHOAL, 1983). The main obstacles to utilization of cerrado areas are due to the soil characteristics. About 56% of the Brazilian "cerrados" have Ferrasols (or oxiols) soils (HOEFLICH *et al*., 1976), which combine extremely low nutrient status with problems of high phosphate and aluminium toxicity (GOODLAND & POLLARD, 1973; GOEDERT & BLUMENSCHEIN, 1977; RATTER *et al*., 1977).

The needs for alkaline additives and fertilizers in such soils are extremely demanding in order to achieve commercial, competitive crop production and, due to the high costs of nutrients supplement, alternative means of increasing the nitrogen availability in the soil must be sought.

The role of leguminous taxa in this situation is clear because of their successful association with nitrogen-fixing organisms, thus improving the fertility condition of poor soils (ALLEN & ALLEN, 1981).

Almost all of the traditionally exploited legume crops belong to the tribes Vicieae, Phaseoleae, and Trifolieae, with few exceptions, e.g., Arachis of the Aeschynomeneae. These crops are generally adapted to base-rich, fertile soils and are nodulated by "fast-growing" strains of Rhizobium, which are also adapted to such soils (ALLEN & ALLEN, 1981; BERGERSEN, 1982). In contrast, the genera dealt with in the present work, Sesbania and Lupinus, belong to the Robinieae and Genisteae, respectively, and in Brazil species of both genera are found on poor quality soils such as the "cerrados" and seasonally inundated lowlands.

The tropics and subtropics already have a wealth of native legume taxa which are adapted to low-fertile soils but these taxa are either largely unknown or underexploited. This situation was emphasised by the recent Brazilian project **"Coleta, Identificaçāo e Distribuiçāo de Leguminosas Forrageiras Tropicais Brasileiras"** which collected native leguminous species for forage evaluation in an area encompassing southeast, central and eastern Brazil. The report of this project (ROCHA et al., 1979) states that of the 49 legume genera which were sampled almost all contained some collections which are still unidentified due to the lack of basic taxonomic revisions available for these taxa. *Lupinus*, *Sesbania*, *Zornia* and *Macroptilium* are examples of such genera among many others cited in this report for which difficulties were encountered in the identification of collected species. All of these genera are potentially useful and need to be more intensively studied, but a clear understanding of their taxonomy is a pre-requisite to an exploration of their agricultural use.

2.1 - *Lupinus*

Lupins are herbs or rarely shrubs which tend towards a variety of growth habits found in the Genisteae (POLHILL, 1976; BISBY, 1981) and many species are adapted to infertile, sandy, alkaline soils (GLADSTONES, 1980, 1982a). The nodulation of *Lupinus* species is typically achieved by the "slow-growing" strains of *Rhizobium* (ALLEN & ALLEN, 1981; CORBY, 1981; BERGERSEN, 1982) which survive better in such soils than the strains adapted to the Vicieae and Phaseoleae legumes.

Despite the fact that *Lupinus* is a large genus of some 200-300 species (NICHOLLS & BOHM, 1983), commercial lupin crops are largely restricted to the cultivation of just three species : *L. albus* L., *L. luteus* L. and *L. angustifolius* L. Historical, agricultural and agronomical aspects of these species have been discussed by GLADSTONES (1970), HONDELMANN (1984) and WILLIAMS (1984). All three are species of Old World origin which are cultivated for forage, grains, and soil improvement in eastern

Europe, south-eastern U.S.A., Australia, South Africa, Chile and New Zealand (GLADSTONES, 1981; CHATEL & ROWLAND, 1982; NULSEN, 1982). Two other species which are becoming fully domesticated are L. cosentinii Guss. and L. mutabilis Sweet., the former from Morocco and west Mediterranean, and the latter, the only New World species which has ever been cultivated on a large scale (WILLIAMS, AKHTAR & FALUYI, 1980; GLADSTONES, 1981, 1982a) comes from the highlands of South America, mainly Peru (RACHIE et al., 1979).

The development of lupins as commercially exploitable crop plants became possible only with the first selection of low-alkaloid cultivars in Germany in the late 1920's and 1930's (RACHIE et al., 1979; GLADSTONES, 1982b). These strains (the "sweet-lupins") have been thoroughly studied with regard to their nutritional values and the results show that the protein and oil content of the seeds is very high and that they are virtually free from the toxic and anti-metabolic factors which are common in the seeds of many other leguminous species that have been established as commercial varieties (GLADSTONES, 1981).

Several other biochemical properties are known for Lupinus species and although these studies relate to taxa that occur in the Old World (WILLIAMS, DEMISSIE & HARBORNE,1983) or in the temperate areas of North America (NICHOLLS & BOHM, 1983), it is assumed (MEARS & MABRY, 1971) that the alkaloid presence is a constant feature of the whole genus. Thus, although the Central- and South-American species have not been fully studied as yet in this respect it is expected that these taxa will also contain levels of alkaloids as high as the temperate species.

However, it is known that alkaloid-free, sweet-tasting types can be developed by conventional breeding methods (GLADSTONES, 1982b). Cross-compatibility studies between Old and New World species have been made on a small scale by FALUYI (1980) and WILLIAMS, AKHTAR & FALUYI (1980) and these studies suggest that crossing-barriers and genetical isolation between some of the species could be overcome. Other studies (RACHIE _et_ _al_., 1979) have shown that _L_. _mutabilis_ easily crosses with several North American species yielding fertile hybrids. This crossability between Old and New World taxa raises the possibility of incorporating alkaloid-free races/genes into the latter (GLADSTONES, 1980).

Thus, no fundamental barrier seems to exist to a wider use of _Lupinus_ in agriculture, provided that we obtain a better knowledge of the potential residing in the New World taxa and that the wild, bitter-seeded species are reduced in their alkaloid contents to acceptable levels.

2.2 - _Sesbania_

Among the genera of the Robinieae (_sensu_ POLHILL & SOUSA, 1981), _Sesbania_ is the only one that has been used as a tropical forage source. Species of this genus are almost all restricted to seasonally wet areas of the lowlands in the tropics and subtropics.

The sesbanias are known to nodulate well but although the nodulation response is promiscuous, it is also found to be often ineffective, that is, the plants nodulate with many non-specific strains of Rhizobium which might result in low nitrogen fixation (ALLEN & ALLEN, 1981; DATE & HALLIDAY, 1980).

The dominant type of nodule in the Robinieae is the "Astragaloid type", which is the commonest of all and also characteristic of the Mimosoideae, Mirbeliaeae (Caesalpinoideae) and several other tribes of Papilionoideae (CORBY, 1981; CORBY, POLHILL & SPRENT, 1983). This kind of nodule, in Sesbania, has some strains of Rhizobium that only produce nodules in host-plants of the same genus, i.e., strains growing in Sesbania plants nodulate all (or nearly all) Sesbania species but the degree of effectiveness varies markedly (BRISCOE & ANDREWS, 1938; ALLEN & ALLEN, 1981; DATE & HALLIDAY, 1981).

Despite this variable response in nodulation, it is reported by BERGERSEN (1982) that sesbanias can also nodulate on parts of the stem that have been submerged and that this process can be profuse and amounting to as much as 40g of fresh weight per plant. This factor, which may compensate to some extent for the ineffective nodulation on the roots, has led to Sesbania species being used as "green-manure" fertilizers as well as for forage plants. Species which have been employed in this way are : Sesbania bispinosa, S. emerus, S. grandiflora and S. sesban (BURKART, 1952; UPPAL, 1955; TURNER, 1959; COOK et al., 1974; RACHIE et al., 1979; ALLEN & ALLEN, 1981; ISELY, 1982).

However, the many possible agricultural uses of sesbanias is an area of research which is under active investigation in different parts of the world. Recently, projects on Sesbania were started in the Department of Agronomy and Soil Science of the University of Hawaii at Manoa (D.O. EVANS, pers. com. and mimeographed announcement) and in the Division of Tropical Crops and Pastures of the CSIRO at St Lucia, Australia (I.M.WOOD, pers. com.).

Two species already in cultivation are *Sesbania bispinosa* and *S. grandiflora*, the latter being the more important due to the diversified uses of its products : wood, pulp, paper, reforestation, food and gum, apart from the uses as forage and green manure (RACHIE *et al.*, 1979; ISELY, 1982). *S. bispinosa* provides almost the same basic products as *S. grandiflora* but it is particularaly adapted to grow on saline and alkaline soils.

One undesirable aspect of sesbanias is that since they grow fast and produce seeds freely, they can become troublesome weeds in association with some crops like rice (TURNER, 1959). In fact, 12 species of *Sesbania* are listed by HOLM *et al.* (1979) as weeds (or potentially weedy if not controlled) in several countries. Therefore, in introducing these plants to new areas much care will need to be exercised.

At the moment, all the New World species of *Sesbania*, except *S. emerus* (above cited) and *S. punicea* (a weed in the U.S.A. and South Africa - HOLM *et al.*, (1979), and an ornamental species in several countries), are unknown for their potential economic uses.

Any breeding program for improvement of sesbanias should include a preliminary study of the potential of the New World taxa in order to establish their genetic variability and relationships with the Old World species. The same applies to *Lupinus* because of the uncertainty about the number and limits of species in the Americas (NICHOLLS & BOHM, 1983).

Therefore, basic taxonomic revisions of these two genera are needed because such studies will permit accurate identification of species, facilitate communication of data about them, and, hopefully, give some insights into their evolutionary relationships.

3 . MATERIAL AND METHODS

3.1 - Herbarium

Herbarium specimens from the following Institutions were examined and annotated :

Arnold Arboretum of Harvard University (A); British Museum, (Natural History), London (BM); California Academy of Sciences, San Francisco (CAS); Botany School, University of Cambridge (CGE); Dudley Herbarium at California Academy of Sciences (DS); Royal Botanic Gardens, Edinburgh (E); Forest Herbarium, Department of Forestry, University of Oxford (FHO); Fairchild Tropical Garden, Miami (FTG); Conservatoire et Jardin Botaniques de La Ville de Genève (G); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); Lundell Herbarium at the Department of Botany, University of Texas, Austin (LL); Botanische Staatssammelung, Munich (M); Herbário Nacional de México, Universidad Autónoma de México (MEXU); Missouri Botanical Garden, St Louis (MO); Biology Department, New Mexico State University, Las Cruces (NMC); New York Botanical Garden (NY); Fielding-Druce Herbarium, Department of Botany, University of Oxford (OXF); Museum National d'Histoire Naturelle (P); Jardim Botânico do Rio de Janeiro (RB); San Diego Museum of Natural History, San Diego (SD); School of Botany, Trinity College, Dubllin (TCD); Department of Botany, University of Texas (TEX); Departamento de Biologia Vegetal, Fundação Universidade de Brasília (UB); Departamento de Morfologia e Sistemática Vegetais, Universidade Estadual de Campinas, Campinas (UEC); Pringle Herbarium, Department of Botany, University of Vermont, Burlington (VT); and Naturhistoriches Museum, Botanische Abteilung, Wiena (W).

Photographs of type specimens have been taken of all taxa for which type material was available. A set of these photographs have been donated to the Royal Botanic Gardens, Edinburgh (E). Photographs of CAVANILLES' type specimens were obtained from Jardín Botánico at Madrid (MA); of ELLIOTT's collection (Sesbania macrocarpa (Muehl.) Ell.) from the Charleston Museum at Charleston (CHARL), and of PAMPANINI's Sesbania tetragona Pamp. from Museo Botanico, Firenze (FI).

The distribution of species are shown in several maps, according to the exsiccata studied.

The citation of specimens are in alphabetical order of continents and countries and then by regions, states or territories, and collector's name. For North American Sesbania specimens the subdivisions of the United States for "Flora North America" (SHETLER & SKOG, 1978) were used (Figure 1a). For Sesbania and Lupinus in Brazil the five political regions recognised by the Brazilian Institute of Geography (CIVITA, 1976; Figure 1b) were employed.

3.2 - Micromorphological studies of seeds.

Studies were made on the testa topography and internal structure of Sesbania (and allied genera) and Lupinus seeds as seen by optical microscopes and the Scanning Electron Microscope (SEM). The seeds were mostly obtained from herbarium specimens or, in a few cases, recent collections made in the field, and via introductions to the University of St Andrews Botanic Garden

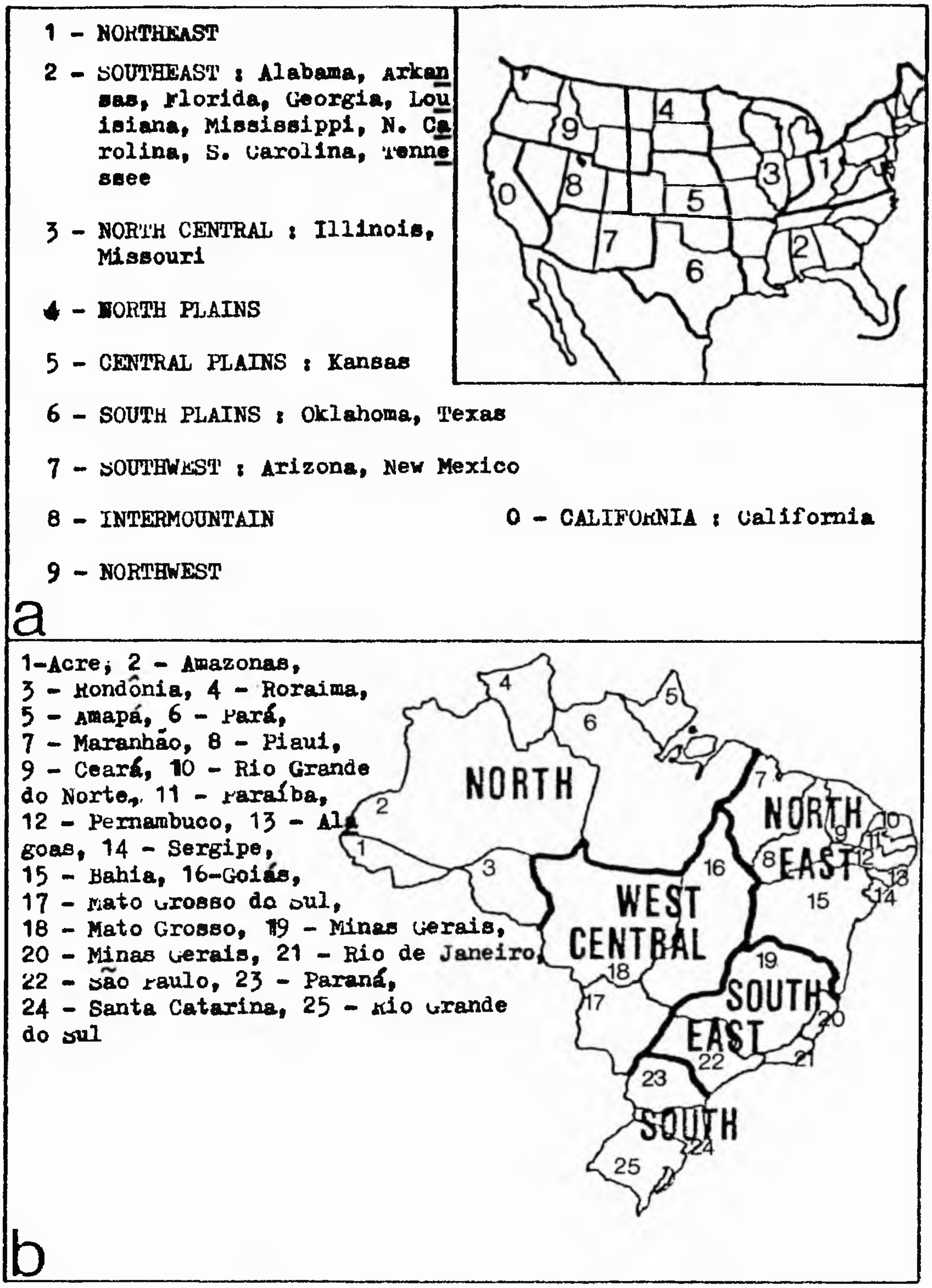

Figure 1 - Maps outlining regional classifications used for distribution purposes. A - North America (after SHETLER & SKOG, 1978, mod.) with list of states where Sesbania species were found.
B - Political geographical regions of Brazil, with a complete list of states and territories (after CIVITA, 1976).

(sections "Seed morphology" on *Sesbania* and *Lupinus*). Wherever applicable, voucher specimens were deposited at the Royal Botanic Garden, Edinburgh (E).

Seeds were examined and photographed using a KYOWA 805116 dissecting microscope and later used for drawings with a camera lucida apparatus. The preparation for the SEM involved washing the seeds for a short time (1-2 minutes) in absolute alcohol after which they were air-dried and mounted on stubs.

Transversal and sagittal sections through the middle of the hilum were made by simple fracture or cutting with a razor blade, following the techniques used by LERSTEN (1982) and LERSTEN & GUNN (1982) so as to display the internal morphology of the hilar region. Whole seeds and sections were mounted on a drop of colloidal silver paste on metal stubs and then coated for five minutes in a Polaron (Royal Botanic Gardens, Edinburgh) or EMSCOPE (Zoology Department, University of St Andrews) sputter coater. Observations were made at 15 Kv using a JEOL JST-200 scanning electron microscope and recorded on ILFORD FP4-120 film.

The terminology used throughout the seeds studies is that of POLHILL (1976) and GUNN (1981) for general seed morphological structures, LERSTEN (1981) for testa topography, and LERSTEN (1982) for seed coat anatomy.

3.3 - Palynology

Pollen material was obtained from herbarium specimens or from cultivated plants for *Sesbania punicea* (Cav.) Benth. and . *virgata* (Cav.) Pers. Pollen samples were first prepared for study using the standard acetolysis method of ERDTMAN (1969). After final centrifugation the samples were divided into two fractions, one was mounted in glycerine jelly on glass slides with paraffin wax-sealed cover slip and used for light microscopical studies. The remaining fraction of the acetolysed pollen was mounted in 95% ethanol on SEM specimen stubs and allowed to air-dry at room temperature before coating. Because the pollen grains are thin-walled, they were found to collapse during drying, even after several attempts of modified acetolysis times or using critical point drying (CPD) techniques. Indeed, the study of non-acetolysed grains with the SEM was found to be the most advantageous technique with many species. For this, dried grains lifted directly from herbarium specimens were mounted on specimen stubs covered with double-sided "Sellotape" and sputter-coated for five minutes using a POLARON or EMSCOPE sputter coaters. Observations were made at 15 Kv using a JEOL JST-200 SEM and recorded on ILFORD FP4-120 film.

3.4 - Cytology

Cytological preparations were made for counting somatic chromosome numbers of _Sesbania_ _emerus_ (Aubl.) Urban, _S_. _exasperata_ H.B.K., _S_. _grandiflora_ (L.) Pers., _S_. _punicea_ (Cav.) Benth., _S_. _virgata_ (Cav.) Pers. and _Glottidium_ _vesicarium_ (Jacq.) Harper. Seeds were obtained from recent collections or _via_ introductions to the University of St Andrews Botanic Garden.

Root tips were prepared for observations following the technique published by GIBBS & INGRAM (1982). The material was treated with 0.05% colchicine for about 1-2 hours and fixed in

Carnoy. The hydrolysis was made with 5N HCl, at 60 °C, for 15-20 minutes. The material was then squashed, stained with propionic-orcein. Although unequivocal counts could be made from these preparations, <u>Sesbania</u> chromosomes were found to be "sticky" and despite the use of various modified techniques it was not possible to obtain metaphase plates with non-overlaping chromosomes suitable for illustrations.

3.5 - Numerical analyses

Computer analyses of morphological characters of specimens of <u>Sesbania</u> <u>emerus</u> (Aubl.) Urban and of unifoliolate and multifoliolate species of <u>Lupinus</u> were made in addition to the taxonomic studies. The programs used for the clustering methods were devised by WISHART (1978) and are available as CLUSTAN in the Computer Laboratory at the University of St Andrews. The data were analysed with a Digital VAX-11/780 computer.

4 - TAXONOMIC REVISION OF NEW WORLD *SESBANIA*

4.1 -TAXONOMIC HISTORY

The first author to describe *Sesbania* species was LINNAEUS (1753) in the *Species Plantarum*, under the binomials *Aeschynomene sesban* L. and *Robinia grandiflora* L. Today, the former taxon is accepted as *Sesbania sesban* (L.) Merrill; the latter was transferred to *Sesban* by POIRET (1806) and subsequently to *Sesbania* by PERSOON (1807) as the species *S. grandiflora* (L.). Pers.

After LINNAEUS, the next reference given to a presently accepted *Sesbania* species was provided by PLUMIER (1757), who described a taxon under the name "*Emerus siliquis longissimis et angustissimis*" and now accepted as *Sesbania emerus* (Aubl.) Urban (see discussion under this species).

In 1763 ADANSON created the generic name *Sesban*, in which he included the two species "Emerus..." as treated by PLUMIER (*loc. cit.*) and *Aeschynomene sesban* L. The same author also created the genus *Agati*, to which the large-flowered species *S. grandiflora* was referred. The original citation of the name *Agati* was made by RHEEDE (1678) but, because it is pre-Linnean, the authority to this generic name is given to ADANSON (*loc. cit.*).

Subsequently, SCOPOLI (1777) published the name *Sesbania* which was treated as a more correct latin name than *Sesban* , and *Sesbania* Scop. is now a conserved name against *Sesban* Adans.

In his *Icones plantarum rariorum* and *Collectanea* JACQUIN (1786, 1787) published the species *Robinia vesicaria* Jacq. However, DESVAUX (1813) recognized that this plant actually differed from a true *Robinia* and created the genus *Glottidium* in order to accommodate this taxon, which he named *Glottidium floridanum* Desv. Subsequently, ELLIOT (1822) re-transferred the species to *Sesbania* with the resulting combination *S. vesicaria* (Jacq.) Ell. A number of subsequent taxonomic treatments variously accepted or rejected *Glottidium* as distinct from *Sesbania*, as is discussed below.

In 1797, CAVANILLES provided descriptions and illustrations of several New World species of *Sesbania*, either under *Aeschynomene* L. or *Piscidia* L., all based on cultivated specimens. Despite his mistaken generic concepts, CAVANILLES' descriptions are useful since they are precise and the species have their types deposited at the Madrid Herbarium (**MA**).

The fourth edition of *Species Plantarum*, published by WILLDENOW (1803), treated the then known species of *Sesbania* partly under *Coronilla* L., a genus regarded as belonging to the Galegeae, and partly under *Piscidia* L., a member of the Tephrosieae. However, two authors who brought together all the species of *Sesbania* thus far known were POIRET (1806) who recognised eight species, and PERSOON (1807) who accepted nine taxa, but in the treatments by both of these authors no new species were described from the New World.

RAFINESQUE (1817), in his *Florula Ludoviciana*, ignored the generic name *Sesbania* and treated the genus as *Darwinia* Raf. If the latter name had already been published, he proposed *Monoplectra* Raf. as a substitute. Although confusing and of little taxonomic value, his work is valuable as the first regional record of plants of southern North American states (EWANS, 1967).

DeCANDOLLE, in Volume 2 of his extensive work, *Prodromus...* (1825) accepted the genus *Sesbania* for which he recognised 17 species. DeCANDOLLE's treatment was conservative in that he considered *Agati* (with *A. grandiflora* (L.) Desv. and *A. coccinea* (L.f.)Desv.) and *Glottidium* (with *G. floridanum* Desv.) as distinct genera. He referred the species with winged pods to the new genus *Daubentonia* DC. which was described, almost simultaneously, in his *Mémoires sur la famille des Legumineuses* (DeCANDOLLE, 1826) and the *Prodromus* (*loc. cit.*) in which he grouped two species, *D. punicea* (Cav.) DC. and *D. longifolia* (Cav.) DC., which differed from *Sesbania* in calyx and pod characters and in their American distributions.

DON (1832) accepted DeCANDOLLE's treatment of *Sesbania*, with *Agati*, *Daubentonia* and *Glottidium* as distinct genera and provided short descriptions for two new species of *Sesbania*, *S. cassioides* and *S. peruviana*, from northern South America (both here treated as synonyms of *S. emerus* (Aubl.) Urban).

BENTHAM (1859) in his contribution to Von MARTIUS' monumental work *Flora Brasiliensis*, listed and provided descriptions of three species of *Sesbania* for Brazil, which were also found in Argentina, Paraguay, and Uruguay. These taxa were classified in two sections : sect. *Sesbania* (containing *S. exasperata* H.B.K.) and sect. *Daubentonia* (with *S. punicea* (Cav.) Benth. and *S. marginata* Benth., the latter being a synonym of *S. virgata* (Cav.) Pers.).

Later, BENTHAM (1865) treated the genus as being a natural group that could be divided in three sections, which were recognised on the basis of fruit characters : sect. *Eusesbania* (with long, linear, many-seeded pods), sect. *Daubentonia* (short to long but 4-winged, several-seeded pods) and sect. *Glottidium* (with short, beaked, 2-seeded pods). With this treatment the group of species with winged pods which had been segregated by DeCANDOLLE (1825) as *Daubentonia*, a distinct but allied genus to *Sesbania*, was demoted by BENTHAM (*loc. cit.*) to sectional level with four species, three in the New World and one in Africa. Furthermore, the genus *Agati* Desv. was reduced to a synonym of the section *Eusesbania* along with *Darwinia* Raf. and *Monoplectra* Raf.

BAKER (1871) erected BENTHAM's sections *Eusesbania* and *Daubentonia* to subgeneric level and provided descriptions for nine species of *Sesbania* for tropical Africa, eight of which under his *Sesbania* subgenus *Sesbania* (pods not winged) and with *Sesbania tetraptera* Hoechst. ex Baker in the new subgenus *Daubentonia* because of its 4-broadwinged pods. Subsequently BAKER (1876) also erected *Agati* to subgenus of *Sesbania*.

A similar treatment was given by TAUBERT (1893) in ENGLER & PRANTL's *Pflanzenfamilien*, where he recognised three subgenera in *Sesbania* (*Eusesbania*, *Daubentonia* and *Glottidium*).

The same point of view was followed by most taxonomists until SMALL (1903), who re-established the generic name *Sesban* (composing the subgenus *Eusesbania* as mentioned above), and recognised as distinct genera *Agati*, *Daubentonia* and *Glottidium*. Again, the basis for such generic splitting was made in fruit morphology, but it was not totally accepted by PHILLIPS & HUTCHINSON (1921), in a revision of the African species of *Sesbania*. These authors treated the genus semi-conservatively, reconizing the sections *Eusesbania* and *Daubentonia* but accepting *Glottidium* as a different genus, as proposed by SMALL (1903).

Daubentoniopsis was another generic name added to this nomenclatural complex by RYDBERG (1923, and later, 1924), which he applied to the species *Daubentoniopsis longifolia* (Cav.) Rydb., with characteristics intermediate between those of *Daubentonia* and *Sesbania sensu stricto*. All five genera (*Sesbania*, *Daubentonia*, *Agati*, *Daubentoniopsis* and *Glottidium*) constitute the subtribe Sesbaniineae of the Galegeae as proposed by RYDBERG (1923).

The species *Sesbania brenningii* Harms, from nothwestern South America (HARMS, 1923), was transferred by BURKART (1969) to a new genus, *Yucaratonia*, on the basis that it has leaves and flowers similar to *Sesbania* but a conspicuous nectar disc below the carpel (absent in all *Sesbania* species) and woody, dehiscent pods. In the present revision, this interpretation by BURKART (*loc. cit.*) is fully accepted and *Yucaratonia* treated as belonging to the tribe Robinieae.

The African and Southern Arabian species of *Sesbania* were revised again by GILLETT (1963), who accepted the views of BENTHAM (1865) and TAUBERT (1893) as to generic limits except that *Glottidium* was maintained as a segregated genus because of the striking differential characters in the pod and seeds. GILLETT (*loc. cit.*) also transferred the two species *Sesbania tetraptera* Hochst. ex Baker and *S. rogersii* Phill. & Hutch.*, which are the

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* G. LEWIS (Royal Botanic Gardens, Kew - pers. com.) proposes to reduce *S. rogersii* to a subspecies of *S. tetraptera* in his treatment of the African species for the *Flora Zambesiaca*.

only African taxa with 4-winged legumes, to a new subgenus *Pterosesbania* Gillett on the basis that the flowers differ from the *Daubentonia* species by the presence of the basal tooth in the wing and keel petals. Therefore, GILLETT (1963) recognised *Sesbania* with four distinct subgenera, i.e., subgen. *Sesbania*, subgen. *Agati* (both comprised of species with non-winged pods), sugen. *Daubentonia* (New World species with 4-winged pods), and subgen. *Pterosesbania* (Old World species with 4-winged pods).

More recently, BURBIDGE (1965), who accepted GILLETT's treatment of *Sesbania* in four subgenera revised the Australian species of *Sesbania* which, except for a solitary representative of the subgenus *Agati*, *Sesbania formosa* (F. Muell.) Burb., all belong to the subgenus *Sesbania*, and LEWIS (pers. com.) has completed a revision of the East African species which will be published in the *Flora Zambesiaca*.

Thus, it can be seen from this synopsis of the taxonomic history of *Sesbania s.l.* that no modern taxonomic treatment of the genus throughout its range exists, with the New World area in particular lacking a modern synthesis, and that varying views as the limits of the genus, and the circumscription of splinter taxa have been put forward by recent authors.

The study presented in this thesis provides a taxonomic revision of the New World species of *Sesbania s.l.* recognising the genus as represented by three subgenera in this area (subgen. *Sesbania*, subgen. *Daubentonia* and subgen. *Agati*). It also aims to give a re-evaluation of the subgeneric limits of the genus as a whole.

4.1.1 - CONSPECTUS

The genus *Sesbania* is here recognised as being divided in the following subgenera:

subgen. *Sesbania*

The subgenus *Sesbania* is the largest one and it is represented by 30 species, 11 subspecies and 10 varieties in Africa and southern Arabia (GILLETT, 1963); nine species and four varieties in Australia (seven species are native, BURBIDGE, 1965); *ca.* ten species in Asia (*Index Kewensis*), and six species in the New World, of which three are introduced.

subgen. *Agati* (Adans.) Baker

The subgenus *Agati* is comprised of two closely related species : *S. formosa* (F. Muell.) Burb. of Australia, and *S. grandiflora* (L.) Pers. which is of Old World origin and cultivated elsewhere. The extension of *S. grandiflora* into southeast Asia is followed by some modifications in the calyx, flower and leaflet shape which become more evident in Australia, mainly in the western region of that country (BURBIDGE, 1965). Although plants having these modified characteristics were earlier treated as *S. grandiflora*, BURBIDGE (*loc. cit.*), in the revision of the Australian species of *Sesbania* recognised enough differential characters to treat them as belonging to a distinct species, *S. formosa*.

S. tomentosa Hook.& Arn., a remarkable species from Hawaii has been treated as *Agati* (RYDBERG, 1924). Only a single specimen of this taxon, not in good condition, has been studied, therefore the author is not able to confirm the inclusion of S. tomentosa in the subgen. Agati.

subgen. Daubentonia (DC.) Baker and subgen. Pterosesbania Gillett

The species with 4-winged pods are split into two subgenera; one of them, subgen. Daubentonia, is native in the New World with five species, and the other, subgen. Pterosesbania, is represented by only one species (S. tetraptera Hoechst ex Baker) distributed in southern Africa.

NEW WORLD SPECIES OF *SESBANIA*

(introduced species are indicated by an asterisk)

- subgen. *Sesbania*
  - *S. bispinosa* (Jacq.) W.F. Wight*
  - *S. emerus* (Aubl.) Urban
  - *S. exasperata* H.B.K.
  - *S. oligosperma* Taub.
  - *S. sericea* (Willd.) Link*
  - *S. sesban* (L.) Merrill*

- subgen. *Daubentonia* (DC.) Baker
  - *S. cavanillesii* S. Watson
  - *S. drummondii* (Rydb.) Cory
  - *S. macroptera* Mich.
  - *S. punicea* (Cav.) Benth.
  - *S. virgata* (Cav.) Pers.

- subgen. *Agati* (Adans.) Baker
  - *S. grandiflora* (L.) Pers.*

4.2 - TAXONOMIC CHARACTERS

4.2.1 - GENERAL MORPHOLOGY

Habit - The sesbanias in general are treelets (subgenera *Agati* and *Daubentonia*), shrubs (most species of the subgenus *Sesbania*) or subshrubs with a herbaceous growth (some species of subgenus *Sesbania*). The differences in habit are not sufficiently outstanding to be important, and those that occur are not always recognizable in herbarium specimens due to their fragmentary nature and lack of adequate habit description.

Vestiture - All New World native species of *Sesbania* are glabrous except for the young shoots which may covered with rather stiff hairs; these may be lost as the leaves mature or may persist as a very sparse cover on the leaflets. Some African species of *Sesbania* subgen. *Sesbania* have the stems , leaf rachis, and leaflets covered with a persistent pubescence. The observation by GILLETT (1963) that in the African species the presence of hairs on the style is associated with a lack of indumentum on other parts of the plant cannot be used for the New World taxa.

Stipules - These are always present on very young shoots but they are caducous in all species. Stipules are commonly narrowly-lanceolate to linear-acuminate and up to 10 mm. In general, the New World species have much shorter stipules than the Old World ones.

Leaves - The leaves of all species are paripinnate and there is a vestigial segment at the terminal end of the rachis. The leaflets are usually paired at the base but often irregularly placed along the upper part of the rachis, which may have a channel on the adaxial face. They are linear-oblong with obtuse or obtuse-apiculate (or acuminate in S. cavanillesii S. Watson) apices, and have oblique-obtuse bases and short petiolules. Size, shape and number of leaflets have been found to be of little diagnostic use for most of the New World taxa despite the fact that these characters have been used in works on African species (PHILLIPS & HUTCHINSON, 1921; GILLETT, 1963). Early deciduous subulate stipels are present at the bases of the petiolules or adjacent to them, where the leaflets are very irregularly arranged.

Although METCALFE & CHALK (1950) stated that the stomata in the Papilionoideae were very variable at the tribal level or even within a genus, data recently published show that, in general, some features concerning stomata can be used quite effectively at the generic and infrageneric levels (for example, in Crotalaria L. (KANNABIRAN & KRISHNAMURTHY, 1974), Genisteae (SAINT-MARTIN, 1976), and several other genera of the three subfamilies (LEELAVATHI, RAMAYYA & PRABHAKAR, 1980)).

The stomata on the leaflets of species of Sesbania have been surveyed by STABER (1909), METCALFE & CHALK (1950), SHAH & GOPAL (1969), and GILL, OLABANJI & HUSAINI (1980, 1982). Because these works do not include the New World species of Sesbania, a survey of the stomata in these taxa, and in Glottidium and Yucaratonia, (both genera of the Robineae) was carried out in connection with the taxonomic characters of the genus and with the ecological adaptations present in these groups (see section 4.4.2).

The pattern present in Sesbania is that all species so far surveyed have amphistomatic leaflets except for S. bispinosa which is epistomatic. Glottidium also shows an amphistomatic pattern but Y. brenningii has hypostomatic leaves, what suggests that other genera of Robinieae might have a pattern of stomata distribution distinct from Sesbania.

Inflorescence - The flowers are in racemes which develop in the axils of the upper, immature leaves and which usually bear from 2-5 flowers (but up to 15-17 in S. virgata (Cav.) Pers. or 18-25 in S. macroptera Mich.). The pedicels are slender and generally longer than the calyx; variation in pedicel length is not diagnostically significant at specific level but very important to differentiate Sesbania from Glottidium Desv. and Yucaratonia Burk. since the species of the latter genera have very long pedicels. At the base of the calyx tube there is a pair of bracteoles, which are deciduous.

Calyx - The tube is more or less cupular when young, but becomes campanulate at anthesis and broadly so below the young pod. It is slightly asymmetrical and in most species the five lobes are usually similar but the upper pair may be shorter or larger in species of subgen. Daubentonia and subgen. Agati.

The venation in the calyx consists of main nerves for each lobe and a fine reticulum of veinlets. In S. exasperata submarginal nerves in the sinus are associated with minute hairs on the internal face.

The colour of the calyx is variable in different shades of green but not significant; nevertheless, the dark pigmentation of the tips of the lobes in species of the subgen. *Sesbania* may be diagnostically useful to separate it from the subgenera *Agati* and *Daubentonia*.

Corolla - The standard petal varies from broadly-ovate through rhomboidal to broadly-obovate. Care is needed when using the shape of the limb as diagnostic as it has been found that the shape may change with the growth of the limb and as the standard becomes reflexed.

The corolla is always glabrous and this feature seems to be an excellent generic character when the genus is compared to Robinieae taxa. The recent treatments of *Sesbania* all agree on the constancy of this character (RYDBERG, 1923, 1924; GILLETT, 1963; BURBIDGE, 1965).

All the native New World species of *Sesbania* have yellow to yellowish corollas except for *S. punicea* which has red flowers. In some taxa there are conspicuous dark spots or streaks on the outer surface of the limb of the standard, as in *S. exasperata*, *S. emerus*, *S. macroptera* and *S. virgata*.

A useful character at subgeneric and specific levels is the nature of the pair of appendages, tubercles or calli at the base of the limb of the standard. The importance of these was first noted by PHILLIPS & HUTCHINSON (1921) and extensively used by GILLETT (1963) for the African species and by BURBIDGE (1965) in the revision of *Sesbania* in Australia. In the subgenus *Sesbania*, these structures are appendages that have their base adnate with the claw of standard but extend to the base of the limb where they may project freely. BURBIDGE (1965) mentions that one of the endemic species of subgen. *Sesbania* in Australia, *S. campylocarpa* (Domin) Burb., the appendages are so reduced that can be interpreted as absent or as a thickening of the claw.

These structures may be absent, as in subgen. *Agati* and some species of subgen. *Daubentonia* (*S. cavanillesii*, *S. drummondii* and *S. macroptera*). However, *S. punicea* and *S. virgata*, also of subgen. *Daubentonia* have a pair of distinct calli located on the upper portion of the claw, close to the base of the limb of the standard.

The wing petals are narrow, with a slender , strongly curved claw, and a slightly curved or oblique limb which in the species of subgen. *Sesbania* has a tooth at the upper basal angle; this structure is absent in the subgen. *Daubentonia*. Adjacent to this lobe the petal is marked by irregular striae whose abundance varies from species to species but always with the same lamellate pattern.

The keel petals have slender claws which are almost as long as the broadly and obliquely-triangular or triangular-ovate limbs. As in the wings, an upper basal tooth is present in the species of the subgen. *Sesbania* (except in *S. oligosperma* Taub.) but absent in the members of the subgen. *Daubentonia*.

Androecium - The androecium is diadelphous, with nine stamen filaments fused for part of their length in a glabrous sheath and one filament free. This free dorsal filament has a conspicuous bend near its base which corresponds to the auricles on the base of the staminal sheath (Figures 2,3,4). The sheath is usually longer than the claw of the keel and reaches the outer angle of

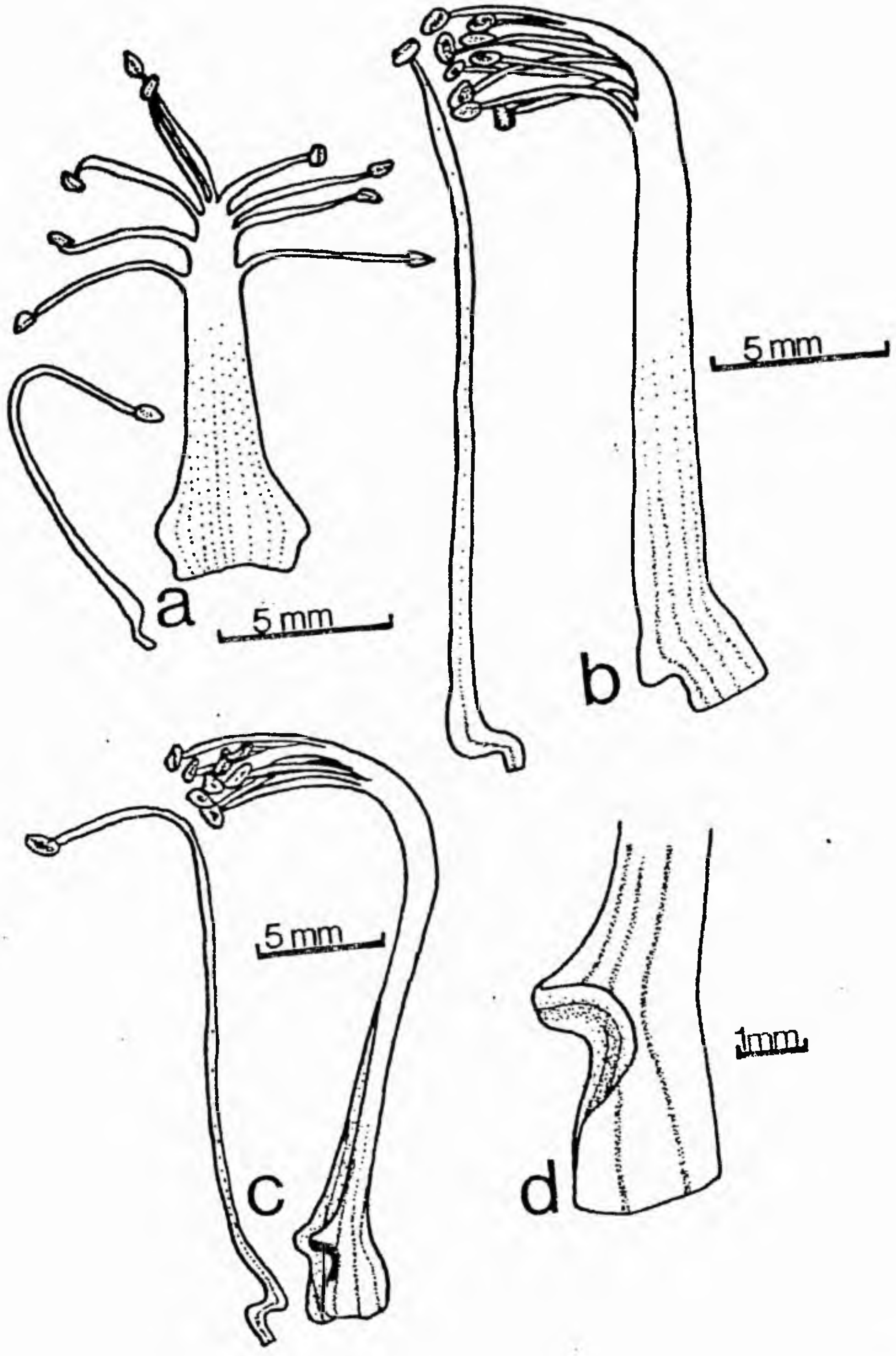

Figure 2 - Androecium of New World species of *Sesbania* subgen. *Sesbania*. a - *S. emerus*; b - *S. exasperata*; c,d - *S. oligosperma* (d, detail of base of the sheath).

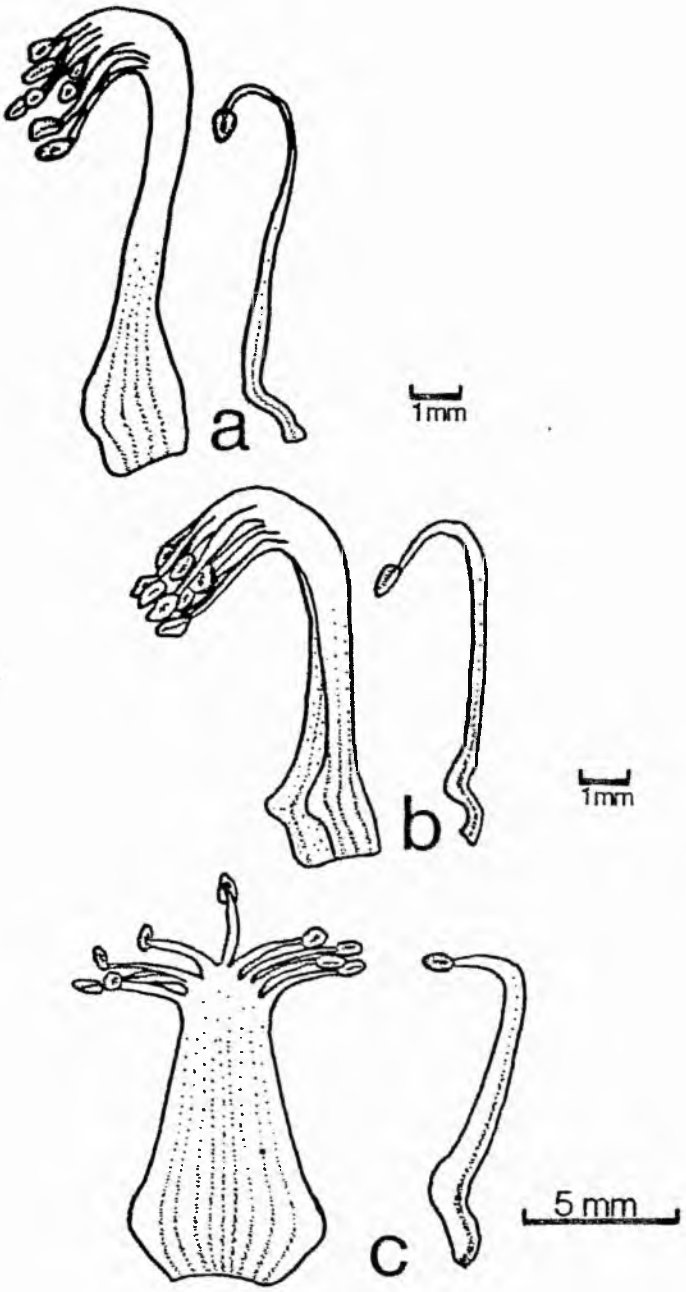

Figure 3 - Androecium of Old World species of *Sesbania* subgen. *Sesbania* introduced in the New World. a - *S. bispinosa*; b - *S. sericea*; c - *S. sesban*.

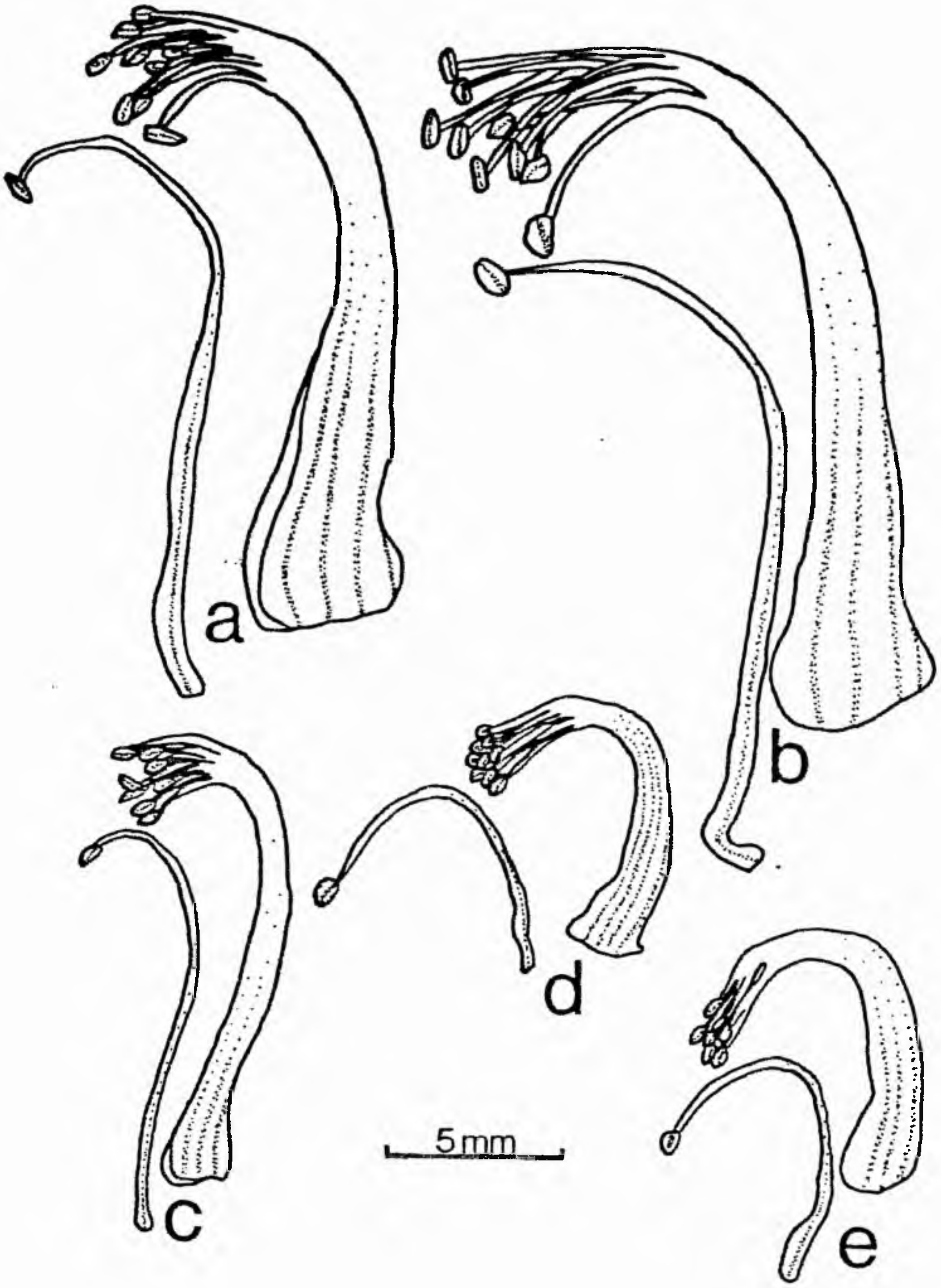

Figure 4 - Androecium of species of Sesbania subgen. Daubentonia.

a - S. cavanillesii; b - S. punicea; c - S. drummondii;

d - S. virgata; e - S. macroptera.

the curve, so that the free parts of the filament are upcurved. The anthers, arranged in two series of five, are generally ovate in the smaller-flowered species, although in the others they may be lanceolate, with the connective broadening towards the base.

Pollen grains - Pollen grains are treated separately in the section "Palynology".

Gynoecium - The slender, flattened ovary is about as long as the staminal sheath, with the style upcurved between the free parts of the filaments. The stigma is capitate (Figure 5). The number of ovules present varies from 4-5(-9) in subgen. Daubentonia to 20-25(-40) in subgen. Sesbania.

Pods - The presence of wings or thickened margins on the pod which characterizes subgen. Daubentonia is a striking feature. Another pod character, surface texture, was used by BURBIDGE (1965) to distinguish the Australian species of Sesbania subgen. Sesbania but very little on this respect has been found useful as a diagnostic character in the New World taxa.

Seeds - The seeds are treated under the section "Seed morphology".

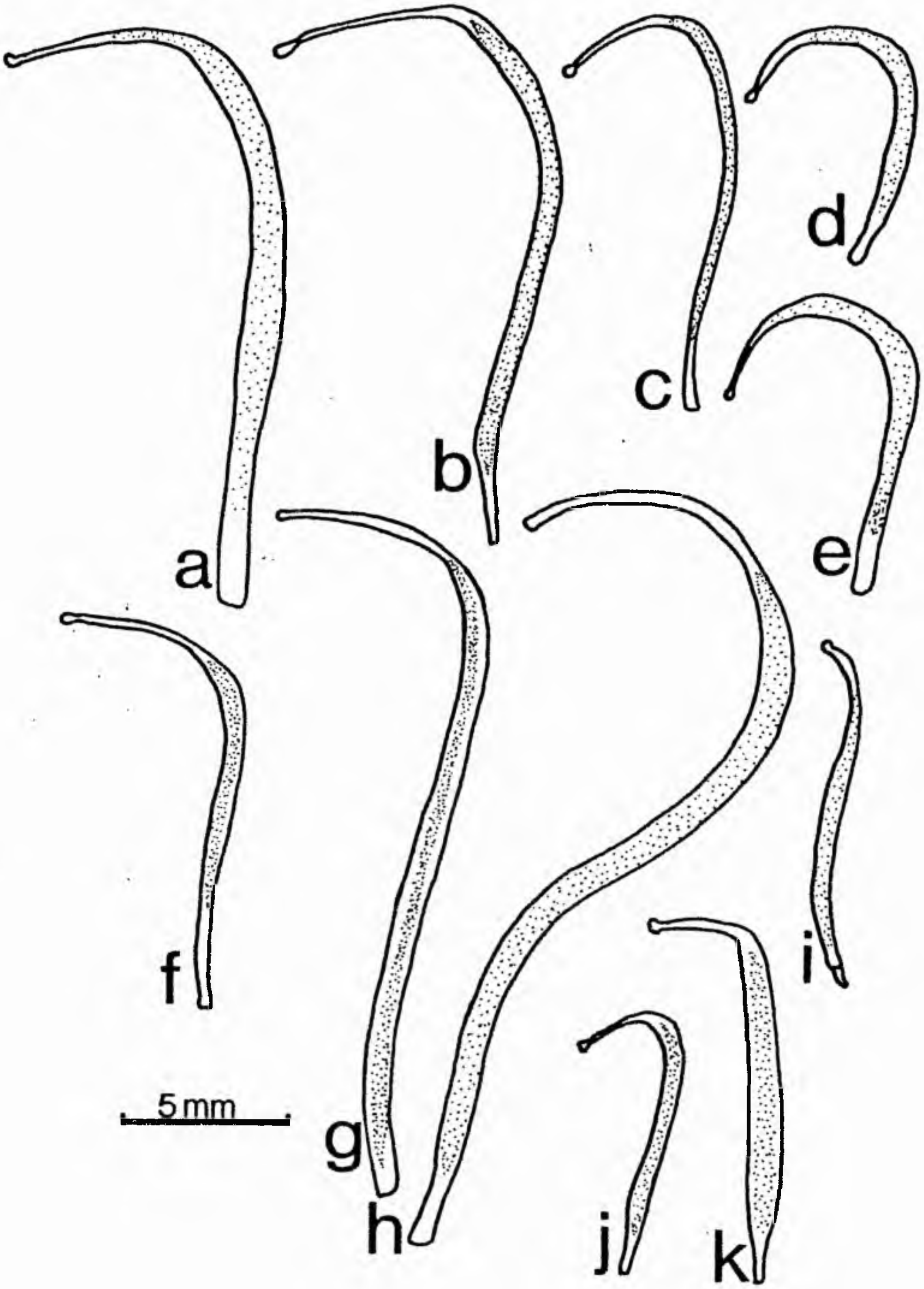

Figure 5 - Gynoecium of species of Sesbania. Subgen. Daubentonia : a - S. cavanillesii, b - S. punicea, c - S. drummondii, d - S. virgata, e - S. macroptera. Subgen. Sesbania : f - S. emerus, g - S. exasperata, h - S. oligosperma, i - S. bispinosa, j - S. sericea, k - S. sesban.

4.2.2 - PALYNOLOGY

In the present work, a survey of the pollen grains of the New World species of Sesbania subgen. Agati, subgen. Daubentonia and subgen. Sesbania, and also of subgen. Pterosesbania (Africa) was made by SEM microscopy for their external exine morphology (Table 3 and Figures 6-11). The mean polar and equatorial diameters were established in acetolysed pollen grains (ERDTMAN, 1969) using light microscopy (Table 5).

With the exception of S. tetraptera (subgen. Pterosesbania) species of Sesbania from the Old World were not studied here because I.K. FERGUSON & G. LEWIS * (unpublished data) have already made an extensive palynological survey of these taxa together with some species from the New World. They (FERGUSON & LEWIS, pers. com.) found that pollen grain features are of little taxonomic value when the Old and New World species of Sesbania are compared since the pollen grains of both regions are extremely similar in their characteristics. Therefore, in the present study the illustrations of S. sesban pollen grains from Africa published by FERGUSON & SKVARLA (1981) were taken as the pattern for the Old World species but, because of the special interest in the winged-pod subgen. Pterosesbania (vis-a-vis) subgen. Daubentonia), material of S. tetraptera was included in the survey of New World species to permit a detailed analysis to be made. For comparison, SEM studies were also carried out for some species of other genera of the Robinieae (Table 4).

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*Royal Botanic Gardens, Kew

Published accounts of pollen studies on Sesbania species are sparse and few electron micrographs have been published. Unfortunately, the revisions of the African (GILLETT, 1963) and Australian (BURBIDGE, 1965) species give no data for pollen grains of the native taxa.

A list of the available data on palynological studies of Sesbania is given in Table 1. In general, previous pollen studies have encompassed a single or very few species of limited geographical areas.

DANA & DATTA (1961, Table 1) based their studies on non-acetolysed pollen grains so that some of the aperture details are certainly lacking. The data given by BAQUAR & AKHTAR (1968) is also based on non-acetolysed grains. Although the latter authors presented measurements of pollen grains of S. bispinosa, S. concolor and S. sesban (three "varieties" of S. sesban), they actually did not specify whether their single figures were for polar or equatorial diameter. Furthermore, aperture type was described only for S. sesban.

VISHNU-MITTRE & SHARMA (1962) and LIEUX (1982) used acetolysed grains and the latter author also used SEM microscopy for his observations. A large part of Table 1 is derived from the work of VISHNU-MITTRE & SHARMA (1962) who studied 326 species of 102 genera of legumes from India which included four Sesbania species. They described 67 "pollen types" which were primarily based on the character of apertures and then subdivided according to the external exine ornamentation pattern. Each type was named after the species which exhibited the particular pollen group

Table 1 - List of pollen grain data available for *Sesbania*.

TAXON	APERTURE	SHAPE	PD	ED	AUTHORITY
subgen. *Agati* *S. grandiflora*	3-colporoidate	subprolate	32 - 34	26 - 30	VISHNU-MITTRE & SHARMA, 1962
subgen. *Daubentonia* *S. drummondii*	3-colporate	oblate spheroidal to prolate-spheroidal	22.8 - 26.7	24 - 26.4	LIEUX, 1982
S. punicea	3-colporate	oblate-spheroidal	25.2 - 28.2	25.8 - 28.8	LIEUX, 1982
subgen. *Sesbania* *S. aculeata* *	3-colpate	prolate	32 - 44	20 - 30	DANA & DATTA, 1961
	3-colporoidate	subprolate	26 - 28	22 - 24	VISHNU-MITTRE & SHARMA, 1962

See Notes in the end of the Table

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Table 1, cont.

TAXON	APERTURE	SHAPE	PD	ED	AUTHORITY
S. aegyptiaca **	3-colpate	subprolate	30 - 32	24 - 26	VISHNU-MITTRE & SHARMA, 1962
S. bispinosa	3-colporate to 3-colporoidate	subprolate	26 - 28	22 - 26	VISHNU-MITTRE & SHARMA, 1962
S. sesban	3-colporoidate	oblate-spheroidate	24 - 30	26 - 28	VISHNU-MITTRE & SHARMA, 1962
	3-colpate	——	——	——	BAQUAR & AKHTAR, 1968
S. sesban var. *bicolor*	3-colpate	subprolate	28 - 30	24 - 26	VISHNU-MITTRE & SHARMA, 1962
S. speciosa	3-colpate	prolate	42 - 48	20 - 24	DANA & DATTA,

NOTES:

* = *S. bispinosa* (Jacq.) W.F. Wight ?
** = *S. sesban* (L.) Merrill ?
PD = polar diameter; ED = equatorial diameter

characteristics. The data presented by VISHNU-MITTRE & SHARMA (*loc. cit.*) is difficult to interpret because, apart from the complexity and lack of precision in the limits of their classification and descriptions of pollen types, VISHNU-MITTRE & SHARMA (1962) also had some problems with the identification of species used in their survey. For example, *Sesbania aegyptiaca* and *S. aculeata*, treated as synonyms of *S. sesban* and *S. bispinosa*, respectively (GILLETT, 1963 and also the present work), were recognised with different "pollen types" from the latter taxa (Table 2).

Under their pollen grain classification, VISHNU-MITTRE & SHARMA (1962) considered the genus *Sesbania* as being eurypalynous because the species studied were found to be represented by six pollen types (Table 2). The colpate aperture was the commonest among the species examined and also present in the taxa studied by DANA & DATTA (1961, Table 1). However, records of compound apertures were also obtained for pollen grains of species of *Sesbania* (Tables 1 and 2). Tricolporate apertures are definitely established for the *Sesbania* species here studied (Table 3), and the illustrations show that they are operculate (Figures 6-11). The colpus is marginate, flat or intruding, with the exine apparently becoming thinner near the furrow rim. The operculum is absent from the pore area in mature grains. The pores are large and slightly elongated along the polar axis (Figures 6,7,9,10).

The results of this survey fully accord with some of the aspects presented in Tables 1 and 2, i.e., the external exine morphological pattern is reticulate except for *S. sesban* pollen

TABLE 2 - Pollen types of species of Sesbania described by VISHNU-MITTRE & SHARMA (1962).

APERTURE	POLLEN TYPE	DESCRIPTION	TAXON STUDIED
3-zonicolpate	Alysicarpus vaginalis var. nummularifolius type	grains granulate, sexine thicker than nexine	S. aegyptiaca *
	Sesbania aculeata type	grains reticulate muri and lumina devoid of any granulation, nexine thinner than sexine	S. aculeata *
	Lupinus polyphyllus type	grains faintly reticulate	S. sesban var. bicolor
3-zonicolporoidate	Trifolium alexandrium type	grains reticulate, lumina distinct	S. grandiflora
	Cicer soongaricum type	grains faintly reticulate	S. sesban
3-zonicolporate	Crotalaria vestita type	grains reticulate, lumina devoid of any ornamentation	S. bispinosa

NOTES : * S. aegyptiaca treated as a synomym of S. sesban and S. aculeata as a synonym of S. bispinosa by GILLETT (1963) and in the present study.

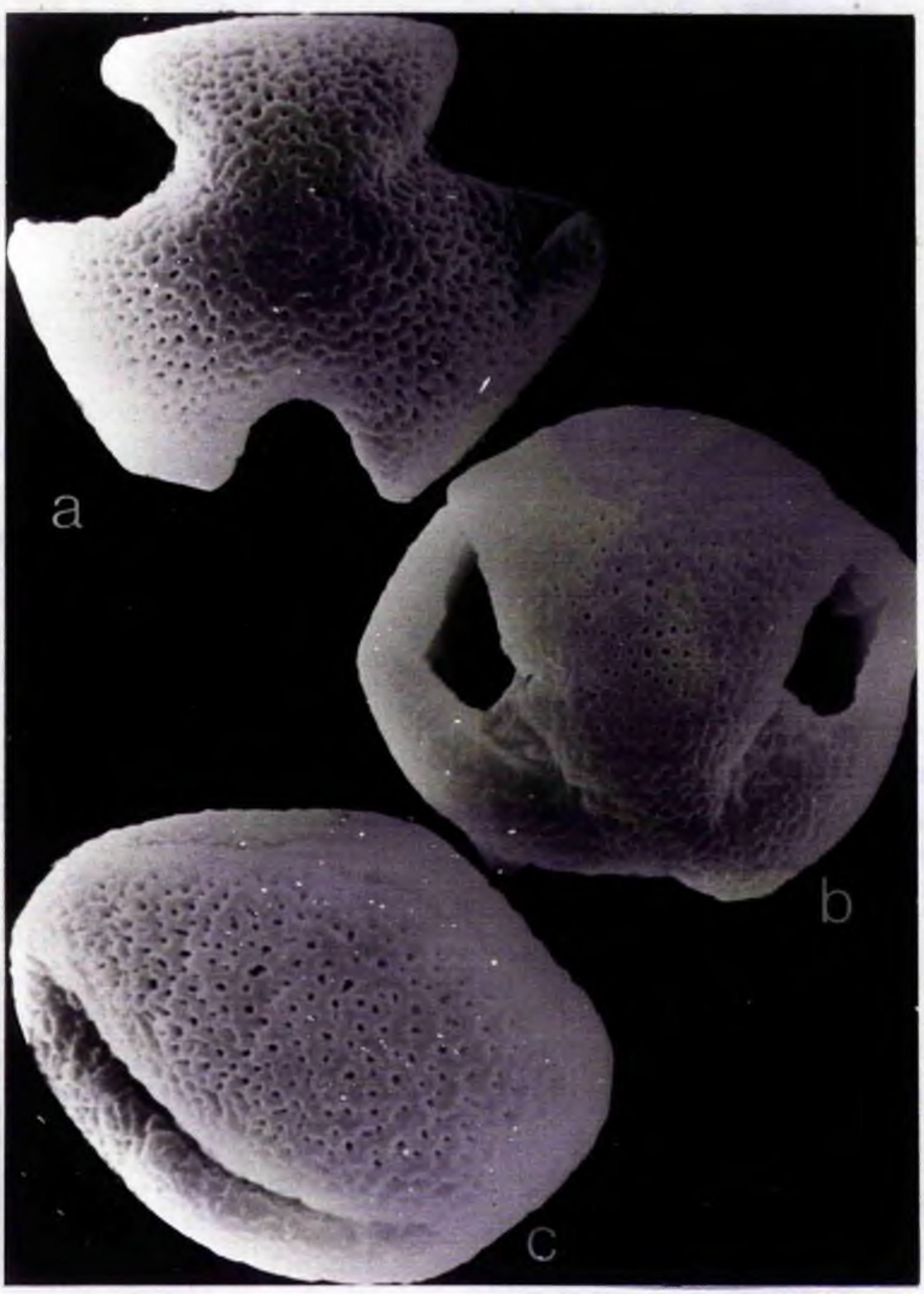

Figure 6 - SEM micrographs of pollen grains of <u>Sesbania cavanillesii</u>. a,b - polar views; c - oblique equatorial view (all 1750x).

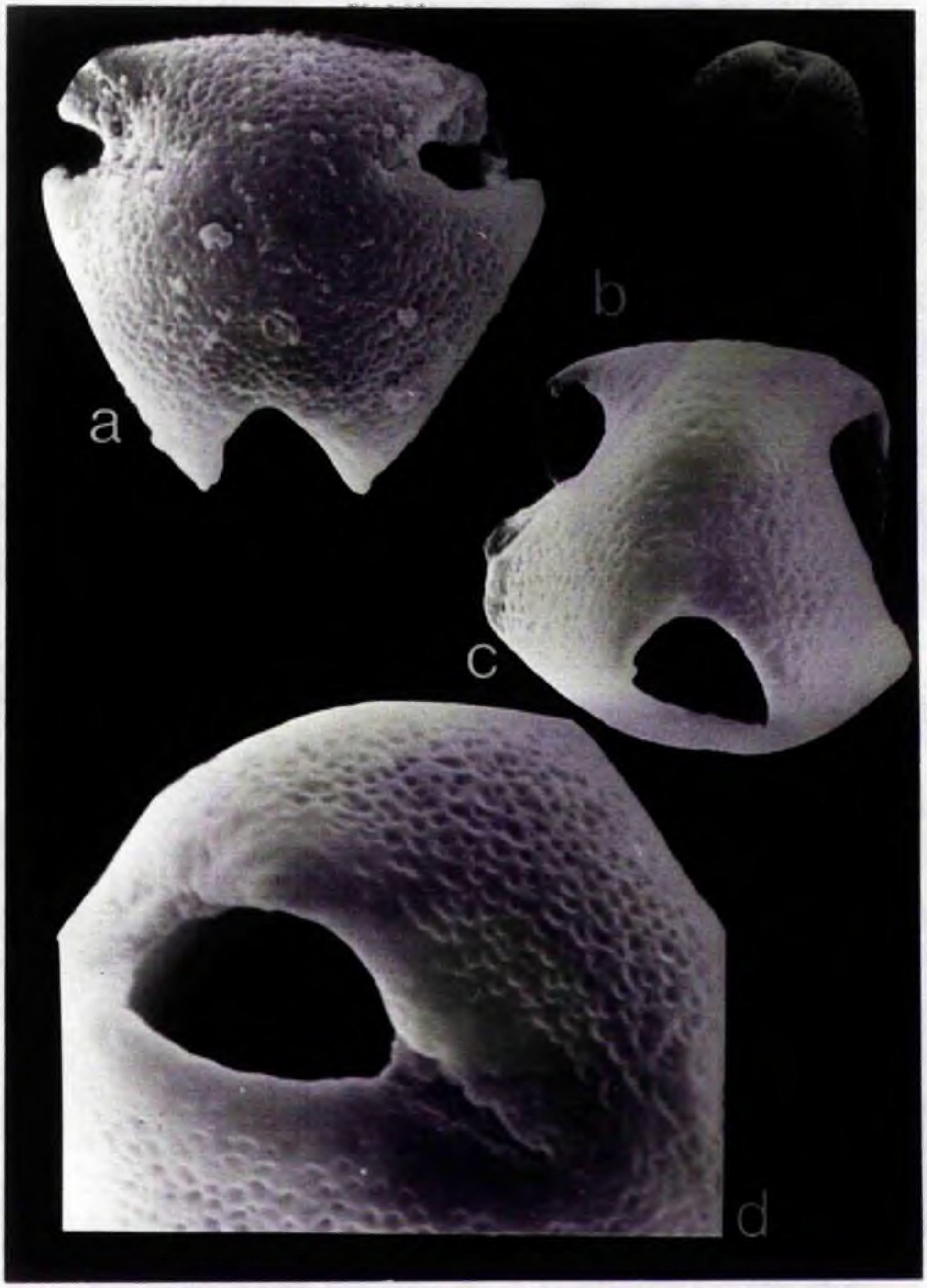

Figure 7 - SEM micrographs of pollen grains of <u>Sesbania macroptera</u>. a,b,c - polar views (1000x); d - colpus and pore (2500x).

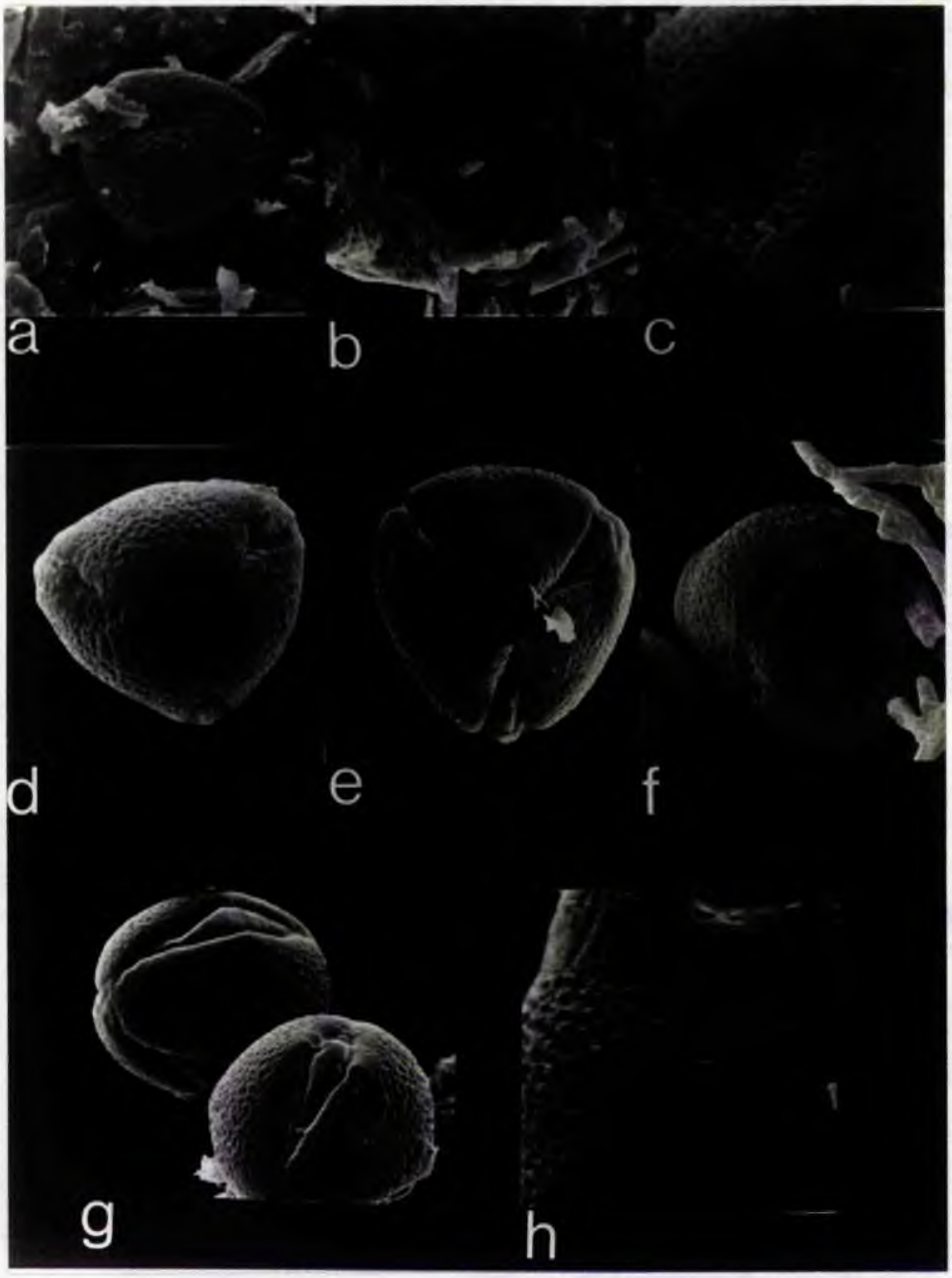

Figure 8 - SEM micrographs of pollen grains of Sesbania drummondii (a,b,c); S. punicea (d,e,f), and S. virgata (g,h). Magnifications : c,h - 2500x; the others, 1000x.

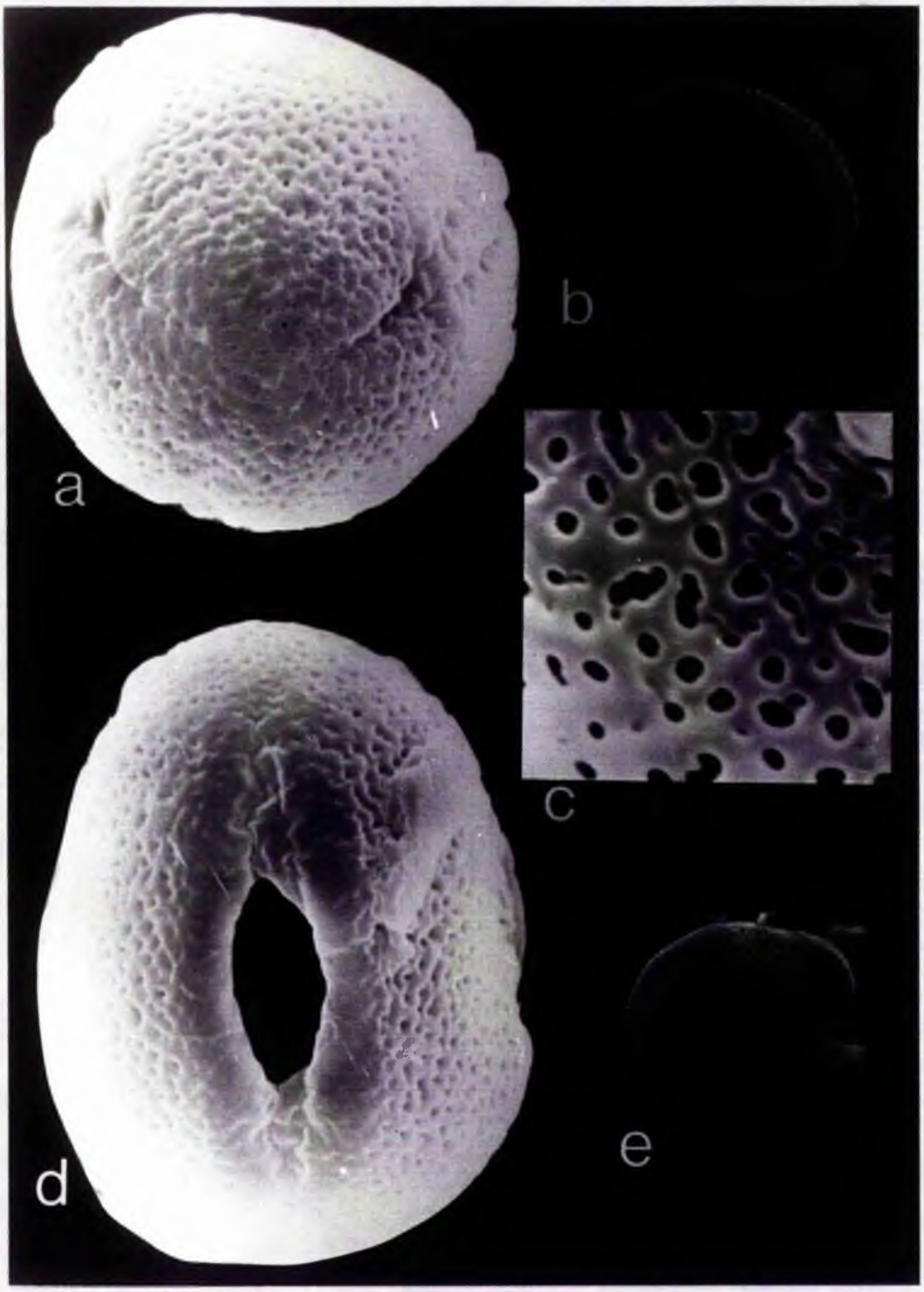

Figure 9 - SEM micrographs of pollen grains of <u>Sesbania</u> <u>emerus</u>.

a - oblique polar view (1750x); b,e - equatorial views (1000x); c - exine pattern (3750x); d - colpus and pore (1750x).

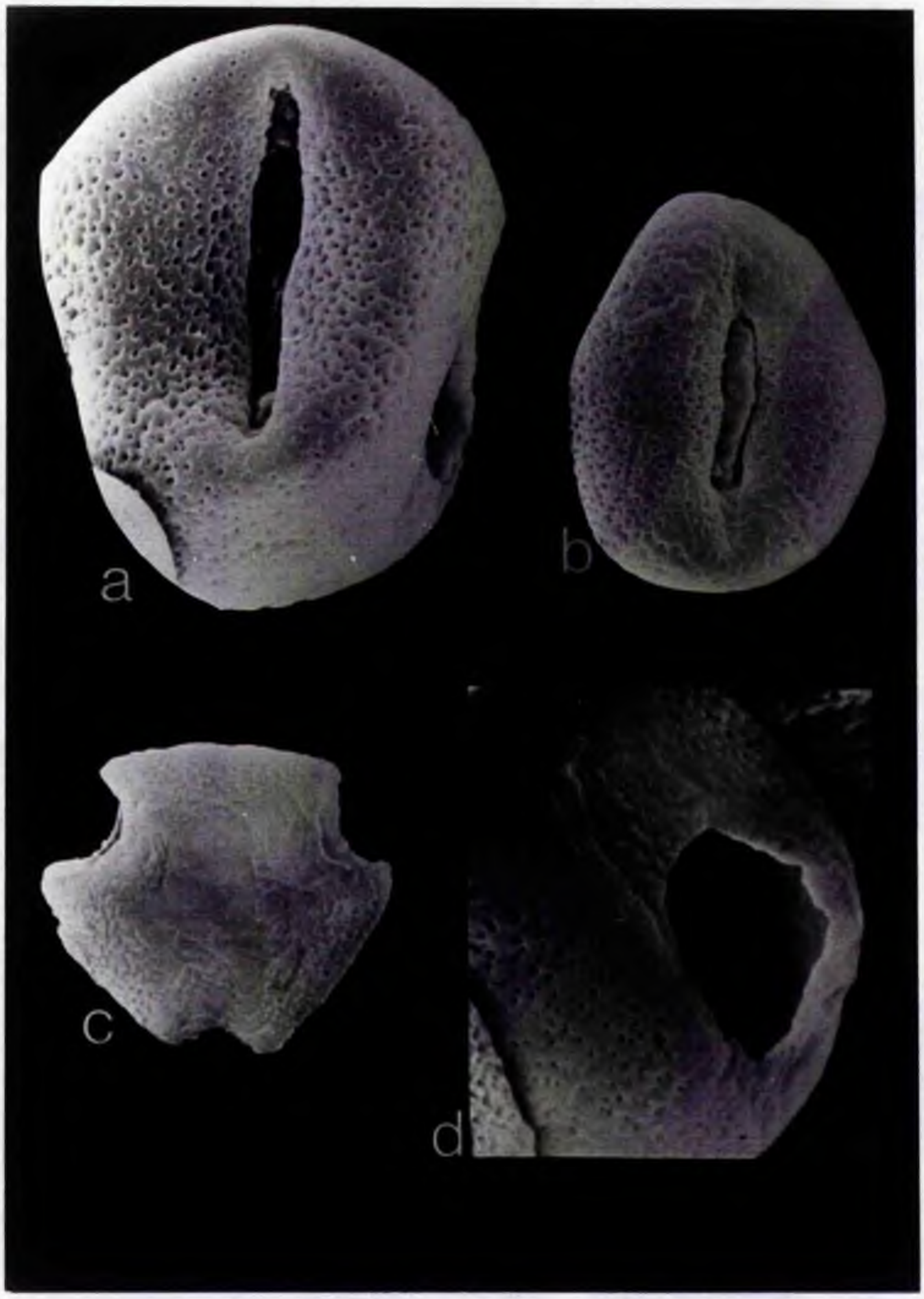

Figure 10 - SEM micrographs of pollen grains of <u>Sesbania exasperata</u>. a,b - equatorial views, grains collapsed (1000x); c - polar view (1000x); d - colpus and pore (1750x).

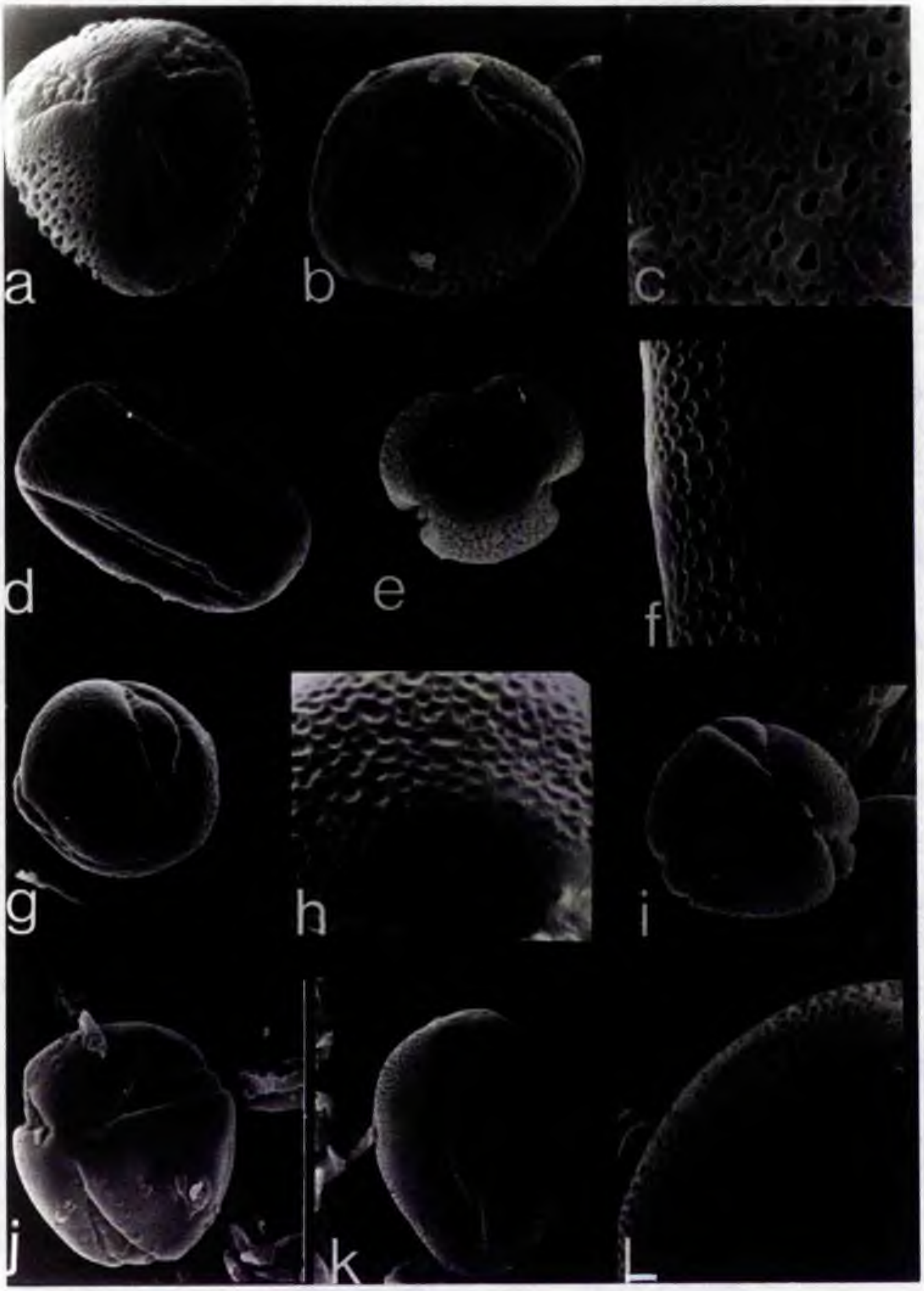

Figure 11 - SEM micrographs of pollen grains of Sesbania.

a,b,c - S. grandiflora; d,e,f - S. bispinosa (grains collapsed);

g,h - S. sesban; i - S. sericea; j,k,l - S. tetraptera.

Magnifications : c,f,h,l - 2500x; the others, 1000x.

grains which may be psilate (Table 3 and Figure 11 h) or probably "faintly-reticulate" (VISHNU-MITTRE & SHARMA, 1962 and Table 2). Basically the pollen grains of Sesbania were described as subprolate but the present study has shown that the pollen may vary from oblate-spheroidal to prolate or prolate-spheroidal (Table 5 and illustrations), and this agrees with the data published by LIEUX (1982) for S. drummondii and S. punicea (Table 1).

Data for polar versus equatorial diameters are given in Table 5 and represented with bar diagrams in Figures 14-16. There is a considerable overlap in dimensions for the pollen grains of the four subgenera of Sesbania but in subgen. Sesbania two species, S. exasperata and S. oligosperma have slightly larger grains than the rest of the taxa studied. This fact correlates well with the spectrum of flower dimensions within the New World species of subgen. Sesbania : S. exasperata and S. oligosperma are the large-flowered taxa while S. emerus, S. bispinosa, S. sericea and S. sesban are the small-flowered ones. Although in subgen. Daubentonia there is also a natural subdivision in small- (S. drummondii, S. macroptera and S. virgata) and large-flowered species (S. cavanillesii and S. punicea) no significant differences in pollen sizes were found among these taxa (Table 5).

The data presented above show a remarkable uniformity of pollen grain features among the species of Sesbania in the New World. They also show that these features are found in the Old World in some species of subgen. Sesbania (Tables 1 and 2, and FERGUSON & SKVARLA, 1981) and in subgen. Pterosesbania (Tables 3

Table 3 - Pollen grain features of species of *Sesbania* studied.

TAXON	EXINE	APERTURE	ORIGIN	FIGURE
subgen. *Agati*				
S. grandiflora	reticulate	3-colporate operculate	Brazil, LEITAO Fo. 1544 (UEC)	11a,b,c
subgen. *Daubentonia*				
S. cavanillesii	reticulate	3-colporate operculate	Mexico, PRINGLE 4738 (E, NY)	6
S. drummondii	reticulate	3-colporate operculate	U.S.A., CORRELL & CORRELL 18984 (LL)	8 a,b,c
S. macroptera	reticulate	3-colporate operculate	Argentina, GOODAL & TIREL, 234 (P) PEREGO 589 (MEXU) Paraguay, WOOLSTON 948 (NY)	7
S. punicea	reticulate	3-colporate operculate	cultivated, Univ. St Andrews	8 d,e,f
S. virgata	reticulate	3-colporate operculate	cultivated, Univ. St Andrews Argentina, PEDERSEN 7015 (NY)	8 g,h

Table 3, cont.

TAXON	EXINE	APERTURE	ORIGIN	FIGURE
subgen. Pterosesbania				
S. tetraptera	reticulate	3-colporate operculate	Malawi, BRUMMITT 8886 (K)	11j,k,l
subgen. Sesbania				
S. bispinosa	reticulate	3-colporate operculate	Dominican Republic, EKMAN 16124a (MO)	11d,e,f
S. emerus	reticulate	3-colporate operculate	Ecuador, DWYER & DWYER 10281 (MO) U.S.A., CORREL 31935 (LL) NASH 2478 (NY) WARNOCK 21621 (TEX)	9
S. exasperata	reticulate	3-colporate operculate	Brazil, HOEHNE s/n (SP) TRAIL, 130 (K)	10
S. oligosperma	reticulate	3-colporate operculate	Argentina, PEDERSEN 6077 (MO) Brazil, PRANCE et al. 26079 (NY)	
S. sericea	reticulate	3-colporate operculate	Porto Rico, JOHNSTON 1102 (NY)	11 i
S. sesban	reticulate to psilate	3-colporate operculate	Brazil, LEITAO Fo, & TARODA, 2548 (UB)	11g,h

and 5). In fact, as mentioned above, I. K. FERGUSON and G. LEWIS (pers. com.) also found an extensive uniformity among the pollen grains of species of Sesbania in Africa. Therefore, it is not surprising that the same situation occurs in the New World and this enhance once more the naturalness of the genus.

Although only part of the genus has been examined, results of the studies of the present work, based on species of two subgenera of Sesbania from the New World plus the African species S. tetraptera (subgen. Pterosesbania), and also of the data for other African species of subgen. Sesbania (FERGUSON, pers. com.) indicate little variability in pollen morphology. Therefore it seems sensible to disagree with the concept given by VISHNU-MITTRE & SHARMA (1962) that the genus Sesbania is eurypalinous, but rather consider it as stenopalynous.

The survey made in the present study of pollen grains of some Robinieae genera (Table 4) showed that these, in fact, do not differ markedly in the aperture and exine ornamentation patterns from Sesbania. However, it must be emphasized that the sampling was relatively small and an extensive, detailed study of pollen grains of Robinieae is needed in order to evaluate its relationships with the other woody tropical tribes of Papilionoideae, including a possibly segregated Sesbanieae.

Due to the collapse of pollen grains during acetolysis, measurements of polar and equatorial diameters of only two genera of the Robinieae were made. The results of these measurements for Glottidium vesicarium and Yucaratonia brenningii are presented in Table 5 and Figure 16. When compared with the value obtained for species of Sesbania (diagrams in Figures 14, 15, 16) G. vesicarium

Table 4 - Pollen grain features of Robinieae genera studied.

TAXON	APERTURE	EXINE	ORIGIN
Cracca Benth. *C. caribaea*	grains collapsed	reticulate	West Indies, RICKSECKER, 391 (E)
Coursetia DC. *C. arborea*	3-colporate operculate	reticulate	Colombia, SMITH 935 (E)
C. dubia	"	"	Ecuador, BALLS B7151 (E)
Diphysa Jacq. *D. carthaginensis*	3-colporate operculate	reticulate	Belize, CASTILLO 29 (OXF) Panama, KLUGE, 28 (OXF)
Gliricidia Kunth *G. maculata*	3-colporate operculate	psilate	Mexico, PALMER 350 (E) Trinidad, BROADWAY s/n (E)
G. sepium	"	"	Nigeria, cultivated CONS. FOR. 28 (OXF)

→

Table 4, cont.

TAXON	APERTURE	EXINE	ORIGIN
Glottidium Desv.			
G. vesicarium	3-colporate non-operculate	reticulate	U.S.A., CHAPMAN 3414a (NY), **Fig. 12** U.S.A., SKEHAN s/n (MO)
Lennea Klotzsch			
L. robinioides	3-aperturate non-operculate	reticulate	Mexico, PURPUS 5891 (E)
Olneya A. Gray			
O. tesota	3-colporate operculate	reticulate	U.S.A., BALLS 10697 (E) U.S.A., LOOMIS 1953 (OXF)
Poitea Vent.			
P. galegoides	grains collapsed	reticulate	San Domingo, TURCHEIM 26 (E)
Robinia L.			
R. pseudacacia	3-colporate operculate	reticulate	U.S.A., BRACELIN & NELSON 68 (E) U.S.A., STEELE s/n (E)
R. viscosa	"	"	Poland, cultivated, BAENITZ s/n (E)
Yucaratonia Burk.			
Y. brenningii	3-colporate non-operculate	psilate to rugulate	Ecuador, PENNINGTON & TENORIO 10807 (K), **Fig. 13**

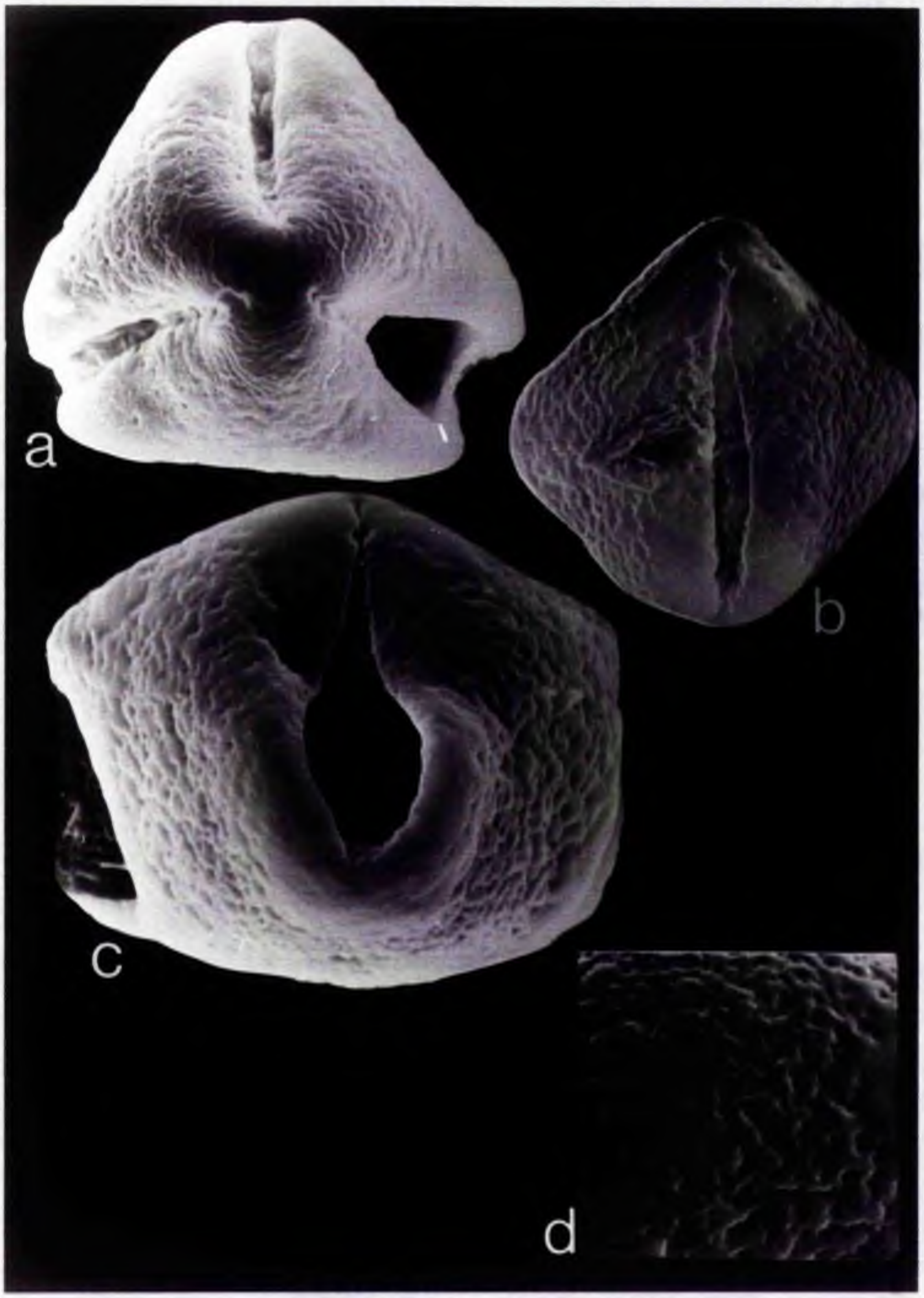

Figure 12 - SEM micrographs of pollen grains of Glottidium vesicarium. a - polar view (1000x); b - oblique equatorial view (1000x); c - aperture, grain collapsed (1750x); d - exine pattern (2500x).

Figure 13 - SEM micrographs of pollen grains of <u>Yucaratonia brenningii</u>. a,c - equatorial views (1750x); b - polar view (1750x).

Table 5 - Pollen grain measurements of species of *Sesbania*, *Glottidium* and *Yucaratonia*.

TAXON	SHAPE	MEASUREMENTS (µm)		
		PD(SD) x ED(SD)	PD(min.-max.)	ED(min.-max.)
Sesbania				
subgen. *Agati*				
S. grandiflora	subprolate to oblate-spheroidal	31.3(±1.5) x 30.4(±2.0)	(28.8 - 34.5)	(27.0 - 33.0)
subgen. *Daubentonia*				
S. cavanillesii	subprolate to prolate-spheroidal	31.9(±1.1) x 27.9(±1.3)	(29.7 - 33.3)	(26.0 - 30.0)
S. drummondii	subprolate-spheroidal	31.1(±1.4) x 30.2(±2.0)	(28.8 - 33.0)	(27.0 - 32.5)
S. macroptera	subprolate-spheroidal	30.4(±2.1) x 26.1(±1.3)	(27.0 - 32.4)	(24.3 - 28.0)
S. punicea	subprolate-spheroidal	31.1(±1.3) x 27.3(±1.5)	(28.0 - 33.0)	(25.0 - 33.0)
S. virgata	subprolate to prolate-spheroidal	31.5(±4.1) x 28.4(±1.4)	(27.0 - 40.5)	(27.0 - 31.0)
subgen. *Pterosesbania*				
S. tetraptera	subprolate to prolate-spheroidal	30.1(±2.8) x 26.5(±2.3)	(24.5 - 33.0)	(23.0 - 31.0)

Table 5, cont.

TAXON	SHAPE	MEASUREMENTS (µm)		
		PD(SD) x ED(SD)	PD(min.-max.)	ED(min.-max.)
subgen. *Sesbania* *S. bispinosa*	subprolate to prolate	28.7(±1.8) x 25.4(±1.6)	(26.0 - 33.0)	(26.0 - 28.0)
S. emerus	prolate-spheroidal	29.8(±2.2) x 24.6(±2.0)	(26.0 - 34.0)	(21.5 - 27.0)
S. exasperata	subprolate to prolate-spheroidal	34.6(±2.4) x 30.0(±2.0)	(32.0 - 40.0)	(27.0 - 34.0)
S. oligosperma	subprolate to prolate-spheroidal	34.0(±1.9) x 31.1(±2.0)	(30.0 - 38.0)	(32.0 - 34.0)
S. sericea	subprolate to prolate spheroidal	28.0(±2.0) x 26.5(±1.4)	(23.0 - 32.0)	(23.0 - 31.0)
S. sesban	subprolate to prolate-spheroidal	29.0(±2.0) x 25.0(±1.5)	(26.0 - 32.0)	(22.0 - 27.0)
Glottidium *G. vesicarium*	oblate-spheroidal	31.8(±2.0) x 25.7(±1.2)	(30.0 - 35.0)	(24.0 - 27.0)
Yucaratonia *Y. brenningii*	prolate-spheroidal	29.4(±2.3) x 30.1(±1.8)	(27.0 - 32.0)	(27.0 - 33.0)

NOTES : ED = equatorial diameter; PD = polar diameter; SD = standard deviation

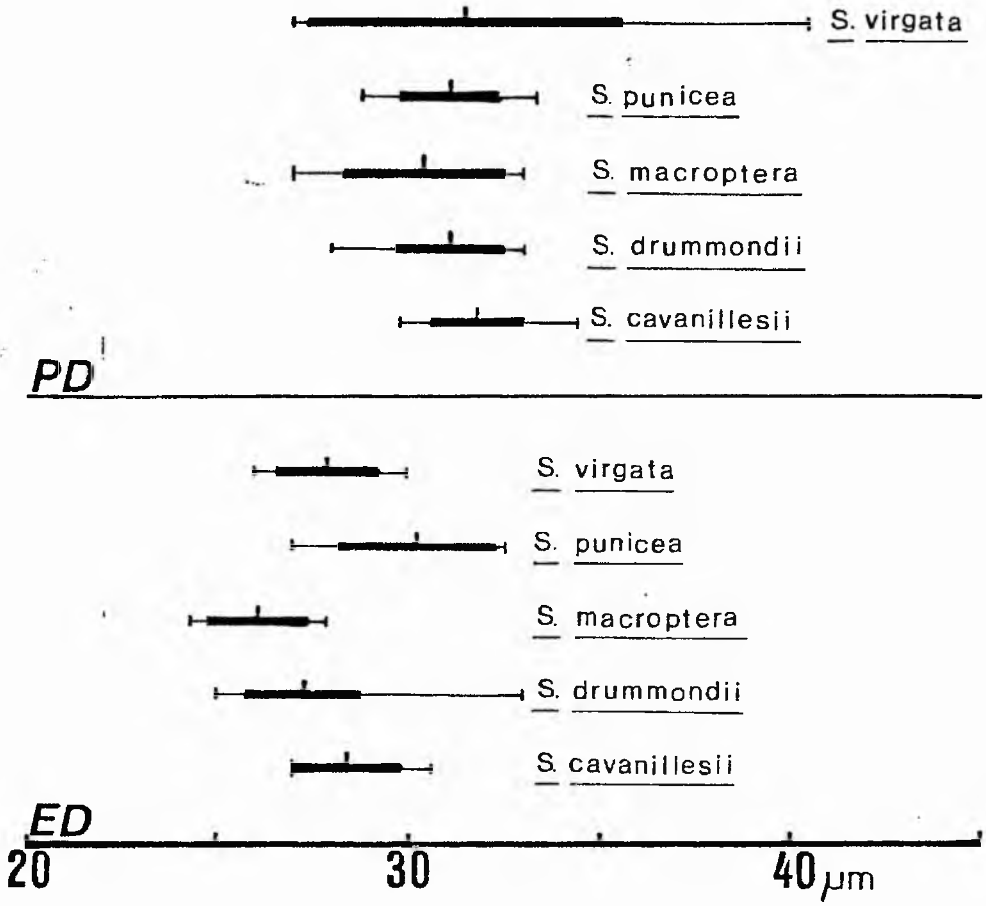

Figure 14 - Comparative diagram for polar (PD) and equatorial (ED) diameters of pollen grains of species of Sesbania subgen. Daubentonia. The horizontal line represents the size range of the grains; the black rectangle marks the standard deviation; the vertical line represents the arithmetic mean.

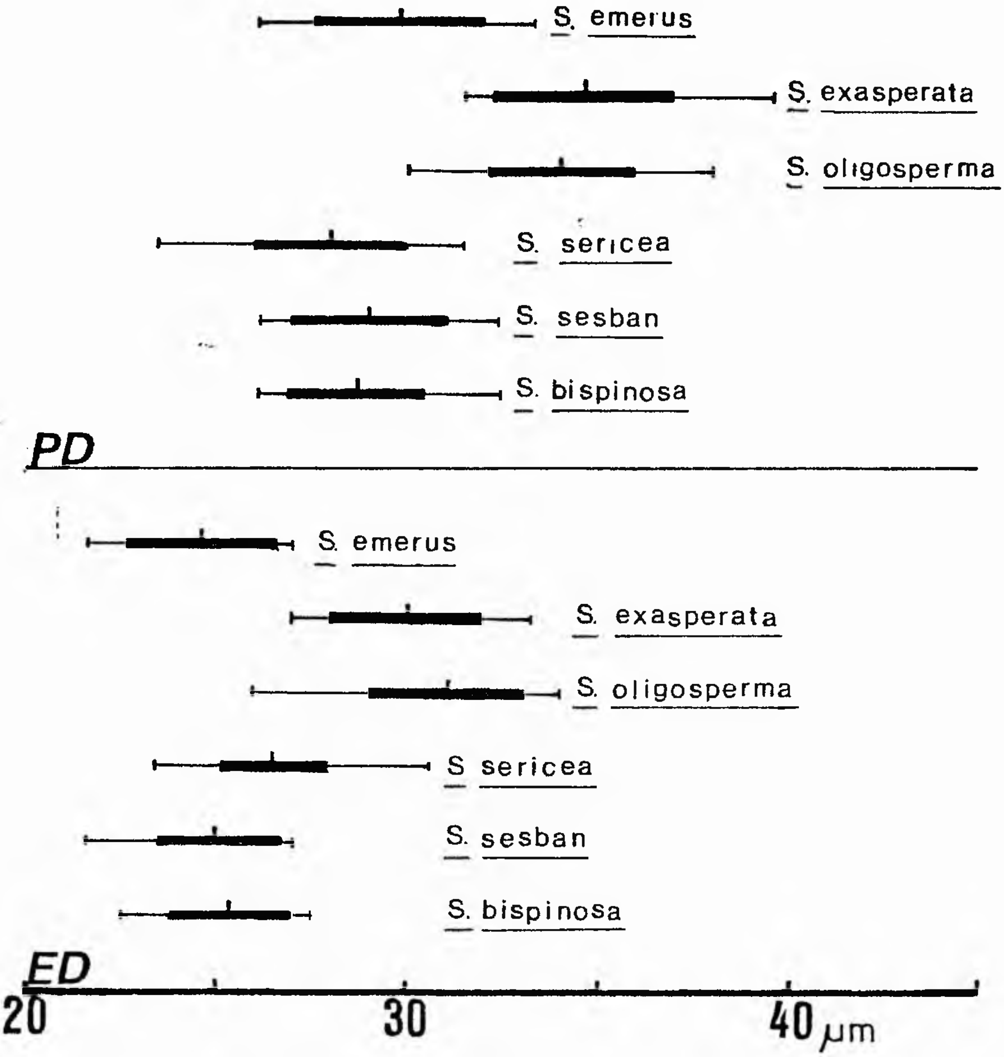

Figure 15 - Comparative diagram for polar (PD) and equatorial (ED) diameters of pollen grains of species of Sesbania subgen. Sesbania. The horizontal line represents the size range of the grains; the black rectangle marks the standard deviation; the vertical line represents the arithmetic mean.

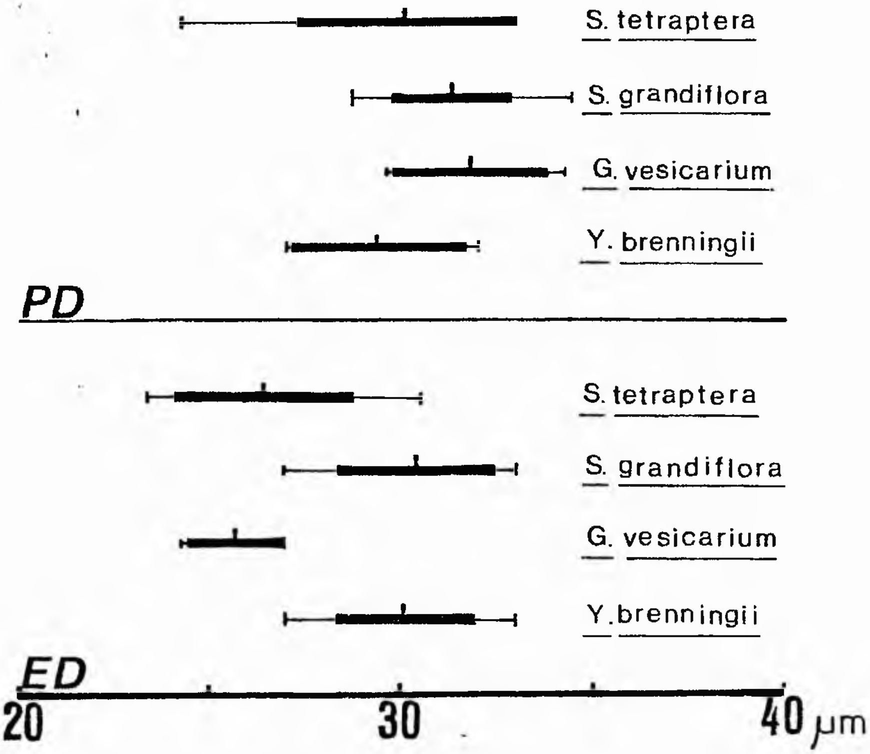

Figure 16 – Comparative diagram for polar (PD) and equatorial (ED) diameters of pollen grains of species of Sesbania subgen. Pterosesbania (S. tetraptera) and subgen. Agati (S. grandiflora), Glottidium, and Yucaratonia. The horizontal line represents the size range of the grains; the black rectangle marks the standard deviation; the vertical line represents the arithmetic mean.

and *Y. brenningii* pollen grains are similar in size. Again, any conclusions at this stage would be too premature because of the small sampling of the tribe in this aspect.

A final observation on pollen size must be made concerning *Sesbania grandiflora*, *S. bispinosa* and *S. sericea*, the only species of *Sesbania* which are known to be polyploids. It is well known that polyploidy produces an effect on plants which is sometimes reflected in the increase in cell sizes of particular organs, such as flowers and seeds, and pollen grains are usually affected by this process (STEBBINS, 1950, 1971). In this survey, however, no differences in pollen dimensions were observed which could indicate any variation on chromosome number of the above taxa.

4.2.3 - SEED MORPHOLOGY

4.2.3.1 - General considerations

In the Leguminosae, seed characters have been widely used as taxonomic parameters at family, tribal, generic, and specific levels. Several broad surveys have been made in many categories of the Leguminosae using seeds as sources of features which support taxonomic classifications and phylogenetic hypotheses (GUNN, 1981).

The classical account by CORNER (1951) has been a primary reference work for interpretation and descriptive terms for the anatomy of the seed-coat but many other isolated works are also useful; for example, MILLER (1967) with Crotalaria L. (Leg. Papilionoideae) and POLHILL (1976) with the Genisteae. In the Kew Conference on Legumes, the general morphology and taxonomic significance of legume seeds were revised by GUNN (1981), while the cotyledon anatomy and seedling structures were studied by SMITH (1981) and DUKE & POLHILL (1981).

Recently, scanning electron microscopy (SEM) techniques have also proved to be useful for the observation of internal structure of seeds and new combinations of several features are being used as taxonomic characters in the Leguminosae (LERSTEN, 1982; LERSTEN & GUNN, 1982; HANNA, 1984).

In the present work, an extensive survey of Sesbania seeds was carried out making the use of optical and SEM microscopy techniques in order to evaluate the usefulness of seed morphological characters in the generic taxonomy. At the same time, several Robinieae genera were also studied for comparison with Sesbania.

The seeds were obtained from herbarium specimens (Table 6 for the list), accessions to the University Botanic Gardens at St Andrews or from recent collections made in the field (as for S. punicea and S. virgata, collected in Brazil by K. Yamamoto and P. E. Gibbs, and for Glottidium vesicarium seeds were sent by D. O. Evans *).

Transverse and longitudinal sections through the centre of the hilum (Figures 17 and 18, and Material and Methods), following techniques used by LERSTEN (1982) and LERSTEN & GUNN (1982) were made in some seeds to show :

a) the position of the tracheid bar relative to the hilar groove
b) the shape of the tracheid bar
c) the packing of the tracheoids
d) the different types of tracheoid pit vesturing
e) the macrosclereid and osteosclereid layers (hypodermis) and,
f) the position and structure of the ovular vascular bundle.

Techniques on preparation of the material for SEM observations have been given under Material and Methods.

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*Dept of Agronomy and Soil Science, University of Hawaii at Manoa.

Table 6 - Collections of Robinieae (*sensu* POLHILL & SOUSA, 1981) specimens studied for seed morphology and testa sculpture patterns.

TAXON	ORIGIN	TESTA PATTERN
Cracca Benth.		
C. caribaea Benth.	Colombia, SMITH 278 (E)	SIMPLE-RETICULATE
C. chrysophylla (Pursh) Kuntze	U.S.A., TRACY 169 (E)	RUGULATE
C. spicata (Walt.) Kuntze	U.S.A., MACKENZIE 1782 (E)	SIMPLE-RETICULATE
Coursetia DC.		
C. arborea Griseb.	Colombia, SMITH 935 (E) Trinidad, BROADWAY 5256 (E) Trinidad, SWABEY 12550 (OXF)	RUGULATE
C. glandulosa Gray	Mexico, PALMER 333 (K)	MULTI-RETICULATE
C. microphylla Gray	U.S.A., PRINGLE s/n (E) PALMER 400 (E)	RUGULATE
C. mollis Rob. & Greenm.	Mexico, SELER 3434 (K)	RUGULATE
Diphysa Jacq.		
D. robinioides Benth.	Honduras, HUGUES & STYLES 122 (OXF)	RUGULATE
Gliricidia Kunth		
G. maculata H.B.K.	Mexico, PALMER 350 (E)	RUGULATE
G. sepium (Jacq.) Steud.	Nigeria, cultivated, CONS. FORESTS 28 (OXF)	RUGULATE

Table 6, cont.

TAXON	ORIGIN	TESTA PATTERN
Glottidium Desv.		
G. vesicarium (Jacq.) Harper	U.S.A., EVANS s/n	RUGULATE
Robinia L.		
R. neomexicana Gray	U.S.A., DUDWORTH s/n (OXF)	RUGULATE
R. pseudacacia L.	U.S.A., HARVARD UNIV. HERB. COLL. (OXF)	RUGULATE
Sesbania Scop.		
subgen. Agati		
S. grandiflora (L.) Pers.	Dominican Republic, AUGUSTO 451 (NY) Porto Rico,SPETZMAN & COLON 189 (FTG)	RUGULATE
S. formosa (F. Muell.) Burb.	Australia, GARDNER s/n (K)	RUGULATE

→

Table 6, cont.

TAXON	ORIGIN	TESTA PATTERN
Sesbania subgen. *Daubentonia*		
S. cavanillesii S. Wats.	Mexico, PRINGLE s/n (MEXU)	RUGULATE
S. drummondii (Rydb.) Cory	U.S.A., FERRIS & DUNCAN 3177 (NY)	RUGULATE
S. macroptera Mich.	Argentina, BURKART 18359 (MO)	RUGULATE
S. punicea (Cav.) Benth.	cultivated, St Andrews Univ.	RUGULATE
S. virgata (Cav.) Pers.	cultivated, St Andrews Univ.	RUGULATE
subgen. *Pterosesbania*		
S. tetraptera Hochst ex Baker	Zimbabwe, GRADNER 561 (K) Namibia, KOTSCHY 131 (K,RB)	RUGULATE
subgen. *Sesbania*		
S. benthamiana Domin	Australia, BLAKE 17698 (K)	RUGULATE
S. bispinosa (Jacq.) W.F. Wight	locality ?, PAVON s/n (G)	RUGULATE

→

Table 6, cont.

TAXON	ORIGIN	TESTA PATTERN
S. brevipeduncula Gill.	Zimbabwe, CORBY 445 (K)	RUGULATE
S. campilocarpa (Domin) Burb.	Australia, BURBIDGE 5353 (K)	RUGULATE
S. emerus (Aubl.) Urb.	Guatemala, KELLERMAN 7882 (NY) Mexico, HINTON 5618 (BM) Mexico ?, BERLANDIER 1934 (P) U.S.A., DRUMMOND 74 (BM) PARRY *et al*. 251c (NY) RUGEL 153 (BM)	RUGULATE
S. erubescens (Benth.)	Australia, SCRYMGEOUR 1977 (K)	RUGULATE
S. exasperata H.B.K.	Brazil, DROUET 2679 (MO,NY) HATSCHBACH 21830 (UEC) Honduras, MOLINA 11134 (NY)	RUGULATE
S. javanica Miquel	Australia, PERRY 4004 (K)	RUGULATE
S. oligosperma Taubert	Argentina, PEDERSEN 7025 (K) Brazil, RIEDEL 2237 (K)	RUGULATE

→

Table 6, cont.

TAXON	ORIGIN	TESTA PATTERN
S. sericea (Wild.) Link.	Trinidad, BROADWAY 6935 (MO) Bahamas, CORRELL 45816 (NY)	RUGULATE
S. sesban (L.) Merrill	Brazil, BUFFARAH *et al.* 281 (UEC) HERINGER 13884 (MO)	RUGULATE
S. simpliciuscula F.Muell. ex Benth.	Australia, LAZARIDES 6776 (K)	RUGULATE
Yucaratonia Burk.		
Y. brenningii (Harms.) Burk.	Ecuador, SPRUCE 6237 (K)	RUGULATE

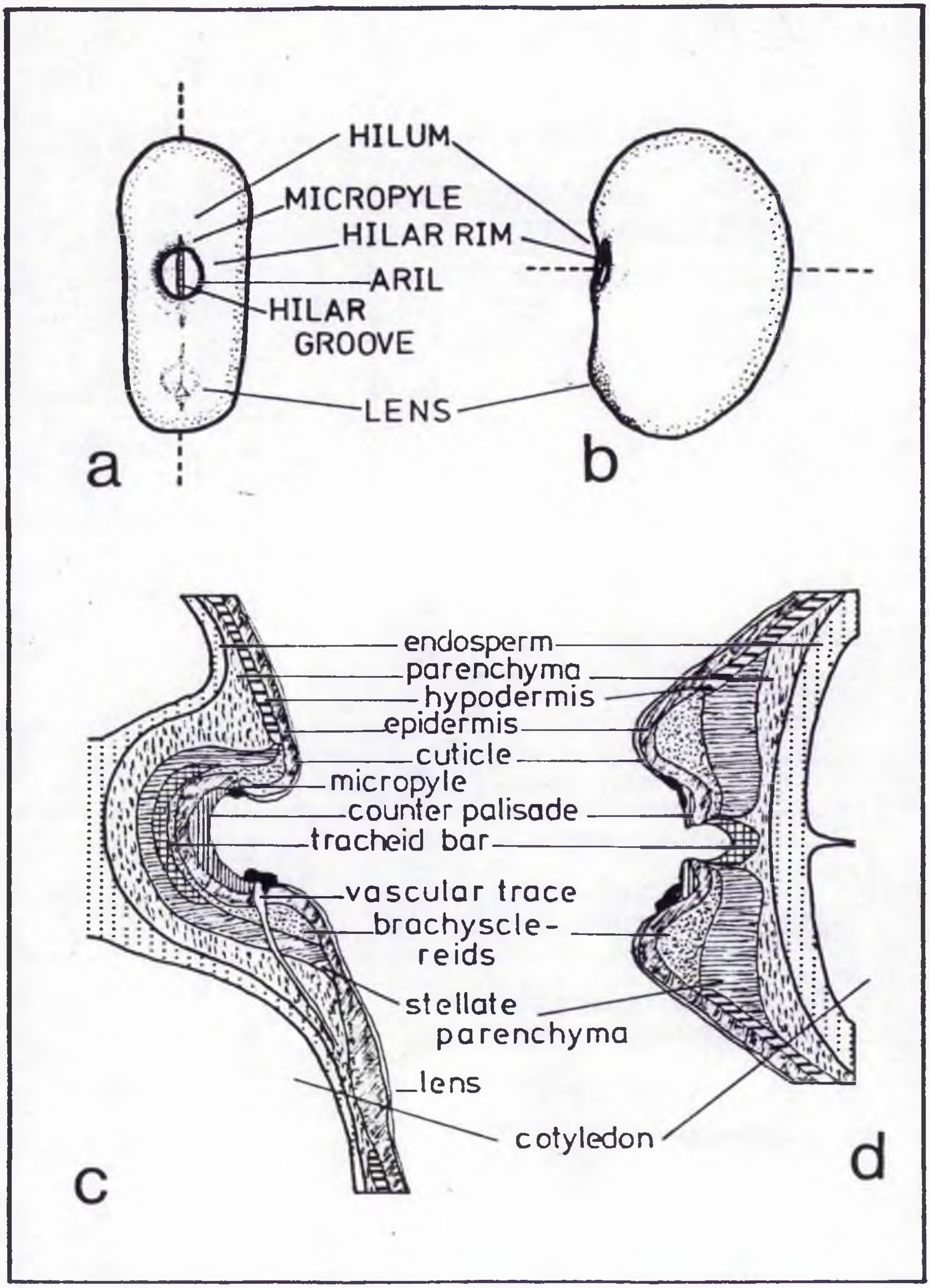


Figure 17 - Diagrams of macroscopical external (a,b) and microscopical internal (c,d) morphological features of legume seeds. a,b - surface and lateral views, respectively, of a legume seed; the dashed lines show the planes of sectioning for anatomical studies. c,d - saggital and transversal sections of the hilar region. (c,d from POLHILL, 1976).

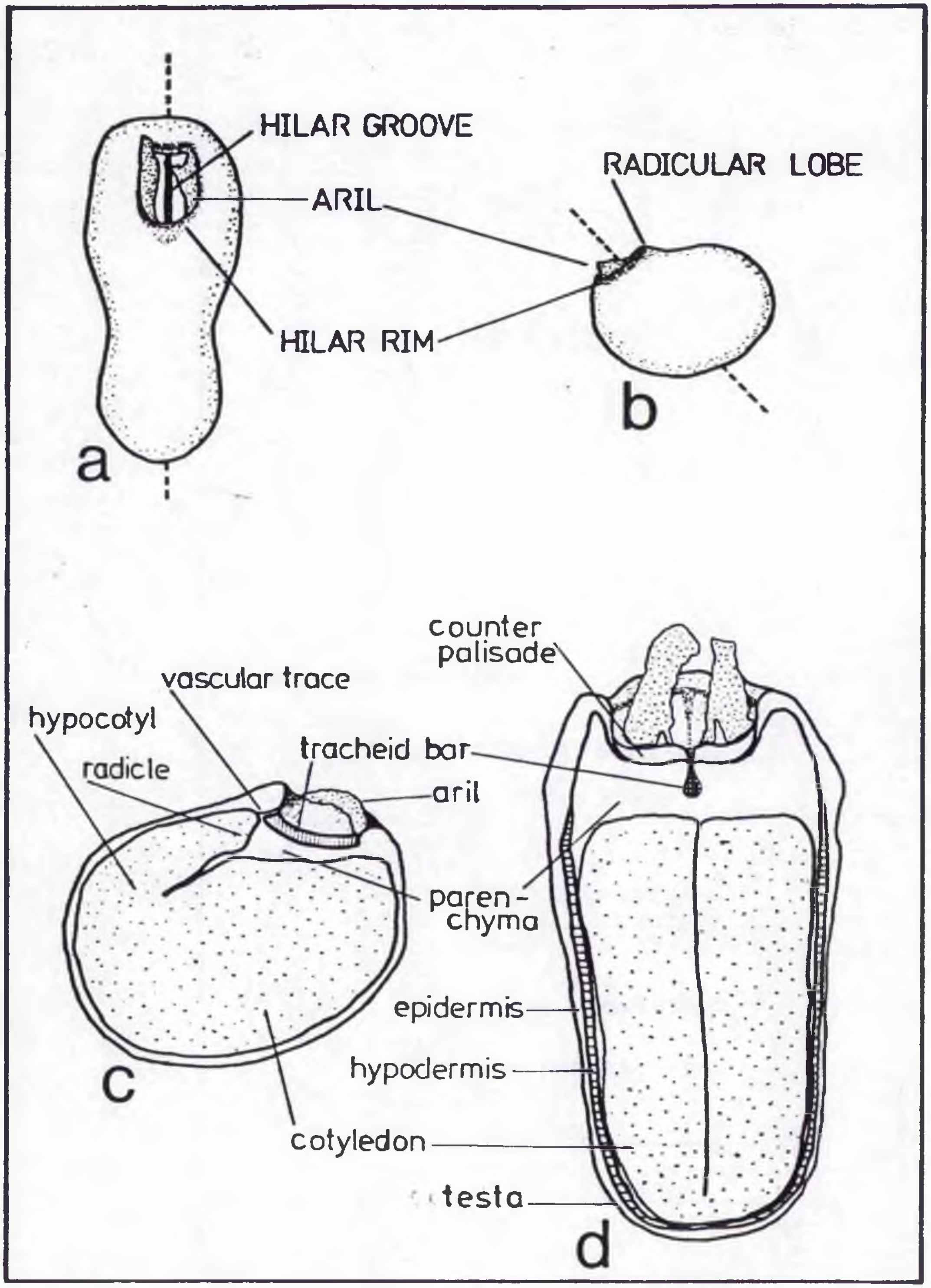


Figure 18 - Diagrams of macroscopical external (a,b) and internal (c,d) morphological features of legume seeds. a,b - surface and lateral views, respectively, of a legume seed; the dashed lines show the planes of sectioning for anatomical studies.
c,d - saggital and transversal sections through the hilar region.

4.2.3.2 - Seed shape

The outlines of the New World *Sesbania* seeds are shown in Figure 19 and a comparison of seed characters of all subgenera is given in Table 7.

Variation in seed shape and size correlates to some extent with the infrageneric classification, i.e., species of the subgenera *Agati*, *Daubentonia* and *Pterosesbania* (Figure 19 A-F and J) are basically reniform and range from 3 mm to over 5 mm, whereas in subgen. *Sesbania* (Figure 19 G-I) the seeds are cylindrical to cylindric-oblong and vary from 2-5 mm. PHILLIPS & HUTCHINSON (1921) have described seeds of the African species *S. cinerascens* Welw. ex Baker emend E.P. de Sousa (subgen. *Sesbania*) as up to 9 mm long, although GILLETT (1963) has cited a length of 4.5 mm for the seeds of the same species. The Australian species of subgen. *Sesbania* have seeds of 4-5 mm, all being oblong in shape (BURBIDGE, 1965).

In comparison with *Sesbania*, the extended, turgid, reniform seeds of the allied genus *Glottidium* Desv. (*G. vesicarium* (Jacq.) Harper, Figure 19 K) are very large, varying from 8-11 mm, and are quite distinct from any *Sesbania* species.

Reniform seeds are common in the Robinieae, as can be seen in the survey on seed shape of this tribe presented in Table 8 but, although not many samples of seeds were available for study, it was observed that some genera are very variable in seed shape, whereas, in comparison, *Sesbania* is relatively uniform.

4.2.3.3 - Hilum, aril, micropyle and lens.

The morphological external features of seeds of *Sesbania* species and Robinieae genera studied, like most of Papilionoideae

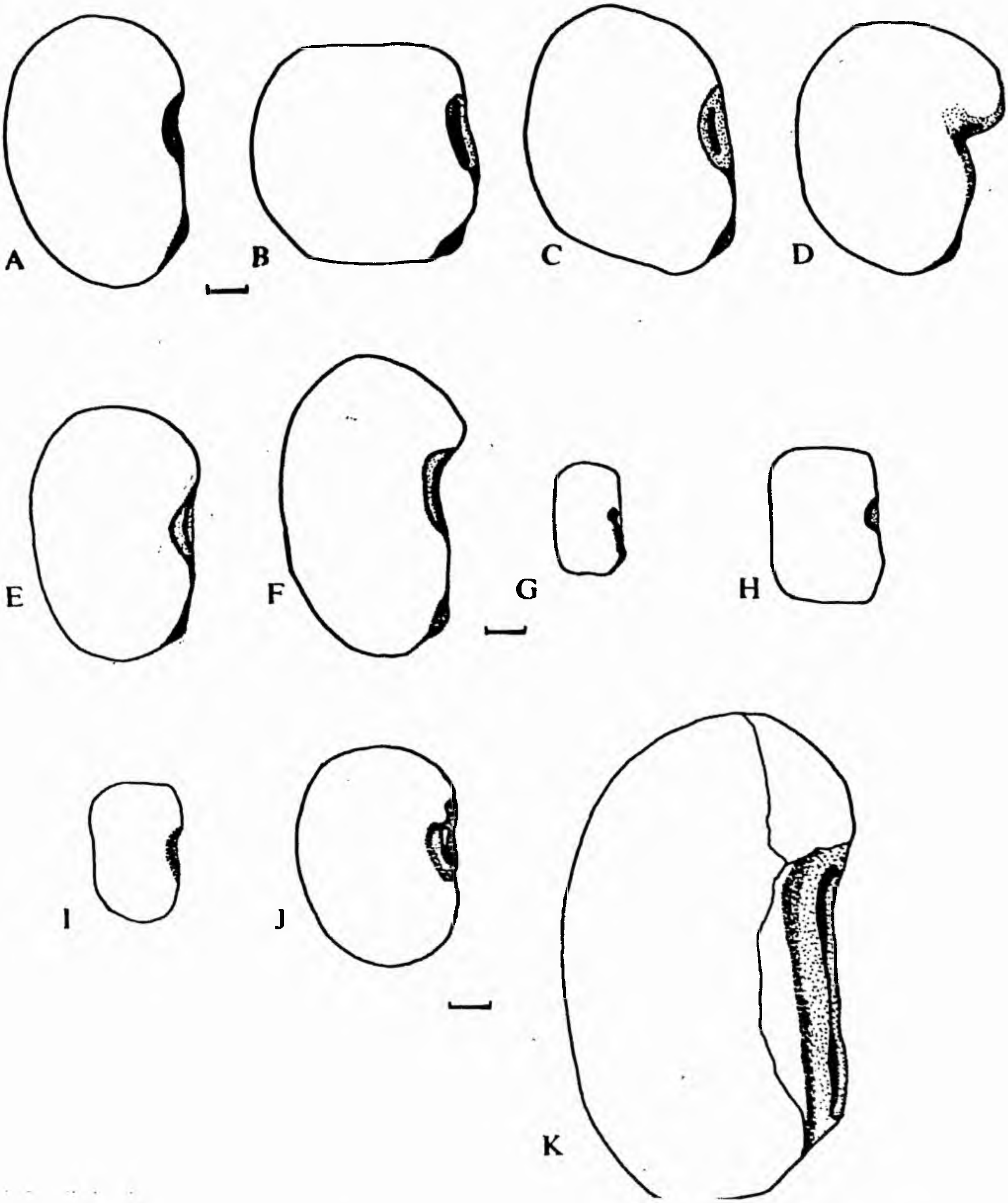


Figure 19 - Seed outlines of some New World species of *Sesbania* and *Glottidium*. A - *S. cavanillesii*; B - *S. drummondii*; C - *S. punicea*; D - *S. macroptera*; E,F - *S. virgata*; G - *S. emerus*; H - *S. oligosperma*; I - *S. exasperata*; J - *S. grandiflora*; K - *Glottidium vesicarium*. (Scale = 1 mm).

Table 7 - Comparative macroscopic features of the seed in subgenera of Sesbania Scop. *

TAXON	LENGTH (mm)	SHAPE	HILUM INSERTION
subgen. Agati	4-7	reniform to reniform-oblong	central to subterminal
subgen. Daubentonia	3-6	reniform	central to subterminal
subgen. Sesbania	2-5(-9)	cyllindric-oblong	central to subterminal
subgen Pterosesbania	4-6	reniform-oblong	central

NOTES :

* Sources : specimens cited in Table 1 and PHILLIPS & HUTCHINSON (1921); GILETT (1963), and BURBIDGE (1965).

consist of testa, hilum, lens, micropyle and radicular lobe (Figures 17, 18, 20 and 21). Details of testa structure are given in the next two sections.

All species of *Sesbania* native to the New World, subgen. *Daubentonia* (Figures 20 a-e), and subgen. *Sesbania* (Figures 4 f,g) as well as the introduced species of subgen. *Agati* (*S. grandiflora*) and subgen. *Sesbania* (*S. bispinosa*, *S. sericea* and *S. sesban*) all have circular to oval hilum. For some African species of subgen. *Sesbania* GILLETT (1963) described the hilum as being ovate-elliptic. In the present work it was found that specimens with non-mature seeds sometimes show differences of hilum shape particularly if the seeds collapse after the drying in the press.

In contrast with *Sesbania*, *Glottidium vesicarium* has an extended, elliptical hilum which promptly differentiates it from any species of the former genus.

In general the hilum is superficial on the seed of subgen. *Sesbania* (Figures 19 G-I and 21 a,b) but in the subgen. *Agati* (Figure 19 J) the hilum may be found sunk in the mid-region of the seed due to an overgrowth of the hilar rim (Figure 17 a,b) or the radicular lobe, as in *S. macroptera* Mich. (Figures 19D, 20c).

The insertion of the hilum is another feature that has been used as a character at many different taxonomic levels although most often at generic level (GUNN, 1981). In *Sesbania* the hilum is lateral and inserted at different positions along the main axis of the seeds in the different subgenera, as can be seen in Table 7 and Figure 20. Sometimes it is difficult to determine the position of the hilum as it extends and becomes larger, as in the subgen.

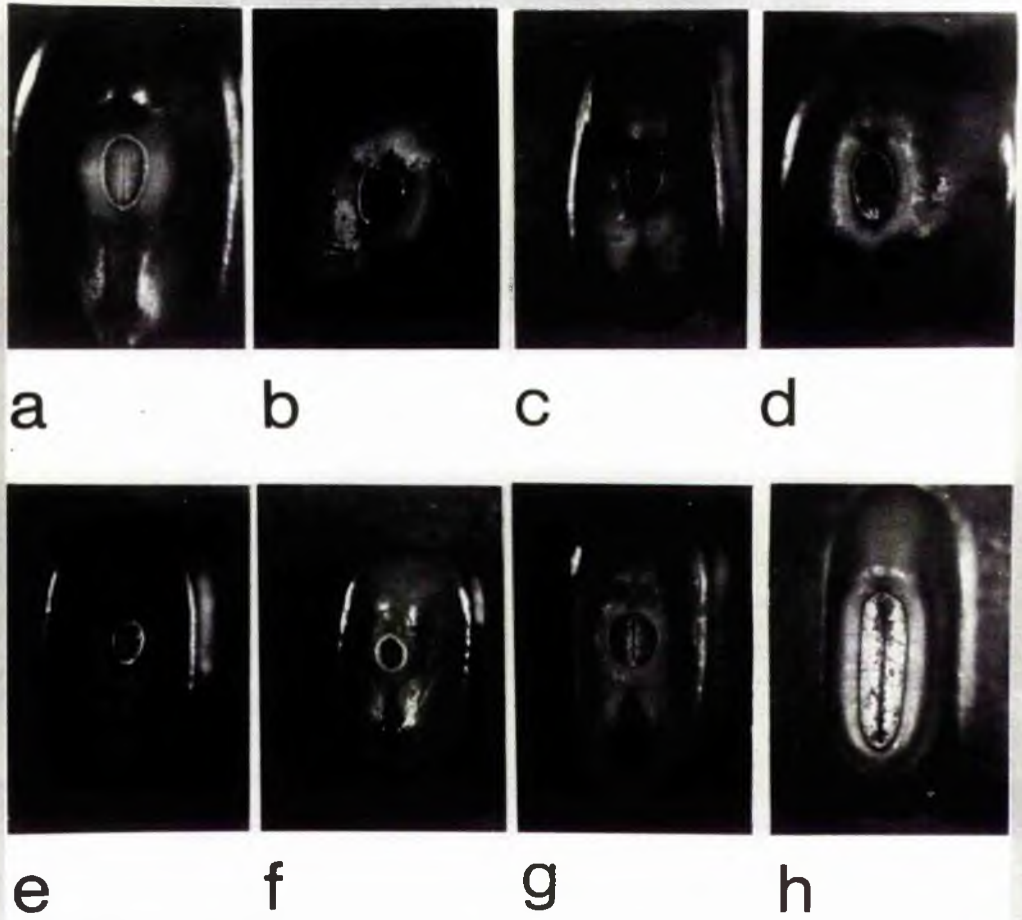


Figure 20 - Photographs of *Sesbania* and *Glottidium* seeds showing shape and insertion of the hilum. a - *S. virgata*; b - *S. punicea*; c - *S. macroptera*; e - *S. drummondii*; e - *S. cavanillesii*; f - *S. emerus*; g - *S. exasperata*; h - *G. vesicarium*. All 10x, except h, 5x.

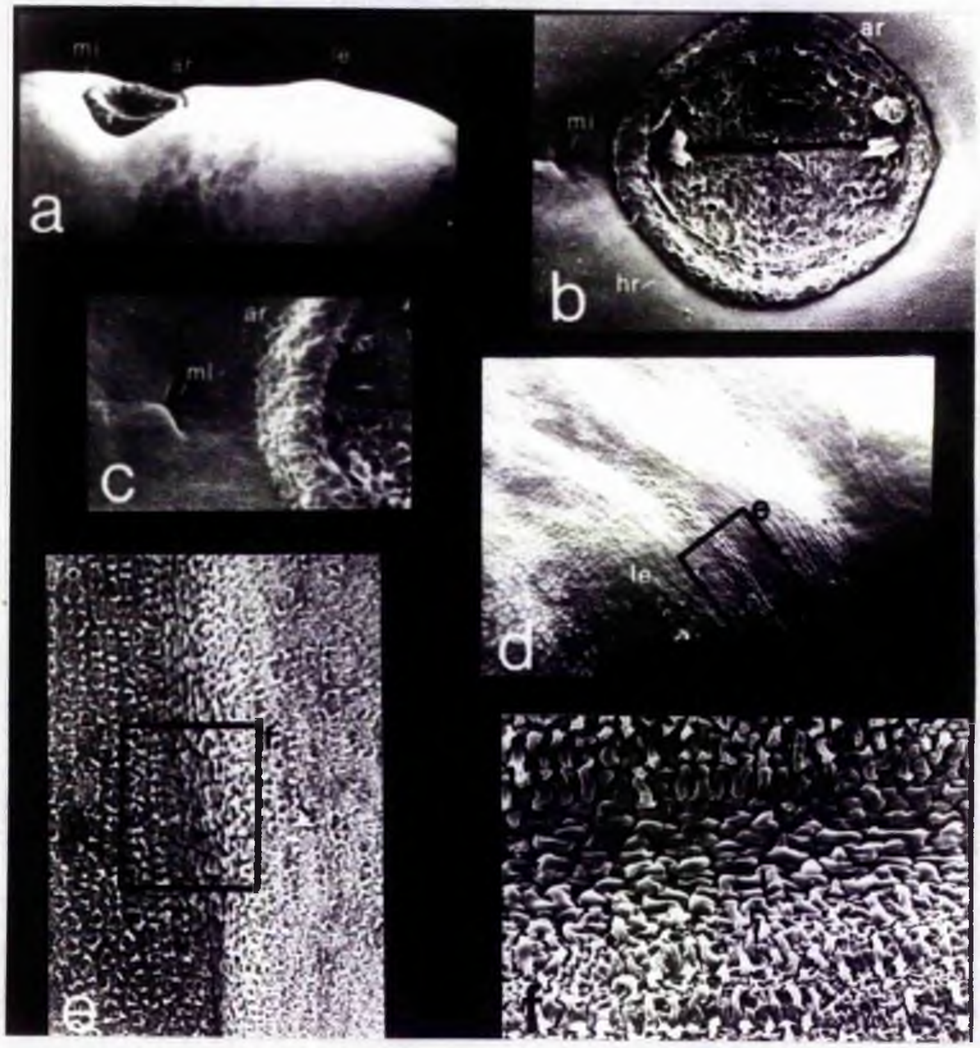


Figure 21 - External morphological features of Sesbania seeds with the use of SEM. a - S. exasperata, surface view (17.5x); b - S. emerus, hilum (25x); c - S. drummondii, hilum and micropyle (100x) d,e,f - S. drummondii : d - lens (100x), e - enlargement of area marked in d (250x), e - testa at mid-lens region (1000x).
(ar = aril; mi = micropyle; le = lens).

Daubentonia. However, the position of the hilum is not correlated with seed shape in Sesbania, and is of little use as a taxonomic character at infra-generic or generic level. The compressed, flat or ovoid seeds of many Robinieae usually have a subapical to apical hilum (Table 8, and POLHILL & SOUSA, 1981) and this certainly contrasts with the lateral hilum of the reniform seeds of Sesbania and Glottidium.

All Sesbanias are arillate with the hilum surrounded by a rim-aril which is regular and conspicuous (Figures 20 a-g and 21 a-c) but does not show any particular feature of taxonomic value at specific level. Some members of the other genera of the Robinieae do not have a conspicuous aril or may lack it completely (RYDBERG, 1923, 1924; HUTCHINSON, 1964). For example, Glottidium vesicarium has an inconspicuous to almost absent annular aril (Figures 19 K and 21 h) and Yucaratonia brenningii does not have an aril (BURKART, 1969; and personal observations).

The micropyle (Figure 17 a) is clearly visible with the naked eye or with low magnification in all Sesbania species. It is deltoid in shape and always positioned on the opposite side of the hilum from the lens (Figures 17 a,b; 20 a-g; 21 a-c). In general, the selected genera of Robinieae which were studied have the same features as in Sesbania.

The lens is another characteristic structure in the hilar area (or close to it), common to all legume seeds but which can be inconspicuous, as in the Robinieae genera Glottidium (Figure 19 K) and Yucaratonia, or extremely conspicuous as in all Sesbania species (Figure 19 A-J). It is usually surrounded and delimited by a differently coloured region of the testa (Figure 20 a-g).

Table 8 - Seed shapes of Robinieae as given by some authors.

AUTHORITY	TAXON	SEED SHAPE
RYDBERG (1923, 1924)	(tribe) Galegeae	
	subtr. Cracciniae	usually reniform or transversely oblong, but oval and compressed in Peteria
	subtr. Sesbaniinae	reniform to subcyllindric
	subtr. Diphysinae	transversely oblong, somewhat oblique
	subtr.Corynellinae	from orbicular to reniform, somewhat flattened
	subtr. Robiniinae	usually compressed, oblong to orbicular, or prismatic in Sphinctospermum
MACBRIDE (1943)	Coursetia DC. (including Benthamantha, Cracca and Poissonia)	suquadrate to rectangular or orbicular
HUTCHINSON (1964)	(tribes) Diphyseae Robinieae Sesbanieae	compressed flat oblong to reniform or subquadrate
POLHILL & SOUSA (1981)	(tribe) Robinieae, including Sesbanieae	ovoid to oblong-reniform or oblong
SOUSA & SOUSA (1981)	(tribe) Robinieae including Sesbanieae	oblong to reniform

4.2.3.4 - Testa sculpture pattern.

The testa sculpture patterns of Sesbania and other Robinieae genera from mid-seed areas as viewed with the SEM at magnifications of 1000x are shown in Table 6 and Figures 22, 23 and 24.

For all Sesbania species the rugulate pattern was found to be present (Figure 22), regardless of subgenus or the origin and distribution of the taxa. This uniformity of the rugulate pattern is, in fact, a characteristic of many Papilionoid genera.

The rugulate pattern was also found in many other genera here studied (Table 6), and was also observed in five of the 11 genera of the Robinieae examined by LERSTEN (1981) in his survey of seed testa topography of the Papilionoideae (Table 9). Furthermore, LERSTEN (loc. cit.) has shown that at least 20 of 32 tribes of the Papilionoideae legumes have rugulate-patterned testa type. It is not surprising, therefore, that seed testa patterning is of little use as a diagnostic character of Sesbania.

LERSTEN (1981) mentioned that the seeds of Sesbania grandiflora which he studied were substriate and not rugulate as in S. bispinosa (Table 9). However, despite making this distinction the same author says that it is not always possible to distinguish clearly the "almost imperceptible" differences in the intermediate configuration (substriate) between the levigate (smooth) and rugulate patterns. In the present study it was concluded that it is not possible to distinguish between rugulate and substriate or levigate patternings. Therefore, S. grandiflora

Table 9 - Seed testa patterns of Robinieae genera observed by LERSTEN (1981).

TESTA PATTERN	TAXON
LEVIGATE	Coursetia microphylla A. Gray Gliricidia sepium (Jacq.) Steud. Olneya tesota A. Gray Sabinea carinalis Griseb.
RUGULATE	Diphysa robinioides Benth. Glottidium vesicarium (Jacq.) Harper Neocracca heteranthera Robinia pseudacacia L. Sesbania bispinosa (Jacq.) W. F. Wight
SIMPLE-RETICULATE	Poissonia hypoleuca
SIMPLE-RETICULATE (AND MOUNDS)	Cracca edwardsii
SUBSTRIATE	Sesbania grandiflora (L.) Pers.

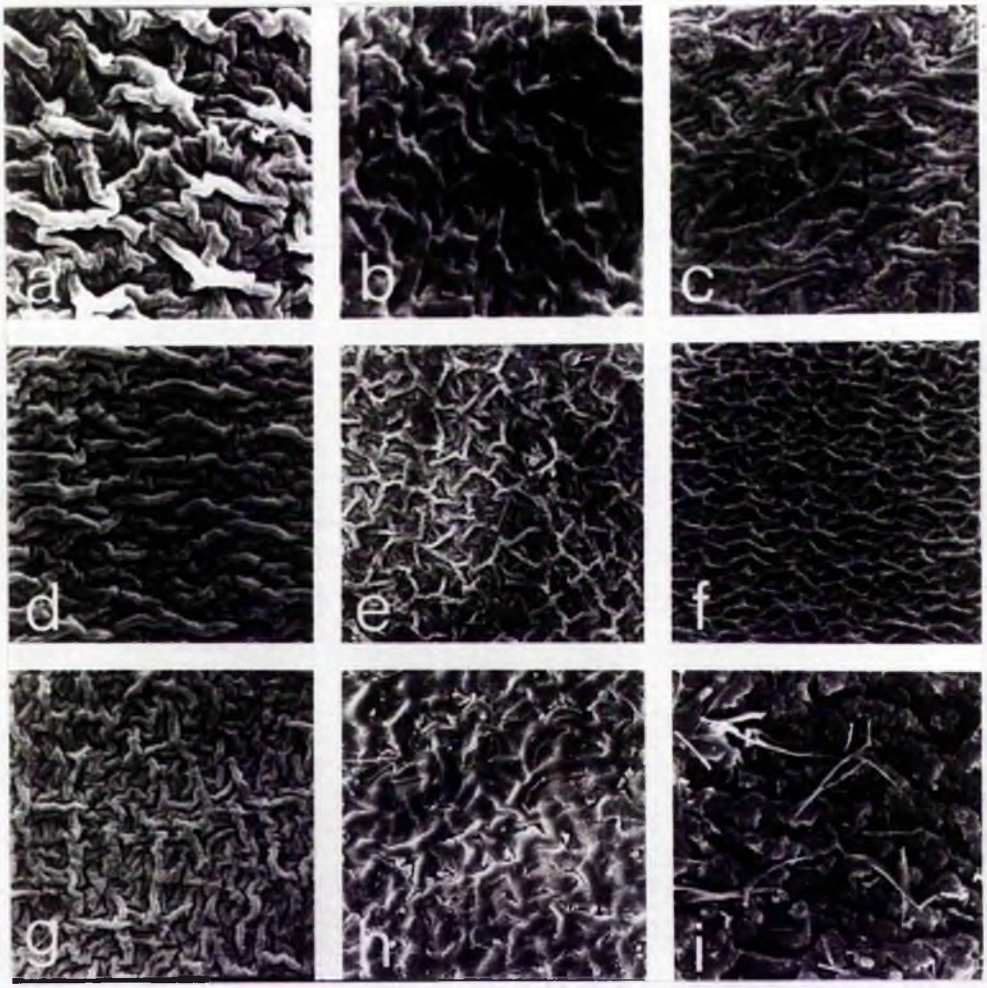


Figure 22 - Seed testa sculpture patterns of Sesbania, Glottidium and Yucaratonia (all 1000x). a - S. emerus; b - S. exasperata; c - S. oligosperma; d - S. sericea; e - S. tetraptera; f - S. tetraptera; f - S. simpliciuscula; g - S. benthamiana; h - Glottidium vesicarium; i - Yucaratonia brenningii.

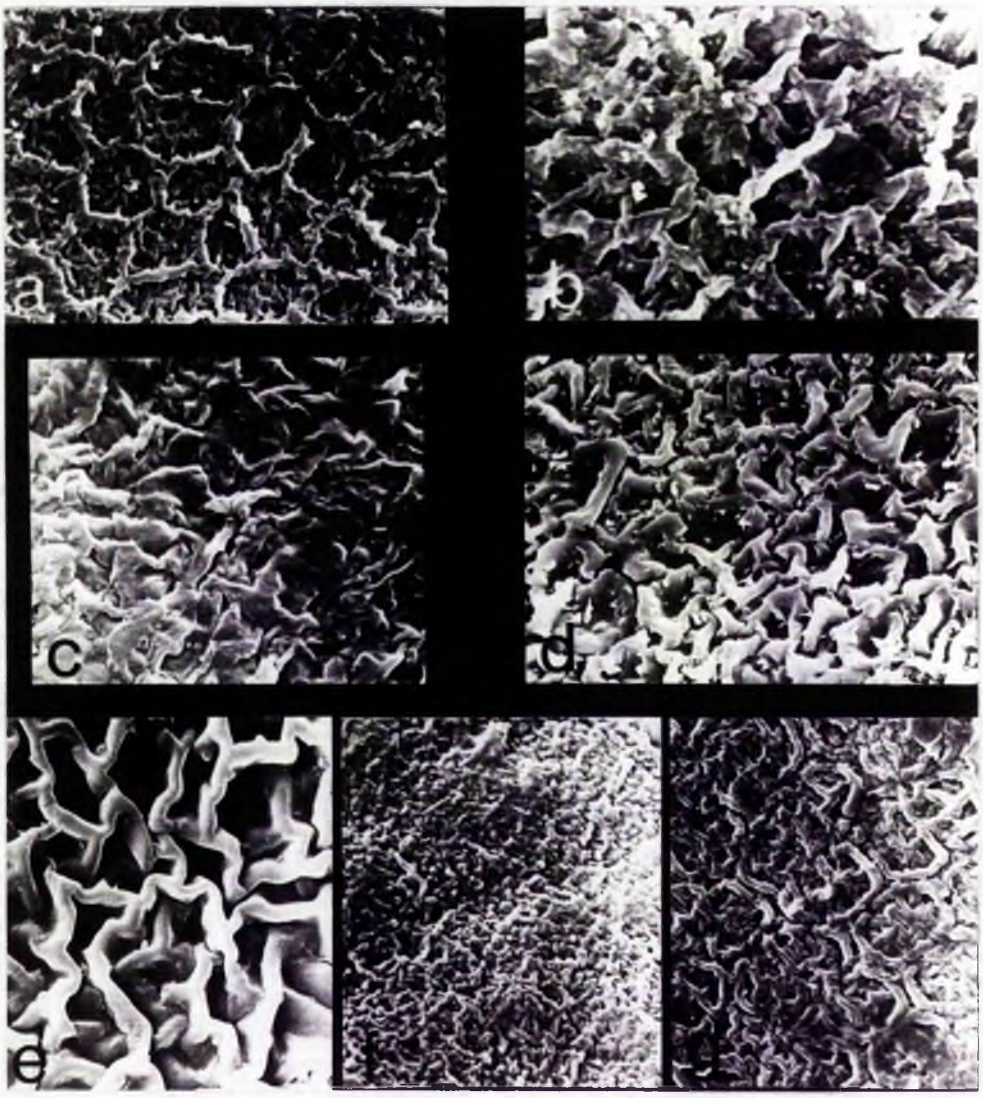


Figure 23 - Seed testa sculpture patterns of Robinieae genera (all 1750x, except a, 1000x). a - Coursetia glandulosa; b - Coursetia arborea; c - Coursetia mollis; d - Robinia pseudacacia; e - Robinia neomexicana; f - Gliricidia sepium; g - Diphysa robinioides.

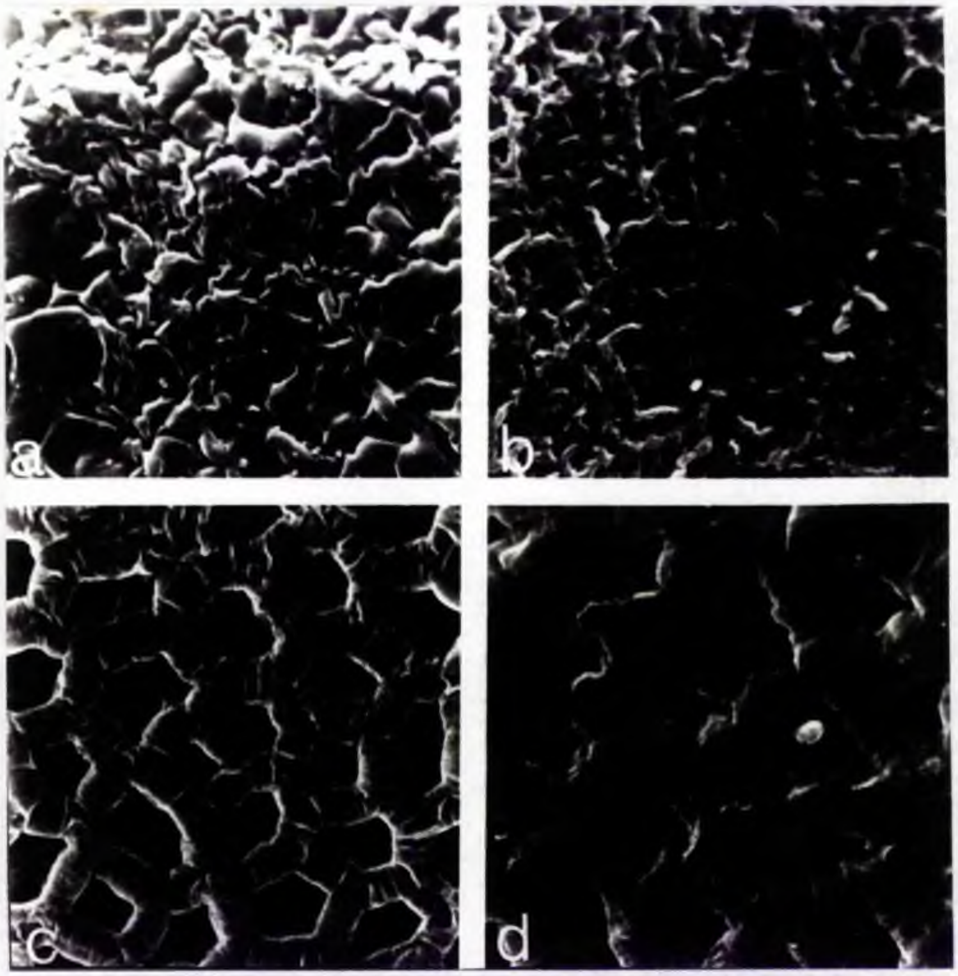


Figure 24 - Seed testa sculpture patterns of Robinieae genera (all 1000x). a - Coursetia glandulosa; b - Cracca chrysophylla; c - Cracca caribaea; d - Cracca spicata.

(subgen. Agati), like the other Sesbanias, is interpreted as having rugulate seed testa.

Other patterns which were observed in the samples of some Robinieae genera (Table 6) include multi- and simple-reticulate (Coursetia glandulosa, Figure 23a; Cracca caribaea and Cracca spicata, Figures 24 c,d), and LERSTEN (1981) gives other examples of levigate seeds in this tribe (Table 9). However, as discussed above, the distinction between the levigate, substriate and rugulate is not always clear although it would certainly depend on the conditions of the samples studied and several effects of the techniques employed for the SEM observations.

In Sesbania, the testa changes its pattern in the lens region (Figures 21 d,e,f), where it becomes clearly distinct from the mid-seed pattern but not always showing a disrupted cuticle. Although this difference is found only in a very small area, it may be correlated with some internal modifications (discussed below) which, altogether, are associated with the function of this structure in the germination process.

As mentioned above, the lens in seeds of Sesbania does not show a disrupted testa but in many other papilionoid legumes it may be found as a partially open passage through the mound formed by the lens (POLHILL, 1976; GUNN, 1981). Although lenses have not yet been properly studied for most species of Leguminosae, those examined show the lens to be an area of weakness through which the water initially penetrates the seed (GUNN, 1972; POLHILL, 1976; ROLSTON, 1978; GUNN, 1981).

The function of the lens in the germination process has also been demonstrated with success by HANNA (1984) in Acacia kempeana (Acacieae, Mimosoideae). Germination of seeds in this species only occurred after heat treatment, which disrupted the testa in the lens region and thus allowed the seeds to imbibe. Certainly, simple scarification of the lens region increased the germination rate of the seeds of all Sesbania species studied.

4.2.3.5 - Internal structure

The internal structure of papilionoid seeds is illustrated diagramatically in Figures 17 c,d and 18 c,d, after sectioning in transversal and longitudinal planes through the hilum, following the techniques given by LERSTEN (1982). The captions for the subsequent illustrations of the anatomy of Sesbania, Glottidium and Yucaratonia seeds are given in Figures 17 and 18, and in the preceding page to Figures 25–43.

A summary of some of the more important features is given in Table 10 and the illustrations for this section are found in Figure 25 for subgen. Agati, Figures 26–31 for subgen. Daubentonia, Figures 32–40 for subgen. Sesbania, Figure 41 for subgen. Pterosesbania, and Figures 42 and 43 for Glottidium vesicarium and Yucaratonia brenningii, respectively.

Except in the hilum, the testa consists of a layer of elongate malpighian cells (essentially the epidermis), together with a subtending layer of sclereids (the hypodermis, formed by the hour-glass cells), and below this a zone of poorly defined cells (the "remnant layer" of some authors) here named as parenchyma (Figures 18 c,d).

POLHILL (1976) reports that the dimensions of epidermal cells

Abreviations used for the illustrations of internal seed morphology (Figures 25 to 43).

Ar = aril
Co = cotyledons
Cp = counter-palisade
Ep = epidermis
Hi = hilum
Hg = hilar groove
Hr = hilar rim
Hy = hypodermis
Le = lens
My = micropyle
Pa = palisade
Pr = parenchyma
Sc = sclereids
Te = testa
Tb = tracheid bar
Tp = tracheoid pit
Tr = tracheoid
Vb = ovular vascular bundle
Vs = vesturing

Figure 25 - Internal seed morphology of Sesbania grandiflora.

a - transversal section of the hilum (75x)

b - tracheoid pits (1000x)

c - transversal section of the testa away from hilum (175x)

d - closeup of ovule vascular bundle in saggital section, in contact with tracheid bar

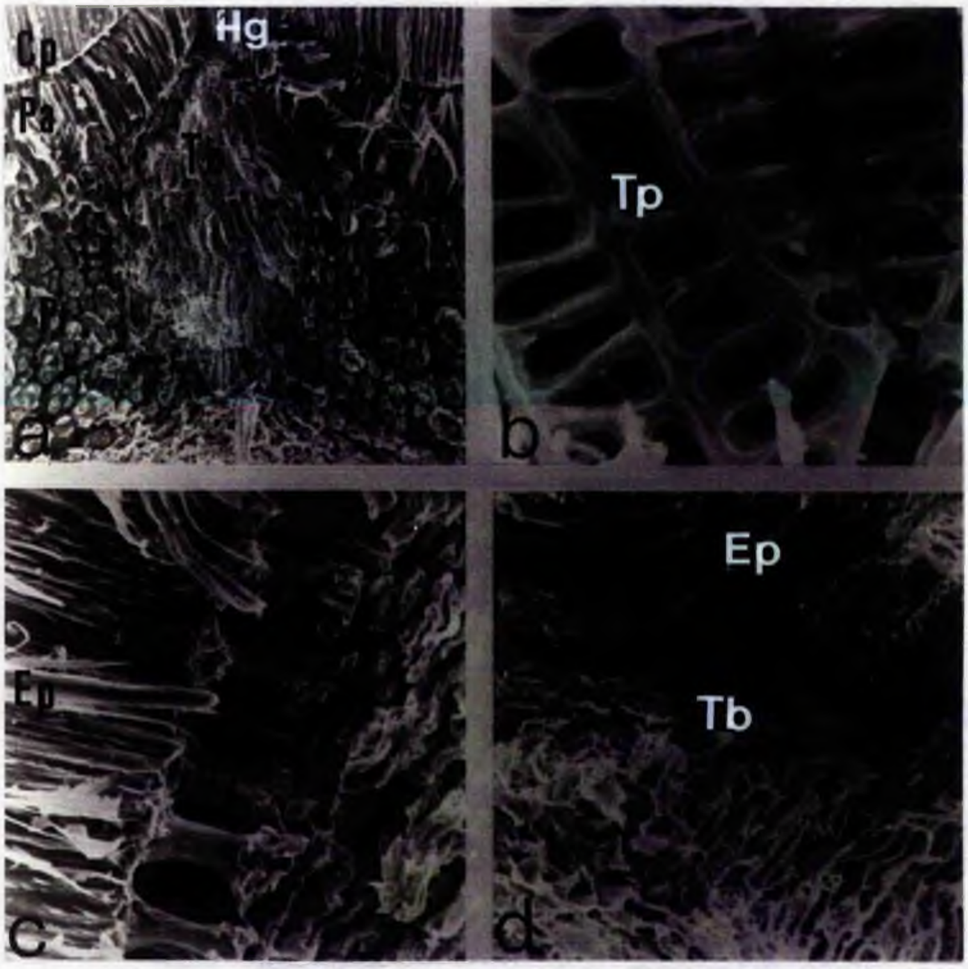
Figure 26 - Internal seed morphology of Sesbania cavanillesii.

a - transversal section of the hilum (17.5x)

b - ibidem (75x) showing tracheid bar shape

c - tracheoid pits (750x)

d - transversal section of the testa away from hilum (100x)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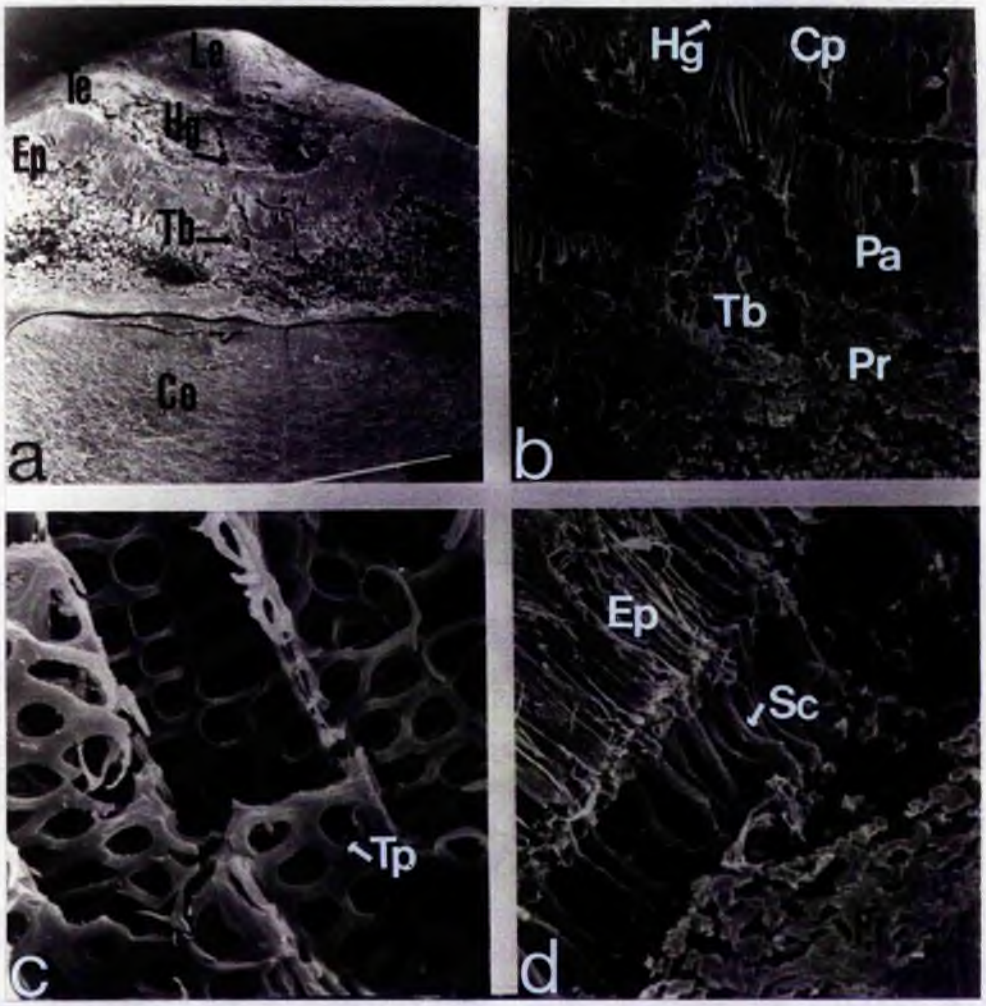
c
Ep
Tb
d

25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Ep
Sc
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26

Figures 27 and 28 - Internal seed morphology of Sesbania drummondii (Figure 27) and S. macroptera (Figure 28).

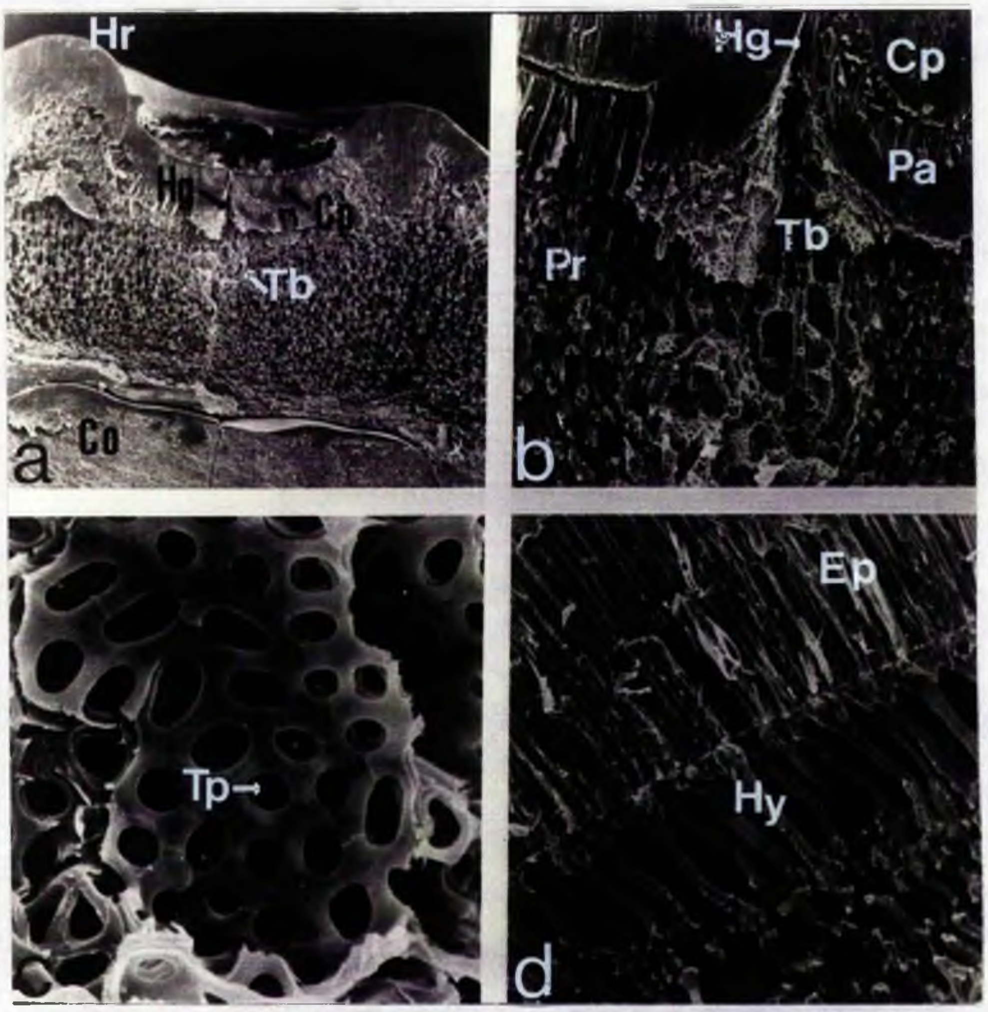
a - transversal section of the hilum (17.5x)

b - tracheid bar and hilum (75x)

c - tracheoid pits (750x)

28d - ibidem (1750x)

27d, 28e - transversal section of the testa (75x, 100x)


Hr
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Hy
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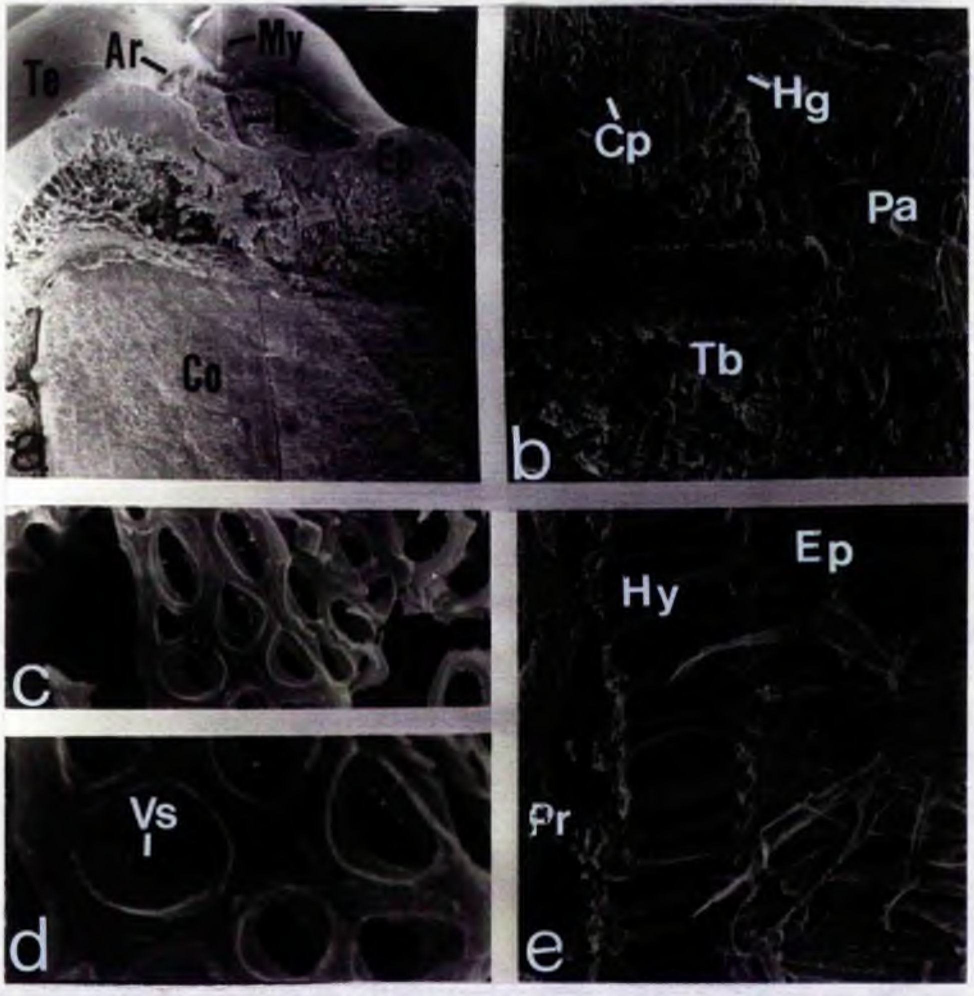
27


Te
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My
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a
Cp
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Pa
Tb
b
c
Vs
d
Ep
Hy
Pr
e

28

Figures 29 and 30- Internal seed morphology of *Sesbania punicea* (Figure 29) and *S. virgata* (Figure 30).

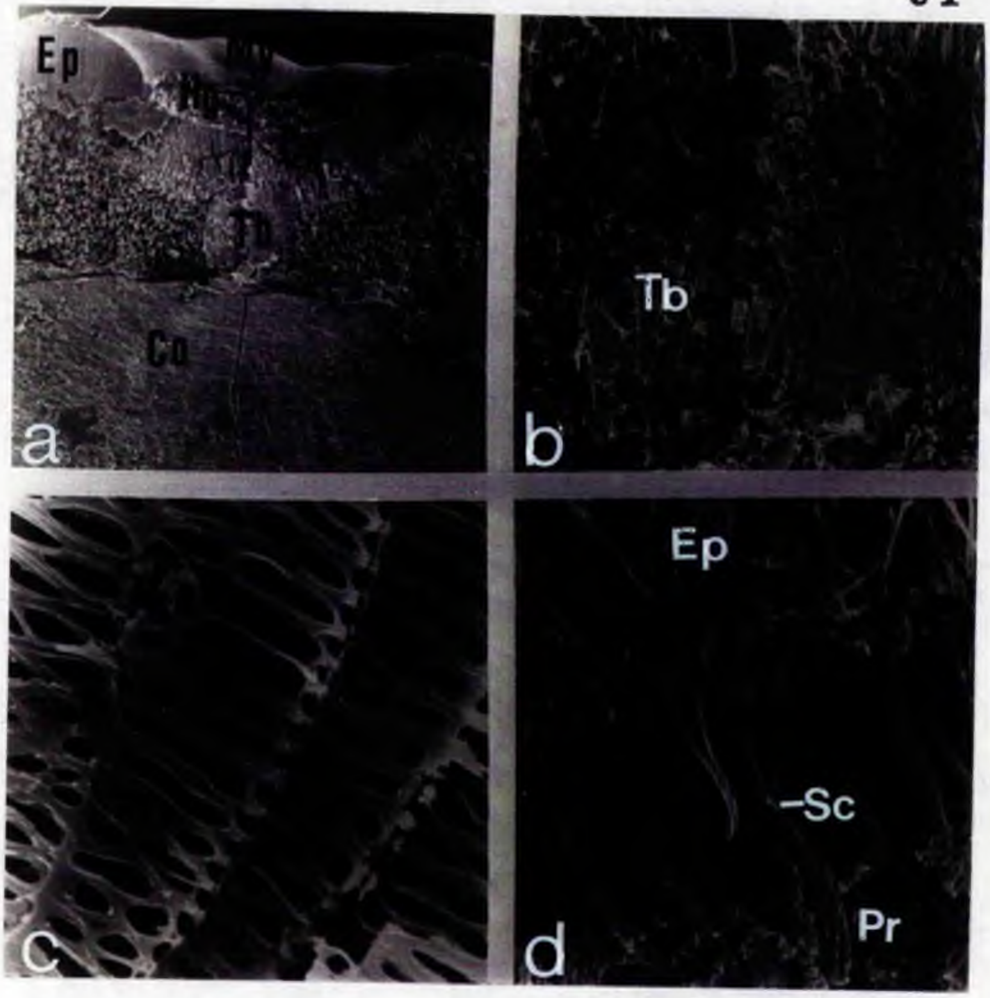
a - transversal section of the hilum (17.5x)

29b - ibidem (75x)

29c, 30b - tracheoid pits (750x)

29d, 30d - transversal section of the testa (100x)

30c - ibidem (75x)



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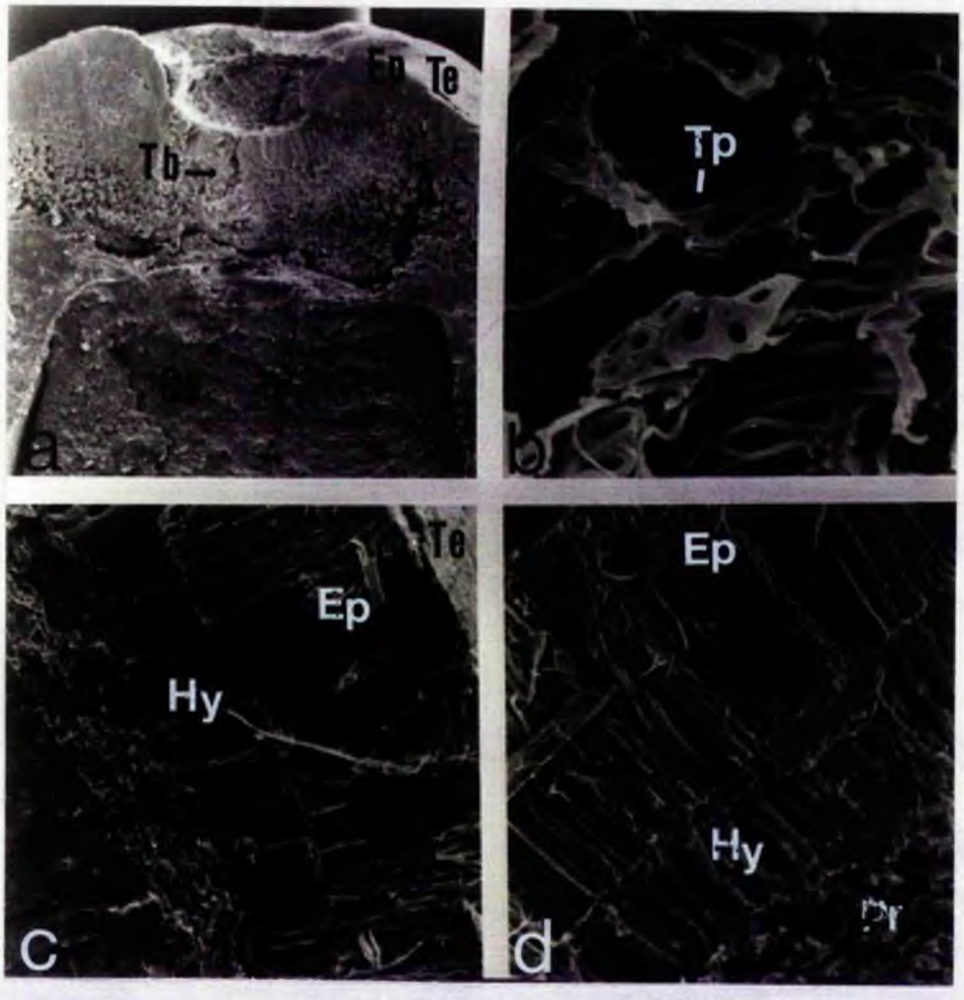

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Figure 31 - Longitudinal sections of seeds through the hilum.

a - *S. punicea* (17.5x)

b - *S. macroptera* (17.5x)

c - *S. cavanillesii* 925x)

d - *S. virgata* (25x)

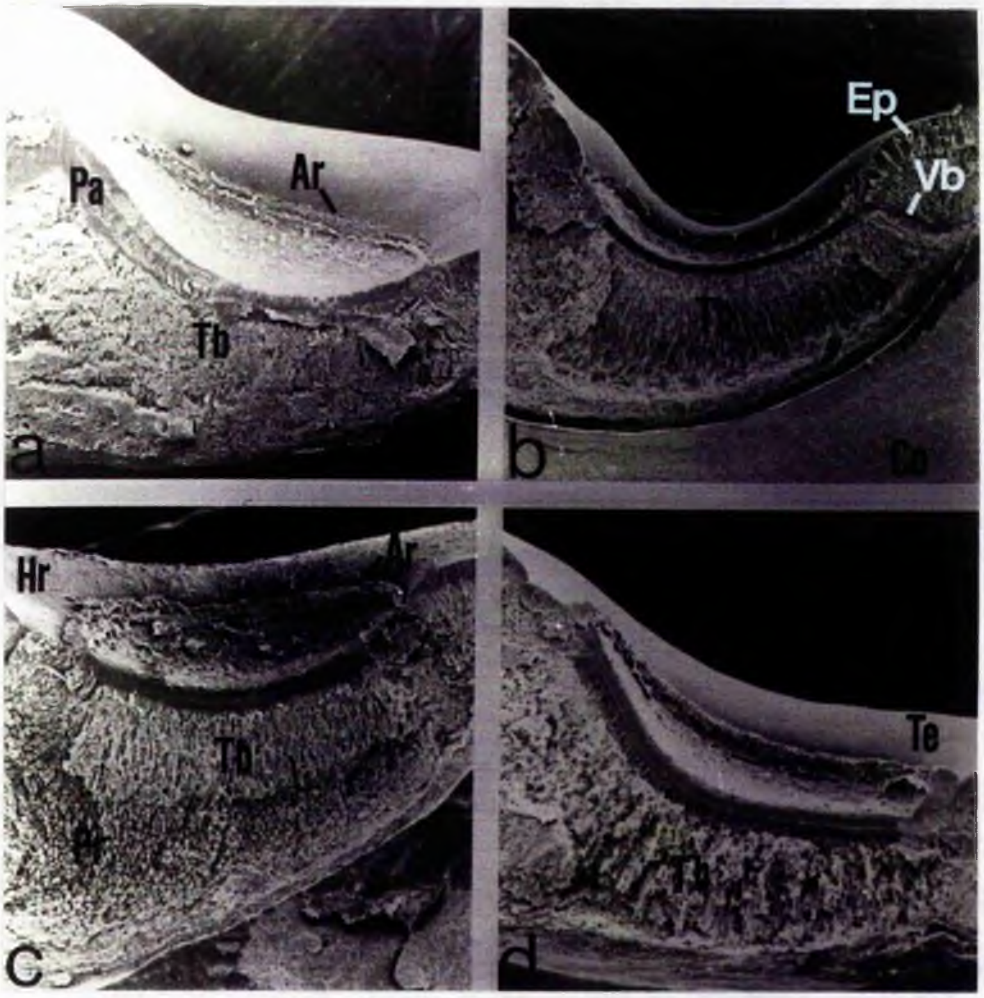
Figure 32 - Internal seed morphology of *Sesbania emerus*.

a - transversal section of the tracheid bar (100x)

b - tracheoid pits (2500x)

c - transversal section of the testa (375x)

d - sclereids (750x) showing striate surface



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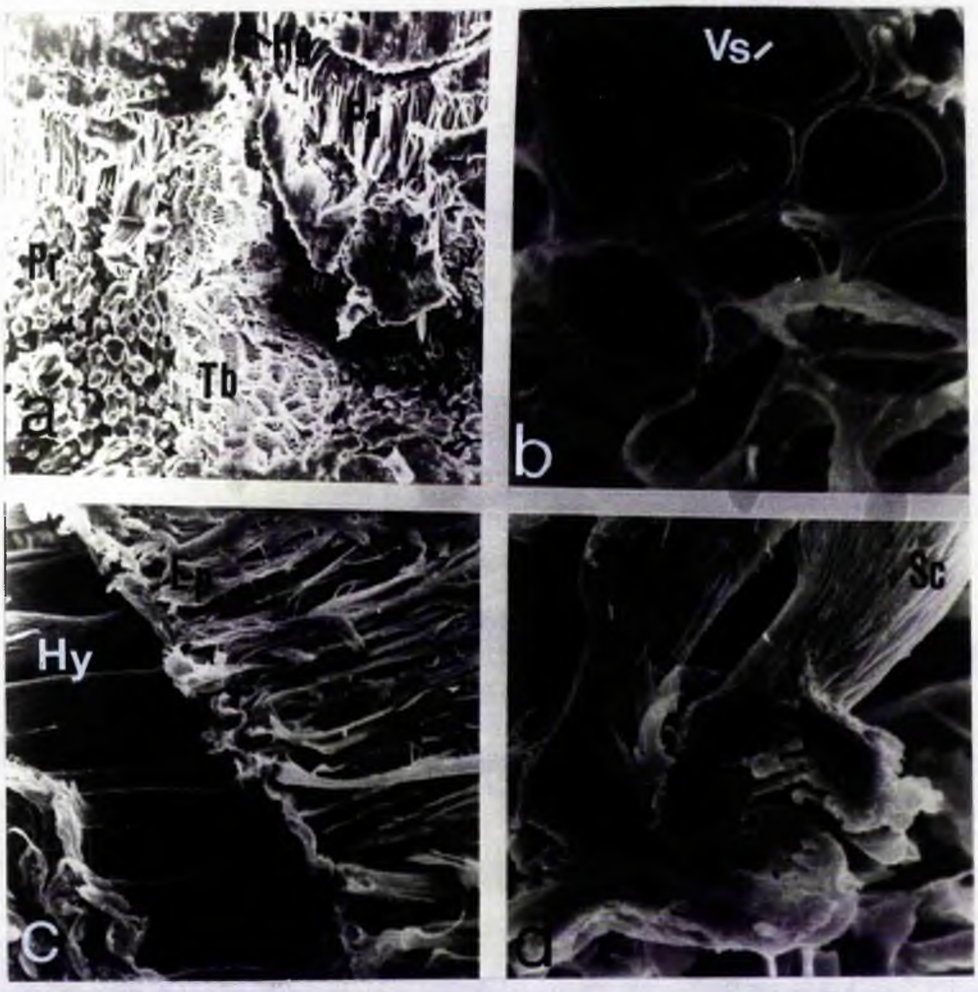

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Figure 33 - Internal seed morphology of Sesbania emerus.

a - longitudinal section through the hilum (75x)

b - transversal section of tracheid bar (100x)

c - tracheoid pits (2500x)

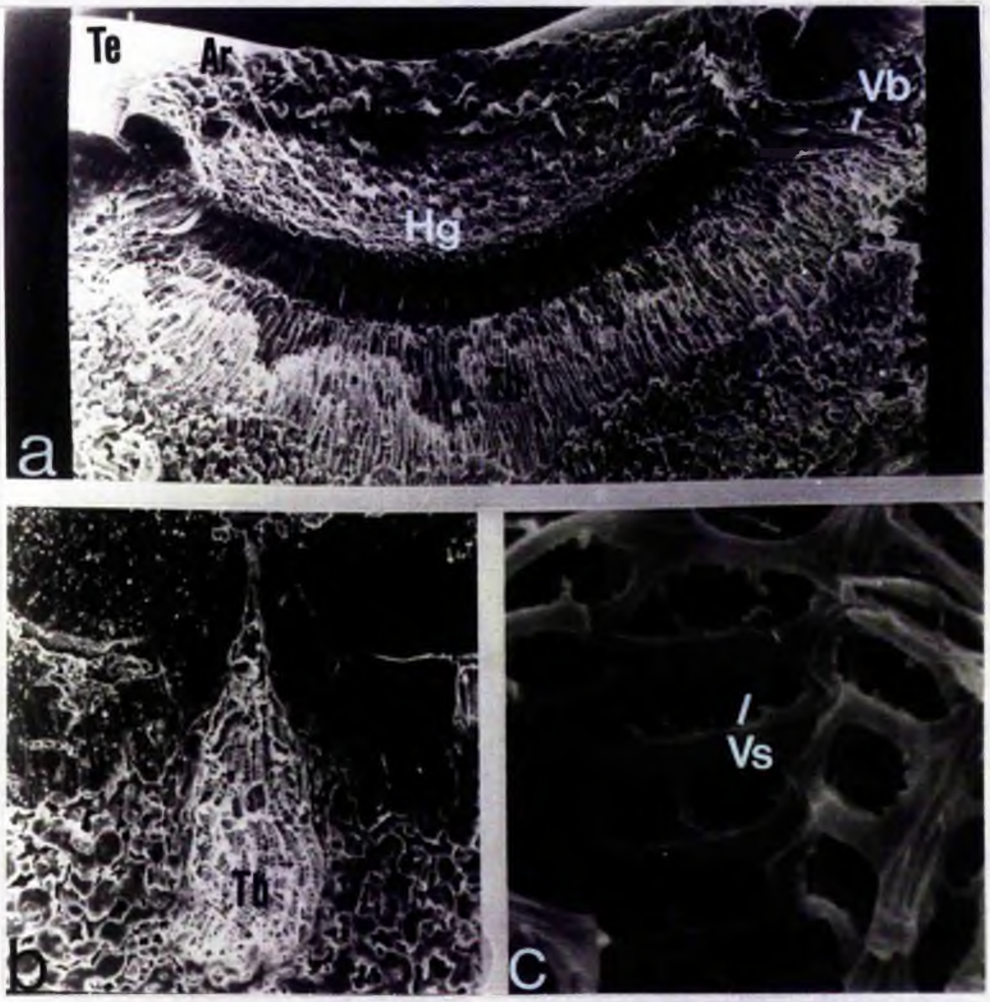
Figure 34 - Internal seed morphology of Sesbania exasperata.

a - longitudinal section through the hilum (17.5x)

b - ibidem (75x)

c - closeup of vascular bundle in contact with tracheid bar (250x)

d - longitudinal section of the testa at lens region (100x)



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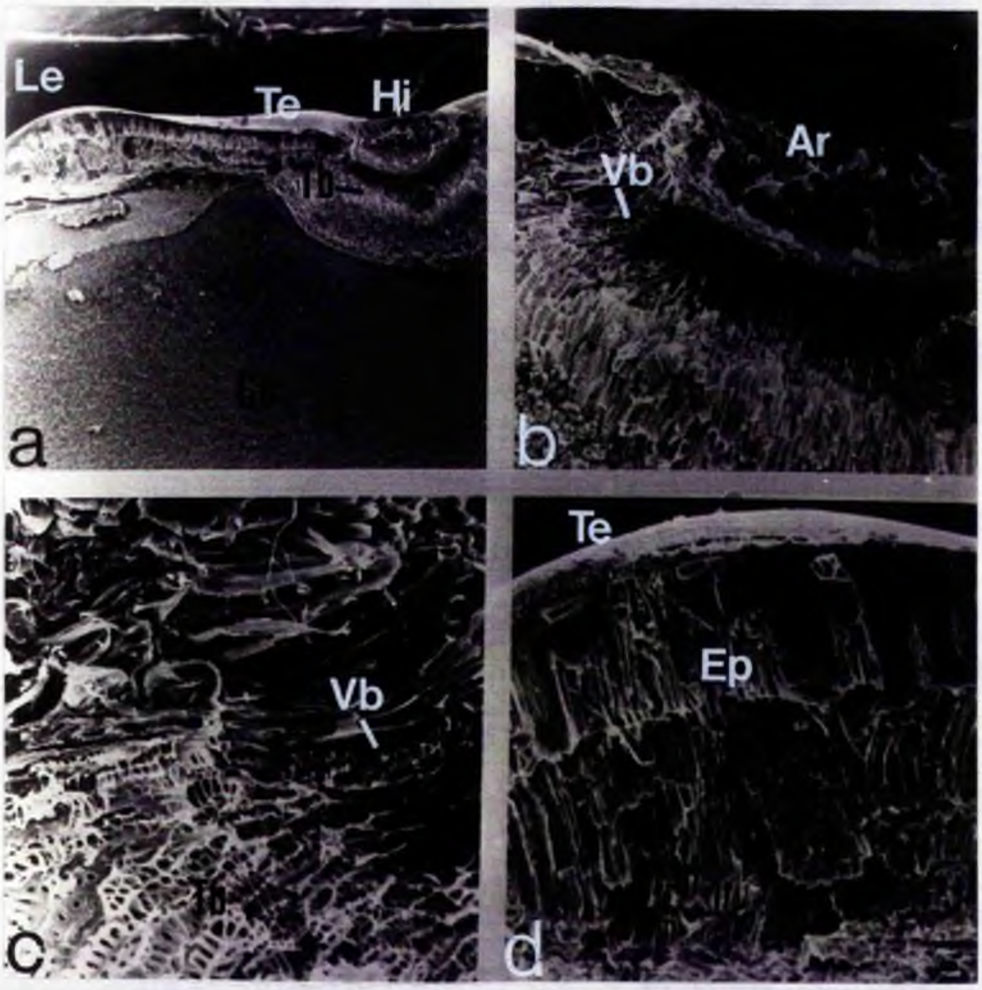

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Figures 35 and 36 - Internal seed morphology of Sesbania oligosperma.

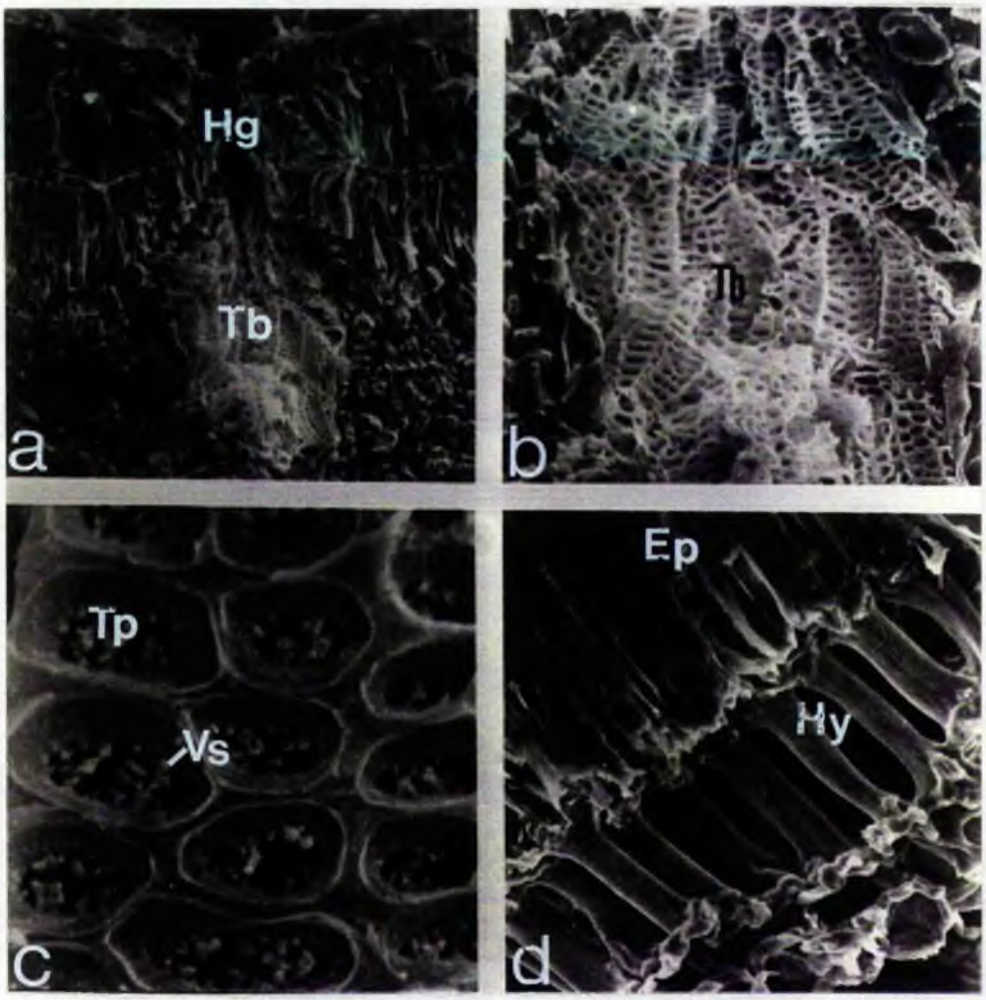
a - transversal section of the hilum (100x)

b - tracheid bar (250x)

c - tracheoid pits (2500x)

d - transversal section of the testa (250x, 3750x)

35



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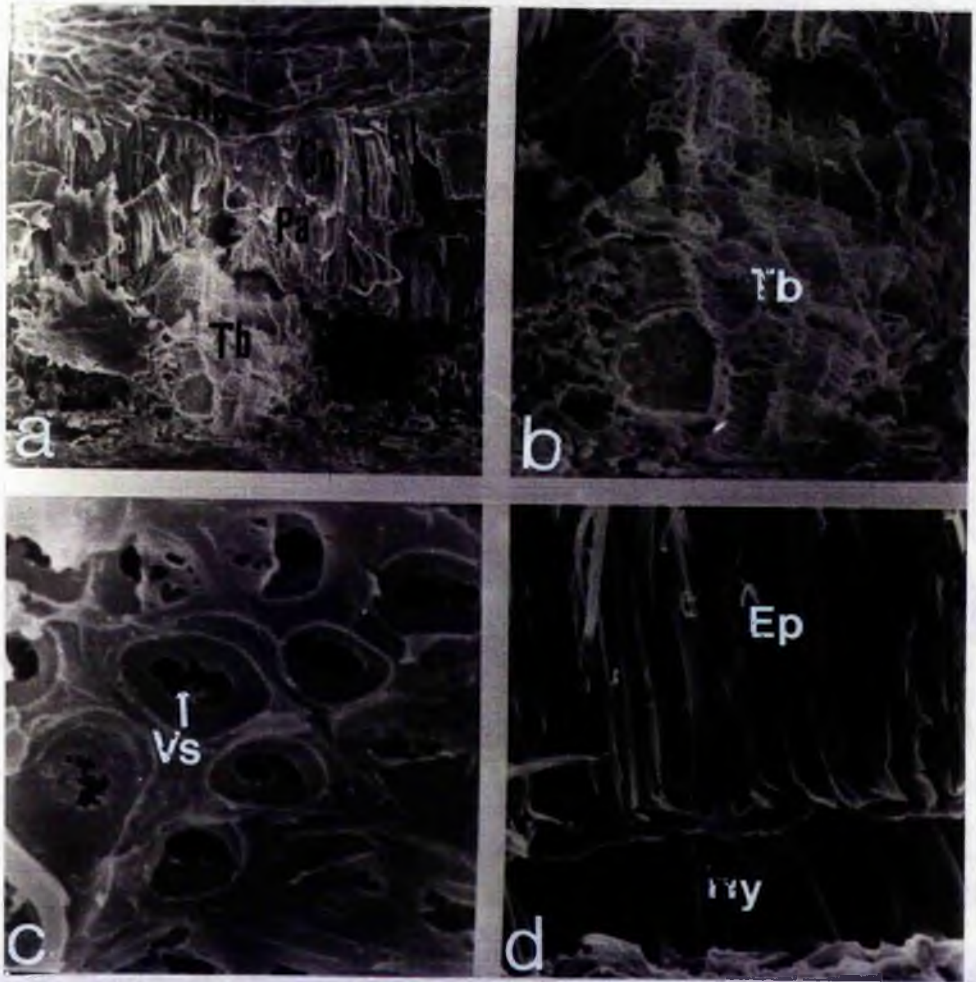


Figure 37 - Internal seed morphology of *Sesbania bispinosa*.

a - transversal section of the hilum (100x)

b - tracheoid pits (2500x)

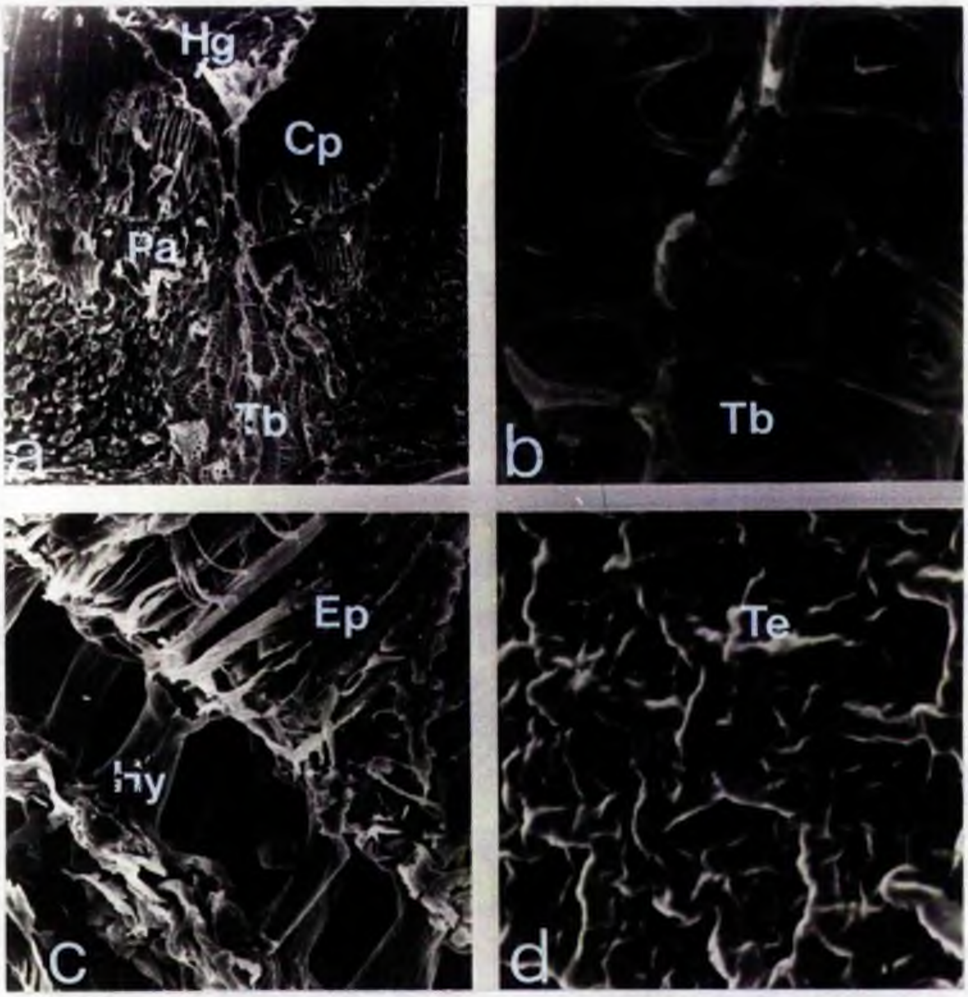
c - transversal section of the testa (375x)

d - testa pattern (2500x)

Figure 38 - Internal seed morphology of *Sesbania brevipeduncula* (a,b) and *S. erubescens* (c,d).

a,c - transversal sections of the hilum (100x)

b,d - tracheoid pits (2500x)



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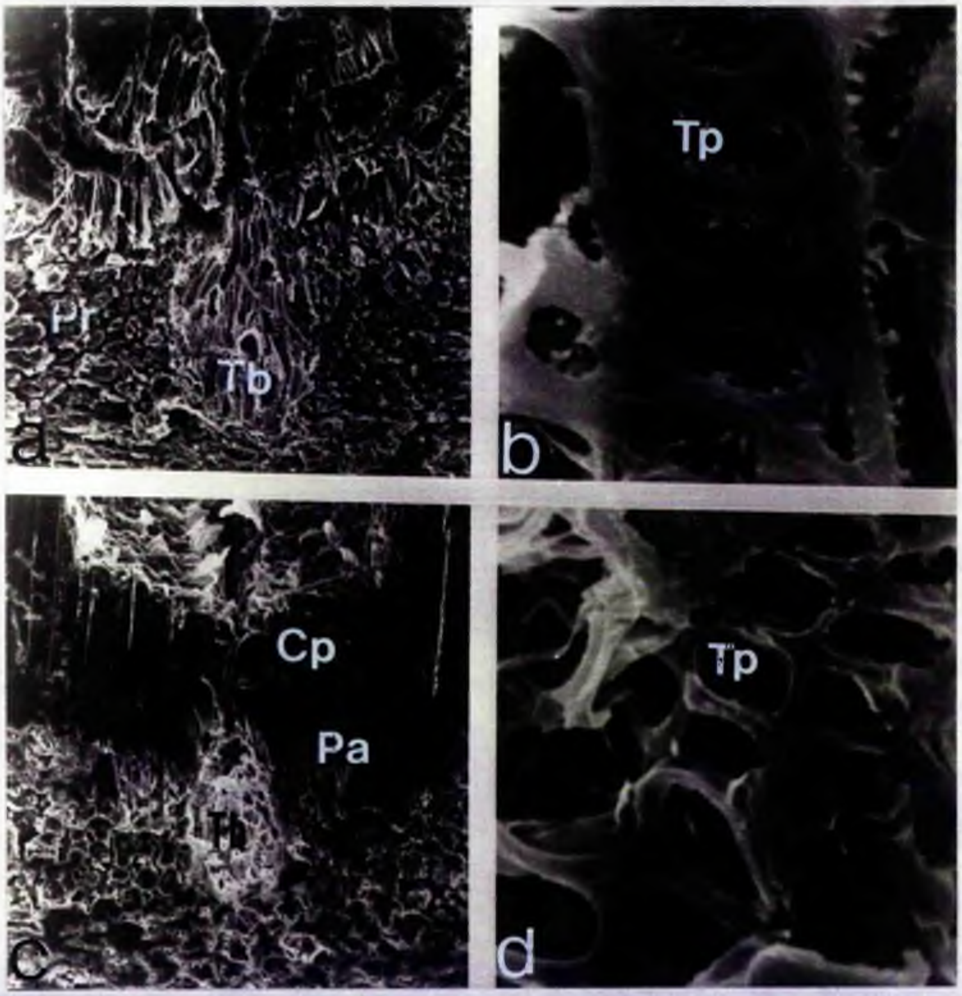

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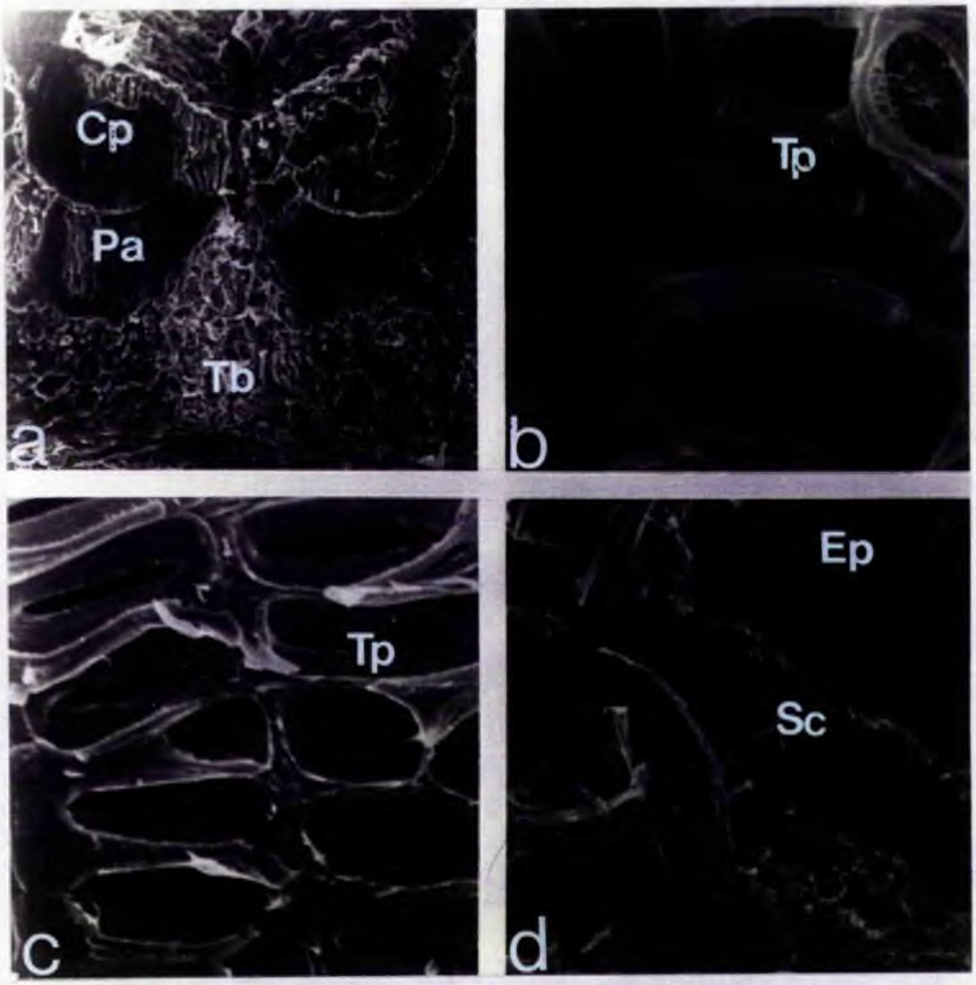
Figures 39 and 40 - Internal seed morphology of <u>Sesbania sericea</u> (Figure 39) and <u>S</u>. <u>sesban</u> (Figure 40).

a - transversal section of the hilum (100x)

b,c - tracheoid pits (2500x)

d - transversal section of the testa (250x, 375x)



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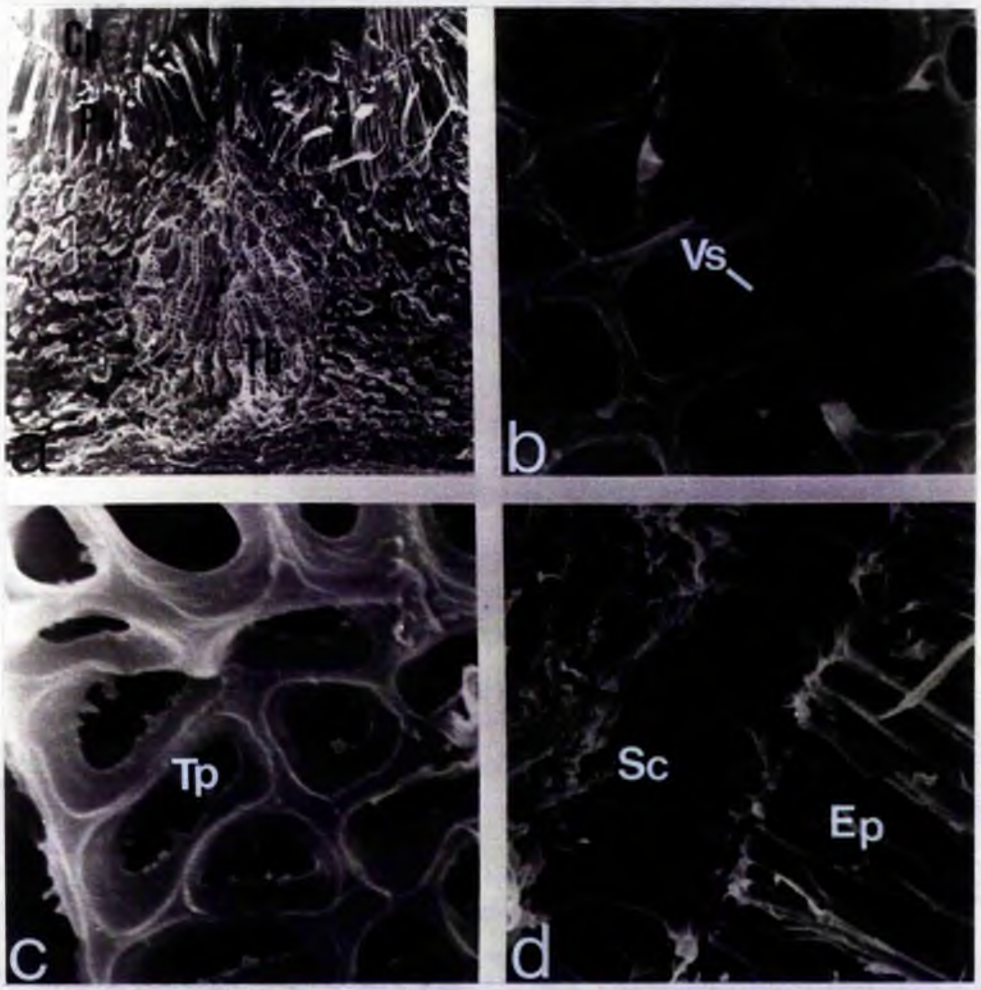

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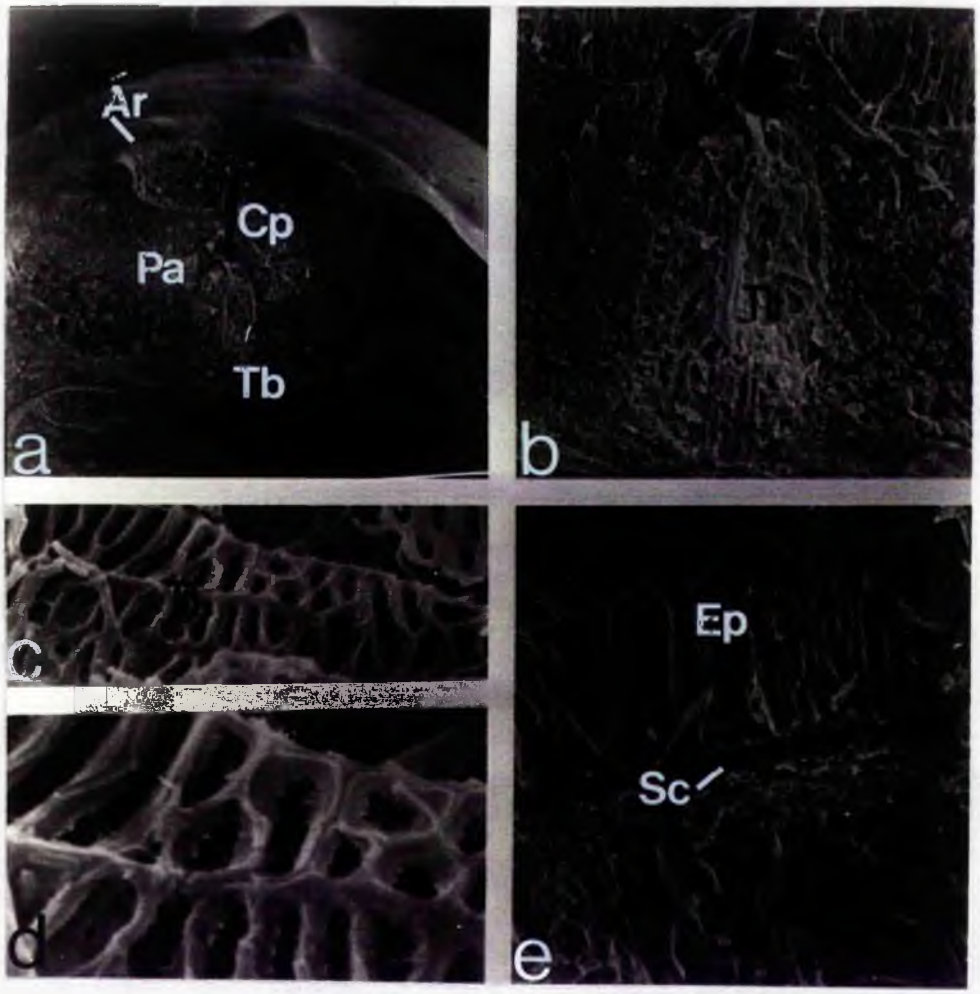
Figure 41 - Internal seed morphology of Sesbania tetraptera.

a - transversal section of the hilum (25x)

b - tracheid bar (75x)

c - tracheoid pits (750x, 1750x)

d - transversal section of the testa (100x)



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Figures 42 and 43 - Internal seed morphology of Glottidium vesicarium (Figure 42) and Yucaratonia brenningii (Figure 43).

a - transversal section of the hilum (17.5x, 37.5x)

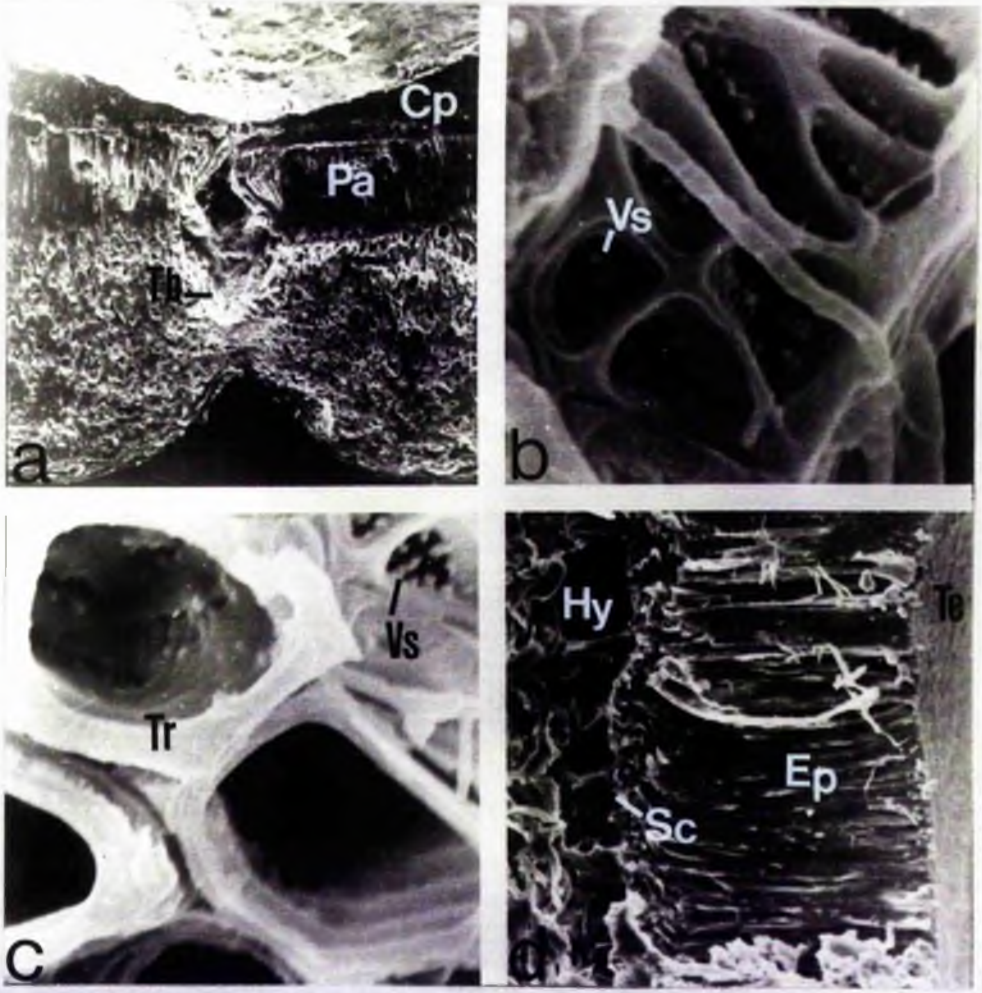
42b - ibidem (75x)

42c, 43b - tracheoid pits (750x, 2500x)

43c - transversal sections through the tracheoids (1750x)

d - transversal section of the testa (100x, 175x)

43



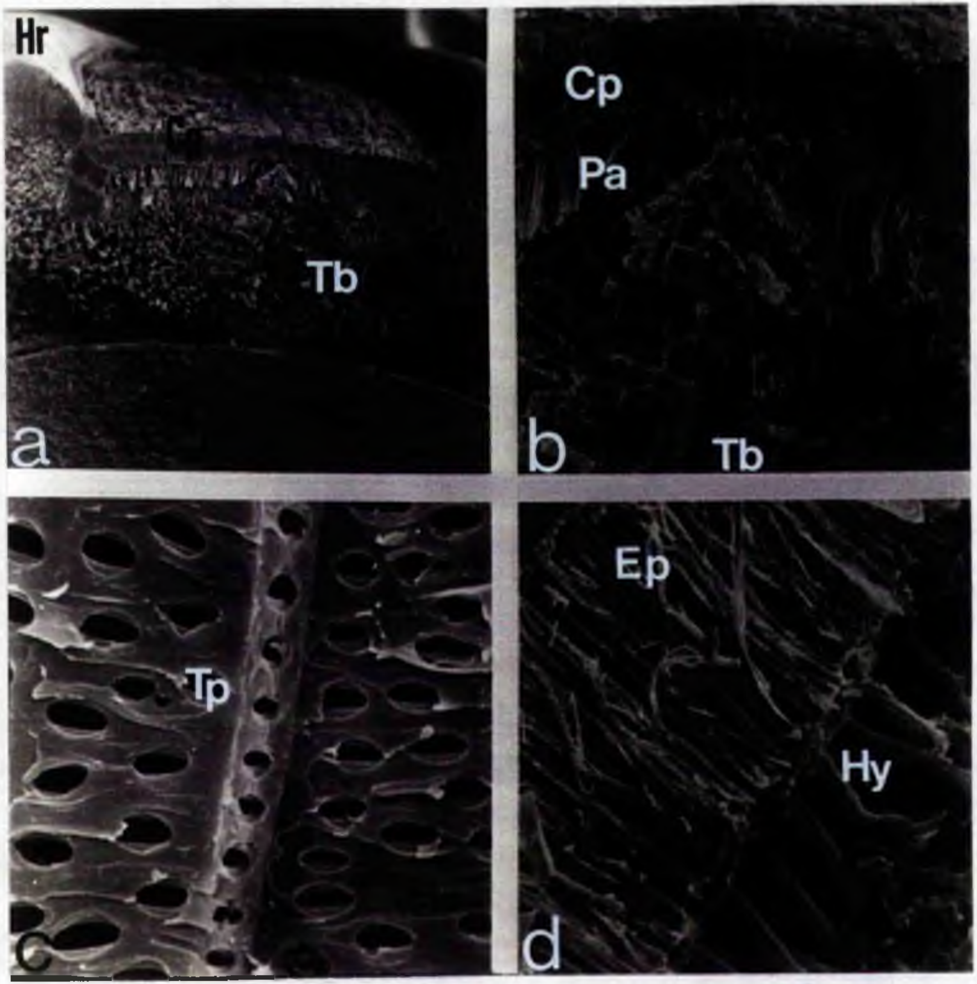


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Table 10 - Summary of testa internal characters of *Sesbania* Scop., *Glottidium* Desv. and *Yucaratonia* Burk.

TAXON	TRACHEID BAR SHAPE	TRACHEOID PIT		SCLEREID		FIGURE
		SHAPE	VESTURING	SHAPE	SURFACE	
Sesbania subgen. *Agati*						
S. grandiflora	elliptical	circular to elongated	non-vestured to sparsely wraty	dumbelloid	striate	25
subgen. *Daubentonia*						
S. cavanillesii	elliptical	circular	non-vestured to sparsely warty	humeroid	striate	26,31c
S. drummondii	elliptical	circular to elongated	non-vestured	humeroid	striate	27
S. macroptera	circular to elliptical	ovate-circular	non-vestured to sparsely warty	humeroid	striate	28, 31b
S. punicea	circular to elliptical	elongated, scallariform	non-vestured to sparsely warty	humeroid	striate	29, 31a
S. virgata	circular to triangular	elongated to ovate	non-vestured to sparsely warty	humeroid	striate	30, 31d
subgen. *Pterosesbania*						
S. tetraptera	elliptical	elongated	warty to piluloid	dumbelloid	striate	41

→

Table 10, cont.

TAXON	TRACHEID BAR SHAPE	TRACHEOID PIT SHAPE	TRACHEOID PIT VESTURING	SCLEREID SHAPE	SCLEREID SURFACE	FIGURE
subgen. *Sesbania*						
S. bispinosa	circular to	elongated	foliate	dumbelloid	striate	37
S. brevipeduncula	elliptical	ovate to elongated	foliate	dumbelloid	striate	38
S. emerus	elliptical	circular to elongated	piluloid to foliate	dumbelloid	striate	32,33
S. erubescens	elliptical	elongated	non-vestured	dumbelloid	striate	38
S. exasperata	circular	ovate to circular	warty, piluloid to foliate	dumbelloid	striate	34
S. oligosperma	elliptical	circular	piluloid to foliate	dumbelloid	striate	35,36
S. sericea	elliptical	elongated	non-vestured to sparsely warty	dumbelloid	striate	39
S. sesban	elliptical	circular-ovate to elongated	foliate to piluloid	dumbelloid	striate	40

Table 10, cont.

TAXON	TRACHEID BAR SHAPE	TRACHEOID PIT		SCLEREID		FIGURE
		SHAPE	VESTURING	SHAPE	SURFACE	
<u>Glottidium</u> Desv.						
<u>G. vesicarium</u>	circular	ovate	non-vestured to sparsely warty	humeroid	striate	42
<u>Yucaratonia</u> Burk.						
<u>Y. brenningii</u>	elliptical	circular	non-vestured to sparsely warty	humeroid	smooth	43

vary enormously in any one seed of the Genisteae genera : "long towards the hilum, shortest towards the opposite side, very long and relatively thin in the lens region". These observations were made using preparations of isolated cells from the different tissue layers (POLHILL, 1976). The SEM technique employed in the present study does not permit such quantitative determinations. However, in *Sesbania* some variation was found in the thickness of the epidermis in different parts of the seed and in Figure 34 A it is possible to see that the epidermis is indeed thicker in longitudinal section in the lens region, indicating that the cells are longer there. Detail of this zone is also shown in Figure 34 D.

Comparative studies were made to determine whether *Sesbania* species showed some variation in the relative proportions of the epidermis and hypodermis layers. Whilst no significant differences in these proportions are present among the four subgenera, it is possible to see that in *Yucaratonia* (Figure 43), a genus of the Robinieae, the epidermis is much thicker than the hypodermis. No published data is available for other Robinieae species with flat, compressed seed like *Yucaratonia brenningii* so that it is not possible to ascertain whether other taxa have a similar testa structure. The hypodermis (or the sclereid layer, which is also called macrosclereid or osteosclereid layer) occurs all around the seed below the epidermis except in the hilar region (Figure 18 d). Although not present at the hilum, the hypodermis is more prominent adjacent to the hilar region and becomes inconspicuous towards the areas in the middle of the seed and opposite the hilum. It consists of a single layer of sclereids that are either humeroid or dumbelloid in shape, the former being generally longer and thinner than the latter and much variation in the dimensions of these cells was found in Sesbania and allies at inter- and intra-generic levels : the subgen. Daubentonia of Sesbania (Figures 26–30) and the genera Glottidium and Yucaratonia (Figures 42 , 43) were found to have persistently humeroid sclereids, whilst in the subgenera Agati (Figure 9), Sesbania (Figures 32, 35, 36, 37, 39, 40) and Pterosesbania (Figure 41) they are dumbelloid (Table 10).

The macrosclereids have a striate surface in all specimen seeds studied, except in Yucaratonia brenningii, where it is smooth (Figure 43).

The hilum is the region in the seed where the epidermis is extended up to the hilar groove and is overlayed by the counter-palisade (Figures 18d, and 25–43). Therefore, both palisade and counter-palisade are interrupted along the longitudinal median line of the hilum by a groove which can be seen with the naked eye (Figures 17,18). There are no particular external structures associated with the hilar groove that are of taxonomic value in Sesbania.

The hilar groove leads to the tracheid bar - a structure only found in papilionoid legume seeds (CORNER, 1951; GUNN, 1981; LERSTEN, 1982), which is always present, extending the length of the hilum beneath the groove (Figures 18 a,c,d and 25–43). The tracheid bar is surrounded by parenchyma tissue except where the palisade and counter-palisade enclose it and, in the uppermost area, where it is in contact with the groove or exposed to the air.

Some of the tracheid bar features which have been found to have taxonomic value are presented in Table 10, viz. shape in transectional view, tracheoid pit shape, and vesturing.

In transversal section the tracheid bar is usually elliptical but it can also be found to be circular or triangular (Figures 25-30, 32, 35-43). Measures of the tracheid bar were made for several species but no correlation was found with hilum or seed sizes.

Compaction and size of the tracheoids (which are perpendicular to the hilar groove) are too variable at intra- and inter-generic levels, and sometimes also found to change in different specimens of the same species. The latter point is illustrated by the observations made in Sesbania oligosperma Taub. (Figure 35, 36). The collection made by RIEDEL 2237 (Figure 35) has seeds which show, at the same magnification used for PEDERSEN 7025 (Figure 36), a longer tracheid bar and the tracheoids less compact. It also has a relatively thinner sclereid layer and a different type of vesturing.

Vesturing and shape of the tracheoid pits are parameters that can vary greatly at inter- and intra-generic levels (LERSTEN & GUNN, 1982) and the present results show two distinct patterns within Sesbania. Species of subgen. Sesbania (including species of New and Old World, Table 10) and subgen. Pterosesbania have predominantly piluloid to foliate pits, whereas in the subgenera Daubentonia and Agati the basic pattern is non-vestured to sparsely warty pits (Table 10 and illustrations).

Glottidium vesicarium (Figure 42) presents the same vesturing pattern as subgen. *Daubentonia* whereas *Yucaratonia brenningii* (Figure 43) has a variation from non-vestured to foliate patterns.

Although showing some minor differences between the allied genera *Sesbania* and *Glottidium*, and also *Yucaratonia*, the tracheid bar is remarkably uniform in many features. Such differences that exist are not taxonomically helpful. For example, the range of variation in tracheid bar morphology and tracheoid pit patterns which LERSTEN (1982) presented for the Robinieae and Sesbanieae have all been observed for the genus *Sesbania* alone in the present study.

The series of longitudinal sections of the seeds of species of different subgenera of *Sesbania* shown in Figures 25d, 31, 33, and 34 can be taken as representative of the whole genus. Figure 31 as well as others show one disadvantage of the technique used : since the seed is simply cut through with a razor blade it is a matter of chance whether a good median sagittal section is obtained. It is therefore difficult, for example, to follow the path of the ovular vascular supply in the hard testa of any particular seed. However, the illustrations of *S. grandiflora* (Figure 25), *S. macroptera* (Figure 31), *S. emerus* (Figure 33 a), and *S. exasperata* (Figure 34 b,c) show that the vascular bundle penetrates the testa in the end of the hilum opposite to the micropyle, turns in the direction of the lens and then merges with the tracheid bar for the whole extension of contact with it. The tracheids of the vascular bundle are much smaller than the tracheoids of the tracheid bar and this comparison is emphasized in Figures 25 d and 33 c). Finally the lens, which in *Sesbania* is located at the non-micropylar end of the hilum appears in surface view as a circular swelling (Figure 21), and in longitudinal section shows unusually elongate epidermal cells (Figure 34 d) and, apparently, absence of a hypodermis. This modification in internal structure, mainly in the length of the epidermal cells is reflected externally causing some change in the testa sculpturing, as already mentioned above.

4.2.3.6 - Cotyledon anatomy.

The study of the cotyledon anatomy was made from seeds of the species of Sesbania cited in Table 11. Despite the potential taxonomic value which has been attributed to cotyledons when they are considered as organs of the seedlings, very little attention was given to their internal morphology in the classical works (CORNER, 1951; 1976) of legume seed anatomy.

Recently SMITH (1981, 1983) has shown with a survey of approximately 900 species of the Leguminosae that the gross anatomy of the cotyledon has correlations with classification at the tribal and generic levels, and so provides a set of characters of taxonomic or phylogenetic value.

SMITH (loc. cit.)recognized two basic types of cotyledons in legume seeds : a leaf-like photosynthetic cotyledon (form 1) which occurs in 60% of the species he examined and a fleshy, storage cotyledon (form 4) which occurs in about 30% of the taxa. Between these two modal forms SMITH (1983) characterized two other types (forms 2 and 3) which combine the features of the basic ones in varying degree.

The foliar cotyledon (form 1) is essentially a functional leaf with leaf-like structure and form, and internally differentiated into palisade and mesophyll tissues. Storage cotyledons (form 4) are thick, fleshy organs, often hemispherical, lacking completely any internal differentiation into palisade and mesophyll layers. The intermediate cotyledons may be thin and leaf-like but lacking a palisade layer (form 2) or thick and fleshy but with palisade (form 3) (SMITH, 1983).

In the Robinieae, SMITH (loc. cit.) investigated seeds of Gliricidia sepium, Robinia luxurians, R. pseudacacia, and four species of Sesbania : S. grandiflora, S. pachycarpa, S. punicea (illustrated in his Figure 2 L), and S. sudanica. Although SMITH (1983) did not specify the form of cotyledon for each of these species, he mentioned that the tribe is characterized by foliar (form 1) and intermediate (form 3) cotyledons. SOUSA & SOUSA (1981) mention that in the Robinieae as a whole the cotyledons tend to be foliaceous but they are fleshy in Hebestigma Urb. and of intermediate form in Lennea Klotzsch, both genera of this tribe.

In order to check the form of the cotyledon anatomy present in the New World species of Sesbania a study was carried out using the seeds of the specimens cited in Table 11. The material consisted of transversal handcut sections of the cotyledons of seeds imbibed for 24 hours; stained in 1% aqueous toluidine blue solution and observed with the bright field optical microscope. The results are shown in Figures 44 and 45.

All species of Sesbania studied have foliar cotyledons and a very clear distinction between palisade and mesophyll layers can

Table 11 - Collections of *Sesbania* specimens studied for cotyledon anatomy.

TAXON	ORIGIN	FIGURE
subgen. *Agati*		
S. grandiflora	cultivated, St Andrews Univ. AUGUSTO 451 (NY)	44 E
subgen. *Daubentonia*		
S. drummondii	CORRELL & JOHNSTON 17485 (LL)	44 A
S. macroptera	BALANSA 1377 (P)	44 B
S. punicea	cultivated, St Andrews Univ.	44 C
S. virgata	cultivated, St Andrews Univ.	44 D
subgen. *Sesbania*		
S. emerus	cultivated, St Andrews Univ.	45 A
S. exasperata	ZEHNTNER 1995 (M)	45 B
S. oligosperma	PEDERSEN 7025 (K)	45 C
S. bispinosa	ADAMS 8312 (MO)	45 D
S. sericea	CORRELL 45816 (NY)	45 E
S. sesban	HERINGER 13884 (MO)	45 F
subgen. *Pterosesbania*		
S. tetraptera	LEMOS & MACUACA 86 (K)	45 G

be observed (Figures 44 and 45). The adaxial face of the cotyledons is adpressed and flat in species of the four subgenera of Sesbania whereas the abaxial side is commonly convex in subgen. Daubentonia (Figures 44 A-D), subgen. Agati (Figure 44 E), and most species of subgen. Sesbania (Figures 45 A-D). However, the adaxial face may also be asymmetrical in some species of subgen. Sesbania (Figures 45 E,F) or grooved in subgen. Pterosesbania (Figure 45 G).

The palisade is usually 3 layers thick and continuous across the adaxial side of the cotyledon (Figures 44 and 45). The ratio of palisade to mesophyll is almost 1:1 regardless the subgeneric classification and dimensions of the cotyledons.

It is possible to see three main veins in transverse section of the cotyledons of Sesbania species and they are all located in the top layers of the mesophyll, adjacent to the palisade. However, in Sesbania grandiflora the mid-vein is at a lower level in the mesophyll (Figure 44 E). In the present study more veinlets were observed between the main vein in the cotyledons of subgen. Sesbania (Figures 45 A-F) which were not observed in seeds of species of subgen. Daubentonia and subgen. Agati. However, this difference may not be clear-cut since the presence of storage substances in the cotyledons of species of the latter subgenera cause problems in the interpretation of sections. Apart from the obvious point that the cotyledons of species of subgen. Daubentonia and subgen. Agati are larger than subgen. Sesbania and subgen. Pterosesbania, the only correlation which can be made is between the shape of the abaxial face of cotyledons and the

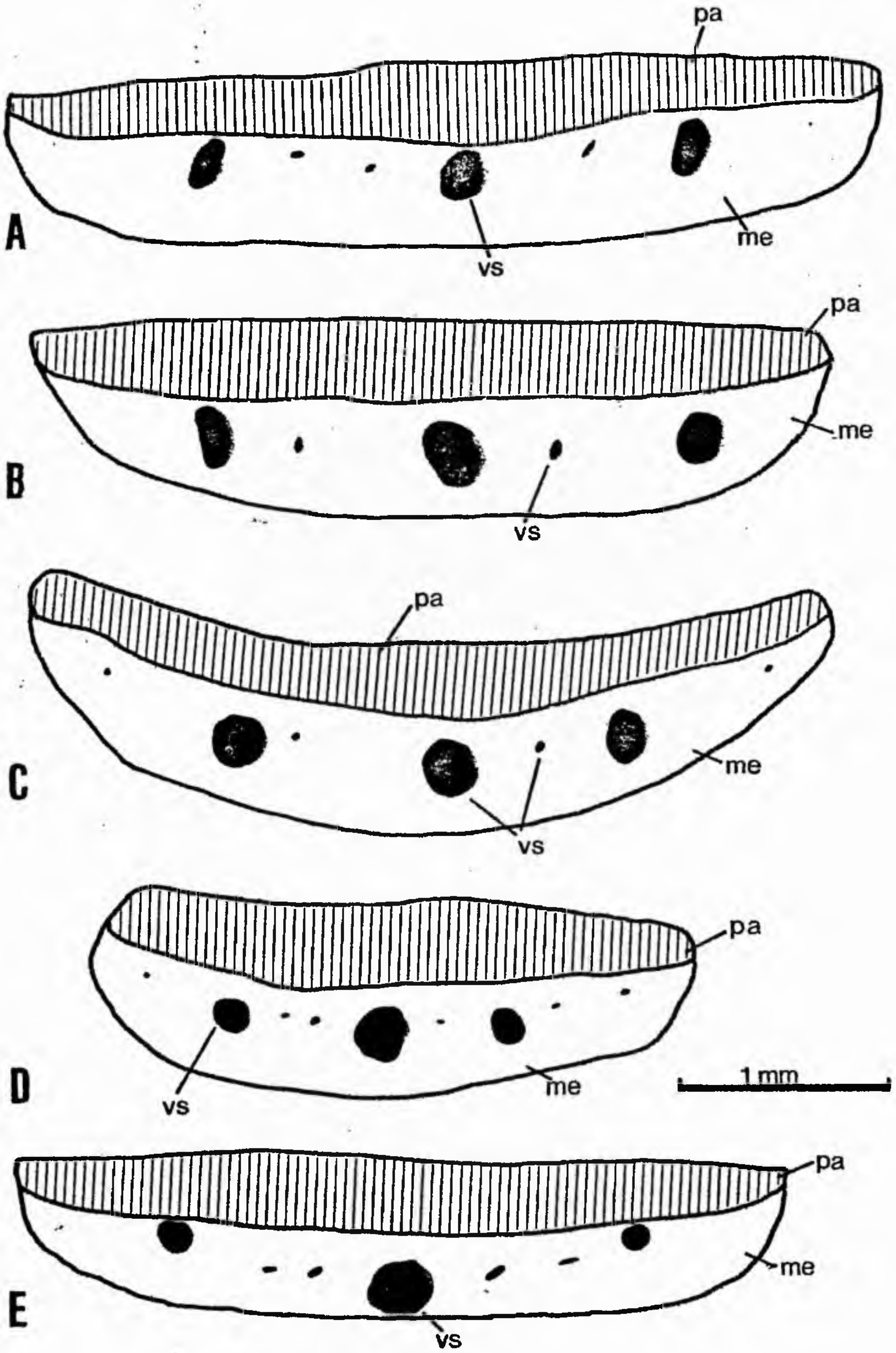


Figure 44 - Transverse sections of cotyledons. *Sesbania* subgen. *Daubentonia* : A - *S. drummondii*, B - *S. macroptera*, C - *S. punicea* D - *S. virgata*; subgen. *Agati* : E - *S. grandiflora*. (pa = palisade; me = mesophyll; vs = veins).

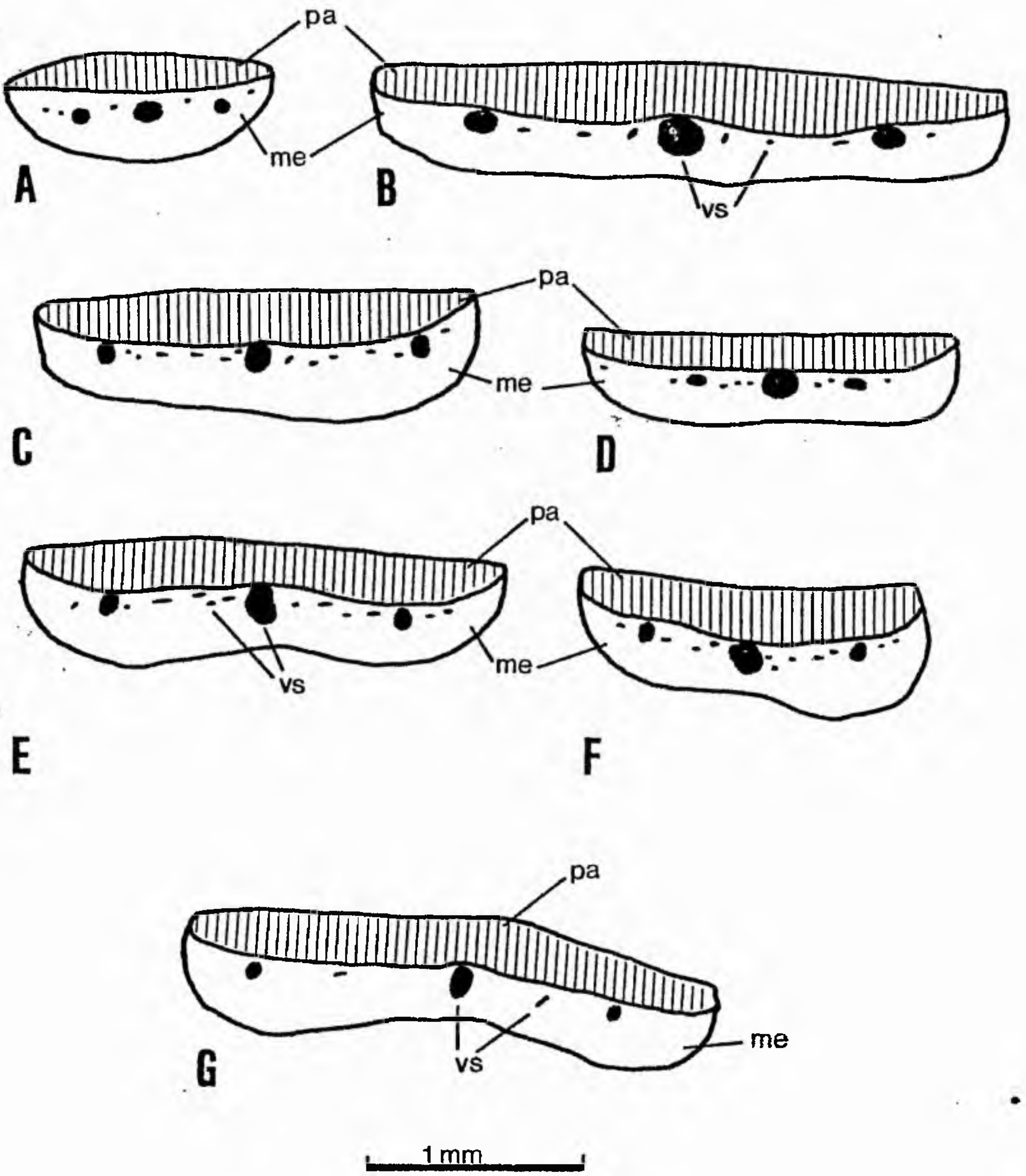


Figure 45 - Transverse sections of cotyledons. Sesbania subgen. Sesbania : A - S. emerus, B- S. exasperata, C - S. oligosperma, D - S. bispinosa, E - S. sericea, F -S. sesban; subgen. Pterosesbania : G - S. tetraptera. (pa = palisade; me = mesophyll; vs = veins).

different subgenera in *Sesbania*. Again, this emphasizes the uniformity of the genus in one more minor but consistent character.

4.2.3.7 - Germination and seedlings

Ecological and physiological aspects of the germination of seeds of *Sesbania* has never been studied in any detail, probably due to the lack of economic uses of the genus. However, such studies are much needed for this genus because of its natural occurrence in water-logged habitats (at least seasonally) despite a typical mechanism of exogenous dormancy (ROLSTON, 1978) in the seed (hard-seedednes).

The ecological aspects of dispersion and germination of this genus in its natural habitat are scarcely known except by some information given by JANZEN (1983) for *Sesbania emerus* in Costa Rica. This author mentions that, once they have fallen on the ground "the seeds may be preyed on by spiny pocket mice (*Liomys salvini*), although these mice do not abundantly leave the forest to forage in the patches of *Sesbania* in the open grasslands. However, *S. emerus* seeds are rich in the uncommon amino acid canavanine, and this may prevent or depress seed predation by rodents and doves" (JANZEN, *loc. cit.*).

Seeds of *Sesbania* may be prevented from germination if predated by beetles (JOHNSON, 1981). A bruchid genus, *Stator*, preys on seeds of Sesbanias and also on seeds of the Robinieae genera *Coursetia*, *Olneya* and *Robinia* (JOHNSON, 1981; SOUSA & SOUSA, 1981). *Stator pruininus* preys directly on seeds of *S. emerus* in Costa Rica and another six species of *Sesbania* elsewhere (JANZEN, 1983). *Acanthoscelides griseolus* was observed to deposit eggs in the locules of *S. emerus* dehisced fruits and the larvae hatched and bore into the seed, completing their development after the seed had fallen onto the ground (JANZEN, 1983).

Dormancy of *Sesbania* seeds can be easily broken by mechanical scarification as observed in seeds of several species studied here (*S. emerus*, *S. punicea*, *S. sesban* and *S. virgata*) or by heat. JANZEN (1983) mentions that seedlings of *S. emerus* are common in places where no adult plants of the same species were present for at least a couple of years. However, germination occurs after fire has burned off the grassland where the seeds were dormant probably due to heat scarification of the seeds.

GILLETT (1963) in his revision of the African and southern Arabian species of *Sesbania* mentioned that successful germination of *S. cinerascens*, *S. kenyensis*, *S. microphylla*, *S. quadrata* and *S. sesban* was achieved with seeds which had been kept in herbarium for up to 19 months or even in the case of *S. sesban* var. *nubica* for 11 years ° There is no indication whether scarification was used to obtain these results (GILLETT, 1963) but they show that viability of *Sesbania* seeds may be very long.

The germination of *Sesbania* seeds is epigeal and this feature is strongly correlated with foliar cotyledons (SMITH, 1981, 1983). This is the case of most of the Robinieae genera except when fleshy cotyledons are present as in *Hebestigma* Urb. and then the germination is hypogeal (SOUSA & SOUSA, 1981).

The seedlings of *Sesbania* have long been observed and associated with its taxonomy (DeCANDOLLE, 1825; GILLETT, 1963). A list of species which have been studied in their seedling features, including the ones for the present work is given in Table 12. Illustrations of seedlings of S. punicea, S. virgata, S. emerus and S. grandiflora are shown in Figure 46.

The following characteristics were observed in all species here studied (Figure 46) and are also a summary of the features described by DeCANDOLLE (1825), GILLETT (1963) and LEITAO FILHO, ARANHA & BACCHI (1975) :

(1) germination epigeal with a long hypocotyl and short epicotyl;

(2) cotyledons foliaceous, very short petiolate and escaping from the testa (Figure 46 D);

(3) first eophyll (eophyll 1 in Figure 46) simple, resembling the cotyledons;

(4) second eophyll (eophyll 2) paripinnate with fewer leaflets than the metaphylls (Figure 46 D);

(5) epicotyl longer than the internode between the first metaphylls.

DeCANDOLLE (1825) described the seedlings of S. punicea as having the eophyll 1 trifoliolate and eophyll 2 as paripinnate. He used these characters to separate Daubentonia as a different genus from Sesbania, the latter possessing the eophyll 1 simple and eophyll 2 imparipinnate. The studies presented by GILLETT (1963, Table 12) and the results of this thesis show that DeCANDOLLE (loc. cit.) was definitely mistaken in the above observations.

Firstly, all S. punicea seedlings which were observed have shown that the eophyll 1 is definitely simple, as in the other species of Sesbania so far studied. Although the seedling stage is extremely vulnerable to environmental changes which might affect the morphology of several organs of the plants (DUKE & POLHILL, 1981), successive observations of different sowings of S. punicea

Table 12 - List of *Sesbania* species studied for their seedling features.

TAXON	AUTHORITY	ORIGIN
subgen. *Agati*		
S. grandiflora	LUBBOCK, 1892 *apud* GILLETT, 1963	Asia
	MONTEIRO, 1984	cultivated *
S. tomentosa	LUBBOCK, 1892 *apud* GILLETT, 1963	Mexico
subgen. *Daubentonia*		
S. punicea (as *Daubentonia punicea*)	DeCANDOLLE, 1825	"America"
	MONTEIRO, 1984	Brazil, cultivated *
S. virgata	SOUSA & SOUSA, 1981	——
	MONTEIRO, 1984	Brazil cultivated *

See NOTES in the end of the Table

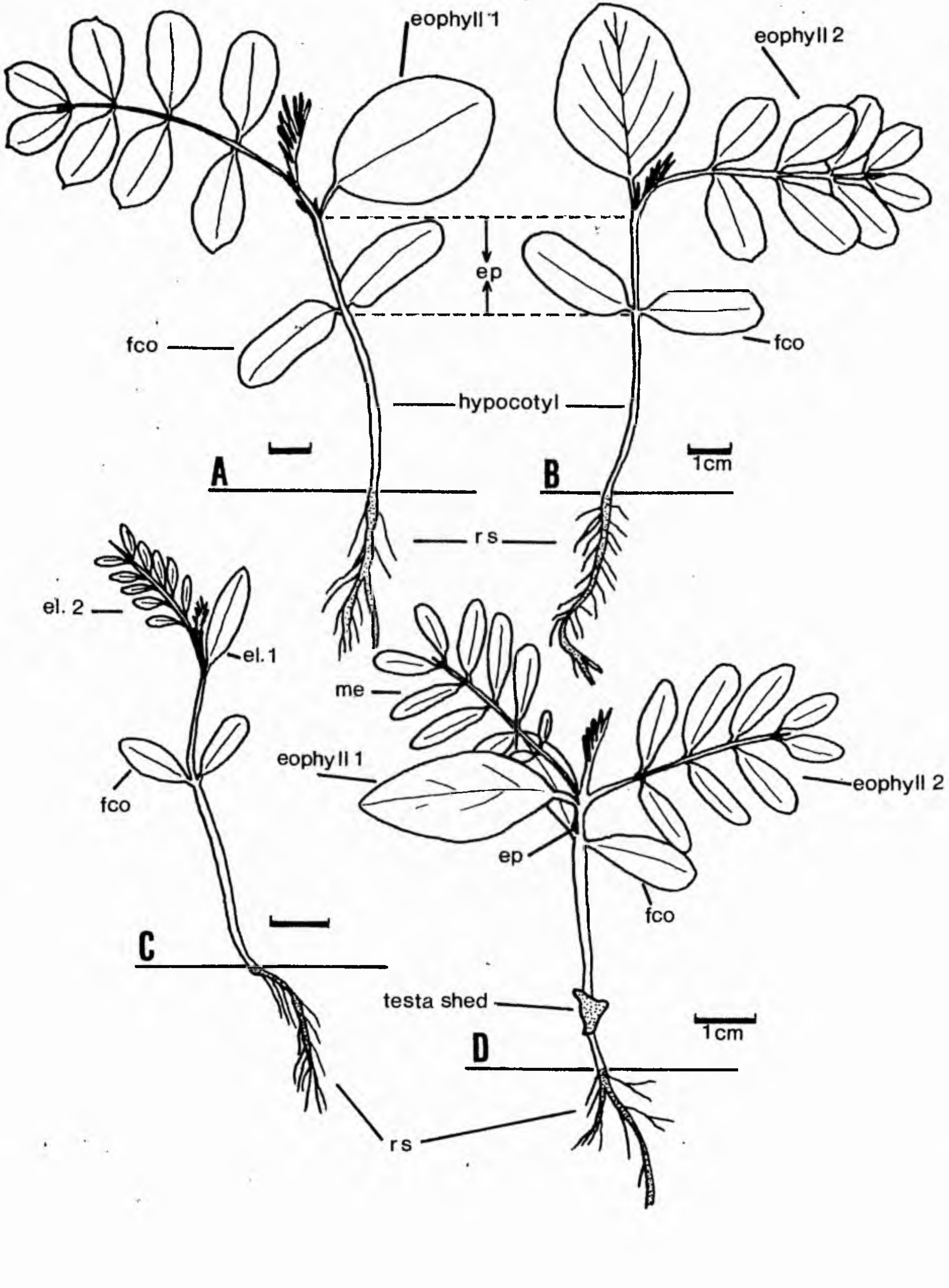
→

Table 12, cont.

TAXON	AUTHORITY	ORIGIN
subgen. *Sesbania* (1)		
S. bispinosa (as *S. aculeata*)	DeCANDOLLE, 1825	----
S. emerus (as *S. occidentalis*)	DeCANDOLLE, 1825	"America"
	MONTEIRO, 1984	Peru ** cultivated *
S. exasperata	LEITAO FILHO, ARANHA & BACCHI, 1975	Brazil
S. keniensis	GILLETT, 1963	Africa
S. microphylla	GILLETT, 1963	Africa
S. quadrata	GILLETT, 1963	Africa
S. sesban (as *S. aegyptiaca*)	DeCANDOLLE , 1825	----
var. *nubica*	LUBBOCK, 1892 *apud* GILLETT 1963	Africa
Sesbania sp (2 unamed taxa)	DeCANDOLLE, 1825	----

NOTES :
* cultivated at St Andrews University Botanic Garden
** seeds sent by D. O. Evans, University of Hawaii at Manoa
(1) or *S. pachycarpa* DC. ? (GILLETT, 1963)

Figure 46 - Seedlings of Sesbania. A - S. punicea; B - S. virgata; C - S. emerus; D - S. grandiflora (el = eophyll; ep = epicotyl; fco = foliar cotyledon; me = metaphyll; rs = root system).


eophyll 1
eophyll 2
ep
fco
fco
hypocotyl
A
B
1cm
rs
el. 2
el. 1
me
eophyll 1
eophyll 2
fco
ep
fco
C
testa shed
1cm
D
rs

seeds resulted in finding the eophyll 1 always simple (Figure 46 A).

Second, the eophyll 2 of *S. emerus* (subgen. *Sesbania*, Figure 46 C) and the other species of the same genus studied by GILLETT (1963) and LEITAO FILHO *et al.* (1975, Table 12) is, in fact, paripinnate like the other succeeding leaves and not imparipinnate as stated by DeCANDOLLE (1825).

DeCANDOLLE (*loc. cit.*) mentions that "*S. aculeata*" (see Table 12) and *Sesbania* sp. have opposite eophylls but, in all seedlings studied here and also in the ones observed by GILLETT (1963) and LEITAO FILHO *et al.* (1975) the eophyls are clearly alternate, although very close together (Figure 46) and each has its own stipule. It has not been possible to study seedlings of *S. bispinosa* (*S. aculeata* for DeCANDOLLE, 1825) or *S. pachycarpa* therefore this information on opposite leaves is yet to be confirmed.

Finally, the epicotyl of *S. grandiflora* (subgen. *Agati*, Figure 46 E) is shorter than the other species studied and it would be interesting to know if *S. formosa* (F. Muell.) Burb., of the same subgenus also shows the same feature.

4.2.4 - CYTOLOGY

4.2.4.1 - Chromosome numbers

An updated list of the chromosome numbers available for *Sesbania* species and *Glottidium* is given in Table 13. It is observed that chromosome numbers in *Sesbania* are an almost constant 2n=12, with the occurrence of three polyploid taxa.

SENN (1938), in his pioneer cytological study of the family Leguminosae, reported chromosome number of three species of *Sesbania* : *S. bispinosa* (sub *S. aculeata*, n=16), *S. grandiflora* (n=7), and *S. tetraptera* (2n=12). The first two records were found to be erroneous and later they were corrected by several authors.

Subsequentely, JACOB (1941) studied the chromosome number and morphology of four species : *S. bispinosa* (2n=24), *S. grandiflora* (2n=24), *S. sesban* (2n=12) and *S. speciosa* (2n=12). Several inconsistent variations in number and morphology of chromosomes in *S. sesban* and *S. bispinosa* were noted by JACOB (*loc. cit.*) whereas the other species were cytologically stable.

Further progress was slow and only TURNER (1955) reported new counts for New World species, one of subgen. *Sesbania* (*S. emerus*) and one of subgen. *Daubentonia* (*S. drummondii*). TURNER (*loc. cit.*) also presented for the first time the count for *Glottidium vesicarium* (2n=12), earlier described as a species of *Sesbania* (*S. vesicaria* (Jaqc.) Ell.)

The works by DATTA & SEN (1960) and DANA & DATTA (1961) only confirmed the numbers previously published for *S. bispinosa* and *S. speciosa*, with some attempts to promote the hibridization between these two species (see section "Reproductive biology").

Table 13 - Chromosome numbers published for *Sesbania* and *Glottidium*.

TAXON	n	2n	REFERENCES
Sesbania			
subgen. *Agati*			
S. grandiflora	6	---	GOLDBLATT, 1981a
	12	24	BAQUAR & AKHTAR, 1968; DANA & DATTA, 1961; DATTA & SEN, 1960; HAQUE, 1946; JACOB, 1941; LUBIS *et al*., 1981; SENN, 1938
subgen. *Daubentonia*			
S. drummondii	6		TURNER, 1955
S. punicea		12	COVAS & SCHNACK, 1946
S. virgata		12	CASTRONOVA, 1945
subgen. *Pterosesbania*			
S. tetraptera		12	SENN, 1938

→

Table 13, cont.

TAXON	n	2n	REFERENCES
Sesbania			
subgen. *Sesbania*			
S. bispinosa	6	12	BAQUAR & AKHTAR, 1968; GOLDBLATT, 1981a; MIEGE, 1960; RAO, 1946
	12	24	BIR & SINDHU, 1966; DANA & DATTA, 1961; DATTA & SEN, 1960; HAQUE, 1946; JACOB, 1941; SAMPATH, 1947
var. *elatior*		12	GOLDBLATT, 1981a
S. cannabina	6		GOLDBLATT, 1981a
S. cinerascens	6	12	GILLETT, 1963; LUBIS *et al*., 1981; PAWAR & BORGAONKER, 1956
S. coerulescens	6		GOLDBLATT, 1981a
S. concolor	12		BAQUAR & AKHTAR, 1968
S. emerus	6		TURNER, 1955
S. javanica		12	LUBIS *et al*., 1981
S. kenyensis		12	GILLETT, 1963
S. leptocarpa		12	BAQUAR & AKHTAR, 1968; GOLBLATT, 1981a
S. macrantha	6	12	GOLDBLATT, 1981a

→

Table 13, cont.

TAXON	n	2n	REFERENCES
Sesbania			
subgen. *Sesbania*			
S. microphylla		12	GILLETT, 1963
S. procumbens		12	GOLDBLATT, 1981a
S. quadrata		12	GILLETT, 1963
S. sericea		24	FRAHM-LELIVELD, 1953
S. sesban	6	12	BAQUAR & AKHTAR, 1968; BIR & SINDHU, 1966; GOLDBLATT, 1981a; GOLDBLATT, 1981b; HAQUE, 1946; LUBIS *et al.*, 1981; RAO, 1946 SAMPATH, 1947; TJIO, 1948
subsp. *sesban*			
var. *bicolor*		12	BAQUAR & AKHTAR, 1968; GOLDBLATT, 1981a
	6,7		BAQUAR & AKHTAR, 1968
var. *concolor*	6,7,8		BAQUAR & AKHTAR, 1968; GOLDBLATT, 1981a
var. *nubica*		12	GILLETT, 1963
var. *picta*		12	GOLDBLATT, 1981a
var. *sesban*	6,7,8		BAQUAR & AKHTAR, 1968
subsp. *punctata*		12	FRAHM-LELIVELD, 1953

→

Table 13, cont.

TAXON	n	2n	REFERENCES
Sesbania			
subgen. *Sesbania*			
S. speciosa		12	JACOB, 1941
S. tomentosa		12	GOLDBLATT, 1981a
f. *arborea*		12	GOLDBLATT, 1981a
Glottidium			
G. vesicarium	6		TURNER, 1955

GILLETT (1963) enlarged the chromosome number records for *Sesbania* and gave as 2n=12 the count for five African species of subgen. *Sesbania* : *S. kenyensis*, *S. sesban* var. *nubica*, *S. cinerascens*, *S. quadrata* and *S. microphylla*.

BAQUAR & AKHTAR (1968) reported *S. concolor* with 2n=12 and confirmed JACOB's (1941) observations about the inconsistency of numbers and structure of chromosomes of *S. sesban*. These authors also found their material of *S. bispinosa* to be diploid with 2n=12 and not a tetraploid (2n=24), as earlier reported by other authors.

LUBIS, OKADA & SASTRAPRADJA (1981) confirmed the counts for *S. sesban*, *S. cinerascens* (both 2n=12) and *S. grandiflora* (2n=24), and contributed with a new record for *S. javanica*, also 2n=12.

In the present study chromosome numbers were obtained from metaphase plate of root tip preparations for five species of *Sesbania* native to the New World (Table 14), *S. emerus*, *S. exasperata*, *S. punicea* and *S. virgata* (all 2n=12), and also *S. grandiflora* (2n=24), and for *Glottidium vesicarium* (2n=12). Of these, the count for *S. exasperata* is a new one and the others are confirmations of previously published counts.

The available chromosome counts for *Sesbania* thus indicate a considerable degree of uniformity in the genus throughout its subgenera and species, and with only two polyploid species, *S. grandiflora* (subgen. *Agati*) and *S. sericea* (subgen. *Sesbania*) and possibly *S. bispinosa* with diploid and tetraploid races if the 2n=24 is confirmed. The data available also conforms to a basic number for the genus of x=6, the same as in *Glottidium* (TURNER, 1955, and the present work).

Table 14 - Chromosome numbers of New World species of Sesbania and Glottidium.

TAXON	2n	Origin
Sesbania Scop.		
subgen. Sesbania		
S. emerus (Aubl.) Urb.	12	Chiclayo, Peru - EVANS s/n (E)
S. exasperata H.B.K.	12	Brazil *
subgen. Daubentonia		
S. punicea (Cav.) Benth.	12	Brazil *
S. virgata (Cav.) Pers.	12	Brazil *
subgen. Agati		
S. grandiflora (L.) Pers.	24	Unknown★
Glottidium Desv.		
G. vesicarium (Jacq.) Harper	12	U.S.A., Texas - EVANS s/n (E)

Notes :
* Root tips obtained from plants cultivated at Univ. of St Andrews Botanic Garden. Seeds collected in Brazil by R. Monteiro, P.E. Gibbs and K. Yamamoto.

★Introduction from seed exchange program at Univ. of St Andrews Botanic Garden (sent by Jardin Botanico Nacional de Cuba).

Although incomplete for the genus as a whole (there are ca. 50 species of Sesbania in the world of which only 23 have their chromosome counted, i.e., more or less 50%), the chromosome numbers of Sesbania species and Glottidium places these taxa in a somewhat anomalous position in the tribe Robinieae, where either x= 11 or 10 have been proposed as basic numbers by GOLDBLATT (1981b). However, GOLDBLATT (loc. cit.) has suggested that these two genera "must be interpreted a derived aneuploids" an explanation that would accord with his view of them as specialised Robinieae.

The polyploid status of S. sericea (Table 13), still only available from one source, has not yet been confirmed by other authors.

4.2.4.2 - Chromosome morphology

JACOB (1941) was the first author to publish karyotypes of four species of Sesbania based on mitosis and meiosis. The karyotype analysis revealed (a) two diploids (S. speciosa and S. sesban, 2n=12) and two polyploids (tetraploids, S. grandiflora and S. bispinosa, 2n=24), and (b) an apparent chromosome homology between these taxa since the karyotype of the tetraploids showed similar morphology to the ones of the diploids.

Based on his data, JACOB (1941) attempted to reconstruct the amphidiploid origin of S. grandiflora and S. bispinosa involving the species S. sesban and S. speciosa (Figure 47). In his reconstruction, JACOB (loc. cit.) was considerably influenced by the assumption that diploid species have two nucleoli, triploids

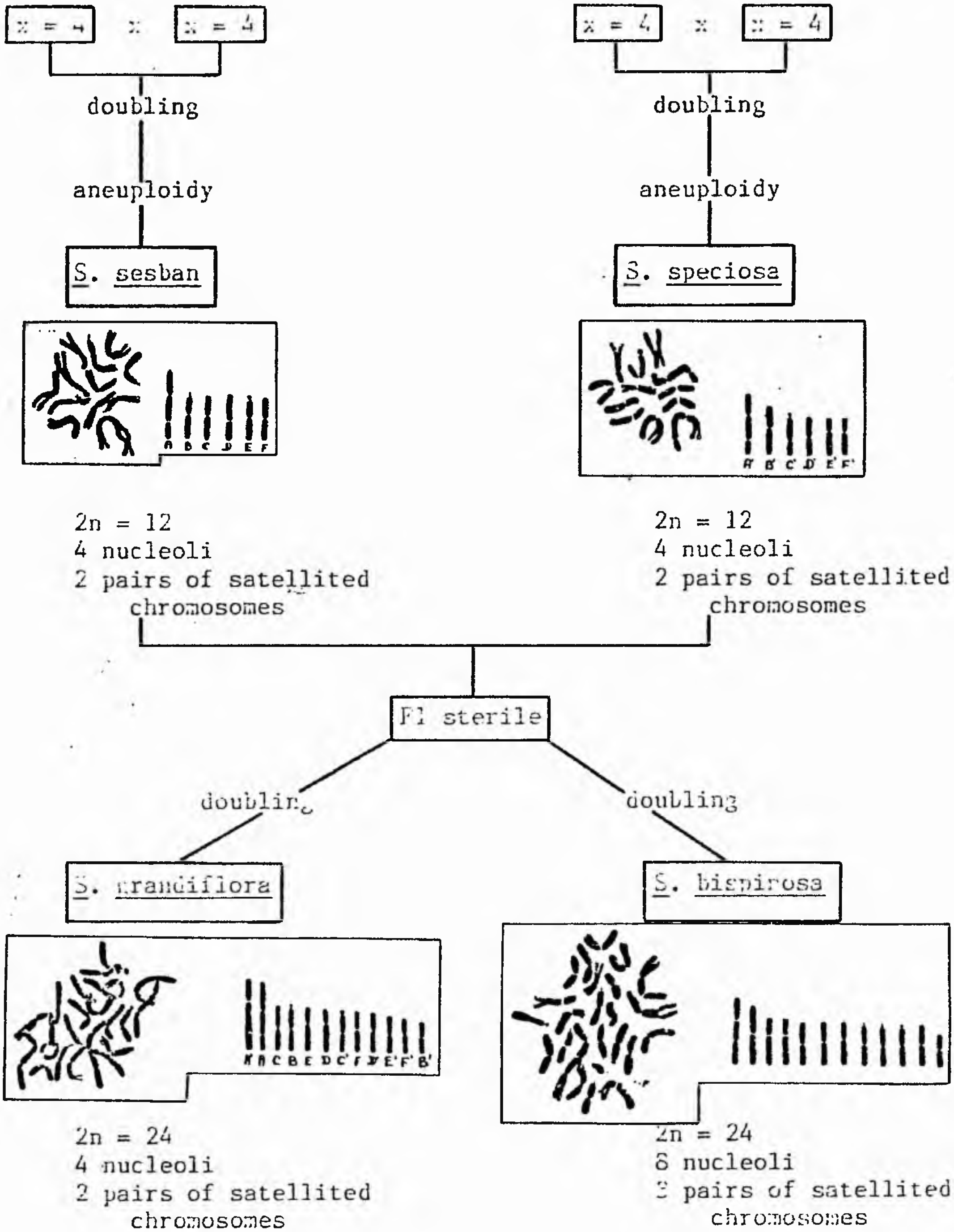


Figure 47 - Cytological relationships between <u>Sesbania sesban</u>, <u>S. speciosa</u>, <u>S. grandiflora</u> and <u>S. bispinosa</u> (after JACOB, 1941).

three, tetraploids four, etc, and he therefore considered that S. sesban, with four nucleoli and four satellited chromosomes, could not be a true diploid. This view was reinforced by the occurrence of several anomalies in mitosis and meiosis (quadrivalent formation, inversions, translocations and fragmentations) in S. sesban and JACOB (loc. cit.) concluded that more than two homologous chromosome sets were present in this species. He also suggested that S. sesban was most probably derived from hybridization between taxa with a lower chromosome number ($x=4$) with subsequent doubling followed by a loss of some chromosomes (Figure 47). Similar reasoning was used for S. speciosa and this taxon was also considered to be of hybrid origin but with the loss of a satellite (Figure 47).

For the polyploids, S. bispinosa and S. grandiflora, JACOB (1941) proposed a hybrid origin based on evidence from similarity of the chromosome morphology, and numbers of satellites and nucleoli (Figure 47). However, if S. grandiflora is a true amphidiploid, then eight nucleolar chromosomes would be expected rather than the four observed. JACOB (loc. cit.) further proposed that in the course of evolution of this species four nucleolar organisers had been lost in two of the satellited chromosomes and that this loss had not, presumably, affected the vigour of the hybrid. Also in S. grandiflora nine pairs of chromosomes were similar to nine pairs in the putative parents : four in S. speciosa and five in S. sesban (JACOB, 1941).

Finally, JACOB (1941) remarks that the natural occurrence of S. sesban, S. speciosa, S. grandiflora and S. bispinosa in Africa indicates this continent as where the polyploids had their origin.

However, GILLETT (1963) has argued that *S. grandiflora* is originally a native species to Indonesia rather than to Africa.

These hypotheses are difficult to confirm because no karyotype studies are available for the majority of species in the genus. Furthermore, the interrelationships between the African and Asian species of *Sesbania* are not yet known since there is not a modern revision of the genus in the latter area.

More recent karyological studies on *Sesbania* were made by LUBIS *et al.* (1981) who worked with the Old World species *S. sinerascence* (= *S. cinerascens* ?), *S. javanica*, *S. sesban* (all three of subgen. *Sesbania*, diploids, 2n=12), and *S. grandiflora* (2n=24). The authors concluded (LUBIS *et al.* , *loc. cit.*) that the diploid taxa had similar karyotypes but the satellite characters (location and position) easily distinguished each species.

The origin of *S. grandiflora* was considered and discussed and, although LUBIS *et al.* (1981) found similarities between the morphology of some of the chromosomes of this species and *S. sesban* as reported by JACOB (1941), the detailed karyotype morphology proved to be different, and consequently these authors were uncertain as to whether this polyploid species originated by auto- or allopolyploidy.

Despite rather different conclusions the authors of both these studies (JACOB, 1941; LUBIS *et al.*, 1981) agree on many aspects of the karyotype analysis of these species and *S. grandiflora* and *S. bispinosa* were accepted unquestionably as *Sesbania* species. The chromosomal evidence would seem to support the inclusion of *S. grandiflora* in *Sesbania* rather than split off as the genus *Agati*.

Unfortunately, no karyological analyses are available for the New World species of *Sesbania*. All attempts in the present study to get good root tip preparations of *S. emerus*, *S. exasperata* (subgen. *Sesbania*), *S. punicea* and *S. virgata* (subgen. *Daubentonia*) failed to produce reliable results, although a wide range of pretreatment and staining techniques were tried, including the ones used in the works above cited. In all cases the chromosomes showed unequal and uneven contractions, making the use of the material unsuitable for karyotype determination.

Therefore, no comparisons can be made at the present between the chromosome morphology of the New and Old World species of *Sesbania* and such a study is still very much needed.

4.3 - GENERIC LIMITS

As seen in the historical review of the taxonomy of Sesbania (section "Taxonomic History"), the genus has been subjected to different treatments by various authors (DeCANDOLLE, 1825; BENTHAM, 1865; BAKER, 1871, 1876; PHILLIPS & HUTCHINSON, 1921; RYDBERG, 1923, 1924; GILLET, 1963).

These changing concepts as to how the genus Sesbania should be delimited have caused many misinterpretations of the generic relationships and tribal position of this taxon. Fortunately, the study of the New World species of Sesbania presented here has provided valuable data which makes it possible to reconsider the limits of the genus and its infrageneric classification and also to analyse some of the difficulties associated with its position in the tribe Robinieae.

4.3.1 - Generic segregates

From the segregate generic names which are linked to Sesbania for nomenclatural and /or biological reasons, Glottidium Desv. and Yucaratonia Burk. are of interest in this section, while Agati Adans., Daubentonia DC. and Daubentoniopsis Rydb. are treated in the following one.

Although PHILLIPS & HUTCHINSON (1921) and GILLET (1963) have enumerated differential characters between Sesbania and Glottidium, it has remained controversial as to whether to accept Glottidium as a section of Sesbania as proposed by BENTHAM (1865), or as completely synonymous with Sesbania (TAUBERT, 1893), or as a separate genus (RYDBERG, 1924; HUTCHINSON, 1964; POLHILL & SOUSA, 1981; and others).

Table 15 presents a list of diagnostic characters of *Sesbania* and *Glottidium*, based on PHILLIPS & HUTCHINSON (1921), RYDBERG (1924), GILLETT (1963), POLHILL & SOUSA (1981), and personal observations.

TURNER (1955) revised some of the information available for chromosome numbers in *Sesbania* and provided new counts for some species, including for *S. vesicaria* (Jacq.) Ell. which is, in fact, a synonym of *Glottidium vesicarium* (Jacq.) Harper. On the basis that the former taxon has the same basic chromosome number as *Sesbania* species, TURNER (*loc. cit.*) proposed that *Glottidium* should be considered as a subgenus of *Sesbania* because the cromosome number was "another character that (linked) the subgenera (of *Sesbania*) together" and that, "from the standpoint of total morphology in the various subgenera, the sum of their resemblances far (exceeded) their differences".

Further evidence for this point of view was given by PRAKASH & HERR (1979) with embryological studies in *Sesbania* and *Glottidium*. These authors pointed out that, in comparing the process of embryo development of *Glottidium* with species of *Sesbania* (RAU, 1951, 1953), there was a striking resemblance between the two genera. Their conclusion was that there was little justification for recognizing *Sesbania* and *Glottidium* as separate genera, and the embryological data provided a close relationship between these taxa.

However, despite TURNER's assertion (1955) to the contrary, the same basic chromosome number and similarity of embryological development in *Sesbania* and *Glottidium* are virtually the only two pieces of evidence for a proximity between these two genera as

Table 15 - Diagnostic characters of *Sesbania* Scop. (*sensu lato*, excluding *Glottidium*) and *Glottidium* Desv.

SESBANIA	*GLOTTIDIUM*
Perennial to short lived or annual	Annual
Racemes with short peduncles	Racemes with long peduncles
Filaments not greatly narrowed towards the tip	Filaments greatly narrowed towards the tip
Vexillary filament curved near the base	Vexillary filament straight
Tip of the style erect	Tip of the style incurved
Pods linear and compressed or linear-oblong; 4-angled or 4-winged, septate, long beaked	Pods elliptic, short-beaked, not septate
Endocarp not splitting away from the exocarp	Endocarp papery, splitting away from the exocarp when the pods dehisces and enveloping the seeds
Ovules and seeds 5 or more	Ovules and seeds 2
Seeds less than 9 mm long, cylindric to reniform	Seeds 10-13 mm long, compressed, oblong-reniform
Hilum usually subcircular	Hilum extended, elongate
Distribution pantropical	Distribution neotropical, exclusively

shown in Table 15. The differences far exceed the similarities and, when compared with the morphological patterns which differentiate the subgenera of Sesbania (Table 16, as studied below), it seems clear that both genera have sufficient characters to support a segregation of Glottidium. As a consequence, in the present study, Sesbania and Glottidium have been maintained as two distinct genera.

The genus Yucaratonia Burk. is monospecific and based on a previously published species of Sesbania (S. brenningii Harms). Although HARMS (1923) and BURKART (1969) have listed some characters in which Yucaratonia resembles Sesbania, three striking features in the former taxon immediately differentiate it from the latter. They are : the presence of a basal nectary (disc) in the ovary; the large, long, compressed and dehiscent pods which are non-winged and without thickened margins; and the transversal, ovate-compressed seeds with an apical hilum (BURKART, loc. cit.).

Therefore, the treatment provided by BURKART (1969) in erecting Yucaratonia as a different genus from Sesbania has been accepted here.

4.3.2 - Infrageneric classification

It was mentioned in the section "Taxonomic History" that the character states "winged, several-seeded/non-winged, few- to many-seeded pods" were the features used for the earliest infrageneric classification of Sesbania by BENTHAM (1865), who proposed three sections for the genus, sect. Eusesbania, sect. Daubentonia and sect. Glottidium. All sections had species occurring in the Old and New World, except for Glottidium which was represented by only one species in "America-boreali".

BAKER (1871, 1876) treated the sections described by BENTHAM (1865) as subgenera but without actually mentioning whether he considered *Glottidium* as another subgenus of *Sesbania* since his treatments were concerned with African and Asian species only.

With the use of the same character states mentioned above, the genus *Sesbania* was later split by SMALL (1903) in several genera. However, PHILLIPS & HUTCHINSON (1921) disagreed with SMALL's treatment and reinstated the sections *Eusesbania* and *Daubentonia* except that *Glottidium* was considered to be a different genus.

RYDBERG (1924) accepted the segregate genera as treated by SMALL (1903), i.e., *Agati*, *Daubentonia*, *Sesban* and *Glottidium*, and also created the new genus *Daubentoniopsis*, which has been interpreted as having some features of *Daubentonia* and some others of *Sesbania*, therefore being intermediate between both.

GILLETT (1963) was of the opinion that RYDBERG's proposal was unacceptable in terms of excessive splitting of *Sesbania* into segregate genera but considered that *Glottidium* should be treated conservatively as a different genus. The same point of view was shared by HUTCHINSON (1964).

However, despite GILLETT's (1963) and HUTCHINSON 's (1964) treatments of the infrageneric classification of *Sesbania*, it was observed that, in many exsiccatae here studied received from several American herbaria the former segregate genera *Daubentonia*, *Agati* and *Daubentoniopsis* are still being used for identifications of *Sesbania* species while *Glottidium* is still accepted as merged with *Sesbania*. This fact apparently indicates that the treatments provided by SMALL (1903) and RYDBERG (1924) are still prevailing, mainly due to the lack of studies in the genus.

Therefore, because the classification of *Sesbania* has been in a state of flux, it was accepted at the outset of this study that the status of the taxa *Agati*, *Daubentonia*, *Daubentoniopsis* and *Glottidium* would be postponed until the assessment of the characters of species of *Sesbania sensu lato* could be completed and weighted in order to revaluate the generic and infrageneric classification appropriate for this group.

The generic and infrageneric concepts and criteria here accepted are those provided by DAVIS & HEYWOOD (1963). Based on the assumption that "the most important *function* of the genus is to bring together species, preferably in a natural manner", DAVIS & HEYWOOD (*loc. cit.*) propose that three fundamental questions must be asked when one has to decide on generic concepts :

(1) "Is the group a natural one, and if not is it possible to make it so ?". At this point, the concept of 'naturalness' in taxonomy is brought about and the authors suggest that it is based on "overall resemblance", that is, on maximum correlation of characters among the members of the group.

(2) "Where should the line be drawn between closely allied genera ?" Here, if the genera are sufficiently distinct from one another, the limits are easily drawn but problems could rise when the differential characters are not clear. Once again, as suggested by DAVIS & HEYWOOD (1963) the decision must be made on using "the sum total of characters manifested in each group studied" and "not by a single arbitrary or artificial character".

(3) "Is it practicable to recognise the group as a separate genus or would it be better included in another ?". This question comes in close relation with the previous one "because, if two genera are not readily separable, infrageneric rank may be preferred" (DAVIS & HEYWOOD, 1963). Any solution to be taken for such a problem is surely reflected by the experience of the taxonomist but that decision is certainly to be affected by some considerations such as size and homogeneity of the groups and number of intermediates between them (DAVIS & HEYWOOD, *loc. cit.*). Furthermore, the authors suggest that "the principle that the size of the gap should be inversely proportional to the size of the groups" usually provides a useful guide as to how to answer this last question.

Finally, it is also proposed by DAVIS & HEYWOOD (1963) that "when in doubt as to whether to accord generic rank to a group, there is much to be said for the *subgenus* as a suitable category; it draws attention to the group in the classification and at the same time allows people to continue to use the old binomial".

If *Sesbania sensu lato* is viewed in the light of these criteria, then the accumulated data (Table 16) indicates that the segregate genera *Agati*, *Daubentonia* and *Daubentoniopsis*, as proposed by SMALL (1903) and RYDBERG (1924) were separated by a "single arbitrary character" and not by a sum of correlated characters. Furthermore, as will be discussed in the next section ("Phytogeography and evolutionary relationships"), the number and occurrence of intermediate characters and taxa among these segregate genera are so obvious that the lines between them cannot

Table 16 - Comparison of morphological characters of the subgenera of *Sesbania* Scop.

	subgen. *Sesbania*	subgen. *Daubentonia*	subgen. *Agati*	subgen. *Pterosesbania*
Habit	shrubs	woody shrubs to treelets	shrubs to treelets	shrubs
Flowers per raceme	2-5(-8)	usually 10 or more	2-3(-4)	4-7
Calyx	broad campanulate, conspicuously lobed	rounded-campanulate, inconspicuously lobed, slightly bilabiate	campanulate, inconspicuously lobed, bilabiate	campanulate, conspicuously lobed
Corolla length (mm)	15-30	10-25	50-85	10-12
Keel and wing petals	toothed	non-toothed	non-toothed	toothed
Standard petal	appendaged	short-appendaged to non-appendaged	non-appendaged	appendaged
Ovary	non-alate	non-alate	non-alate	4-alate
Pods	linear, terete or compressed	linear torulose to linear-oblong, 4-angled or 4-winged	linear, elongate, compressed	linear, compressed to torulose, 4-winged
Seeds	cylindric-oblong	reniform	reniform	reniform-oblong
t.p.v.*	piluloid to foliate	non-vestured to sparsely warty	non-vestured to sparsely warty	warty to piluloid

Note : * t.p.v.= tracheoid pit vesturing be clearly drawn. Consequently, the gaps between the groups are so small that the overall resemblances enhance the naturalness of the genus *as a whole*.

It seems sensible, then, to sink *Daubentoniopsis* Rydb. in *Daubentonia* which, along with *Agati*, is treated at subgeneric level of *Sesbania*. Another natural group within the genus, subgen. *Pterosesbania*, as proposed by GILLET (1963), has also been accepted here (Table 16) based on the same principles outlined above.

Finally, it must be stressed that, when the correlation of characters shown by the various subgenera of *Sesbania* (Table 16) are compared to the diagnostic features between *Sesbania* and *Glottidium* (Table 15), the latter data show many clear discontinuities which support the view taken before that *Glottidium* must be treated as a segregate genus.

4.3.3 - Tribal position

In order to have a better understanding of the actual tribal position of the genus *Sesbania*, it is necessary to summarise here how some of the New World tribes of the subfamily Papilionoideae are delimited and interrelated.

POLHILL (1981) has proposed a scheme for the relationships of the Papilionoid tribes which is illustrated in Figure 48. From this simplified representation of the supposed relationships of the tribes, it is observed that there is a central core composed of the Swartzieae, Sophoreae and Tephrosieae. According to POLHILL (*loc. cit.*), in the groups with a hypothetical ancestral stock closely related to the Tephrosieae, an apparent division is seen

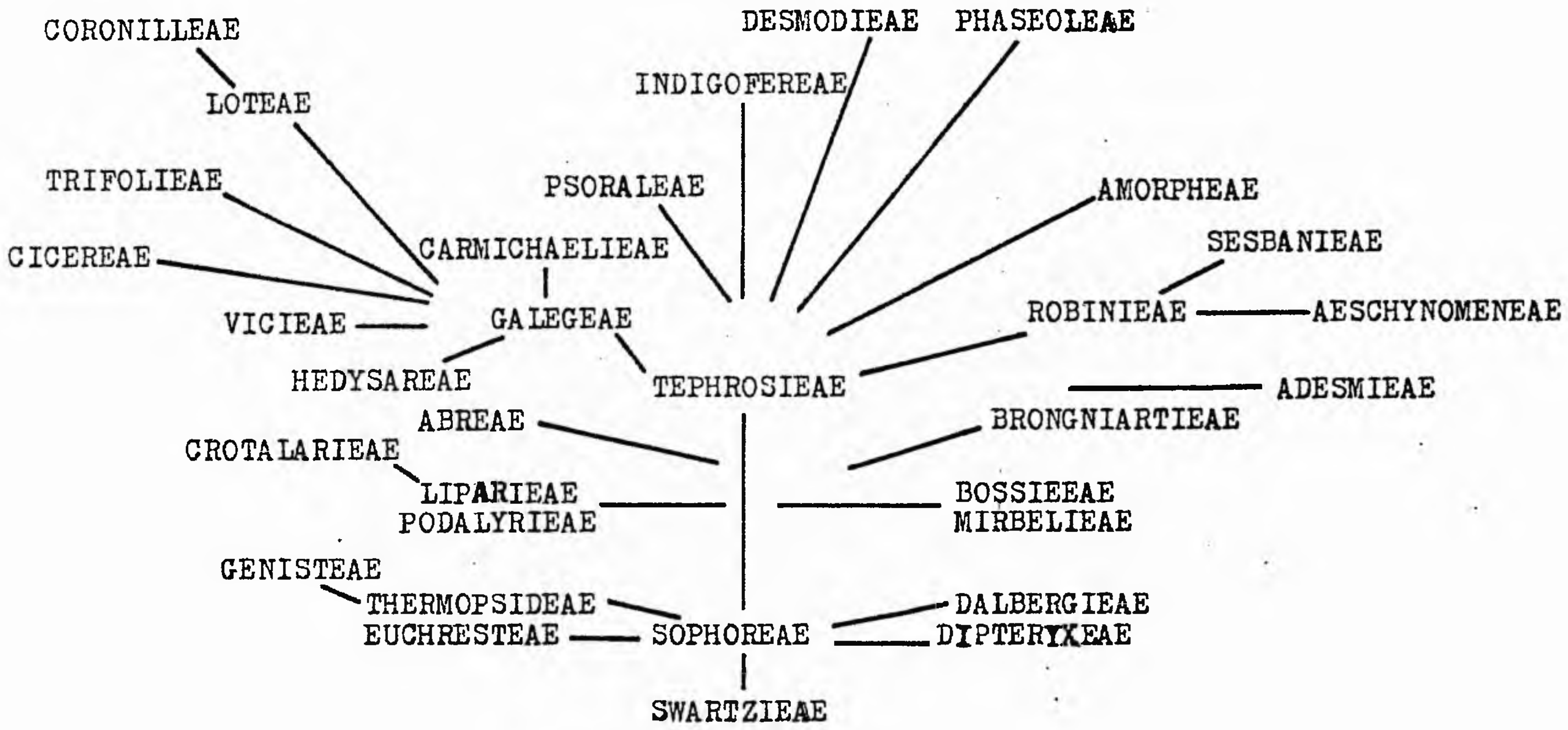


Figure 48 - Tribal relationships in Leguminosae subfamily Papilionoideae (*sensu* POLHILL, 1981).

between "the more advanced" tropical tribes centred in the Old World (Desmodieae, Indigofereae, Phaseoleae and Psoraleeae) and those centred in the New World (Aeschynomeneae, Abreae, Dalbergieae, Dipteryxeae, Brongniartieae, Adesmieae, Amorpheae, Sesbanieae and Robinieae). Interestingly, possible links between these advanced New World tribes were also proposed with the Sophoreae "with the rider that those tribes (Sophoreae and the New World ones) as whole are not sharply distinguished one from another" (POLHILL, loc. cit.).

Thus, the genera listed in Table 17 are from the predominantly New World tribes which have links and share some common features with the Tephrosieae. These taxa are some of the members of the original Galegeae as treated by BENTHAM (1865), mainly in his subtribe Robiniieae, one of the seven subtribes proposed by this author for the tribe Galegeae.

In the following analysis of these genera and their tribal classification, emphasis will be given to the position of Sesbania in the treatments published by BENTHAM (1865), RYDBERG (1924), HUTCHINSON (1964), GEESINK (1981), POLHILL & SOUSA (1981), and SOUSA & SOUSA (1981).

RYDBERG (1923, 1924) rearranged BENTHAM's (1865) classification of the Galegeae and recognised 11 subtribes in which many of the genera were fragmented due to the narrow concepts of the generic limits that RYDBERG (loc. cit.) worked with. Therefore, in his treatment of the Galegeae, the subtribe Sesbaniinae comprised the complex of segregate genera Sesban, Daubentonia, Daubentoniopsis and Agati, and also Glottidium. As

Table 17 - Tribal arrangements of the Robinieae genera and allies (see text in section "Tribal position").

	AUTHORITIES					
TAXON	BENTHAM (1865)	RYDBERG (1923/4)	HUTCHINSON (1964)	POLHILL & SOUSA (1981)	SOUSA & SOUSA (1981)	GEESINK (1981)
Apurimacia			Robinieae		Lonchocarpinae	Tephrosieae
Bembicidium		Corynellinae	Robinieae	Robinieae		
Bergeronia			Aeschynomeneae		Lonchocarpinae	Tephrosieae
Corynella	Robiniinae	Corynellinae	Robinieae	Robinieae		
Coursetia	Robiniinae	Corynellinae Robiniinae	Robinieae	Robinieae		
Cracca	Robiniinae	Craccinae	Sesbanieae	Robinieae		
Dahlstedtia			Lonchocarpeae		Lonchocarpinae	Tephrosieae
Diphysa	Robiniinae	Diphysinae	Diphyseae	Robinieae		
Gliricidia	Robiniinae	Robiniinae	Robinieae	Robinieae		
Glottidium	in *Sesbania*	Sesbaniinae	Sesbanieae	Robinieae		
Genistidium			Barbierieae	Robinieae		
Hebestigma		Robiniinae	Robinieae	Robinieae		

Table 17, cont.

	AUTHORITIES					
TAXON	BENTHAM (1865)	RYDBERG (1923/4)	HUTCHINSON (1964)	POLHILL & SOUSA (1981)	SOUSA & SOUSA (1981)	GEESINK (1981)
Lennea	Robiniinae	Robiniinae	Robinieae	Robinieae		
Lonchocarpus	Tephrosiinae		Lonchocarpeae		Lonchocarpinae	Tephrosieae
Margaritolobium			Robinieae		Lonchocarpinae	Tephrosieae
Muellera	Tephrosiinae		Lonchocarpeae		Lonchocarpinae	Tephrosieae
Neocracca			Sesbanieae	Robinieae		
Notodon			Sesbanieae	Robinieae		
Olneya	Robiniinae	Robiniinae	Robinieae	Robinieae		
Peteria	Robiniinae	Cracciinae	Tephrosieae	Robinieae		
Poissonia			Sesbanieae	Robinieae		
Poitea	Robiniinae	Robiniinae	Sesbanieae	Robinieae		
Robinia	Robiniinae	Robiniinae	Robinieae	Robinieae		
Sabinea	Robiniinae	Corynelliinae	Robinieae	Robinieae		
Sesbania	Robiniinae	Sesbaniinae	Sesbanieae	Robinieae		
Sphinctospermum		Robiniinae	Tephrosieae	Robinieae		
Willardia		Robiniinae	Robinieae		Lonchocarpinae	Tephrosieae
Yucaratonia				Robinieae		

with other classifications proposed by RYDBERG (1923, 1924), this concept of Sesbaniinae was not widely accepted and GILLETT (1963), in the revision of the African species of *Sesbania*, was of the opinion that RYDBERG's proposal was only correct as to the isolation of this genus from the other Galegeae but, as discussed above, unacceptable in terms of the excessive splitting of *Sesbania* into segregate genera.

The next major tribal classification of the Leguminosae was published by HUTCHINSON (1964), who adopted BENTHAM's (1865) treatment of subtribes as a basis but raised them to tribal level and created several others. For example, *Diphysa* Jacq., originally in subtribe Robiniinae was placed in a new tribe of its own, Diphyseae Hutch. *Sesbania* was separated from the original Galegeae in an isolated tribe, Sesbanieae Hutch. which also included the genera *Glottidium* Desv., *Cracca* Benth., *Poissonia* Baill., and *Neocracca* O. Kuntze. However, a detailed analysis of the characters used by HUTCHINSON (*loc. cit.*) in the key for his Leguminosae tribes and also in the descriptions of these taxa revealed that the habit *herbaceous* in the proposed Sesbanieae is the only difference with the Robinieae which is comprised of *woody* plants.

The system created by HUTCHINSON (1964) was rather artificial and still left the tribal position of *Sesbania* and other genera questionable. Nevertheless, the tribes Sesbanieae and Robinieae as proposed by HUTCHINSON (*loc. cit.*) prevailed until the Kew Conference on Legume Systematics in 1978 (POLHILL & RAVEN, 1981).

GEESINK (1981) prepared an updated treatment of the tribe Tephrosieae in which he transferred from the Robinieae *sensu* HUTCHINSON (1964) to the Tephrosieae (Benth.)Hutch. a number of genera which were occupying an anomalous position in the former tribe (*Apurimacia* Harms, *Margaritolobium* Harms and *Willardia* Rose). Curiously, these genera and also *Bergeronia* Mich., *Dahlstedtia* Malme, *Lonchocarpus* Kunth, *Muellera* Linn.f. and *Piscidia* L., all in Tephrosieae *sensu* GEESINK (1981) were treated by SOUSA & SOUSA (1981) as belonging to the subtribe Lonchocarpinae. SOUSA & SOUSA (*loc. cit.*) also proposed that the same genera could comprise a modified tribe Lonchocarpeae, which would make this tribe rather different to that originally circumscribed by HUTCHINSON (1964). However, this proposal to treat these genera at tribal level was not formally effected and it is the treatment at subtribal level, i.e., Lonchocarpinae which is considered here.

There is no doubt that after the removal of the tephrosioid and lonchocarpoid elements from the original Robinieae *sensu* HUTCHINSON (1964), GEESINK (1981) and SOUSA & SOUSA (1981) made a more coherent concept of the tribe Robinieae but some difficulties still remain with regard to the tribal classification of *Diphysa* Jacq., *Genistidium* I.M. Johnston, *Glottidium* Desv., *Peteria* A. Gray, and *Sesbania* Scop. These difficulties arise because, unfortunately, a modern revision of the Robinieae was not presented in the Kew Conference (POLHILL & RAVEN, 1981) and no other studies have been published since. As pointed out by POLHILL & SOUSA (1981), "(this) neglect is unfortunate as Robinieae seem to be crucial to understanding the development of more advanced tribes in the New World".

Nevertheless, an appraisal of the Robinieae was given by POLHILL & SOUSA (1981), who mentioned that "habit, flowers, fruits and seeds of Robinieae are at the same level of organisation as those of Tephrosieae, their antecedents were certainly closely related, and in practice components of the two tribes have been confused and are still difficult to differentiate".

POLHILL & SOUSA (1981), however, reconsidered the limits of this tribe and also of Sesbanieae Hutch. (Table 17), and based on a suggestion given by M. SOUSA (POLHILL, 1981), they merged Sesbanieae into the Robinieae.

Although POLHILL & SOUSA (1981) stated that "as pointed out by SOUSA & SOUSA (1981) ... to put both (Sesbania and Diphysa) in Robinieae seems more sensible, especially in view of the recent erection of Yucaratonia (BURKART, 1969)", SOUSA & SOUSA (1981) did not in fact add much further explanation to support this classification.

As a result of the fusion of Sesbanieae and Robinieae the limits of the latter were expanded in order to accommodate the variation present in its diverse members. However, some problems still remained with regard to Sesbania, Glottidium and Diphysa.

These problems are reflected in the morphological, cytological and partially, in the palynological data available for the tribe. Morphologically, the problems raised concern the presence of the axillary "simple racemose inflorescence" in the regularly bracteolate genera of the Robinieae : Sesbania, Glottidium and Diphysa (POLHILL & SOUSA, 1981). The racemes are unbranched but SOUSA & SOUSA (1981) have interpreted these inflorescences as being once branched. From their point of view, the bracteoles indicate a cymose origin of these racemes, in which the lateral flowers of a dichasium abort and the pedicel below the bracteoles becomes the secondary bracts and the inflorescence is named "Diphysa-type" (Figure 49). In all specimens of Sesbania studied, no other indications of this "once-branched" inflorescence were found except by the presence of the bracteoles.

Other genera of the Robinieae (Coursetia DC., Gliricidia Kunth, Robinia L., and Sabinea DC.) were regarded by SOUSA & SOUSA (1981) as having their inflorescences derived from the "Gliricidia-type" of inflorescence; these taxa, as most of the genera in the tribe, are non-bracteolate. Therefore, two members of the tribe Sesbanieae Hutch. (Sesbania and Glottidium) and the genus Diphysa Jacq. are placed rather uncomfortably in the latter tribe as far as the type of inflorescence and presence of the bracteoles are concerned.

With the exception of Sesbania and Glottidium, both genera with n=6 (and probably x=6), the tribe Robinieae sensu POLHILL & SOUSA (1981) seems to be characterised by basic chromosome numbers of x= 11,10,9 or 8 (GOLDBLATT, 1981b). Cytologically, therefore, these two genera "must be interpreted" as specialised members of the Robinieae because of their derived aneuploidy from a basal stock which has x=11 (GOLDBLATT, loc. cit.). These facts place Sesbania (and Glottidium) in a somewhat anomalous position in the Robinieae.

Regrettably, there is no cytological data available for all

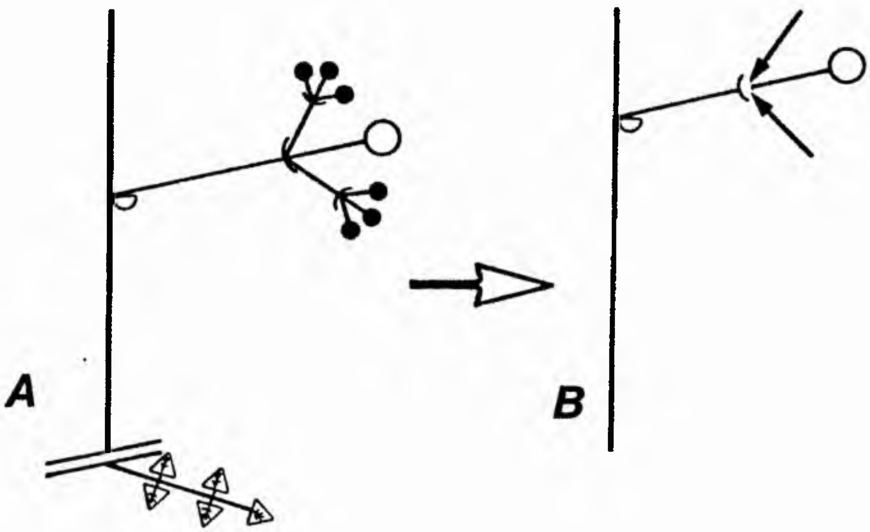


Figure 49 - Evolutionary diagram of the "Diphysa-type" of inflorescence in the Robinieae, after SOUSA & SOUSA (1981). Open circles represent fertile flowers; closed circles represent abortive flowers. The interpretation of B is that it represents the bracteolate, simple, racemose inflorescence as found in Sesbania, Glottidium, Diphysa and other Robinieae genera, which is derived from A through the abortion of the lateral flowers. The setae indicate the articulation point of the pedicel above the bracteoles; when the flower falls off, the lower pedicel with the bracteoles remain. A step further, with a subsequent reduction, there are no bracteoles present but the pedicel is articulated in the middle, as is found in most species of Robinia, Coursetia, Gliricidia, and Sabinea (SOUSA & SOUSA, 1981).

or even most of the Robinieae genera and it is not possible to know if the unusually low chromosome number is shared with Sesbania and Glottidium by other taxa.

In the palynological account of the Papilionoideae provided by FERGUSON & SKVARLA (1981), the tribes Sesbanieae and Robinieae (sensu POLHILL, 1981) are kept separate. These authors mention that the basic pattern of the Robinieae (Rydb.) Hutch. is of a tricolporate and unspecialised pollen grain similar to that of the Galegeae, while in Sesbanieae the pollen grains are operculate and have a well defined, circular endoaperture. The differences between the palynological features of the two tribes are not clearly stated but it is interesting to note that the conservative view of maintaining two separate tribes has been taken.

Finally, the pantropical distribution of Sesbania is an atypical feature for a Robinieae genus because all the other members of this tribe are only found in the tropics and subtropics of the New World. Although this is not an uncommon situation in the tribes of the Leguminosae, it must be taken into account in order to consider the tribal position of Sesbania and its allies.

Sesbania is, then, a somewhat anomalous genus within the limits of the Robinieae sensu POLHILL & SOUSA (1981) because the relationships of this genus with the other members of the tribe are largely unknown. Furthermore, the enormous lack of knowledge of the generic limits in Robinieae still remains and makes comparative studies very difficult.

Yucaratonia is another sesbanioid genus which is problematical at tribal level. As observed by BURKART (1969), the features of Yucaratonia, a monospecific genus based on a previously published species of *Sesbania* (*S. breninngii* Harms), place the genus as an intermediate between the *tribes* Sesbanieae and Robinieae (both as classified by HUTCHINSON, 1964). In Sesbanieae, *Y. brenningii* (Harms) Burk. comes close to *Sesbania* from which it differs mainly by the presence of a nectary and some other characters, as observed above (section "Generic relationships"). In the Robinieae, *Yucaratonia* is closely related to *Gliricidia* (BURKART, 1969), differing from it in having the ovary with a basal disc, absence of brachiblasts , racemes not in leafless stems; calyx campanulate, and yellow flowers.

The characteristic basal disc of *Yucaratonia* is, in fact, unique among the Robinieae genera (POLHILL & SOUSA, 1981) and seems a rather awkward feature if the genus is to be treated as a member of this tribe. Furthermore, the Robinieae contains a number of monospecific, geographically restricted and seemingly rather specialised genera, *viz*. *Hebestigma* Urb. in Cuba; *Olneya* A. Gray and *Sphinctospermum* Rose in northwestern Mexico and southwestern U.S.A.; *Neocracca* Kuntze in Andes of Bolivia and Argentina; *Genistidium* I.M. Johnston in Mexico; *Bembicidium* Rydb. in Cuba; *Yucaratonia* Burk. in Ecuador and Peru; and *Glottidium* Desv. in southeastern U.S.A. (POLHILL & SOUSA, 1981).

The presence of these rather disparate elements clearly makes tribal delimitation difficult. The generic limits in the tribe (Table 17) are so unclear that, for example, MACBRIDE (1943) has included *Poissonia* and *Cracca* in *Coursetia* and, on the other hand, POLHILL & SOUSA (1981) have questioned the distinction of *Olneya* from *Coursetia*.

In conclusion, it seems for the author that the tribe Robinieae constitutes a good example of a group with features of a "dustbin" taxon (DAVIS & HEYWOOD, 1963) which these authors define as one for "which good taxonomic characters are hard to find, or in which distinctive characters are found only in the minority of species". Although, at the moment, the members of the Robinieae apparently constitute an unnatural agglomeration, it is expected that further study may help to disentangle the group. However, in the present study, it has been accepted that while more critical data is being accumulated for other genera of the tribe, the genus Sesbania is treated as a member of the Robinieae. This is certainly a decision which will have to be revised when modern revisions of the other Robinieae genera are available.

4.4 - PHYTOGEOGRAPHY AND EVOLUTIONARY RELATIONSHIPS

4.4.1 - Hypothetical geographical origin

The interpretation of the origin and subsequent dispersal of any angiosperm group is fraught with difficulties. In some cases macrofossils and pollen fossil records permit some insights, but for the majority of taxa reconstruction has to be speculatively undertaken based on the understanding of the modern group alone. The Leguminosae as a whole are clearly no exception to the latter situation.

A hypothetical explanation for the present-day distribution of the species of Sesbania (Figure 50) can be based, at least in part, on current theories of continental drift as applied to angiosperm biogeography (RAVEN & AXELROD, 1974), particularly to the Leguminosae (RAVEN & POLHILL, 1981).

Although the legumes are extremely diverse in South America, (for example, the core groups Tephrosieae and Sophoreae of the Papilionoideae have more taxa in this area than in Africa (POLHILL, RAVEN & STIRTON, 1981)), there are few endemic genera and no marked concentration of archaic genera in this continent. Such "archaic genera" are relatively concentrated in the Old World which, according to RAVEN & POLHILL (1981), "points to Africa as a prime centre for the earliest evolution of the family".

It has been postulated that the origin of the Papilionoideae and Mimosoideae took place by the mid-Eocene (ca. 50 m.y. BP) when South America was about equidistant between Africa and North America (RAVEN & AXELROD, 1974; RAVEN & POLHILL, 1981). At this time, "there was undoubtedly an early interchange of legumes

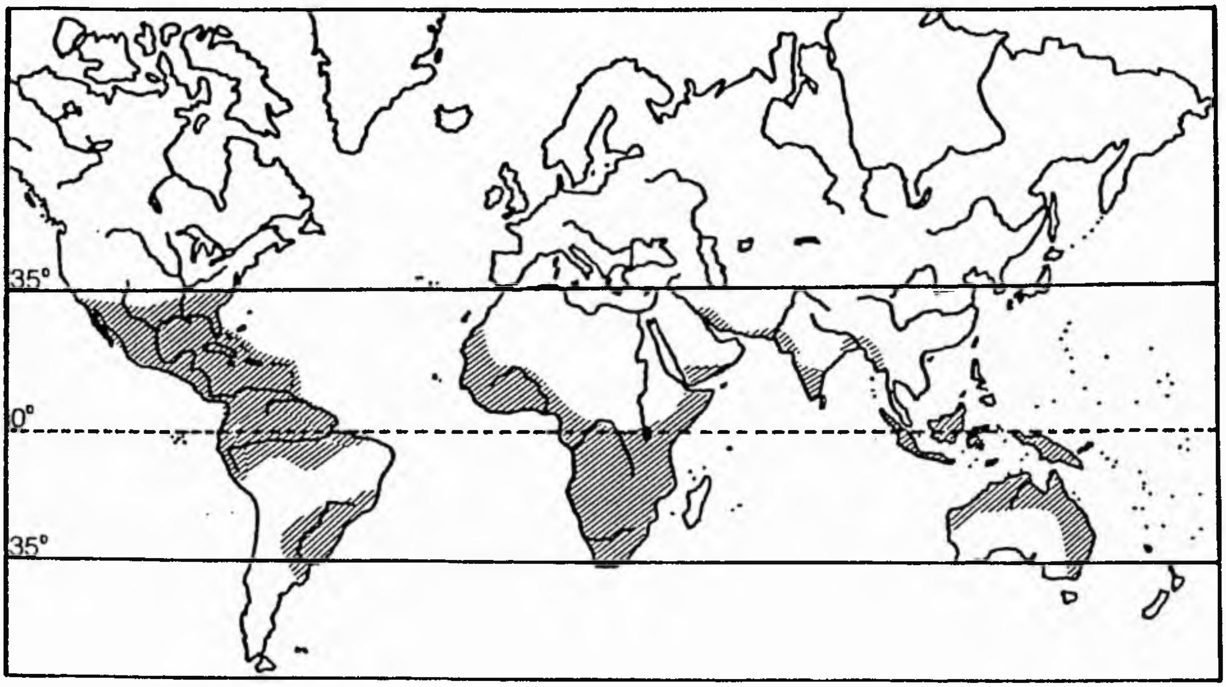


Figure 50 - Distribution of Sesbania Scop.

between Africa and South America" (RAVEN & POLHILL, *loc. cit.*). Such mobility (of legumes) is attested by the often pantropical distributions of the genera and tribes of legumes (GOOD, 1974; RAVEN & AXELROD, *loc. cit.*; RAVEN & POLHILL, *loc. cit.*). However, these pantropical taxa show much more diversity in the New World, which indicates, at least for the tropical plants, that most of the evolution of the rich and varied South American legume flora took place in isolation following separation of this continent from Africa (RAVEN & AXELROD, 1974; GENTRY, 1982). This hypothesis is supported by the adaptive radiation of "more advanced " tribes of Papilionoideae in the New World (RAVEN & POLHILL, 1981; POLHILL, 1981).

Although the history of the separation of South America from Africa is clear, the geological evidence of the earlier separation of North America from the Gondwanan-Laurasian landmass are still uncertain (CONEY, 1982; GENTRY, 1982). The separation seems to have occurred earlier than the split of South America from Africa (CONEY, *loc. cit.*) or at least the distances between South and North America increased at a much higher rate than between Africa and South America (RAVEN & AXELROD, 1974; CONEY, *loc. cit.*). The legumes, however, reached North America frequently from South America throughout the Tertiary until the two continents finally joined at *ca.* 5.7 m.y. BP (RAVEN & POLHILL, 1981). There is evidence that the tropical legume flora of North America is for the most part derived from South America via Central America (RAVEN & AXELROD, *loc. cit.*; GENTRY, 1982). The scarcity of archaic tropical legume genera in North America lends support for the hypothesis of late colonization of this continent by legumes from South America (RAVEN & POLHILL, 1981).

According to RAVEN & POLHILL (1981) the relative easy mobility of legumes compared to other families also allowed the group to move northwards and eastwards from Africa, certainly associated with the geological movement of land masses of the African, Eurasian and Indo-Australian plates (RAVEN & AXELROD, 1974; RAVEN, 1983). However, the legume flora is considerably poorer in tropical Asia than in Africa or South America, a situation which is "attributed largely to a lack of penetration into well-established ecosystems once access was relatively easy" (RAVEN & POLHILL, 1981). Although RAVEN & AXELROD (loc. cit.) have mentioned that the Papilionoideae are considered to be "relatively old" in Australia, it is supposed that the Leguminosae as a whole are very recent in this region (RAVEN & POLHILL, 1981). This view is supported by BURBIDGE (1960) who has demonstrated that the Australian tropical legume flora has strong connections with the Malaysian and New Guinean elements which were, in turn, largely derived via the tropical Asian-African connections (RAVEN & AXELROD, 1974; RAVEN & POLHILL, loc. cit.; RAVEN, 1983).

It seems, therefore, that plate tectonics can provide a convincing scenario to explain the origin, evolution and early dispersal of legumes through direct land migration between the continents. However, this rather vaguely perceived sequence of early continental-dispersion in the Leguminosae has been overlain by, on the one hand, repeated long-distance dispersal events, and on the other hand, migrations and extinctions due to the effects on the tropical flora of the southern hemisphere ice-age (16-13 m.y. BP for the expansion of the east Antartic ice sheet, 9–5 m.y. BP for the west Antartic sheet *cf.* RAVEN, 1983). This latter phenomenon stimulated other events such as the Northern Hemisphere ice–age, flux of forest *versus* savanna vegetation in South America and Africa, and expansion of dry habitats whose effects continue to the present–day (RAVEN, 1983). As a consequence, unravelling this complex of events to delineate the biogeographical history of any one genus can only be a largely speculative exercise based on

(1) taxonomic delimitation and distribution limits of each species,

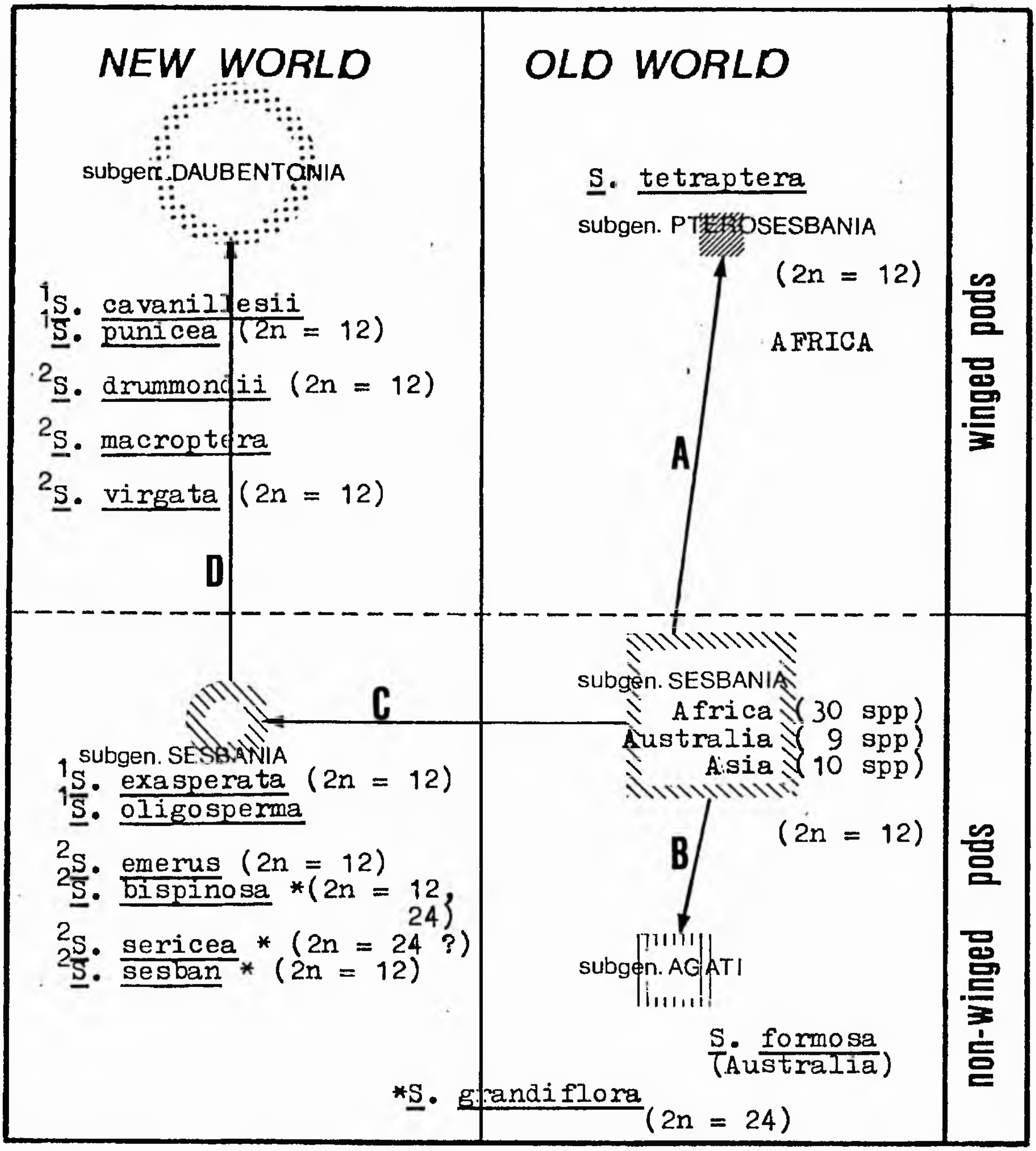
(2) relationships of species groups as reflected in infrageneric classification,

(3) interpretation of relationships in terms of primitive *versus* derived characters,

(4) present–day distribution of other genera of the same tribe or other alliance of taxa.

Using these facts and also the evidence of supposed geological history of the legumes mentioned above, at least an approach to the phytogeography of *Sesbania* can be made if we consider the genus and its infrageneric taxa under the scheme of Figure 51 and Table 16.

Sesbania has *ca.* 32 species in Africa (GILLETT, 1963), ten in Australia (BURBIDGE, 1965), *ca.* 10–11 in tropical Asia, and in the present work, eight native species are recognised in the New World. One can speculate, therefore, that having the majority of species, Africa is certainly the centre of diversity and, possibly, the continent where *Sesbania* had its origin.



Notes :

1 = large-flowered species
2 = small-flowered species
* = introduced species

Figure 51 - Interrelationships between the subgenera of Sesbania Scop. in the New and Old World. Steps A-D are explained in the text.

We can further speculate that a common stock for the whole genus in Africa produced a large group of species on that continent which share a number of characters, i.e, the subgenus *Sesbania*. From this basal stock a new species (*S. tetraptera* Hoechst ex Baker) arose (Figure 51, step A – subgen. *Pterosesbania*).

The main differential character of *S. tetraptera* with the members of subgen. *Sesbania* is the ovary which has four wing-like expansions which develop to winged pods and, as is shown in Table 16, the accumulation of other characters of subgen. *Sesbania* in the subgen. *Pterosesbania* make the winged-pod in the latter the only possible discontinuity between both.

Although no time scale can be provided for the evolutionary steps indicated in Figure 51, it is possible to speculate that while subgen. *Pterosesbania* was evolving in Africa, a very small part of the subgenus *Sesbania* (one species ?) established itself in the New World either through long-distance dispersal or migration through land bridges provided by continental movements (Figure 51, step C). In addition to diversification to produce other species of subgen. *Sesbania*, this stock also gave rise by parallel evolution to another group, subgen. *Daubentonia*, which also has members with winged pods, like subgen. *Pterosesbania* (Figure 51, step D). Independent evolution of these two groups is supported by the lack of consistency in their characters as seen in Table 16.

GILLETT (1963) using the nature of the appendages on the claw of the standard petal, considered *S. tetraptera* (subgen. *Pterosesbania*, in central and eastern Africa) to be closely related to *S. macrantha* Welw. ex Baker (central, southwest and southeast Africa) and to *S. pachycarpa* DC. *emend* Gill. & Parr. (west Africa, mainly), both of subgen. *Sesbania*. Apart from this relationship, no other character provides evidence of links between subgen. *Sesbania* and subgen. *Pterosesbania*.

In the New World, however, two intermediate species between the subgenera *Sesbania* and *Daubentonia* are evident. *S. oligosperma* Taub. (Brazil, Argentina) has reduced or lost the tooth in the keel petals and the pods have diminished in length with the number of seeds subsequently decreased.

The next step was achieved by *S. cavanillesii* S. Watson (Mexico) which lost the teeth in the wing *and* keel petals and the pair of appendages on the claw of the standard, and suffered a further reduction of the pod; the latter became more torulose and gained a thickening of the margins. Both of these species can therefore be considered as New World subgen. *Sesbania* species with subgen. *Daubentonia* character tendencies.

The appendages of the standard did not completely disappear in subgen. *Daubentonia* and can be found in *S. punicea* and *S. virgata* as short, small calli. A further step is seen in *S. virgata* which has an accentuated thickening of the margins of the pods, which perhaps represents an advance on the condition found in *S. cavanillesii*.

Therefore, just as there seem to be evident links between subgen. *Pterosesbania* and some African species of subgen. *Sesbania* (GILLETT, 1963), likewise in subgen. *Daubentonia* is possible to find a series of intermediate stages linking this group with the

New World representatives of subgen. Sesbania, and hence supporting the independent origin of subgen. Daubentonia vis-a-vis the African winged-pods species. The present disjunct distributions found in species of subgen. Daubentonia in North and South America are here interpreted in terms of exchange of taxa between these areas through long-distance dispersal. This view is discussed under the taxonomic treatments of S. punicea and S. drummondii.

An interesting aspect of subgen. Sesbania in the New and Old World is the natural occurrence of small- and large-flowered species in both areas. In Africa the two groups do not show distinct distribution patterns (GILLETT, 1963) but in the New World the native small-flowered species S. emerus is distributed mainly in Central and North America and West Indies, whereas the large-flowered taxa (S. exasperata and S. oligosperma) occur more often in South America. One can speculate, therefore, that the species of Sesbania subgen. Sesbania in South America may be derived from more than one introduction from Africa, although there is no firm evidence for this hypothesis.

The species of subgen. Sesbania here regarded as recently introduced in the New World (S. bispinosa, S. sericea and S. sesban) are considered to owe their distributions in this area to their weedy characteristics and also to their association with disturbed habitats caused by Man's agricultural practices. All of them have been introduced in other areas of the tropics and subtropics in the same way.

It is difficult to interpret the relationships of the Australian species of subgen. Sesbania with other areas of occurrence of the genus. No connections can be made with the South American species and this is valid for the family as a whole (BURBIDGE, 1960; RAVEN & AXELROD, 1974; RAVEN & POLHILL, 1981).

In Australia, *Sesbania* is restricted to the tropical zone and adjacent parts of northern Eremaea. BURBIDGE (1965) recognised nine species of subgen. *Sesbania* in this country, six of which are endemic. Of the other three, BURBIDGE (*loc. cit.*) mentioned that *S. javanica* Miq. is believed to be conspecific of *S. roxburghii* Merrill (= *S. paludosa* Prain ?), which also occurs in southeast Asia and Malaysia; *S. cannabina* (Retz.) Poir. which GILLETT (1963) considered to be native to Malaysia and Australia and has probably extended recently into cultivated areas of Iraq, India, Burma and Indo-China; and *S. sesban* is the only certain introduction by Man in Australia (BURBIDGE, *loc. cit.*).

In one native species, *S. campylocarpa* (Domin) Burb., the appendages on the claw of the standard petal are apparently absent and BURBIDGE (1965) has mentioned that "since calli (= appendages) developed in many non-Australian species it seems probable that their absence in *S. campylocarpa* does not indicate a primitive condition for the genus". This hypothesis of primitiviness of presence of the appendages on the standard's claw is accepted here since the reduction and/or absence of appendages is also noted in species of subgen. *Daubentonia*, mainly in the intermediates between this taxon and subgen. *Sesbania*.

While the connections of some of the Australian species with the southeastern Asian seems acceptable because of the strong correlations of the floras of both regions (BURBIDGE, 1960), the origin and relationships of the endemics are still obscure (BURBIDGE, 1965). Indeed, G. LEWIS * (pers. com.) considers that many of these Australian "endemic species" of Sesbania are in fact conspecific with taxa occurring in southern and southeastern regions of Africa. A careful evaluation of this situation must await the publication of a modern revision of the African species.

The origin and relationships of subgen. Agati (S. grandiflora and S. formosa, Figure 51, step B) are obscure and, therefore, very confused. The first record of S. grandiflora is from India (RHEEDE, 1678) and, indeed, GILLET considered this species as originally from Indonesia. However, due to its potential economic value and many uses by Man (see section "Economic Uses") the species has certainly been introduced elsewhere. Nevertheless, with its dispersal to the islands of southeast Asia, it probably acquired some modifications which finally became more marked in Australia. BURBIDGE (1965) has argued that such Australian plants show enough discontinuity with the Malaysian ones to treat the former as S. formosa (F. Muell.) Burb., although BENTHAM had previously treated its basionym (Agati formosa F. Muel.) as a synonym of S. grandiflora (BURBIDGE, 1965).

While the ploidy status of S. formosa is not known, JACOB (1941) and LUBIS et al. (1981) have proposed two different origins for the tetraploid S. grandiflora (these hypotheses are discussed in the section "Cytology").

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JACOB (1941), who worked with plants of *Sesbania* growing in India, considered *S. grandiflora* as an amphidiploid possibly derived from two species with karyotypes similar to the ones he found in *S. sesban* and *S. speciosa*, both of subgen. *Sesbania* and of African origin but introduced and cultivated in India. LUBIS *et al.* (1981), using observations on the cytology of four *Sesbania* species from Java, suggested that *S. grandiflora* may be an autopolyploid with *s. sesban* as the putative ancestral species.

Although these studies seem to be apparently contradictory, they simply reflect the lack of a better understanding of the interrelationships between the infrageneric taxa of *Sesbania* due to the absence of cytological data for the majority of its species. However, the polyploid nature of *S. grandiflora* may possibly explain its rather distinct position within the genus as reflected by its isolation as a separate subgenus. However, polyploidy did not have the same effect in *S. bispinosa* (subgen. *Sesbania*).

It is reasonable then, to accept *Sesbania* as a coherent natural genus with a pantropical distribution and subdivided in four distinct but interrelated subgenera (Table 16). The species that comprise each subgenus certainly share a common stock of characters and, as intermediate taxa between the subgenera occur in the New World, it is unacceptable that the disjunct distributions should be used as an argument to treat the New World taxa as separate genera.

4.4.2 - Habitat and Ecological Adaptations

Members of the genus *Sesbania* are found in areas where water is abundant at least for part of the year in tropical, subtropical, and warm temperate latitudes between 35 N and 35 S (Figure 50). *Sesbania* has been cited as one of the aquatic taxa in the book "Water plants of the world" by COOK *et al.* (1974). This characteristic of aquatic to semi-aquatic habitat is well established in the genus, and in fact accounts as an ecological requirement for its species to grow although some of them may also occur in seasonally arid areas (BURBIDGE, 1965).

UPPAL (1955) and GILLET (1963) mentioned that some species of *Sesbania* have their distributions closely related with differences in the alkalinity and salinity of the water which they seem to tolerate well. Unfortunately this physiological adaptation has been studied in detail only in *S. bispinosa* (UPPAL, 1955) but it is probably found in other species which are associated with coastal sand dunes and old mangrove mudflats in southern U.S.A. (*S. emerus*, *S. drummondii*), southeastern South America (*S. punicea*, *S. virgata*), and Australia (species of subgen. *Sesbania* - BURBIDGE, 1965).

Some internal morphological adaptations for aquatic habitats are reported by SCOTT & WAGER (1888) and SCHENK (1889) for *S. bispinosa* and *S. virgata*. In these taxa a well developed aerenchyma is found in the roots. STABER (1909), however, did not find the same root anatomy in *S. emerus*.

Other anatomical studies on *Sesbania* are sparse : STABER (1909) dealt with the general anatomy of the stem and leaves of *S. emerus* and also received some of the scattered data on anatomy of the genus published up to that time. COZZO (1948) gave an account of the wood morphology of *S. punicea* and *S. virgata* in a comparative study focused on the tribal position of the genus (Galegeae, at that time). METCALFE & CHALK (1950) mentioned the genus sporadically but provided no new information.

In a revision of "Stomata and stomaty in the Leguminosae", STIRTON * (in prep., pers. com.) suggests that the distribution pattern of stomata is a reliable character for taxonomic purposes and can also be associated with the habitats in which the plants occur. It is proposed that taxa of tropical lowland rain forests, montane forests, European and Asian woodlands, trees and shrubs are most likely to have <u>hypostomatic leaves</u>, and plants of coastal marshes, coastal strands, meadows, disturbed habitats and open aquatic habitats often show <u>amphistomatic leaves</u>.

The previously published data available for the occurrence and stomata types in species of <u>Sesbania</u> is shown in Table 18. Despite its fragmentary nature these observations indicate that (a) some species are variable for stomatal-type and (b) amphistomatic leaves are a feature of the genus.

The stomatal occurrence on the leaves of the New World species of <u>Sesbania</u>, <u>Glottidium</u> (<u>G</u>. <u>vesicarium</u> (Jacq.) Harper) and <u>Yucaratonia</u> (<u>Y</u>. <u>brenningii</u> (Harms) Burk.) was studied in the present work. The material consisted of

(1) samples of leaflets collected from several exsiccatae for each taxon, which were resuscitated in boiling water, or

(2) epidermal peels from flesh leaflets in the case of cultivated specimens (<u>S</u>. <u>punicea</u> and <u>S</u>. <u>virgata</u>).

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Table 18 - Stomatal occurrence and types in species of *Sesbania*.

TAXON	STOMATA					REFERENCE
		% OF TYPES				
	DISTRIBUTION	PARACYTIC	ANISOCYTIC	ANOMOCYTIC	DIACYTIC	
S. bispinosa	Epistomatic	---	---	---	100 %	GILL *et al.*, 1980, 1982
S. emerus	Amphistomatic	n.a.	n.a.	n.a.	n.a.	STABER,1909
S. grandiflora	Amphistomatic	22.5 %	32.2 %	39.0 %	6.3 %	SHAH & GOPAL, 1969
S. macrantha	Amphistomatic	---	80.0 %	---	20.0 %	GILL *et al.*, 1980 1982
S. sesban	Amphistomatic	31.43 %	37.14 %	20.0 %	---	SHAH & GOPAL, 1969
	Amphistomatic	---	---	100.0 %	---	GILL *et al*, 1980 1982

Observations were made by means of direct observation of the leaf surface or peels with the use of high magnifications in a KIOWA 805116 dissecting microscope.

The results show that

(1) all species of *Sesbania* of the subgenera *Sesbania* and *Daubentonia* have amphistomatic leaves, except for *S. bispinosa*, which is epistomatic (confirming the results found by GILL *et al*., 1980, 1982);

(2) the genus *Glottidium* (*G. vesicarium*) is also amphistomatic, and,

(3) the monospecific genus *Yucaratonia* (*Y. brenningii*) has amphistomatic leaves.

These results confirm that the the distribution of stomata on the leaves of *Sesbania* seems to be characteristic at generic level, but exceptions certainly occur, e.g., *S. bispinosa*. Furthermore, the correlation of amphistomatic distribution with palustrine habitats (mentioned above) is supported by the predominance of this stomatal type in *Sesbania*.

Another successful adaptive feature found in *Sesbania* is the fact that seeds germinate better after being scarified either mechanically or by heat (see section "Germination and seedlings"). This hard-seededness characteristic is essentially a dormancy mechanism which avoids immediate germination of seeds once they fall on the possibly still inundated ground around the mother plant.

The adaptation of species of Sesbania to the disturbed soils of wet lowlands and river valleys has apparently allowed them to invade and colonise successfully areas where the environment has been disturbed by human activities, resulting ultimately in their present wide distributions.

4.5 -REPRODUCTIVE BIOLOGY

4.5.1 - Pollination mechanism

The typical papilionoid flower of Sesbania can be readily associated with melitophily but one record of ornithophily in S. grandiflora is given by ARROYO (1981) in the comprehensive review of the breeding systems and pollination biology of the Leguminosae.

Apparent nectar guides are provided by streaks and dots on the reflexed standard. However, in the cultivated plants of S. virgata and S. punicea which were studied no nectar could be detected and no references concerning the presence of nectar in species of Sesbania have been found.

The pollination in Sesbania is achieved through mechanical activation of the wing and keel petals and their interaction with the pistils and stamens. The wing petals may also act as attractants in helping to shape the overall morphology of the flowers but their roles are certainly associated as landing platform for bees and as levers to lower and raise the keel (LEPPIK, 1966; ARROYO, 1981). These functions are enhanced by the existence of the sculptures on the outer surfaces of the wing petals, as discussed by STIRTON (1981).

The types of wing petal sculpturing were revised by STIRTON (1981) and from his work and also observations in the present study of a wide range of New and Old World species of Sesbania, Glottidium, Yucaratonia and other genera included in Robinieae sensu POLHILL & SOUSA (1981) it would seem that the lamellate type is consistent throughout the whole group. The distribution of the sculpture in the wing petals of S. punicea is shown in Figure 75d and represents the lamellate pattern for Sesbania and other genera cited above. The structure is made up of foldings of the epidermis which give the appearance of stripes running along from the upper basal portion to the middle of the petal.

STIRTON (1981) noted that some species of Robinia have wing petals with smooth outer surfaces. The absence of sculpturing on the wings is not uncommon among the Papilionoideae and it is the pattern found in the members of tribes such as Trifolieae, Loteae, Amorpheae and Indigofereae. When the sculpturing (or indentation) is absent, the presence of pockets in the upper margin of the wings or the folding of the whole petals provide the necessary mechanical reinforcement for these organs to withstand the pressure exerted by the visiting insects.

In Sesbania, the exposure of the pollen and the stigma through the "simple valvular arrangement" (LEPPIK, 1966) of the stamens and stigma, illustrated by the flowers of S. virgata in Figure 78e, ensures that the latter structures can emerge from the keel as long as the pressure of the visitor continues and then return to their former position when the pressure ceases. As this pollen-presentation mechanism allows the flowers to receive repeated visits, self- and cross-pollinations can possibly occur quite often in these plants.

Manipulation of the flowers of Sesbania and collection of pollen by insects are enormously facilitated by this pollen-presentation mechanism. The rigid structure of the filament sheath retains the pistil inside the staminal tube so that both are exposed simultaneously when the keel petal is lowered. The pollen grains, which are found to be already released from the anthers just prior to anthesis, accumulate as a massive plug on and around the stigma and anthers. From that point onwards, a simple mechanical activation on the wings and keel petals expose the whole system for the pollinator.

BURBIDGE (1965) mentions that several species of *Sesbania* are well known to have upper flowers of the raceme which are functionally male due to the reduction or lack of development of the pistil. This is the case of *S. simpliciuscula* var. *simpliciuscula* and *S. cannabina* var. *sericea* in Australia and, in the former taxon, this condition may be correlated with modifications in size of the appendages at the base of the standard (BURBIDGE, *loc. cit.*).

Because of this statement, a detailed study of gender distribution of flowers in the inflorescence of New World *Sesbania* species was made for this work. As far as the material available in exsiccatae permitted, a check for the presence of stamens and pistils in the flowers at different insertions in the racemes revealed no indications of such functional unisexuality. Furthermore, the specimens with fruits likewise did not give any evidence of the occurrence of female-sterile flowers in any part of the inflorescence.

Flowering plants of *S. punicea* and *S. virgata* that were cultivated in the experimental glasshouses of the University of St Andrews Botanic Garden were regularly checked for the occurrence of staminate rather than hermaphroditic flowers but the many observations carried out over two flowering seasons (summers of 1982 and 1983) again did not give any indication of the occurrence of unisexual flowers.

It is intriguing that, although cited as a well known feature of the genus (BURBIDGE, 1965), no mention of such unisexuality was mentioned by ARROYO (1981) in her extensive study of reproductive biology of legumes.Whilst female sterility is widespread in members of the subfamily Mimosoideae, no examples were given by ARROYO (*loc. cit.*) for the members of the Papilionoideae. Therefore, the unisexuality of *Sesbania* demands further investigations, preferably in conjunction with field studies on floral biology. If some staminate flowers or gender separation do not occur, it is therefore concluded that the single fowers function as the pollination units in species of *Sesbania*.

4.5.2 - Hybridization

The proportions of self- and cross-pollinations, the rates of incompatibility, and the extention of sterility barriers are not known for any species of *Sesbania* except for the work of DATTA & SEN (1960) with *S. bispinosa* (a tetraploid) and *S. speciosa* (diploid), both African/Asian members of subgen. *Sesbania*. The results of attempts at hybridization between these two taxa showed that both were fully self-compatible but, regardless of the pollen-donor, all interspecific crossings resulted in infertile seeds. It should be mentioned here that, although plants of *S. bispinosa* used by DATTA & SEN (*loc. cit.*) were polyploids, DANA & DATTA (1961) did find that their behaviour through meiosis was regular, with only rare multivalents formation. DATTA & SEN (1960) concluded that the genomic difference of the two species was the main cause of the failure of hybridization.

Several attempts to study the reproductive aspects of *S. punicea*, *S. virgata*, *S. sesban* var. *nubica*, *S. macrantha* and *S. rostrata* in cultivation at the Botanic Garden of the University of St Andrews were made in two summers (1982 and 1983) but all resulted in failures associated with premature flower drop in both manipulated and untouched flowers. *S. sesban*, *S. macrantha* and *S. rostrata* did not flower during the three years of cultivation.

However, a few flowers of *S. punicea* and *S. virgata* left untouched but occasionally visited by some bees produced a very low number of pods, but it is not known whether these fruits were results of self- or cross-pollinations.

This lack of success with reproductive biology studies with the two species that came into flower in cultivation was unfortunate because they could render some insights on how to design possible genetical improvement programs.

4.6 - GENERIC DESCRIPTION[*]

Sesbania Scopoli, Introd. : 308, 1777, *nom. conserv.*

Agati Adanson, Fam. Pl. *2* : 326, 513, 1763

Sesban Adanson, Fam. Pl. *2* : 327, 604, 1763

Sesbana R. Brown *ex* W. & W. Aiton, Hort. Kew (ed.2) *4* : 330, 1812 - *orth. var.*

Darwinia Raf., Fl. Ludov. : 106, 1817

Monoplectra Raf., Fl. Ludov. : 106, 1817 - *nom. superfl.*

Daubentonia DC., Prodr. *2* : 264-6, 1825; Mem. Leg. : 285, 1826

Resupinaria Raf., Sylva Tell. : 115, 1838

Sesbania Pers., Bentham *in* Gen. Pl. *1* : 502, 1865 - *pro majore parte* (excl. sect. *Glottidium* = *Glottidium* Desv.)

Emerus Kuntze, Rev. Gen. Pl. *1* : 180, 1891. *Non Emerus* Mill., Gard. Dict. (ed. 4), 1754

Daubentoniopsis Rydb., AM. J. BOT. *10* : 497, 1923; N. AM. FL. *24* : 206, 1924.

Annual or perennial *herbs*, *shrubs* or small *trees*; stem and branches terete, smooth to striate or 4-angled, striate; glabrous to sparsely strigose or sericeo-villous (*S. sericea*, subgen. *Sesbania*), usually unarmed or with small whitish prickles or spines (*S. bispinosa*). *Leaves* alternate, compound, paripinnate, multifoliolate; the rachis with a setaceous tip and often with a channel on the adaxial side; leaflets entire, linear-oblong, oblong-ovate or oblong-lanceolate to elliptic (*S. cavanillesii*),

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[*] As represented in the New World

obtuse to acute at the apex, rounded at the base, green on the adaxial face but usually glaucous beneath and with sparsely scattered small, black dots (glands ?), often glabrous but covered with minute stiff hairs when young, short petioluled; stipules oblong, minute to absent. Racemes axillary, shorter than the leaves (except for S. sesban), pedunculate, with (1-)2 - 12(-17) flowers; with a pair of bracts at the base of the pedicel and a pair of bracteoles subtending the flower; both bracts and bracteoles deciduous. Calyx, in subgen. Sesbania broadly campanulate, as broad as long, green or brown-spotted externally on the lobes, with 5 long, triangular, acute to acuminate lobes or, in subgen. Daubentonia and subgen. Agati, rounded-campanulate, broader than long, with 5 short lobes and then slightly bilabiate. Flowers glabrous, with a slender pedicel, usually yellow but the standard spotted with green or red (black ?) dots or streaks, or white to pinkish (subgen. Agati) or red (S. punicea, subgen. Daubentonia); standard longer than the other petals, reflexed (subgen. Sesbania and subgen. Agati) or strongly reflexed (subgen. Daubentonia), suborbicular to orbicular, emarginate, the short claw usually with a pair of appendages sometimes decurrent and with free tips; wing and keel petals with an upper basal tooth (subgen. Sesbania) or non-toothed (subgenera Agati and Daubentonia), both lanceolate-lunate in S. grandiflora; wing petals free, oblong to oblong-lanceolate, short clawed, the claw bent; keel petals curved or straight, joined below, lunate to semi-lunate, the claw about as long as the blade. Stamens 10, diadelphous, nine of subequal length fused in a glabrous sheath bearing an auricle at the base and the vexillar filament free, geniculate near its base; anthers dorsifixed, uniform, ovate to lanceolate; pollen grains triaperturate, colporate, exine reticulate. Ovary glabrous, linear, compressed or cylindric, circular to elliptical in transection (tetralate only in *S. tetraptera*, subgen. *Pterosesbania*, Africa), with 4 to many ovules; style filiform to linear, stipitate; the stigma small, capitate. *Pods* coriaceus, long and slender, terete or compressed, beaked, dehiscent, 2-valved and multi-seeded *or* 4-angled or 4-winged, oblong-linear, compressed, beaked, indehiscent and with 4-9 seeds; septate between the seeds within, sometimes externally indented between the seeds; calyx not persistent in the fruit. *Seeds* brown and smooth, cylindrical to cylindric-oblong to reniform-oblong with a subcentral circular to elliptic hilum. 2n = 12 (2n = 24 in *S. grandiflora* and *S. bispinosa*).

Type species : *Sesbania sesban* (L.) Merrill

The genus has been treated in various ways by taxonomists since its earliest descriptions by ADANSON (1763) as *Sesban* and by SCOPOLI (1777) as *Sesbania*, both based on *Aeschynomene sesban* L. The recent edition of the "International Code of Botanical Nomenclature" (=ICBN, STAFLEU, 1983) states that *Sesbania* Scop. is a conserved name against *Sesban* Adans., despite the fact that SCOPOLI (*loc. cit.*) did not propose a new name but only introduced a variant of "Sesban" more conformable to latin usage.

GILLETT (1963) accepted RICKETT & STAFLEU's interpretation and considered that binomials in *Sesban* should be treated as if they were binomials in *Sesbania*. This subsequently led to the conclusion that the names published by POIRET (1806) under *Sesban* (in "Encyclopaedia Methodique") had priority over those by PERSOON ("Synopsis Plantarum", 1807). BURBIDGE (1965) also retained the same treatment for the revision of the Australian species of *Sesbania*.

However, with the later recognition and establishment that *Sesbania* Scop. was a *nomen conservandum* and *Sesban* Adans. a *nomen rejiciendum* (FARR, LEUSSINK & STAFLEU, 1979; ICBN, 1983) the treatment used by GILLETT (1963) has been rejected. The interpretation here accepted is that *S. grandiflora* (L.) Poir. as cited by GILLETT (*loc. cit.*) should be *S. grandiflora* (L.) Pers. Other nomenclatural corrections which may require to be made to GILLETT's interpretation of *Sesbania* do not concern the species treated in this thesis and are therefore not further discussed here.

ADANSON (1763) based his new genus *Agati* on the Linnean *Robinia grandiflora* (= *S. grandiflora* (L.) Pers.) but its type was initially listed in the 1961 edition of the ICBN and by RICKETT & STAFLEU (1959) as *Robinia caragana* L. This was subsequently corrected to *R. grandiflora* and *Agati* became a rejected name against *Sesbania* Scop.

The binomial of the type species, *Sesbania sesban* (L.) Merrill was discussed by NICOLSON (1975), TERRELL (1977) and WHITE (1980) as a possible source of confusion regarding tautonyms and paratautonyms since both words are very similar. A consultation to the ICBN concerning this matter brought the following articles into consideration :

Article 23 - defines a tautonym as a binary combination in which the specific epithet exactly repeats the generic name , i.e., the two are identical;

Article 55 - rejects a specific epithet if on transfer to another genus it forms a tautonym;

Article 73 - specifies that the original spelling of a name is to be retained, except for correction of orthographic or typographic errors;

Article 75 - states that generic and specific names so similar they are likely to be confused are treated as orthographic variants, i.e., variant spellings of the same word.

From the statements of the articles cited above it is clear that (a) if Sesbania Scop. is a conserved name against Sesban Adans., then (b) the binomial Sesbania sesban is not a tautonym (TERRELL, 1977) because the two words making up the specific name are not orthographic variants. The species name Sesbania sesban is therefore used here.

Darwinia was a generic name given by RAFINESQUE (1817) to a Sesbania plant growing in southern Louisiana, U.S.A., which he named D. exaltata (see discussion under S. emerus) although, unknown to RAFINESQUE (loc. cit.), RUDGE (1815) had already published Darwinia as a genus in the Myrtaceae. Nevertheless, RAFINESQUE (1817) proposed the alternative name Monoplectra in case of the name Darwinia had been used before. The name Darwinia must be rejected, of course, as a later homonym; Monoplectra has no status, but in any case is unnecessary since Darwinia exaltata, i.e., Sesbania emerus, is a good species of Sesbania.

Daubentoniopsis Rydb. also presents no problem for the interpretation of synonymy because it was based on a previously published Sesbania species, S. cavanillesii S. Watson (WATSON, 1878; RYDBERG, 1923, 1924).

Originally a number of Old World species present in the New World were treated as distinct species, consequently inflating the number of specific names/epithets available. Most of the problems were solved by PHILLIPS & HUTCHINSON (1921) and GILLETT (1963) in their revisions of the African species but since these studies deal only with the African taxa, they did not treat with names related to S. sesban, S. bispinosa and S. sericea in the New World. Therefore, for these African taxa, the synonymy has been carefully studied for the present study.

4.7 - KEY TO THE SUBGENERA AND SPECIES OF *SESBANIA* IN THE NEW WORLD

1 . Flowers large, 5–8.5 (–10.0) cm, white or pinkish; standard elliptic; pods (25–)30–40 cm; seeds reniform oblong ———————————————————————— subgen. *Agati* ((12) *S. grandiflora*)

1'. Flowers small, less than 5 cm, yellow, pale orange or red; standard suborbicular; pods 15–30(–40) cm, non-winged, or 6–15 cm with thickened margins or 4-winged; seeds cylindric-oblong to reniform ———————————————————————————— 2

2 . Calyx campanulate, as broad as long, conspicuously 5-lobed, lobes deltoid, acute or acuminate, usually dark-pigmented outside, 1.5–4.0 mm; wing and keel petals with a basal tooth (lacking in *S. oligosperma*); standard with a pair of elongate decurrent appendages along the claw; pods slender, terete or slightly compressed, many-seeded; seeds cylindric-oblong ———————————————————————— subgen. *Sesbania*

2'. Calyx rounded-campanulate, broader than long, inconspicuously 5-lobed, lobes very short, non-pigmented outside, 0.5–1.5 mm; wing and keel petals without a basal tooth; standard petal lacking appendages along the claw (a pair of small divergent appendages near base of claw sometimes present); pods 4-angled or often 4-winged (but torulose with thickened margins in *S. cavanillesii*); seeds reniform ———————————————————— subgen. *Daubentonia* subgen. Sesbania

1 . Abaxial surface of the leaflets and stem uniformly silky-villous; racemes with 3-4 flowers ———————————— (6) S. sericea

1'. Leaves and stem glabrous; racemes with (2-)4-12 flowers ———— 2

2 . Racemes longer than the leaves; leaves with 10-20 pairs of leaflets ———————————————————— (1) S. sesban

2'. Racemes shorter than the leaves; leaves with 25 or more pairs of leaflets ——————————————————— 3

3 . Spines present on the stem branches and on the abaxial face of the leaf rachis; flowers less than 15 mm ————— (5) S. bispinosa

3'. Plants unarmed; flowers 15-30 mm —————————————— 4

4 . Stem terete, smooth to striate; calyx up to 5 mm long; corolla up to 20 mm; wing and keel petals oblong —————— (2) S. emerus

4'. Stem angled, striate; calyx 7-10 mm; corolla 18-30 mm; wing petals oblong to obovate ——————————————— 5

5 . Keel petals obovate, with a conspicuous upper basal tooth; calyx lobes broadly triangular, mucronulate, 2.5-3.0 mm; pods up to 30 cm, not constricted —————————— (3) S. exasperata

5'. Keel petals ovate, with the basal tooth very reduced or lacking calyx lobes triangular-acuminate, 2.5-3.5 mm; pods 15-20 cm, slightly moniliform ———————————— (4) S. oligosperma subgen. Daubentonia

6 . Claw of the standard petal with short appendages ———————— 7

6'. Claw of the standard petal without appendages ————————— 8

7 . Flowers yellow to greenish yellow, 10-15 mm; standard with green streaks externally; pods 4-7 cm; with thickened margins, 4-6 seeded ——————————————————————— (11) S. virgata

7'. Flowers red, 20-25 mm; standard not mottled or streaked; pods 5-12 cm, with 4 undulate wings, 5-9 seeded ——— (10) S. punicea

8 . Pods not winged, torulose, with thickened margins, conspicuously constricted between the seeds; flowers 20-25 mm, pale-yellow; leaflets oblong-lanceolate to elliptic ——— (7) S. cavanillesii

8'. Pods with 4 striate wings; flowers 8-15 mm, pale- to bright-yellow; leaflets linear-oblong ———————————————————— 9

9 . Standard externally green-streaked or mottled, strongly reflexed; calyx slightly to conspicuously bilabiate; style strongly curved; pods 4-6 cm with 4 folded wings ———————— (9) S. macroptera

9'. Standard not mottled or streaked, reflexed; calyx equally short 5-lobed; style straight to slightly curved; pods 7-10 cm, with 4 patent wings ————————————————— (8) S. drummondii

4.8 - Subgenus Sesbania

subgen. Sesbania

Sesbania sect. Eusesbania Benth., Gen. Pl. 1 : 502, 1825; Phill. & Hutch., BOTHALIA 1: 40-46, 1921

Sesbania subgen. Sesbania Baker, Fl Trop. Afr. 2 : 133, 1871; Gillett, KEW BULL. 17 : 91-159, 1963; Burbidge, AUSTR. J. BOT. 13 : 103-141, 1965

Sesbania sect. Moniligeram Taub., FLORA 72 : 423, 1889

Sesban Adans. Small, Fl. Southeast. Un. St. : 614, 1903; Rydberg, AM. J. BOT. 10 : 496, 1923, FL. N. AM. 24 : 202-5, 1924

Woody herbs, subshrubs or shrubs (rarely short-lived, slender trees) evergreen or deciduous, glabrous to sparsely strigose or sericeous. Racemes (1-)2-6(-8)-flowered. Calyx broadly campanulate, conspicuously 5-lobed; lobes shorter than the tube, subequal, triangular (or deltoid in S. oligosperma), acute to acuminate. Standard suborbicular, with 2 decurrent, callous appendages on the claw and sometimes terminating in the base of the limb with free projections. Wing and keel petals with an upper basal tooth (reduced or absent in the keel of S. oligosperma); wing petals oblong-lanceolate to oblong; keel petals broadly lunate, long-clawed. Staminal sheath auriculate at the base. Pod stipitate, linear, terete or slightly compressed, beaked, 15-30

(-40) cm; seeds cylindric to cylindric-oblong, hilum circular, central.

Type species : Sesbania sesban (L.) Merrill

The subgenus Sesbania comprises the main core of the genus and is distributed in the tropics and subtropics of the New and Old World, although much more abundantly in the latter region.

(1) Sesbania sesban (L.) Merrill

PHILLIP. JOURN. SC., BOT. 7 : 235, 1912

syn. : Aeschynomene sesban L.
Sp. Pl. : 714, 1753
Aeschynomene picta Cav.
Ic. 4 : 7, 1797
Coronilla sesban (L.) Willd.
Sp. Pl. 3 : 1147, 1803
Coronilla picta (Cav.) Willd.
Sp. Pl. 3 : 1148, 1803
Sesban aegyptiacus (Willd.) Poir.
Lam., Encycl. 7 : 128, 1806
Sesban pictus (Cav.) Poir.
Lam., Encycl. 7 : 129, 1806
Sesbania aegyptiaca (Willd.) Pers.
Syn. Pl. 2 : 316, 1807
Sesbania picta (Cav.) Pers.
Syn. Pl. 2 : 316, 1807
Emerus sesban (L.) Kuntze
Rev. Gen. : 180, 1891
Sesban sesban (L.) Britton
BROOKLIN BOT. GARD., MEM. 1 : 54, 1918
Sesbania sesban (L.) Fawc. & Rendle
Fl. Jam. 4 : 23, 1920

Woody herb of 1-1.5 m or shrub 2-3 m tall; stem terete sparsely hairy on the younger parts. Leaves 8-15 cm, with 10-20 pairs of leaflets; leaflets linear-oblong, 20-30 x 4-6 mm; petiolules 1.0-1.2 mm; stipules linear-lanceolate, 4-6 mm long, brownish. Racemes 10-17(-20) cm with 3-6(-8) or up to 12 flowers on slender pedicels of 4-8(-12) mm; bracts and bracteoles linear-subulate. Flowers yellow, 12-15(-18) mm; calyx campanulate, 4-5 mm (including the lobes), the lobes 1.0-1.5 x 1.2 mm, broad-triangular; standard orbiculate-rhomboidal, wider than long and with the appendages decurrent but broadened above in the base of the blade and with free obtuse-acute tips, externally dense dotted with dark purple or all purple outside; wing petals oblique-lanceolate 13-15 mm, with a rounded upper basal tooth; keel petals upcurved, oblong, 12-14 mm, the claw 8-10 mm with a linear-triangular tooth lying almost parallel to the claw. Staminal sheath 10-12 mm long. Pod 150-200 x 3.0-4.5 mm, short-beaked, somewhat twisted, more or less torulose. Seeds oblong-cylindric, 15-25(-30) per pod, 3.5-4 x 2.0-2.2 mm, brown. Figure 52.

Type - of *Sesbania sesban* (L.) Merrill subsp. *sesban* var. *sesban* : Egypt, cultivated, HASSELQUIST s/n, date ? (LINN, sheet 922.13, microfiche E!).

- *S. sesban* subsp. *sesban* var. *bicolor* (Wight & Arn.) F. W. Andr. Fl. Pl. Sud *2* : 232, 1952

  syn. : *Sesbania aegyptiaca* var. *bicolor* Wight & Arn. Prodr. Fl. Ind. : 214, 1834

  Type - India, WIGHT 906, date ? (K!)

GILLETT (1963), in his revision of the African species of *Sesbania*, recognised two subspecies of *S. sesban*, *viz.*, subsp. *sesban* with four varieties, and subsp. *punctata* (DC.)Gill. The former subspecies is widespread in the tropics and subtropics of Africa, Asia and part of the New World, while the latter occurs

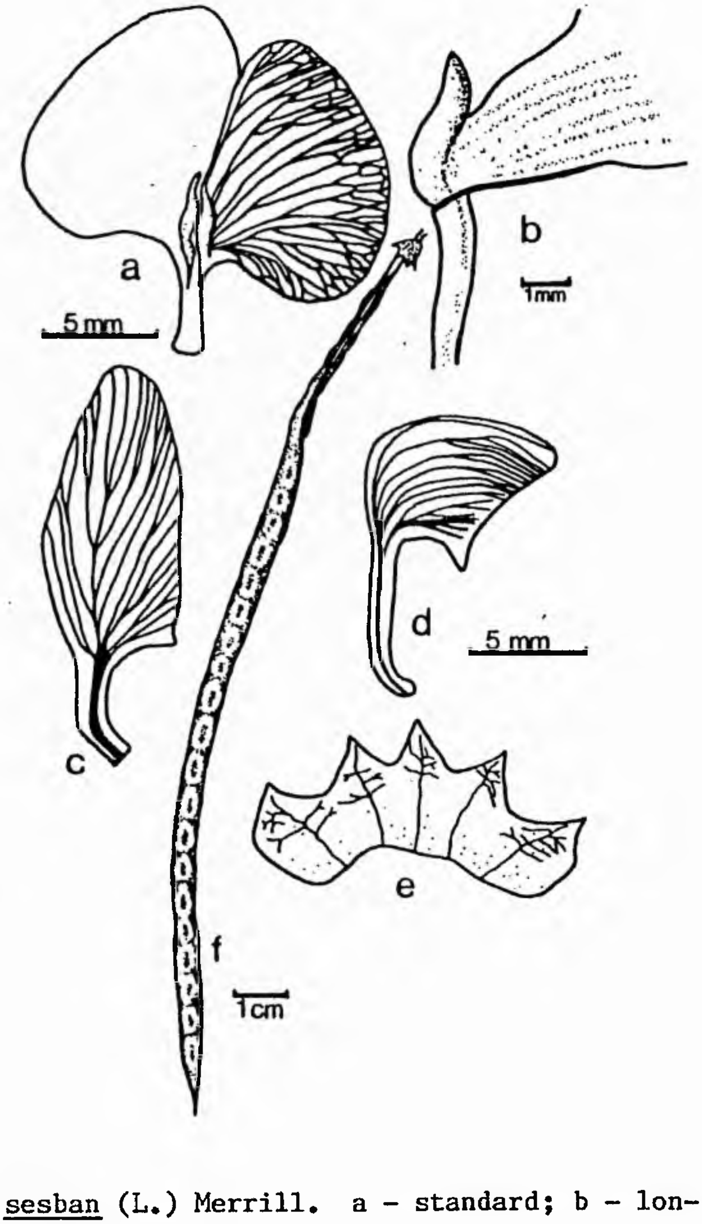


Figure 52 - Sesbania sesban (L.) Merrill. a - standard; b - longitudinal section of standard base showing appendage; c - wing petal; keel petal; e - calyx, flattened out; f - pod.

mainly in west Africa but also in some regions of Central and North-east regions of this continent. They can be differentiated as follows (*apud* GILLETT, *loc. cit.*) :

(1) Filament-sheath 15-24 mm long

Pods with fewer than 30 seeds, the septa 6-8 mm apart, filament-sheath 15-17 mm; inflorescence occasionally branched -- subsp. *punctata*

(2) Filament-sheath 9-13 mm long, inflorescence never branched --- subsp. *sesban*

(3) Standard entirely suffused with purple ----- var. *bicolor*

(3) Standard yellow speckled with purple, or rarely pure yellow

(4) Septa of pod 6-8 mm apart; pod 3-5 mm wide

(5) Plant glabrescent or glabrous -------- var. *sesban*

(5) Stems and leaf-rachises very pubescent -- var. *zambesiaca*

(4) Septa of pod 4-6 mm apart; pod 2-4 mm wide; plant more or less pubescent, at least at leaf bases ---var. *nubica*

All the specimens from the New World which have been seen have unbranched inflorescences, and are therefore referred to subsp. *sesban*. Furthermore, the distinction "externally purple-suffused standard" *versus* "standard yellow-speckled" was easy to apply to herbarium material and it appears that all New World material is referable to var. *bicolor*.

This is supported by the fact that GILLETT (1963) cites only var. bicolor as cultivated in tropical regions outside Africa.

S. sesban is cited in many publications concerning the New World legume flora but very few of them provide a full, detailed description. Therefore, it is difficult to decide which subspecies (and variety) most of these descriptions refer to, unless specimens are cited which can be examined.

Apart from the character of racemes longer than the leaves, another feature which distinguishes S. sesban from the other species of Sesbania subgen. Sesbania in the New World, and which may be useful in the field, is the twisting of the pods. This feature was also noted by BURBIDGE (1965) in the revision of the Australian species of Sesbania but, due to the lack of descriptions in GILLETT's revision of Sesbania in Africa, it is impossible to know whether the pods of var. bicolor are also twisted in that geographical region. A restriction on the use of this character in herbarium studies is that it is not always apparent in pressed specimens.

Distribution (Figures 63, 65)

SOUTH AMERICA

Brazil

North - Amazonas state : lower Rio Purus, Lago de Beruri, PRANCE & PRANCE 14781, 20.ix.1971 (K,NY); Para state : Conceição do Araguaia, FROES 30006, 3.vii.1953 (UB).

North-east - Bahia state : Serra do Jatobá, Milagres, HARLEY et al. 19413, 6.iii.1977 (K,MO); Ceará state : no locality mentioned, ROCHA 13, no date (SP); Fernando de Noronha Territory : no loc.

ment., RIDLEY, LEA & RAMAGE s/n, 21.viii.1887 (BM); Pernambuco state : São João dos Pombos, FALCÃO et al. 1010, 11.ix.1954 (RB); Olinda, PICKEL 654, iii.1924 (SP).

South-east - Rio de Janeiro state : near Rio de Janeiro, GLAZIOU 10505, ix.1879 (K); São Paulo state : São Paulo, Jardim Botânico, CAMARGO 44, vi.1966 (SP); Nova Odessa, Instituto de Zootecnia, GOMES & MANTOVANI 6, 9 and 11, 20.ix.1978 (SP); São José do Barreiro, HOEHNE & GEHRT s/n, 3.v.1926 (SP); São Paulo, cultivated, HANDRO s/n, 10.ii.1936 (SP); ibidem, cultivated, JUNG 26, v.1977 (SP); municipio of Campinas, district of Barão Geraldo, LEITAO FILHO & TARODA 2548, 12.viii.1976 (K,NY,UB); São Paulo, Cidade Universitária, MARTINS 2254, 5.viii.1976 (NY,UEC); Matão, MOURA 101, 18.i.1963 (SP); Nova Odessa, NUNEY s/n, viii.1052 (RB); São Paulo city, cultivated, PICKEL 1316, 10.xi.1945 (MO); ibidem, ibidem, PUTTEMANS s/n, ii.1900 (SP).

West Central - Federal District : Chapada da Contagem, ca. 30 Km NE of Brasília, IRWIN et al. 8466, 19.ix.1965 (K,MO,NY,RB,SP,UB); Brasília, HERINGER 13884, 16.vi.1974 (MO); ibidem, cerrados near Universidade de Brasília, ONISHI & FONSECA 35, 24.ix.1970 (NY); Mato Grosso do Sul state : municipio of Corumbá, Fazenda Marilândia, PEREIRA et al. 287, 8.x.1953 (RB).

Colombia - Province of Córdoba : Aguas Negras, 12 km NE of Montería, ANDERSON 1910, 2.i.1970 (K).

French Guyana - Kourou, BENOIST 1340, 6.vii.1914 (P); no loc. ment., RICHARD s/n, no date (P).

Guyana - Georgetown, PARKER s/n, no date (K).

Paraguay - Terere River, HASSLER 2528, date ? (G); "Paraguaria

Septentrionalis", HASSLER 7219, 1901/2 (BM); upper regions of River Apa, HASSLER 7719, xi.1901/2 (G,K,MO,NY,P).

<u>Peru</u> - Departamento of Loreto : Pucallpa, on Rio Ucayali, FOSBERG 28955, 2.xi.1947 (NY).

<u>Surinam</u> - no loc. ment., KOSTMANN 670a, no date (MO); Wiawia Reserve at the coast, ca. 2 km S of camp, 3 km E of Motcreek, STERRINGA 12498, 20.iii.1969 (NY); no loc. ment., SULLIVANT s/n, no date (NY); no loc. ment., collector ? 1263, no date (E).

<u>WEST INDIES</u>

<u>Bahamas</u> - Great Inagua : Matthew Town, NASH & TAYLOR 1466, 6.xi.1904 (NY).

<u>Bonaire</u> - no loc. ment., ARNOLDO 2292, xii.1962 (NY).

<u>Cuba</u> - Bayamo, CONSTANTE s/n, iii.1922 (NY); prov. of Oriente, EKMAN 7522, 22.viii.1916 (NY); La Prenda, HIORAM & MAUREL 6054, vi.1922 (NY); Santa Clara, LUNA 595, v.1920 (NY); no loc. ment., WRIGHT s/n, no date (NY).

<u>Guadeloupe</u> - no loc. ment., DUSS 4140, 15.iv.1903 (NY).

<u>Jamaica</u> - Hope Gardens, HARRIS 8617, 11.i.1904 (NY); Westmoreland, besides pond ca. 0.7 mi. N.N.W. of Locust Tree, PROCTOR 26788, 9.i.1966 (LL).

<u>Martinique</u> - no loc. ment., BELANGER 857, 1860 (P).

<u>Puerto Rico</u> - Trujillo Plant Station, BRITTON & BRITTON 9165, 22.i.1929 (NY); Mayaguez, HESS 2013, 16.V.1913 (NY).

<u>St Kitt's</u> - Basseteme, Botanic Station, BRITTON & COWELL 352, 8.ix-5.x.1901 (NY).

<u>St Thomas</u> - La Grange's Howe, BORGSEN s/n, 1905-6 (P).

(2) . *Sesbania emerus* (Aubl.) Urb.

REPERT. Sp. NOV. *16* : 149, 1919

syn. : *Aeschynomene emerus* Aubl.
Pl. Guian. : 775, Tabl. Noms 1, 1775
Emerus siliquis longissimis et angustissimis Plumier
Pl. Am., Cat. Amer. : 19, 1703; Pl. Am. fasc. 5 :
115, pl. 125 fig. 1 (ed. Burman), 1757
Emerus caule erecto, ... Mill. (polynom.)
Gard. Dict. : 67, 1759 (7th ed.)
Emerus herbacea ... Mill. (polynom.)
Gard. Dict. : 67, 1768 (8th ed.)
Coronilla occidentalis Willd.
Sp. Pl. *3* : 1147, 1803
Sesban occidentalis (Willd.) Poir.
Lam. Encycl. *7* : 129, 1806
Sesbania occidentalis (Willd) Pers.
Syn. Pl. *2* : 316, 1807
Sesbania macrocarpa Muhl.
Cat. : 65, 1813 , *nom. nud.*
Darwinia exaltata Raf.
Fl. Ludov. : 106, 1817, *nom. nud.*
Sesbania cassioides Don
Gen. Hist. *2* : 240, 1832
Sesbania peruviana Don
Gen. Hist. *2* : 240, 1832
Sesbania macrocarpa var. *picta* S. Watson
PROC. AM. ACAD. *24* : 46, 1889
not *Sesban pictus* Poir. nor *Sesbania picta* Pers.
Emerus sesban occidentalis Kuntze
Rev. Gen. Pl. : 181, 1891
Sesban emerus (Aubl.) Urban *ex* Britton & Willson,
orth. var., SCI. SURV. PORTO RICO *5* : 395, 1924
Sesban exaltatus (Raf.) Rydb.
NORTH AM. FLORA *24* : 204, 1924
Sesban sonorae Rydb.
NORTH AM. FLORA *24* : 205, 1924
Sesbania exaltata (Raf.) Rydb. *ex* A. W. Hill
Ind. Kew. *7* : 223, 1929
Sesbania exaltata (Raf.) Cory
RHODORA *38* : 404-408, 1936

Erect herb or shrub up to 2 m tall. Leaves 15-25(-30) cm, narrow, with (20-)35-50(-60) pairs of leaflets; leaflets narrowly-oblong, rounded at both ends, mucronate at the apex, 25 x 3 mm; petiolules 1-1.2 mm; rachis 20-30 cm; stipules linear to narrow-lanceolate, acuminate, 4-5(-10) mm, brownish, deciduous. Racemes 2-8 cm with (1-)2-5 flowers on slender pedicels of 5-15 mm; bracts and bractlets linear. Flowers yellow, 15-20(-25) mm; calyx campanulate, 4.5-5.5 mm (including the lobes), the lobes 1.0-1.5 x 0.3 mm, triangular with acuminate tips; standard suborbicular with raised appendages at the base of the blade, yellowish, streaked and mottled with purple externally; wing and keel petals with an upper basal triangular, acuminate tooth; wing petals oblong, up to 15 mm; keel petals upcurved, the blade oblong and almost of the same length of claw. Staminal sheath 9-12 mm. Pod 100-250(-300) x 3.5 mm, beaked, stipitate, the margins slightly thickened, glabrous, usually constricted between the seeds when young. Seeds oblong, 25-40(-50) per pod, 3-4 x 2-2.5 mm brown and sometimes mottled with black. Figure 53.

Type : Plate 125, fig. 1, PLUMIER, Pl. Amer., fasc. 5 (ed.Burman), 1757; Nov. Pl. Am., Cat. Amer. : 19, 1703.

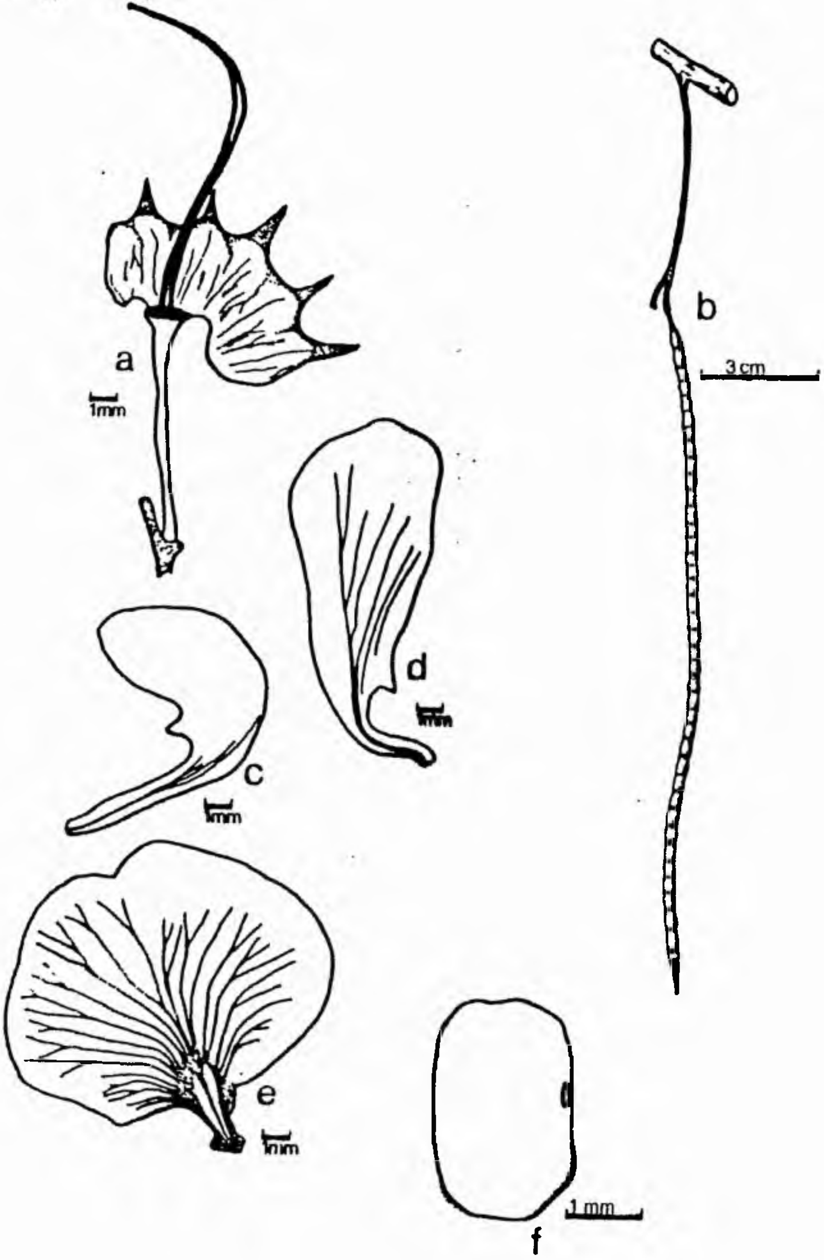


Figure 53 - Sesbania emerus (Aubl.) Urban. a - calyx (open) and ovary; b - pod; c - keel petal; d - wing petal; e - standard; f - seed.

According to STAFLEU (1967) there are no type specimens for PLUMIER's (1703) American plants, except for those collected by Surian, who accompanied PLUMIER to the West Indies in 1689-1690. The Surian herbarium was consulted in Paris (P) and no specimen was found for Emerus siliquis longissimis et angustissimis. However, the illustrations provided by PLUMIER (1703, 1757) can be considered as the types of his New World taxa (STAFLEU, 1967) and this interpretation has been fully accepted by several taxonomists, including for problems related to typification of taxa in the Leguminosae (POLHILL & STEARN, 1976).

PLUMIER's drawing for S. emerus was first published in his "Catalogus Plantarum Americanarum" (Figure 54) and then, later, when BURMAN edited a new version of PLUMIER's illustrations in "Plantarum Americanarum" (Figure 55).

In the BURMAN edition the drawing of S. emerus was accompanied by an illustration of an Equisetum species, two plants obviously bearing no relationship whatsoever to each other (Figure 55). Some other modifications to the original version were done for the later edition and these changes in general represent improvements of the original illustration. The drawing shows a branch of a plant with compound paripinnate leves and opposite leaflets. In the first edition (Figure 54) the leaflets were drawn with acute to acuminate base and apex, but in the later version they appeared rounded at both ends. A separate flower was originally drawn with a dotted vexillum only but subsequently the wing petals were also depicted with black dots on them (Figure 54, 55). No Sesbania species is known to have such ornamentations on the wing petals.

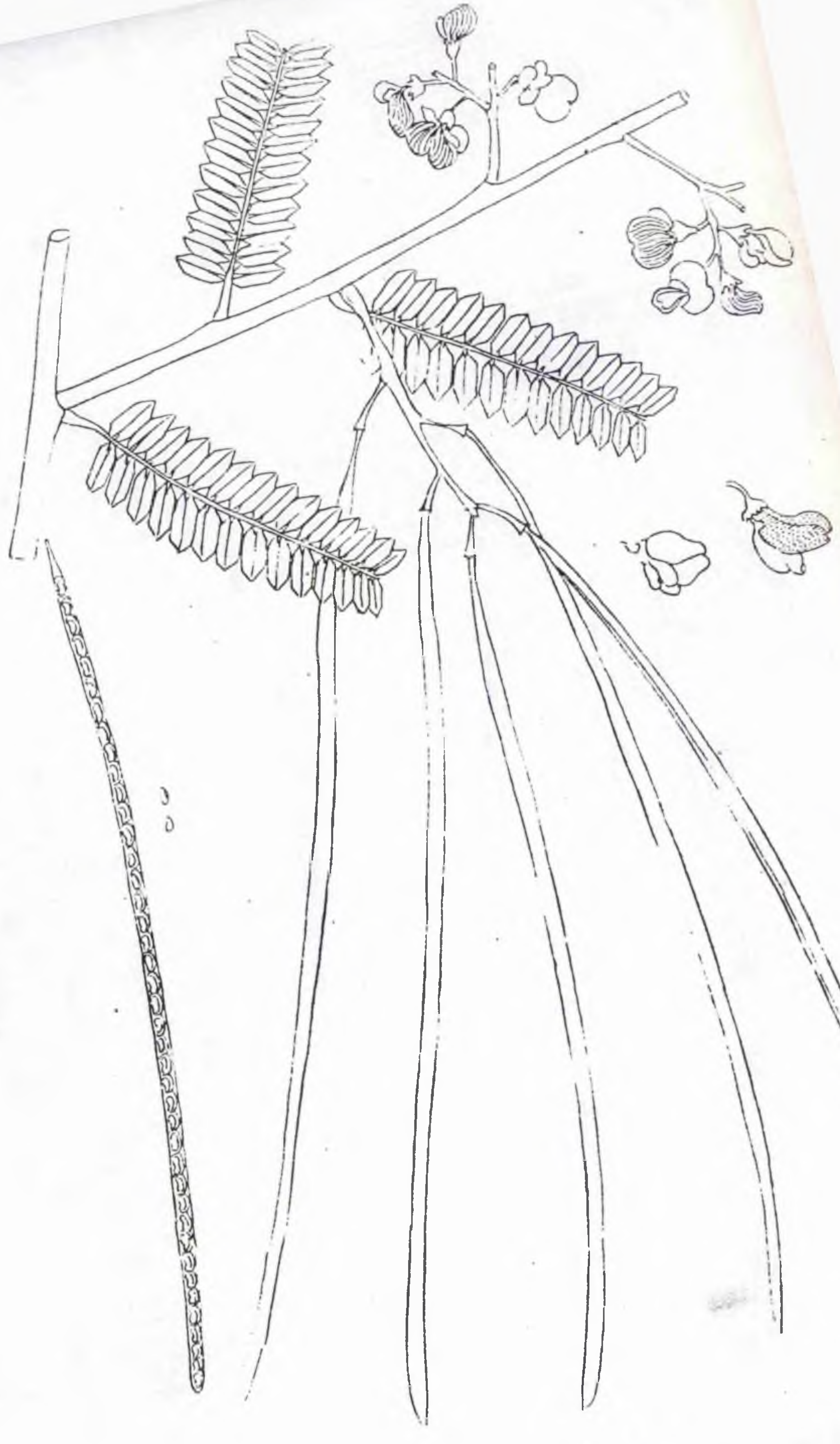
The inflorescences in both drawings are axillary, a feature which makes certain that this plant is a Sesbania species, although not many details of petal shape can be seen (Figures 54, 55).

The pods, however, are very similar in shape to those of specimens of S. emerus which have been studied and they are depicted in correct proportional size to the leaves and flowers (Figures 53, 54, 55).

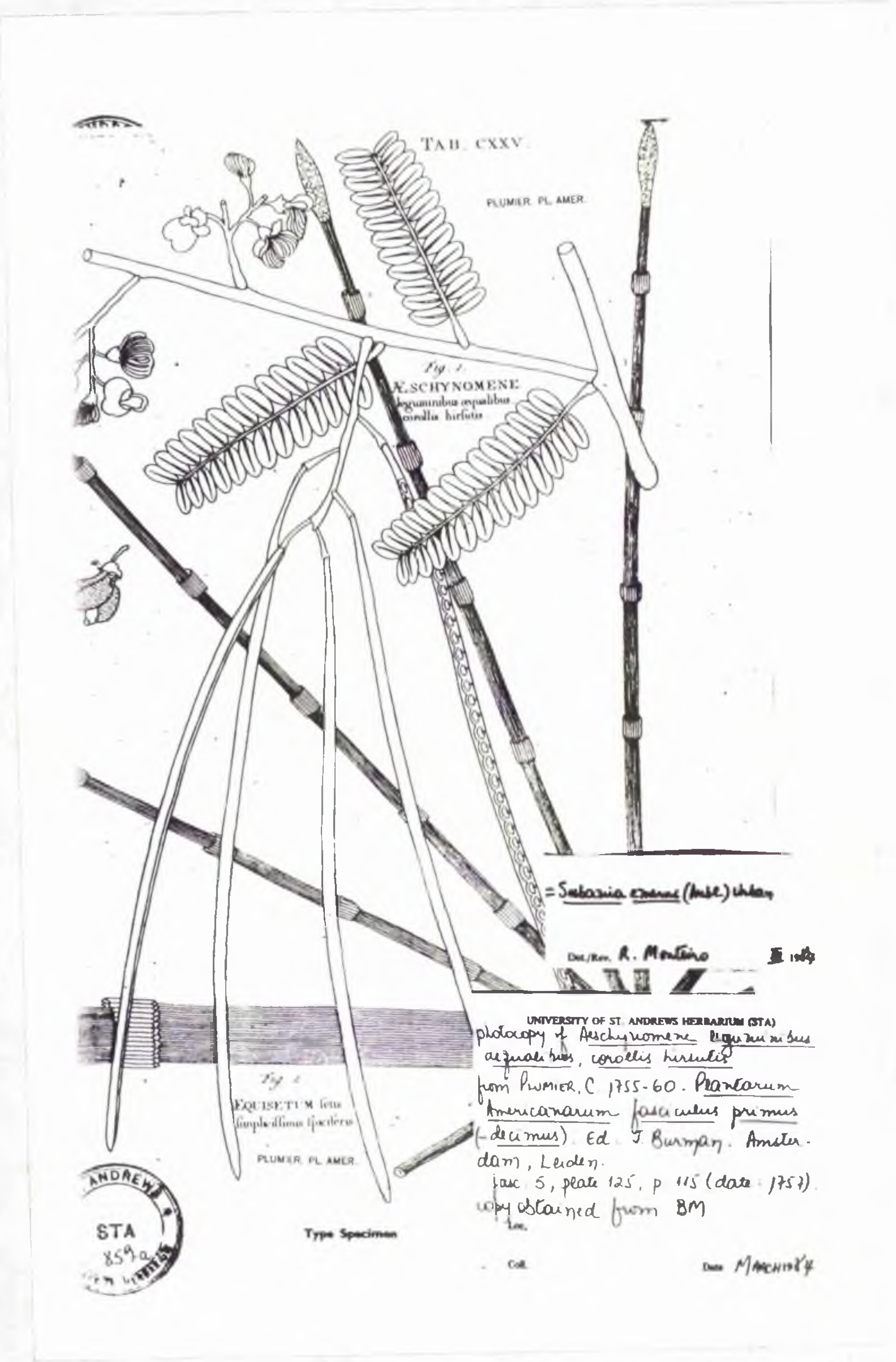
As a whole the drawings obviously lack details which one would wish for a certain identity with Sesbania emerus. However, further support for this interpretation is given by MILLER (1759) when he described "Emerus herbacea...".

In the seventh and eighth editions of his "Gardener's Dictionary", MILLER (1759, 1768) gave the information that the plant which PLUMIER (1703) referred to the name "Emerus siliquis..." was found by the latter in the "French settlements" of the West Indies and then subsequently seen and collected abundantly in Vera Cruz, Mexico, by HOUSTON, who travelled with the South Sea Company to Central America and the West Indies between 1729 and 1733. MILLER (loc. cit.) mentioned that HOUSTON had collected seeds from these specimens, which were sown in England and succeeded to produce plants that MILLER later described as "Emerus caule erecto..." (MILLER, 1759) and as "Emerus herbacea..." (MILLER, 1768). The type of these polynomials is at BM and certainly is a typical specimen of S. emerus Therefore, this confirms the identity of the plants seen by PLUMIER (1703).

Figure 54 - Illustration of "Emerus siliquis ..." given by PLUMIER (1703) in "Nova Plantarum Americanarum". Photocopy supplied by the Department of Botany of University of Oxford, England (x 0.71).



ſiliquis longiſsimis & anguſtiſsimis Cat.19.



= Sesbania emerus (Aubl.) Urban

Det./Rev. R. Monteiro III 1984

UNIVERSITY OF ST. ANDREWS HERBARIUM (STA)
photocopy of Aeschynomene leguminibus
aequalibus, corollis hirsutis
from PLUMIER, C. 1755-60. Plantarum
Americanarum fasciculus primus
(-decimus). Ed. J. Burman. Amster-
dam, Leiden.
fasc. 5, plate 125, p. 115 (date: 1757).
copy obtained from BM
Loc.

Coll.
Date MARCH 1984

Figure 55 - Illustration of "Emerus siliquis ..." given by PLUMIER (1757, ed. BURMAN) in "Plantarum Americanarum", fasc. 5, plate 125. Photograph of a photocopy supplied by the Department of Botany of Oxford University of Oxford, England.

The first binomial to be applied to PLUMIER's taxon was Aeschynomene emerus which was published by AUBLET (1775). Subsequently, three names were launched by other authors, all of them bearing relationships with the early name "Emerus siliquis..." Coronilla occidentalis Willd. was the first, followed by Sesban occidentalis Poir., and then Sesbania occidentalis Pers. The epithet published by AUBLET (1775) did not appear in these works in which the above names were listed.

The next name apllied for this species was Sesbania macrocarpa Muhl. In his "Catalogus..." MUHLENBERG (1813) published many new names without descriptions, mostly as nomina nuda, although MERRILL & HU (1949) have argued that some of these names were actually validated by the citation of synonyms. One of such nomina nuda is Sesbania macrocarpa, which was cited by the "Index Kewensis" as published (or validated) after RAFINESQUE. This interpretation was corrected by MERRILL & HU (loc. cit.) in listing the invalid names published by MUHLENBERG (1813).

On the other hand, RAFINESQUE (1817) included S. macrocarpa Muhl. as a synonym of Darwinia exaltata Raf., Darwinia being a generic name which is superfluous for Sesbania. According to RAFINESQUE (loc. cit.), the names of the species published in "Florula Ludoviciana" were based on the short descriptions given by ROBIN (1807) in "Voyage dans l'interieur de la Louisiane" and also on the actual specimens collected by ROBIN. However, no herbarium and types of ROBIN are known to exist (STAFLEU, 1967) and the extant specimens of Rafinesque's herbarium do not include a type for D. exaltata; therefore, Darwinia exaltata is also a nomen nudum, a situation already studied by MERRILL (1949).

In 1919, URBAN, who had the opportuniy to revise PLUMIER's and other botanists' types of plants from the West Indies, gave an extensive discussion and provided modern nomenclature for the taxa of this area. In "Sertum Antillanum IX", URBAN (loc. cit.) made the combination Sesbania emerus (Aubl.) Urban, therefore correcting the species name. The PLUMIER drawing was cited at the end of a short list of synonyms which consisted of C. occidentalis Willd. and S. occidentalis Pers.

Unfortunately, some of the specimens cited by URBAN (1919) do not belong to Sesbania emerus but to S. exasperata H.B.K. These specimens are RUGEL 229 (Cuba) and SINTENIS 102 and 3802 (Porto Rico). Other exsiccatae listed by URBAN could not be traced in the specimens on loan.

The name Sesban was applied again by BRITTON & WILLSON (1924) and RYDBERG (1924) for other S. emerus synonyms but these have no validity since they are based on a rejected generic name and also because they were derived from a nomen nudum. Again, the same reasons apply to S. exaltata (Raf.) Rydb. ex A.W. Hill and S. exaltata (Raf.) Cory.

However, one binomial, S. sonorae Rydb. deserves further comments at this point. RYDBERG (1924) recognised three different species in North America, following the complex of names for S. emerus : Sesban emerus (Aubl.) Britton & Willson; S. exaltatus (Raf.) Rydb., and S. sonorae Rydb.

These taxa were separated as follows (RYDBERG, 1924) :

Corolla 15-20 mm long; plant shrubby at the base ——— *S. emerus*
Corolla 15 mm long or less; plant herbaceous, annual
  Leaflets 30-70; pod 30-40 seeded; calyx lobes with subulate tips ——————————————————— *S. exaltatus*
  Leaflets 16-30; pod 15-30 seeded; calyx lobes short-acuminate ——————————————————— *S. sonorae*

Under *S. emerus*, a species from southeastern U.S.A. (Florida), Mexico (Vera Cruz, Morelos), Central America (Guatemala, Panama) and West Indies, RYDBERG (1924) listed as synonyms the nomenclatural complex *C. occidentalis* Wiild., *Sesban occidentalis* Poir. and *S. occidentalis* Pers., and had doubts as to whether or not *S. macrocarpa* Muhl., as described by ELLIOTT (1823) in "A skecth of the botany of South Carolina and Georgia", should also be considered as another synonym.

The specimen seen and annotated by ELLIOTT (*loc. cit.*) is at the Charleston Museum Herbarium (CHARL), from where a phototype of it was obtained. The specimen, although slightly damaged, can be recognised as *S. emerus*. Therefore, there is no doubt that ELLIOTT (1823) dealt with the same taxon as AUBLET (1775) and other authors.

For *S. exaltatus* (Raf.) Rydb., RYDBERG (1924) regarded as synonyms the binomials *Darwinia exaltata* Raf. and, again, *S. macrocarpa* Muhl. (both *nomina nuda*). The same author mentioned *S. exaltatus* as occurring in the United States, from Missouri to Louisiana and Texas.

Finally, for *S. sonorae* Rydb., which was said to occur in western U.S.A. (Arizona and southern California) and northern Mexico (states of Sonora, Sinaloa and Baja California), the species names *S. macrocarpa* Muhl. var. *picta* S. Wats. and *Sesban macrocarpa* Standley were listed as synonyms. These latter binomials were all based on the earlier *nomen nudum S. macrocarpa* published by MUHLENBERG (1813).

Therefore, it is clear that RYDBERG (1924), although apparently aware of the many nomenclatural problems involved in the complex of *S. emerus* and other segregate species, as reflected by the repeated citations of synonyms based on the same original types, also worked with very narrow concepts of species limits and used small differences in some characters to treat different populations of the same taxon as distinct species (*S. emerus*, *S. exaltatus* and *S. sonorae*).

However, it is observable from RYDBERG's (1924) key and descriptions that the differences between these species were only in degree of measurements (corolla length), number of leaflets and seeds, rather minute changes of calyx lobe shapes, and in their distributions. The interspecific differences are not of the same magnitude as the significant modifications applied as the diagnostic characters for the identification of the other species in the present work, therefore making it difficult to recognise the limits of each taxon involved in this species complex.

It must be emphasized at this point that, as shown by the descriptions provided by RYDBERG (1924), differences in petal shape of "*S. emerus*, *S. exaltatus* and *S. sonorae* " were not diagnostic for any of these taxa. In fact, the dissections of flowers from the specimens available for the present study showed a remarkable uniformity of petal shape, regardless of their geographical origin.

Therefore, because of this regional treatment imposed by RYDBERG (1924), based on degree of numerically measurable characters, an extensive numerical analysis of S. emerus was undertaken by means of a study of 116 herbarium specimens which were blocked in the geographical areas listed in Table 19.

The method consisted in obtaining a matrix of numerical data derived from (a) measurements for 22 characters listed in Table 20, which (b) were treated as the ratios listed in Table 21 so as to create the data matrix of Table 22. From this matrix the ratios were plotted by means of the STATPACK graphic program available for microcomputers to give the series of scatter diagrams illustrated in Figures 56 - 59. In these scatter diagrams each point represents a mean value for the parameters concerned for the group of specimens available form the various geographical areas listed in Table 19. Numbers beside each point are those which refer to areas in Table 19.

Thus, for example, the geographical areas from which the specimens of "S. sonorae Rydb." come from are numbered 1,2 and 4, i.e., south-western U.S.A. (states of Arizona and New Mexico), Mexico (states of Baja California, Sinaloa and Sonora), and the state of California, respectively. Also of interest for this discussion is area 10, viz., South America. The other areas can be located with the use of Table 19 and Figure 1 (section "Material and Methods").

Table 19 - Number of specimens per area studied in the numerical analysis of <u>Sesbania emerus</u> (Aubl.) Urban.

AREA		
Number	Locality *	Number of specimens
1	U.S.A., Southwest	4
2	Mexico	24
3	Caribbean and West Indies	4
4	U.S.A., California	6
5	U.S.A., South Plains	22
6	U.S.A., North Central	6
7	U.S.A., Central Plains	2
8	Central America **	20
9	U.S.A., Southeast	24
10	South America	4

Notes :

* The location of the areas in North America is based on SHETLER & SKOG (1978) (see also Figure 1, section "Material and Methods)

** Excluding Mexico

Table 20 - List of characters used in the numerical analysis of *Sesbania emerus* (Aubl.) Urban.

Stem diameter (mm)

Internode length (cm)

Leaf length (cm)

Pairs of leaflets per leaf

Leaflet length (mm)

Leaflet width (mm)

Petiolule length (mm)

Mucron length (mm)

Inflorescence length (cm)

Flowers per inflorescence

Peduncle length (mm)

Interpedicel length (mm)

Pedicel length (mm)

Bract length (mm)

Flower length (cm)

Calyx length (mm)

Calyx lobe length (mm)

Calyx lobe width (mm)

Pod length (cm)

Pod width (cm)

Seed length (mm)

Seed width (mm)

Table 21 - List of ratios used in the numerical analysis of *Sesbania emerus* (Aubl.) Urban, based on the measurements of Table 20.

Ratio 1 = leaf length/internode length
Ratio 2 = leaflet length/leaflet width
Ratio 3 = leaf length/petiolule length
Ratio 4 = leaflet length/mucron length
Ratio 5 = petiolule length/mucron length
Ratio 6 = inflorescence length/peduncle length
Ratio 7 = peduncle length/pedicel length
Ratio 8 = peduncle length/corolla length
Ratio 9 = internode length/interpedicel length
Ratio 10 = corolla length/calyx length
Ratio 11 = lobe length/lobe width
Ratio 12 = pod length/pod width
Ratio 13 = seed length/seed width
Ratio 14 = no. seeds per pod/no. leaflets per leaf

Table 22 - Set of data used in the numerical analysis of *Sesbania emerus*, according to its distribution (areas of Table 19).
R = ratios of Table 21; SD = standard deviation.

	RATIOS													
Area	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12	R13	R14
1	1.7	5.1	20.0	62.5	3.2	15.3	3.6	6.9	2.5	2.3	2.1	65.3	1.9	1.5
2	3.1	4.3	19.8	53.4	2.8	3.5	2.8	1.5	5.9	2.3	1.9	55.3	1.5	1.2
3	3.3	5.8	27.3	58.6	2.2	4.0	2.6	1.5	8.2	2.1	1.2	69.7	1.7	1.2
4	3.3	5.5	20.3	78.8	3.4	2.2	5.8	3.2	4.0	2.2	1.6	77.6	1.8	1.2
5	3.5	5.5	24.2	72.6	2.4	2.7	4.8	2.6	4.3	2.2	1.6	55.6	1.7	1.5
6	3.6	5.3	35.7	72.2	2.3	2.2	2.9	1.6	4.4	2.1	1.8	43.6	2.0	1.3
7	4.2	5.7	19.1	61.7	3.3	2.4	3.3	2.0	2.9	2.7	1.5	60.1	1.7	1.3
8	4.3	5.7	17.1	58.4	3.1	2.9	2.1	1.5	8.3	1.9	1.5	55.7	1.5	1.4
9	4.4	5.7	21.6	58.8	2.7	2.7	3.9	1.9	4.6	2.5	1.3	53.8	1.5	1.2
10	6.1	5.0	18.4	73.3	4.0	3.2	2.1	1.0	7.4	2.0	2.0	75.9	1.6	1.6
Min.	1.7	4.3	17.0	53.4	2.2	2.2	2.1	1.0	2.5	1.9	1.2	43.6	1.5	1.2
Max.	6.1	5.8	35.7	78.8	4.0	15.3	5.8	6.9	8.3	2.7	2.1	77.6	2.0	1.6
Mean	3.8	5.4	22.4	65.3	2.9	4.1	3.4	2.4	5.3	2.2	1.7	61.3	1.7	1.3
SD	1.1	0.5	5.5	8.5	0.6	3.9	1.2	1.7	2.1	0.2	0.3	10.7	0.2	0.2

Some caution is necessary with the interpretation of the results from this numerical analysis because of the uneven sampling of the specimens in the different areas (Table 19). However, these specimens represent all the suitable material of this species complex available for the present study.

It can be seen clearly that the specimens of areas 1 (SW U.S.A.), 2 (Northern Mexico), 4 (California) and 10 (South America) are isolated in some of the graphical plottings of the parameter ratios of Table 20 (for example, Figures 56 A–C; 57 A,C; and 58 A). However, these geographical species clusters (areas 1, 2, 4 and 10) are not consistently isolated in all scatter diagrams but rather they separate in different plottings.

The areas represented by numbers 1, 2 and 4 (southwestern U.S.A., Mexico and California) include all the specimens which were treated by RYDBERG (1924) as S. sonorae. It can be seen that whilst some scatter-plots (Figures 56 A,B; 57 A) show a separation of plants from areas 1 and 2, those from area 4 (California) are not equally segregated. It is also important to note that the characters used in these plots (Figures 56 and 57, ratios 1,2,6) are not in fact those employed by RYDBERG (loc. cit.) to distinguish between S. sonorae and S. exaltatus and S. emerus. When characters which were used by RYDBERG (ratios 8,10,11,12,13 and 14, Table 20) are plotted, as in Figures 56 C, 58 A–C, and 59 A–B, taxa represented by areas 1 and 2 are not segregated from the remaining populations.

Another peculiarity observed in these results is that the specimens from the north and NW Mexico (represented by area 2 in this study) are more often plotted together with specimens of

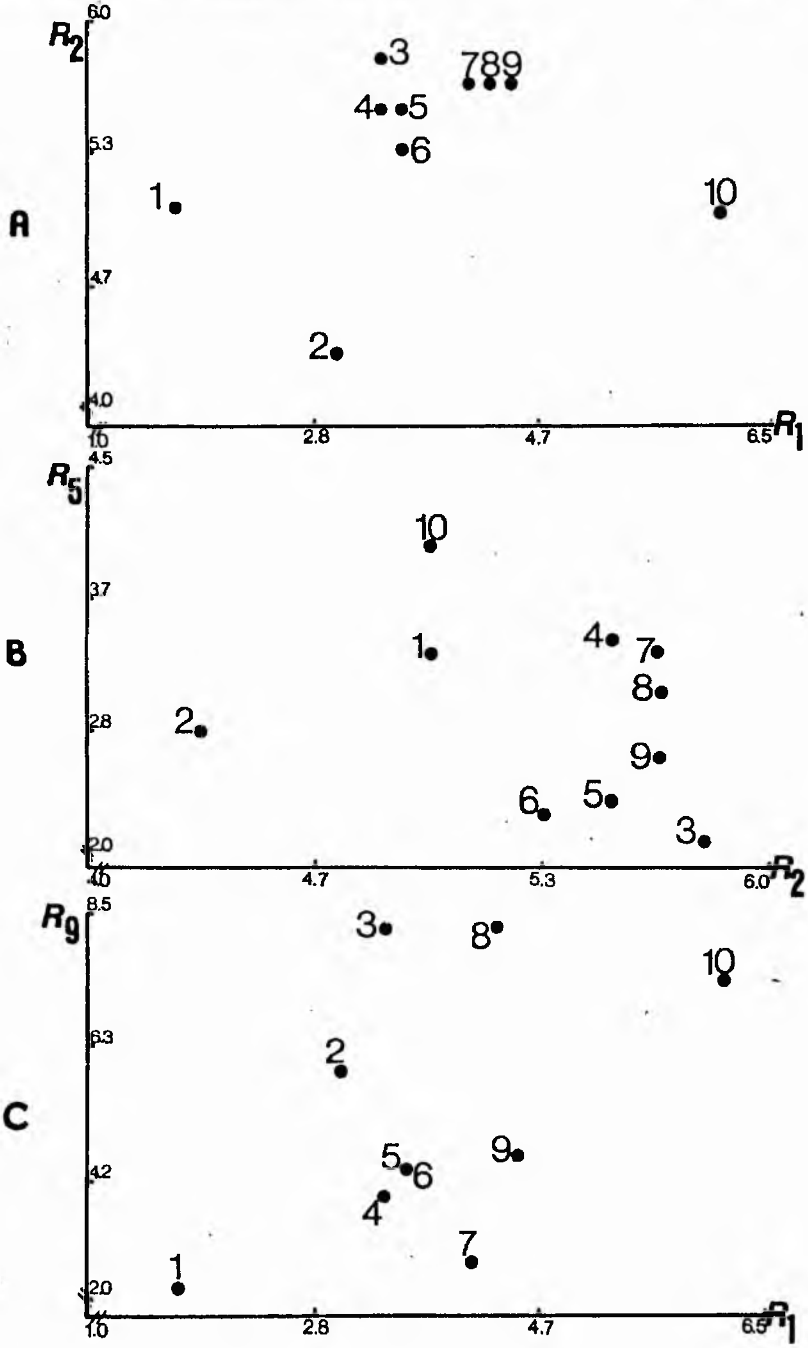


Figure 56 - Scatter diagrams of the data in Table 22, for S. emerus. The values of axes x and y are the values of the ratios of Table 21 and the number besides each plot represents the areas in Table 19.

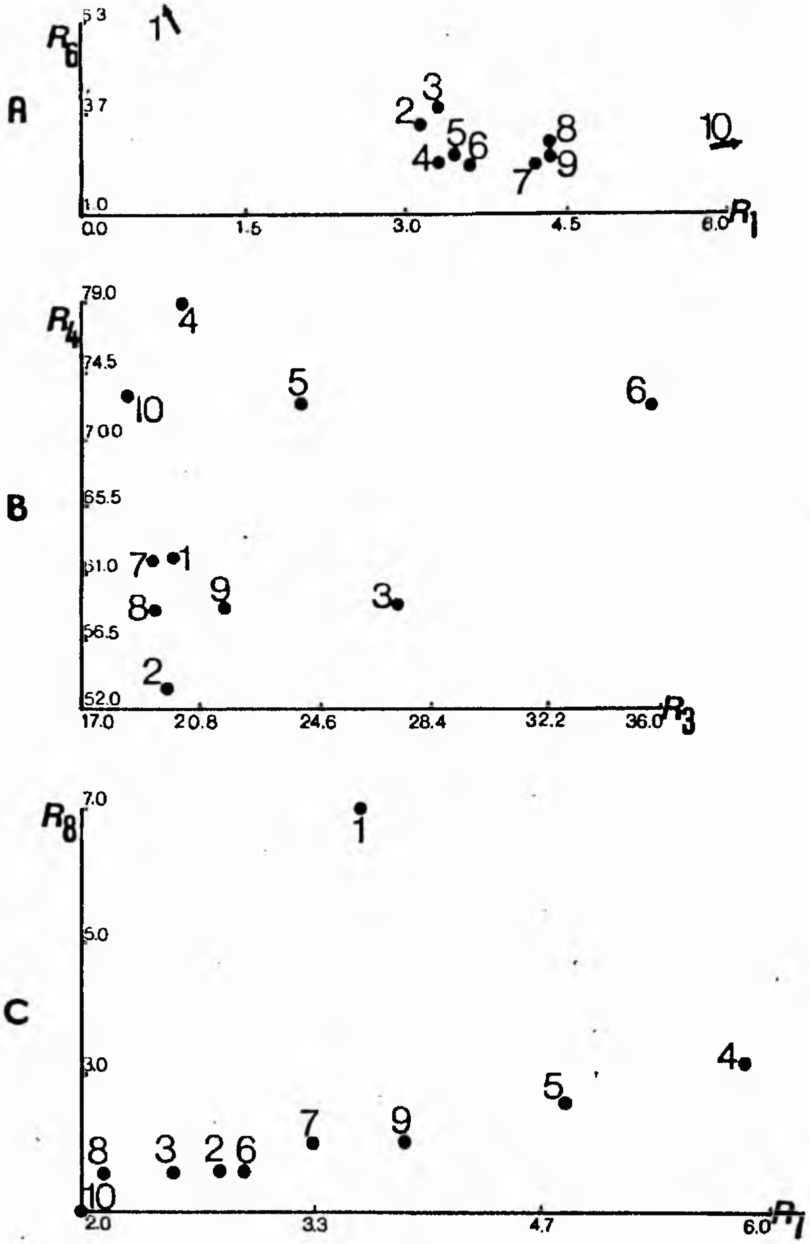


Figure 57 - Scatter diagrams of the data in Table 22, for S. emerus. The values of axes x and y are the values of the ratios of Table 21 and the number besides each plot represents the areas in Table 19.

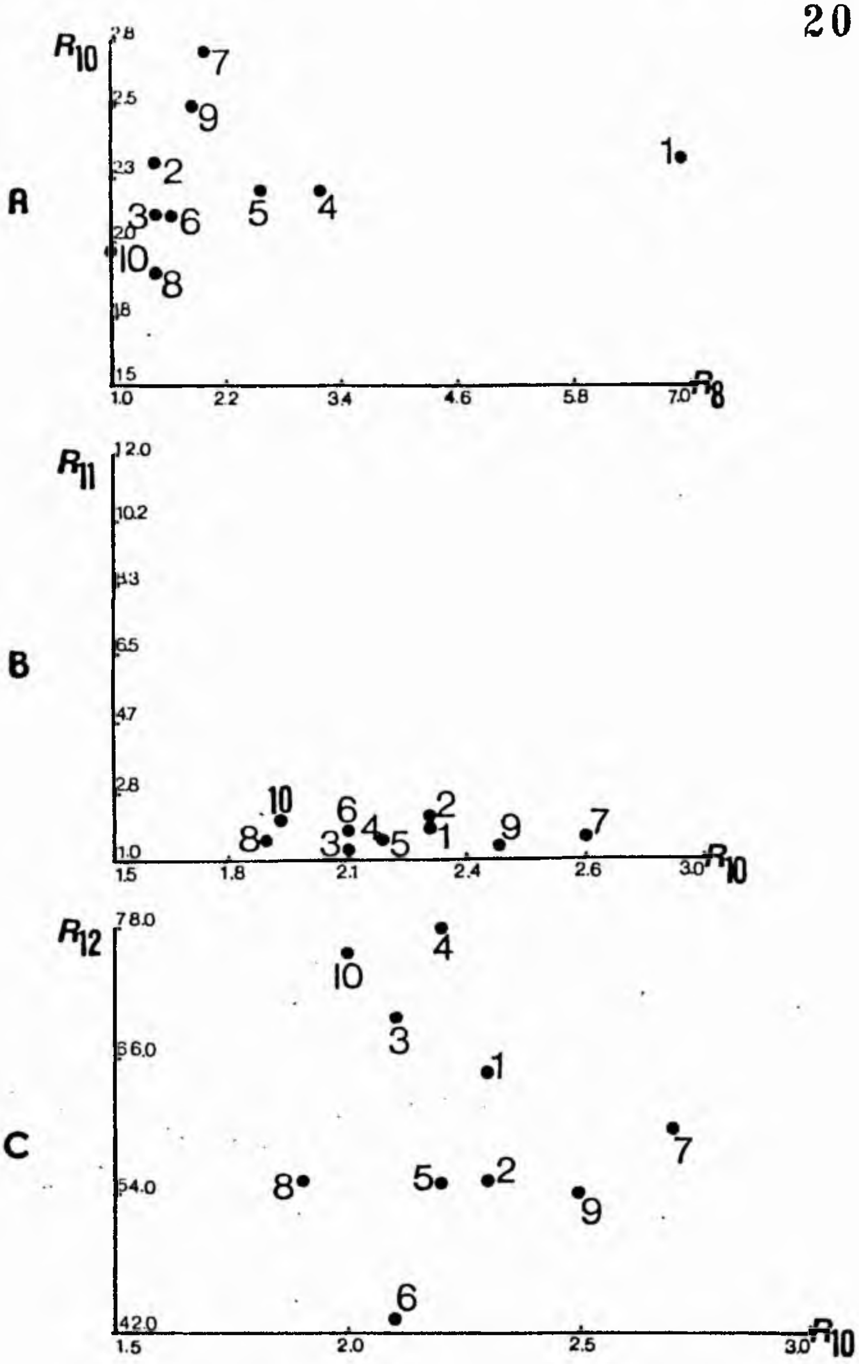


Figure 58 - Scatter diagrams of the data in Table 22, for S. emerus. The values of axes x and y are the values of the ratios of Table 21 and the number besides each plot represents the areas in Table 19.

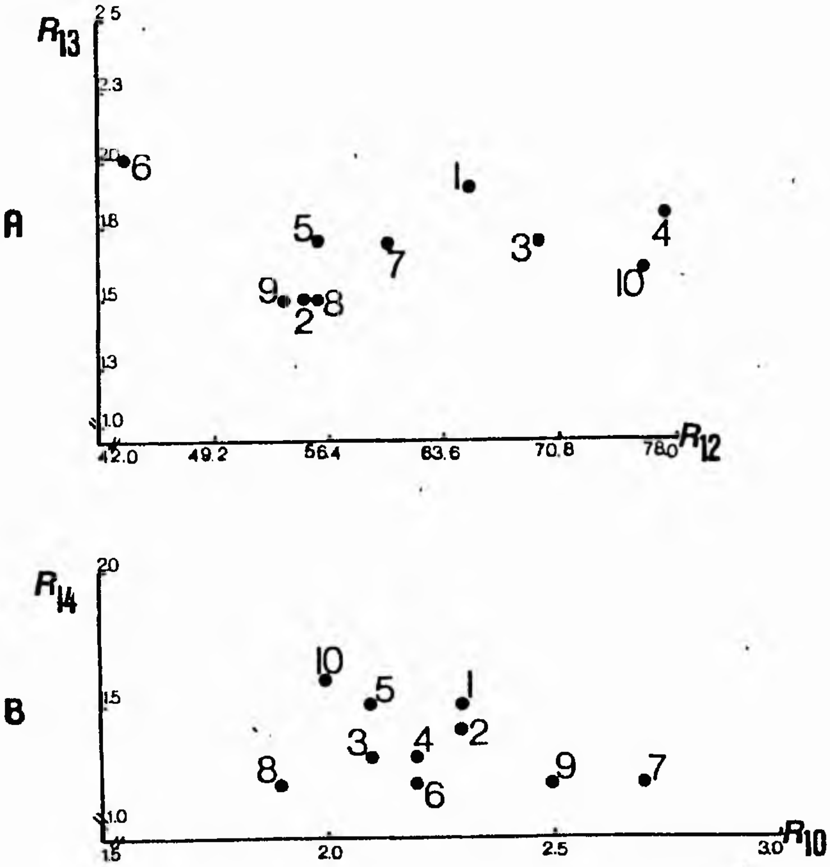


Figure 59 - Scatter diagrams of the data in Table 22, for S. emerus. The values of axes x and y are the values of the ratios of Table 21 and the number besides each plot represents the areas in Table 19.

other areas than those of the neighbouring area 1. This raises the possibility that the plants from the latter area, i.e., southwestern U.S.A., including also specimens of area 4 (California), perhaps represent populations of S. emerus which may be under environmental stress at the northern limit for S. emerus, and as consequence they differ from the more characteristic facies of this species found in populations from the Gulf of Mexico states and southeastern U.S.A.

The stress may well be exerted by the change in environment in this area imposed by the dry areas of the Sonora and Mohave deserts (Figure 60). Indeed, this region is the zone which the natural geographical, climatic and edaphic barriers limit the distribution of a number of genera in the state of California, as discussed by RAVEN & AXELROD (1978). These authors considered that the expansion and consequently a further enrichment of the "California floristic province" flora were limited by the climatic conditions of mountains and deserts to the east and south of the province (RAVEN & AXELROD, loc. cit.). The dry areas to the south are represented by the Mohave and and Sonora deserts. In California, the latter area is represented by its northern portion here called "Colorado desert" (Figure 60 B, RAVEN & AXELROD, loc. cit.).

Interestingly, the Mohave and Sonora (=Colorado) deserts have distinct climatic conditions : the Mohave is characterised by rains and low temperatures during the winter, while the Sonora (=Colorado) has summer rains and warmer temperatures (RAVEN & AXELROD, 1972; SOLBRIG, 1972). These conditions restrict many taxa

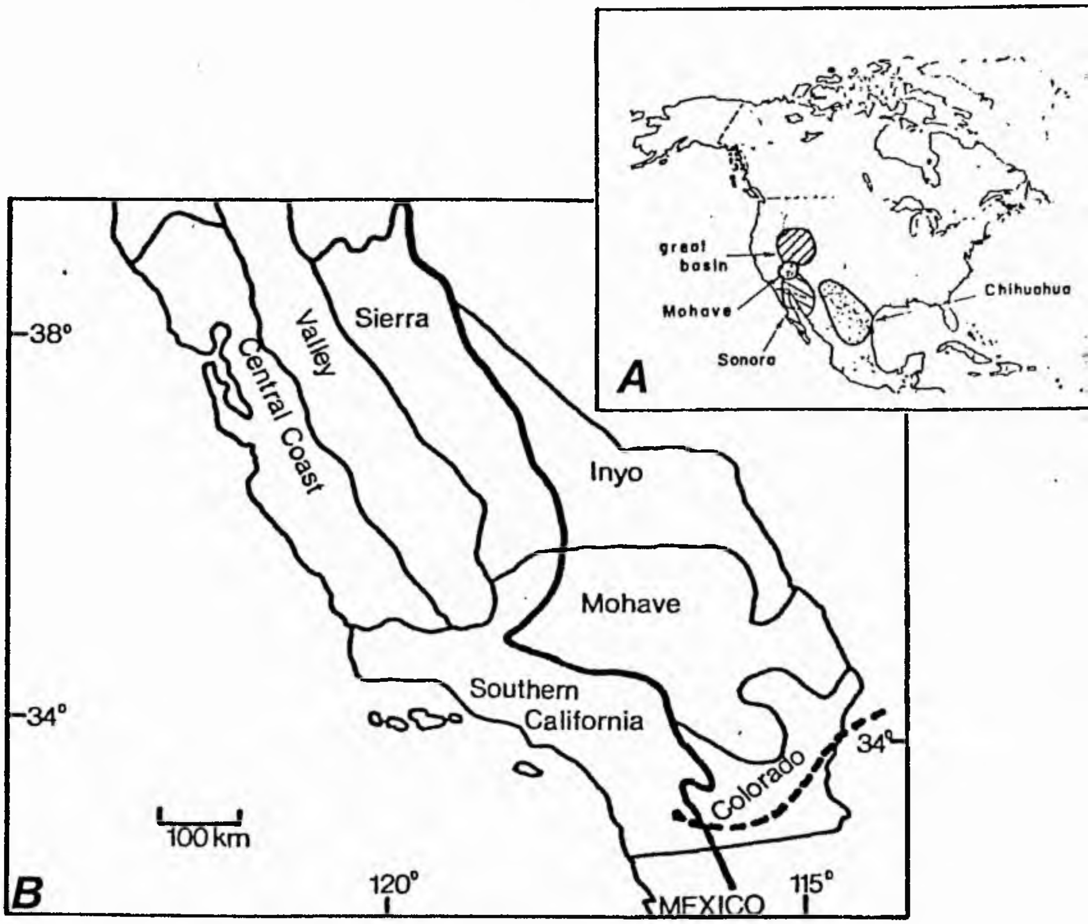


Figure 60 - (A) - Map showing the "semi-desert" to "desert" areas of North and Central America (after SOLBRIG, 1972).

(B) - Part of the Californian Floristic Regions map given by RAVEN & AXELROD (1978, modified). The area west of the heavy line is a portion of the "California Floristic Province". The discontinuous line in the right hand corner marks the limits south of which <u>Sesbania emerus</u> occurs naturally; above this limit the climatic conditions of the desert areas Colorado and Mohave restrict the distribution of this species.

of tropical to subtropical distributions to their range to the Colorado desert. Among these taxa, RAVEN & AXELROD (*loc. cit.*) have included *Sesbania* and the observations of the present work fully support this inclusion. However, it must be noted that the geographical area in question certainly represents an extreme limit of the distribution of *S. emerus* in North America, as shown in Figure 62.

Although plant populations in 'stressful habitats' at the extreme limits of species distributions may produce independent species as proposed by MAYR (1963), SOLBRIG (1970) and GRANT (1971), this situation does not seem to apply in *S. emerus*. This conclusion is supported by the fact that discontinuities observed for different populations of *S. emerus* here studied are not sufficient to reach the necessary level in which distinct species or even infraspecific taxa are recognised (GILLETT, 1963; BURBIDGE, 1965; and the present work).

The character states "length of flowers and pods" and "number of leaflets and seeds" have been used to recognise infraspecific taxa in species of *Sesbania* *but always* associated with some morphological modifications in petal shapes or colour, as in *Sesbania sesban* and *S. bispinosa* (GILLETT, 1963). Very often these taxa also have different distribution ranges and even when introduced and/or cultivated outside its natural areas, these varieties maintain their discontinuous characteristics, as is the case of the taxa here studied, *S. sesban* subsp. *sesban* var. *bicolor* and *S. bispinosa* var. *bispinosa*.

The data matrix of Table 22 was also used for a clustering analysis to ascertain to what extent these data would support the assumption that S. emerus does indeed comprise just one species throughout its distribution range.

The study consisted of the application of several methods of hierarchical analysis available through CLUSTAN (WISHART, 1978), a clustering program designed at St Andrews University Computer Centre. As is commonly the case, a variety of dendograms were produced by the different clustering techniques but only the dendograms given by the Group Average and Ward's methods are presented here (Figures 61 A,B, respectively).

The results show that the two methods are basically similar in the dendograms produced although higher levels of similarity are presented in the Group Average tree (Figure 61 A), where area 10 (South America) becomes isolated from the others. This fact does not happen with Ward's method (Figure 61 B) but here the same area, although belonging to a single S. emerus cluster, is linked linked with the rest of the groupings at a high coefficient level. In both methods, however, the general result is quite clear in the sense that, apart from South America (area 10), the populations of S. emerus from different geographical areas show no striking differences. This confirms the view that the species has not differentiated to any marked extent into isolated populations with their own character correlations which would warrant treatment as either infraspecific or still less independent species status.

The situation with regard to the South American specimens is not well understood and certainly this is a case where more extensive collections should be made in order to provide

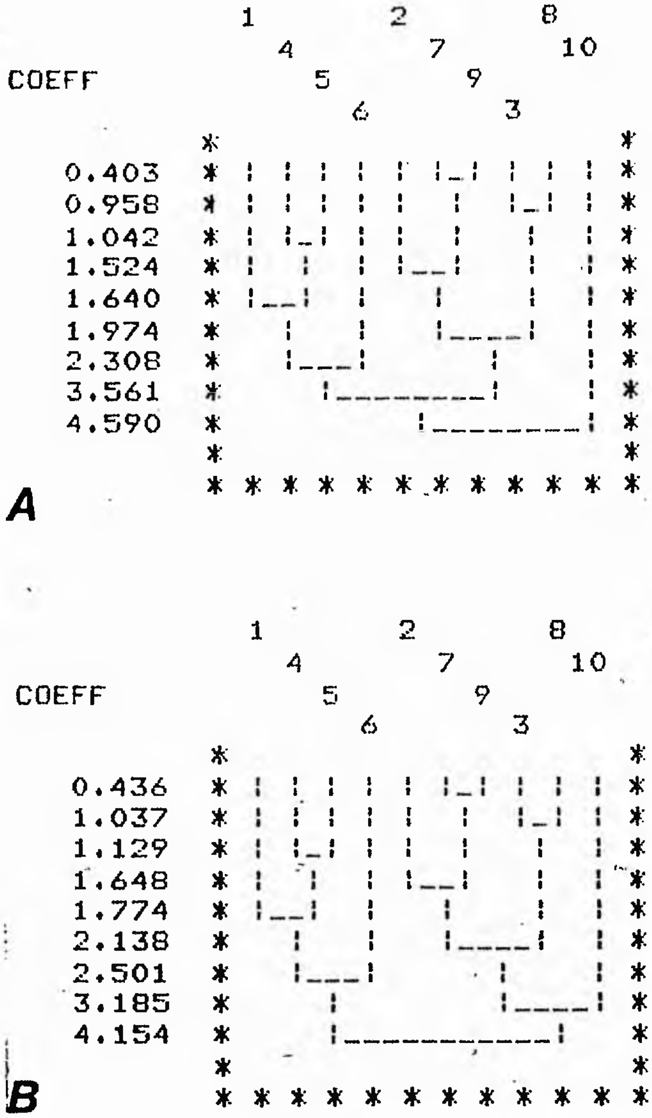


Figure 61 - Dendrogram trees of Group Average (A) and Ward's (B) methods of clusering analysis of the data matrix in Table 22. Numbers above each vertical line represent the geographical areas of Table 19.

sufficient material for a broader study of the variations present within *S. emerus* in South America.

The distribution of *S. emerus* is, then, very wide-ranging, from North America to occasional populations in South America (Figures 62, 63). It is interesting to notice that although it is so successfully adapted to warmer areas of the southeast and south Plains of North America, *Sesbania emerus* does not occur abundantly in South America, even in the regions with the same climatic conditions. HILL (1982) has presented and illustrated with many examples the remarkable similarity between the Texas coastal bend region flora (an area within the radius of 30-60 miles of Corpus Christi, 27°48'N - 97°24'W) to that of the Paraná basin of South America. The most reasonable explanation of this similarity given by HILL (*loc. cit.*) was that of successive occurrences of long-distance seed dispersal by birds to give now conspecific or similar species of both areas. The same long-distance dispersal origin could account for the few collections of *S. emerus* which occur in Paraguay (Figure 63).

A possible reason for why *S. emerus* has not yet become more widely established in the warm wet regions of South America may be due to its weedy habit (TURNER, 1955; HOLM *et al.*, 1979) in cultivated and disturbed areas which seem to be more frequent in the south-eastern region and the Plains of North America than in the Paraná basin. Interestingly, *S. emerus*, like many other species of *Sesbania*, can adapt well to low nutrient soils, and these conditions do not seem to cause variations in the number of seeds per pod but only in the seed weight (WILLSON, 1983), a factor which might favour a wider dispersion of this species.

Distribution (Figure 62, 63)

CENTRAL AMERICA

Belize - Indian Church, ARNASON 17834, 24.x.1977 (MO); Belize City roadside at St John's College campus, DWYER, ELIAS & MAXELL 15, 15.iii.1967 (MO); Northern River, GENTLE 1371, 15.viii.1934 (LL,MO,NY); Belize City, roadside near St John's College, LAZOR & TYSON 2130, 10.iv.1969 (MO).

Costa Rica - Guanacaste : Cañas - Pan American Highway 5 km N of Finca La Pacifica, FRANKIE 287a, 1.x.1969 (MO); Cañas : roadside N of Finca La Pacifica, JANZEN 10038, 17.xi.1971 (MO); Guanacaste : Sabana, near Pan American Highway, 4-6 km S of La Cruz, WESTON, WESTON & WESTON 2799, 13.x.1966 (MO).

El Salvador - Ateos, CALDERON 1865, x.1923 (NY); Sonsonate : vicinity of Santa Emilia, alt. 135 m, STANDLEY 22058, 22-25.vii.1922 (MO,NY)

Guatemala - Province of Zacapa : Zacapa, KELLERMAN 7882, 1.i.1908 (NY).

Honduras - Dept of Morazán : El Zamorano, MOLINA 11134, 7.xi.1962 (NY);drainage of the Rio Yeguare, at about 87 W-14 N, Jicarito, WILLIAMS 17300, 4.xi.1950 (BM,MO); Dept of Valle : thickets along Raton Island beach, MOLINA & MOLINA 22801, 12.x.1968 (NY).

Mexico -

Baja California - San José del Cabo, BRANDEGEE 138, 3.xi.1891 (DS); Baja Norte, eastside of Sierra Juarez, Canon de Guadeloupe, BURGESS et al. 6082, 11.x.1981 (MEXU); Mulegé, HOWE 4006, 28.ix.1964 (SD); low land near Hardy River, MacDOUGAL 101, 3.iv.1905 (NY); Saltillo, Vale de Mexicali, MORAN 29760, 18.vii.1981 (SD); vicinity of San José del Cabo, WIGGINS 5687A, 16.v.1931 (CAS,DS,NY).

Chiapas - mun. of Jiquipilas : 16 km eastsouth of Tierra y Libertad along road to Villa Flores, BREEDLOVE 27322, 23.viii.1972 (DS,MEXU,MO,NY,TEX); mun. de Suchiapa, BREEDLOVE 28042, 26.ix.1972 (DS,MEXU,MO,NY,TEX); mun. of Tonalá : on the northwest side of Cierro Vernal, 25-30 km SE of Tonalá, BREDLOVE 28325, 4.x.1972 (DS,MEXU,MO); mun. of Cintalapa, seasonal Evergreen Forest along the Rio Cintalapa, 5-6 km NW of Las Cruces along logging road to la Cienega, BREEDLOVE 28423, 5.x.1972 (DS,MEXU,MO); mun. of Arriaga : 15 km NW of Arriaga, BREEDLOVE 36763, 25.viii.1974 (DS,MEXU); mun. of Villa Corzo : 58 km S of Mexican Highway 190 on road to Nueva Concordia, BREEDLOVE 37651, 11.ix.1974 (DS,MO); mun. of La Concordia, 96 km S of Mexican Highway 190 on road to Nueva Concordia, BREEDLOVE 38496, 10.x.1974 (MEXU); mun. of Tonala : NW of Puerto Arista, BREEDLOVE 52825, 16.ix.1981 (CAS); ibidem : east shore of Mar Muerto, N of Paredon, BREEDLOVE 20785 & THORNE, 18.x.1971 (MEXU,MO,NY); mun. of Acalá : wooded slope along the Rio Grijalva, 10 km S of Mexican Highway 190 along the road to Acalá at Nandaburri, LAUGHLIN 2639, 24.x.1966 (DS,MEXU,NY); Escuintila, MATUDA 49, ix.1936 (LL,MEXU); mun. of Escuintila : Cacaluta, MATUDA 16987, 3.ix.1947 (MEXU); ibidem, ibidem, MATUDA 17062, 12.x.1947 (DS,NY); mun. of Tonala : Mojarra, MATUDA 17230, 27.xi.1947 (MEXU); mun. of Tonala : camino Tonala a Arriaga, MIRANDA 7278, 28.viii.1951 (MEXU); ca. 50 mi. W of Tapachula, PENNELL, DUNN & DZIEKANOWSKI 321, 8.v.1978 (MEXU,NY); Colonia Ocotal, 7 km NW of Tonala, SOUSA 4245 <u>et al</u>., 8.ix.1973 (CAS, MEXU); 4 km NW of Jerico, alt. 500 m, SOUSA 11481 <u>et al</u>., 12.xii.1980 (MEXU); Angel Albino Corzo, 10 km E of Revolucion Mexicana, SOUSA 11504 _et al._, 12.xii.1980 (CAS).

Guanajuato - en el Ingenio Alvaro Obregon, TELLEZ 3446, CABRERA & RICO, 6.ix.1980 (MEXU).

Guerrero - road Puerto Marquez-Revolcadero, BOEGE 870, 20.ix.1968 (MEXU); mun. of Iguala : km 41 of the road Iguala-Teleoapan, DELGADO 545, 25.ix.1976 (MEXU); mun. of Acapulco : 3 km S of Base Naval Icacos, road to Puerto Marquez, GRETHER 902 & QUERO, 21.xii.1977 (MEXU); 27 km W of San Luis de La Loma, 3 km S of Papanoa, LADD 210 _et al._, 20.x.1977 (MEXU); near Rio Balsas, ORCUTT 4383, viii.1910 (BM,MO); mun. of Acapulco, PARAY 2312, 15.xi.1956 (MEXU); Bahia de Zihuatanejo, SOUSA 6161, 2.x.1976 (MO).

Jalisco : Estación Biologica de Chamela, DELGADO 114 _et al._ , 19.ix.1968 (MEXU); "environs de Guadalajara", DIGUET 39, no date (P); mun. of Colima : road Manzanillo- Colima, km 40, LUNA 3522, 30.ix.1972 (MEXU); mun. of La Huerta : Chamela, "Las Islas", MAGALLANES 804, 27.ix.1977 (MEXU); Chamela, MAGALLANES 870, 3.xi.1977 (MEXU); mun. of Guadalajara : Valle de Chuatulco, URBINO s/n, ix.1885 (MEXU).

Michoacan - 4-5 km W-NW of Apatzingan, along the road to Buena Vista-Tomatlán, DIETERLE 4362, 10.ix.1972 (MEXU); Tacupa, Huetamo, HINTON 5618 _et al._, 13.ii.1934 ((BM,G,NY); mun. of Tiquicheo : El Guayabo Zancon, SOTO 289, 22.ix.1977 (MEXU); 8 km SE of Tziotzio, en La Calavera, SOTO 984, 7.ix.1978 (MEXU); 6 km NW of Buenavista, carretera Apatzingan-Tepalcatepec, SOTO 1051, 10.ix.1978 (MEXU).

Morelos - Oaxtepec, HARKING 400, 31.viii.1952 ((MEXU); valley below Cuernavaca, PRINGLE 9094, 20.ix.1900 ((MEXU,MO,P).

Nayarit - San Blás, FERRIS 5472, 10.x.1925 (DS); ibidem, JOHNSON 97-73, 6.i.1973 (MO); 5 mi. N of Acoponita on road to Tuxpan, IRWIN 1291, 25.viii.1957 (TEX); San Blás, LAY & COLLIE s/n, xii.1827-ii.1828 (BM); Isla Isabel, alt. 10-75 m, RAMOS 10, 16.xii.1977 (MEXU).

Oaxaca - mun. of Santa Maria Chimalapa : district of Juchitán, 4 km NO of Ejido La Esmeralda, DELGADO 953, GARCIA & PERINO, 8.iii.1978 (CAS,MEXU,MO); San Geronimo, MELL 2151, 20.x.1933 (NY); Tahueca, 15 km NE of Pochutla, district of Pochutla, OILVARES 650, 3.x.1980 (MEXU); mun. of Tehuantepec : Puente Espuela, 15 km SW of Morro, E of Huamelula, SOUSA 8671 & TELLEZ, 27.x.1977 (MEXU,MO); La Pita, 3 km W-NW of Puerto Escondido, district of Juquila, SOUSA 6378 *et al.*, 21.x.1976 (MEXU); 3 km W of Rio Huatulco, 22 km E of Pochutla, district of Pochutla, SOUSA 7591 *et al.*, 24.vi.1977 (MEXU); Estacion San Vicente, district of Tuxtepec, SOUSA 7990 *et al.*, 13.viii.1977 (CAS,MEXU,MO); Laguna de Los Bajos, SOUSA 8422 *et al.*, 21.x.1977 (MEXU,MO); 6 km S of Salina Cruz, district of Tehuantepec, SOUSA 9530 *et al.*, 19.ix.1978 (CAS,MEXU); en el Pueblo de San Mateo del Mar, TELLEZ & MAGALLANES 161, 20.ix.1976 (BM,MEXU); Colonia Reforma, 250 m de la carretera por camino carreta, ZIZUMBO & COLUNGA 331, 13.ix.1978 (MEXU).

Sinaloa - 2.6 mi. S of San Miguel, N of Los Machis, FELGER 8724, 22.x.1963 (MEXU); Labradas, FERRIS & MEXIA 5215, 20.ix.1925 (CAS,DS); 16 km SE of Escuinapa, GRETHER 1102 & QUERO, 19.ix.1978 (MEXU); Temascaltepec ; Naranjo, HINTON 1985 *et al.*, 5.x.1932

(BM,MEXU); ibidem, HINTON 4729 *et al*., 10.ix.1933 (G); 2 mi. N of Mazatlan, JOHNSON 190-72, 29.xii.1972 (MO); 53 mi. S of Culiacán, JOHNSON 1880-72, 26.xii.1972 (MO); mun. of Mazatlán : Mazatlán, ORTEGA 5979, xii.1925 (DS); El Quelite cut off, Rt 15, 3.4 mi.S of Elota, OZMENT 114, 9.x.1962 (MO).

Sonora - mun. of Huatabampo : along Mexico Highway 15, 5 mi.N of Estacion Don, BREEDLOVE 18639 & THORNE, 7.x.1970 (CAS); Guaymas, GENTRY 4678, 22.x.1939 (topotype of *S. sonorae* Rydb., CAS,DS,MO, NY,SD); Agua Caliente, N of Los Alamos, GENTRY 4850, 2xi.1939 (DS,MEXU); 35 mi. of Hermosillo along road to Mazatan, GENTRY 17854, 21.ix.1959 (LL); Sierra San Pedro Nolasco, Talea, JURGENSEN 510, 1813-4 (BM,FHO,MO); Guaymas, PALMER 286. x.1887 (holotype of *S. macrocarpa* var. *picta* S. Watson, GH); coastal plain scrub ca. 13 mi. NW of Vicam, ca. 27 45'N-110 30'W, WEBSTER & BRECKON 15611, 14.x.1970 (MO); crossing of Rio Sonora, 13 mi. S of Ures, WIGGINS 7318, 19.ix.1934 (DS).

Tabasco - Cardenas, COWAN 2425, 13.ix.1979 (CAS,MEXU,MO,NY); Pajonal, 12 km E of Villahermosa, GERMAN *et al*. 1936, 8.x.1979 (MEXU); mun. of Paraiso, 50 mi. S of Paraiso, GLEZ & MIRANDA 22, 16.vii.1979 (MEXU); E. Zapata, LLUCH 20, 25.ii.1964 (MEXU); Ingenio Benito Juarez, road Cárdenas-Coatzalcoalcos, MAGANA 307 & ZAMUDIO, 16.VI.1981 (MEXU); Frontera, km 15 E of Frontera, OROZCO *et al*. *sub* COWAN 2262, 9.vi.1979 (CAS); Chable, 11 km NE of Chable, 32 km SE of Balancan, SOUSA 12375 *et al*., 10.v.1982 (BM,MEXU); "7 km S del entronque de carretera Villahermosa-Chetumal sobre carr. a Balancan, TELLEZ 932 & MARTINEZ, 23.ix.1979 (BM,MEXU).

Tamaulipas - mun. of Ciudad Rio Bravo : road Rio Bravo-Reynosa, RODRIGUEZ 1498, 16.vii.1975 (CAS,MEXU).

Veracruz - mun. of Veracruz ; Nevería, road Tamarindo-Veracruz, BAEZ 278,362, and 499, 1.ix.1981 (MEXU); Ciudad Alemán, CALDERON 1024, 20.viii.1966 (CAS,MEXU,MO,NY); mun. of Panuco : Nuevo Poblado Chicayan, CALZADA & MARQUEZ 4549, 13.vii.1978 (MEXU); km. 23 of road La Granja-El Temascal, cerca Ejido B. Vista, CHAVELAS & PEREZ 210, 9.ix.1964 (MEXU); Laguna Salada, DORANTES *et al.* 1031, 26.vi.1972 (CAS); Veracruz, GOUIN s/n, 1867 (P); Vera Cruz, HOUSTON s/n, 1731 (type of "*Emerus herbacea*..." Mill., holotype BM, NY phtotype); 4 mi.E of Tolomé on Highway 140, edge of the road, MAXELL & HEIDINGER 168, 3.vii.1965 (MO); Tampico-Tuxpán, NEVLING & GOMEZ-POMPA 466, 5.ix.1967 (MEXU); Pozo de Arena, 16 km de Ignacio de La Llave, Laguna de San Marcos, NOVELO 235, 28.vii.1976 (MEXU); Antigua, 5 km N of Laguna Salada, SOUSA 2546, 6.ix.1965 (MEXU); mun. de Actopán, 4 km SE of Laguna Verde, El Viejon, SOUSA 4591 *et al.*, 28.ix.a975 (MEXU).

Yucatan - Izamal, GAUMER 907, no date (BM); Sacnicte, GAUMER *et al.* 23425, ix.1916 (G).

Mexico, no locality mentioned : BERLANDIER 1773 ? (BM,G,P); BERLANDIER 1934, ix.1828 (P); HARVEY 1773, 1844 (DS); JURGENSEN 167, iv.1844 (TCD); El Calabazal ?, LANGLASSE 462, 16.x.1898 (G,P); PALMER 775, 3-15.x.1890 (BM,G,NY); PARRY *et al.* 251c, xii.1854 (NY).

Mexico, localities not traced - Mun. of Ixtaltepa : Mezquite, alt. 200 ms, SOUSA 5005, SCHUBERT & RUDD, 3.X.1975 (K,MEXU); Puerto Escondido, SOUSA 5555 *et al.*, 19.iv.1976 (CAS,MEXU,SD); Cobá :

orilla de La Laguna de Coba, TELLEZ 3768 et al., 19.x.1980 (BM,CAS,MEXU).

Nicaragua - Dept of Leon : sector NW of Momotombito Island, ARAQUISTAIN 99, 20.viii.1979 (MEXU); Dept of Esteli : along road on way to San Juan Limay, MOLINA 23178, 6.xi.1968 (NY); Dept of Chontales : ca. 4.5 km S of Highway 7 on road to Nueva Guinea, STEVENS 4932, 1.xi.1977 (MEXU); Managua : ca. 4 km from Highway 12, near bridge of Rio La Adnana, 12 02'N-86 31'W, STEVENS 5389, 27.xi.1978 (MEXU); Managua : S shore of Lago Managua, STEVENS 11060, 12.xii.1978 (MEXU); Dept of Leon : Isla Momotombito, along beach from Louse (W side), to Punta Troza Quemada (N side), STEVENS 13224, 10.vi.1979 (MEXU); Carazo : ca. 3.3 km SE of Casares on road to Huehuete, SE of La Bocana Grande, STEVENS s/n, 23.ix.1977 (MEXU); Managua : along Highway 1, ca. km. 58, ca. 8 km. N of Las Maderas, ca. 11 29'N, 86 03'W, STEVENS & ARISQUITAIN 14875, 16.x.1979 (MEXU).

Panama - Dept of Chiriquí : Burica Península, 1 mi. W of Puerto Armuelles, CROAT 22037, 20.ii.1973 (MO); Panama City : weedy area S of Tocumen Airport, D'ARCY 9662, 15.xi.1975 (MO); Los Santos : ca. 10 km SW of El Cortezo, HAMMEL 5405, 28.x.1978 (MO); Rio Grande Station, HAYES 772, xii.1859 (NY); no local. ment., HAYES, s/n, no date (BM); Rio Grande Station, HAYN. ? 297, x.1861 (K); 9 km E of Santiago, JOHNSON 2207-80, 30.iii.1980 (MO); Pan American Highway, 2 km W of El Lano, NEE 7953, 11.xi.1973 (LL,MO); Veraguas roadsides and fencerows along Santiago-San Francisco road at Bridge over Rio Santa Maria, alt. 60 ms, NEE 8195, 18.xi.1973 (MO); Chiriqui : David, Calle Estudiante, RIOS 31, 1.xii.1975 (MO); Panama City : via Tumba Muerto, ca. 2 km from Universidad de

Panama, TAYLOR s/n, 29.x.1971 (MO); Distr. of Los Santos : Managre Beach, 5 mi. SE of Chitre, TYSON, DWYER & BLUM 3018, 22.i.1966 (MO); vicinity of Miraflores Lake, WHITE 263, 4.xii.1938 (VT).

NORTH AMERICA

California - Riverside Co : Blythe, Colorado River bottom lands, HUTCHINSON 6822, ix.1931 (DS); Imperial Co : Winterhaven, JOHNSON 197, 1.ix.1965 (TEX); Riverside Co : 2 mi. N of Indio, NOBS & SMITH 500, 3.ix.1948 (DS); Imperial Co : Salton Basin, canal area near Imperial, SALTON BASIN PARISH 83090, 15.x.1912 (DS,NY); ibidem, canal banks on western outskirts of El Centro, elev. 12 m.,RAVEN 16385, 8.x.1961 (CAS); Bard, U.S. Experimental Station, RIXFORD s/n, vii.1913 (CAS); The Needles, RUSBY 566, 15.ix.1883 (NY,P); San Diego Co : 3 mi.from escondido, San Pasqual Rosa, SCARBERY s/n, 14.viii.1937 (SD); Los Angeles Co : 2 mi. NE of La Verne, WHEELER 1354, 8.ix.1932 (CAS,DS); Imperial Co : Colorado Desert, Wister, SE of Salton Sea, WOLF 4329, 13.x.1932 (SD).

Southwest - Arizona : Yuma, Colorado River, BRANDEZEE s/n, iv.1884 (DS); ibidem, FORBES s/n, ix.1904 (CAS); no local. ment., PALMER s/n, 1885 (NY); Yuma, SALTON BASIN PARISH 8310, 20.x.1912 (DS); New Mexico : vicinity of Roswell, DUNN s/n, 31.viii.1951 (NMC).

South Plains - Oklahoma : Verdigris, BUSH 76, 2.viii.1894 (MO,NY); ibidem, BUSH 77, 5.x.1894 (NY); Cherokee Co : along the Illinois River, 2.5 mi. S of Scraper, CORRELL & CORRELL 39802, 18.ix.1970 (L) Johnston Co : Tishomingo, PALMER 6459, 18.ix.1914 (P); Atoka Co : ditch, 12 mi. W of Atoka, WATERFALL 8397, 5.viii.1948 (TEX); Johnson Co : no local. ment., collector ?, 27.ix.1957 (NMC).

Texas : Harris Co, ANDERSON 36-1, ix-x.1936 (TEX); Brazos Co : College Station, BALLESTER 63, 17.x.1963 (NY); Travis Co : Daffan, BODIN s/n, ix.1891 (DS); no local. ment., BOLL s/n, 1871 (G); Columbia, BUSH 1455, 11.x.1900 (MO); Hidalgo Co : McAllen, CAMERON 9, 18.vi.1937 (TEX);

Walker Co : 8 mi. NW of Huntsville, CORRELL 14173, 27.viii.1946 (LL,NY); Montgomery Co : in water and moist sandy soil along stream at Ferris Chapel, N of Montgomery, CORRELL 31935, 6.x.1965 (LL); Bowie Co : on and about wooded hills along McKinnery Bayou, 6.5 mi. N of Texarkana, CORRELL 33430, 14.viii.1966 (LL); Uvalde Co : Blewet, CORRELL & CORRELL 26164, 2.x.1962 (LL); Van Zandt Co : just west of spillway, Lake Tawakoni, CORRELL & CORRELL 35003, 24.ix.1967 (LL); Aransas Co : Aransas Refuge, CORY 45845, 29.ix.1944 (TEX); Jefferson Co : 10.5 mi. S of Beaumont, CORY 50508, 14.xi.1945 (NY); Ellis Co : 9 mi. NE of Ennis, CORY 52312, 13.ix.1946 (DS,NY); Kaufman Co : Bois d'Arc Island, CORY 52544, 28.x.1946 (DS,NY); Williamson Co : Brushy Creek, Round Rock, CRUTCHFIELD 784, 9.ix.1965 (LL); Montgomery Co, DIXON 482, 18-21.vii.1909 (NY); no local. ment., DOUNI ? 74, no date (NY); no local. ment., DRUMMOND 74, 1835 (BM, G,NY,TCD); ibidem, DRUMMOND 1174, no date (P); Bastrop Co, DUVAL 101, no date (TEX); Bexar Co : San Antonio, EGGERT s/n, 7.ix.1900 (MO); Cameron Co : Brownsville, FERRIS & DUNCAN 3219, 1-5.viii.1921 (DS); Brazos Co, FERRIS & DUNCAN 3283, 13.viii.1921 (CAS,DS,MO,NY); Houston, FISHER 50186, 20.ix.1950 (CAS); ibidem, FISHER s/n, 15.ix.1929 (BM); Hidalgo Co : Santa Ana National Wildlife Refuge, S of Alamo, FLEETWOOD 3087, vii.1959 (TEX); Brazos Co : about 3 mi. SW of College Station, GOULD 7690, 20.ix.1957 (TEX); Bexar Co : San Antonio, alt. 180 m., HELLER 1831, 9.vi.1894 (NY); ibidem, no local. ment., JERMY 26, no date (NY); ibidem, ibidem, JERMY 75, 1907 (NY), JERMY 110, no date (MO); Gillespie Co, JERMY 489, no date (MO); Hays Co : 4 mi. N of San Marcos below railroad bridge over Blanco River, JOHNSON 357, 23.viii.1948 (TEX); Cameron Co : near San Benito, JOHNSTON s/n, 8.ix.1953 (TEX); Harris Co, JOOR 45, 15.ix.1876 (P); Dallas, LETTERMAN s/n, 25-30.vii.1880 (MO); no local. ment., LINDHEIMER 261, 1846 (MO); Comale Creek, LINDHEIMER 371, viii.1846 (BM,FHO,G,K,MO,NY,P,TCD); locality ?, LINDHEIMER 498, viii.1845 (MO); New Braunfels, LINDHEIMER 787, 1849 (MO); Comanche Spring - New Braunfels, LINDHEIMER 788, viii.1850 (BM,E,G,MO,NMC,NY,P,TEX); Dallas Co : Bachmans Dam, LUNDELL 11634, 24.viii.1942 (LL); San Saba Co : above Camp Billie Gibbons on Broad Creek, 15 mi. SW of Richland Springs, MCGREGOR 40, 17.x.1965 (TEX); Harrison Co : Rag Island, Caddo Lake, o.5 mi. E of Crips Camp, MITCHELL 3954, 25.viii.1967 (LL); Jefferson Co : Port Arthur, NOGLE 2064, 10.x.1942 (TEX), NOGLE 2065, 11.x.1942 (MO); San Antonio, PALMER 278, 18-27.ix.1879 (K,MO,P,W); Anderson Co : Palestine, PALMER 10728,15.ix.1916 (DS,MO); Brazos Co : Bryan, PARMALLE 61, 18.x.1949 (TEX); Winter Spring, REEVES 1094C, 13.ix.1941 (TEX); Dallas, REVERCHON s/n, vi.1876 (G), REVERCHON s/n, vii.1877 (NY); Olmito, in low ground, RUNYON 675, 20.x.1924 (TEX); Brownsville, highway S of Olmito, RUNYON 3023, ix.1934 (TEX); ibidem, Ringgold Park, RUNYON 3024, 1.ix.1938 (TEX); Tarrant Co : Handley ?, RUTH 129, 1.x.1910 (TEX); along railroad near Forth North, RUTH 280, 29.ix.1910 (MO,NY); San Marcos and vicinity, STANFIELD s/n, iv-vi.1897 (NY); Jefferson Co, THARP 3446, 4.ix.1924 (TEX); Gonzales Co : Palmetto State Park, TARP s/n, 18.x.1940 (TEX); Travis Co : Hamilton Creek, 3-4 mi. SE of Marble Falls on Travis Peak road, THARP & YORK 50-134, 20.viii.1950 (TEX); locality ?, THURBER. 3, 1851 (NY); Harris Co : Lake Houstton Park, 2-3 mi. E of Great Bayou, TRAVERSE 1701, 9.ix.1960 (TEX); Travis Co, TURNER 3655, 17.viii.1954 (TEX); Jackson Co : 7 mi. W of Edna, TURNER 3291 & THARP, 15.ix.1953 (TEX); Galveston Co : deep sand ca. 100 yards from Gulf Beach, Bolivar Peninsula, ca. 8 mi. E of Bolivar Point, WALLER & BAUML 3153, 23.ix.1974 (TEX); Travis Co : abundant in creek bottom above Barton Springs, Austin, WARNOCK 21621, 10.ix.1944 (DS,G,MO,NY,TEX); near San Antonio, WILKINSON s/n, 1900-1902 (MO), WILKINSON 179, no date (MO); Travis Co : Barton Creek, YOUNG s/n, 29.viii.1912 (TEX); Brazos Co : White Creek bed, 3 mi. SW of College Station, collector ?, 20.ix.1946 (DS); Brownsville, collector ?, 22.xi.1965 (TEX).

<u>Central Plains</u> - <u>Kansas</u> : Rilley Co : Manhattan, GATES 18565, 27.ix.1935 (MO), GATES 18579, 28.ix.1935 (TEX); Wilson Co : 2 mi. SE of Noodesha, McGREGOR 5729, 30.viii.1952 (NY).

<u>Southeast</u> - <u>Alabama</u> : Spring Hill, GRAVES 1091, vii.1919 (MO); Mobile, MOHR s/n, 1878 (NY), MOHR s/n, date ? (W); roadsides near Montgomery, SMITH s/n, 19.viii.1884 (P); <u>Arkansas</u> : Marked Tree, BUSH 256, 1.xi.1897 (NY); Pulaski Co : Little Rock, bottoms of Arkansas River, DEMAREE 8196, 17.ix.1931 (DS,MO,NY); no local. ment., DEMAREE 9196, 17.ix.1931 (NY); Monroe Co : Clarendon, White River bottoms, DEMAREE 10912, 2.ix.1934 (DS,MO); Crittenden Co : between Leeve and Mississippi River, West Memphis, DEMAREE 11107, 8.ix.1934 (DS,MO); Miller Co : Texarkana, DEMAREE 13464,

20.viii.1936 (MO,NY); Desha Co : McGhee, DEMAREE 13781, 26.ix.1936 (DS,MO,NY); Chicot Co : Eudora, DEMAREE 13828, 4.x.1936 (DS,NY); Jefferson Co : Pine Bluff, DEMAREE 16250, 17.ix.1937 (MO,NY); Jackson Co : Newport, White River bottoms, DEMAREE 20374A, 25.viii.1939 (CAS,MO,NY); St Francis Co : Madison Junction, DEMAREE 21561, 3.ix.1940 (MO,NY); Drew Co : Wilmar, DEMAREE 24591, 7.viii.1943 (MO,NY); Chicot Co : coastal plain, Lake Village, DEMAREE 67925, 1.x.1973 (MOO; Tulaski Co, EGGERT s/n, 3.vii.1894 (MO); Clay Co : Corning, EGGERT s/n, 21.viii.1896 (MO,NY); Hempstead Co : Fulton, GREENMAN 4435, 5.x.1923 (MO); near Little Rock, HASSE s/n, 25.viii.1886 (DS), HASSE s/n, 18.viii.1895 (NY), HASSE s/n, 25-31.viii.1896 (NY); Port Arkansas, KELLOG s/n, 27.ix.1909 (MO); Fulton, KELLOG s/n, 29.viii.1910 (MO); no local. ment., NUTTALL s/n, no date (NY); Ozark Mountains, TRELEASE s/n, 5.viii.1887 (MO); Florida : Hillsborough Co : 11 mi. N of Bradenton, BALTZELL 6616, 3.x.1974 (BM); Lee Co : Western Sanibel, BRUMBACH 9056, 1.x.1976 (NY); ibidem : Upper Captiva, BRUMBACH 9294, 12.x.1977 (NY); no local. ment., CHAPMANs/n, 1845 (BM); marshes along the coast, near Apalachicola, CHAPMAN 4569, viii.1879 (NY); no local. ment., CHAPMAN s/n, no date (NY,P); Okloosa Co : near Allison Lake, ca. 8 mi. N of Fort Walton, CHAPMAN & CHAPMAN 203, 25.x.1966 (SD); Dade Co : Homestead Bayfront Canal, CORRELL & POPENOE 48338, 9.iv.1977 (FTG,NY); no local. ment., CURTISS s/n, 1880 (NY); Pensacola, CURTISS 6917, 26.ix.1901 (E,G,K,MO,NY,P,W); shores of St John's River, CURTISS 590 ?, date ? (BM,NY); Dade Co : Pine Island, Everglades National Park, CRAIGHEAD s/n, 14.viii.1964 (FTG); Monroe Co : Flamingo, CRAIGHEAD s/n, 14.xii.1965 (FTG); Tampa, GARBER s/n, ix-x.1877 (NY); Pinellas Co : clearwater, SR 5888, Princeton Ave, W of US19, GENELLE & FLEMING 320, 7.ix.1970 (NY); Dade Co : between Homestead and Biscayne Bay on wet muck, GILLIS 6958, 9.x.1968 (FTG,MO); Framklin Co : brackish awales along the mouth of the Ochlockenee River, GODFREY 54124, 8.x.1955 (NY); ibidem : near Carrabelle, GODFREY & KRAL 54220, 16.x.1955 (NY); Collier Co : Immokalee City limits, LAKELA 30138 & ALMEDA, 30.viii.1966 (NY); Polk Co : Bartow near Winter Haven, McFARLIN 6572, 19.viii.1931 (CAS); Lake Co : Eustis, MOLDENKE & MOLDENKE 29798, 18.v.1975 (LL); Alachua Co : Newman's Lake near Gainesville, MURRIL s/n, 24.ix.1939 (MO); Hillsborough Co : Tampa, NASH 2478, 24.viii.1895 (G,MO,NY,P,W); Monroe Co : Stock Island, Key West, POPENOE 607, 24.iv.1976 (FTG); near Jamony, RUGEL s/n, viii.1843 (MO,NY); Lake Jamony, RUGEL 652, viii.1843 (BM,G); Tallahassee, RUGEL 153, ix.1845 (BM,G,NY,P); on cultivated hammock land N of Hendryx Wharf, Manattee River, SIMPSON 104, 12.ix.1890 (NY); Monroe Co : Lower PMatecumbe Key, SMALL 8393, 24.v.1917 (NY); Everglades W of Coconut Grove, SMALL 8814, and 8820, 23.v.1918 (NY); Everglades Park, Lake Okeechobee, SMALL & SMALL 4304, 11-25.xi.1913 (NY); Georgia : Wayne Co : 1 mi. S of Jesup, DUNCAN 7860, 13.ix.1947 (MO,NY); McIntosh Co : near S end of Sapelo Island, DUNCAN 20632, 14.x.1956 (TEX); Coloquitt Co : Coaspal Plain Province, 3.1 mi. SSE of Berlin, FAIRCLOTH 4838, 6.ix.1967 (MO); Lowndes Co : shoulders of roadside ditch on Ga-94 in the SE section of Valdosta, FAIRCLOTH 4931, 10.x.1967 (MO); Thomas Co : 3.1 mi. E of Boston, FAIRCLOTH 6251, 27.ix.1969 (MO); McIntosh Co : low field just W of Biol. Lab., Sapelo Island, HARDIN 348, 21.viii.1954 (TEX); Louisiana : vicinity of Covington, ARSENE et al. 11774, 29.vi.1920 (NY,P); New Orleans, BAHENI 243, 2.x.1934 (G); ibidem, BIDDELL s/n, date ? (FHO); East Baton Rouge Parish : Baton Rouge, BROWN 1211, 6.x.1927 (NY), Melville, BUSH 400, 29.vii.1897 (MO,NY); Port Allen, banks of Mississippi River, DEMAREE 13489, 21.viii.1936 (MO,NY); St Bernard-New Orleans, DEMAREE 13502, 23.viii.1936 (MO,NY); Assumption Parish : 8 mi. W of Tibodeaux, EWAN 18903, 11.xi.1956 (MO); New Orleans, EWAN & BRETTING 22241, 22.ix.1974 (TEX); ibidem, INGALLS s/n, 1834 (NY); vicinity of Lake Charles, MACKENZIE 411, 25.viii-10.ix.1898 (MO); near New Orleans, Mississippi banks, NUTTALL s/n, no date (BM); West Feliciana Parish : Cataipa, PENNELL 4333, 24.viii.1912 (NY); New Orleans, RIDDELL s/n, no date (NY); no local. ment., SMITH s/n, 1836 (G); Port Eads, TRACY & LLOYD 191, 22.viii.1900 (E,G); West Louisiana, collector ?, date ? (NY); no local. ment., collector ?, date ? (E); Mississippi : Harrison Co : Henderson point, DEMAREE 32760, 8.xii.1952 (TEX); Edwards, RHOADES S/N, vii.1927 (NY); Pearl River Co : Picayune, SARGENT 8361, 15.viii.1964 (CAS); ibidem, ibidem, SARGENT 8394, 25.viii.1964 (CAS); ibidem, ca 8 mi. NW of Picayune, SARGENT 10319, 17.viii.1970 (MO); Horn Island, TRACY 1385, 19.vii.1891 (MO); North Carolina : New Hanover Co : Wilmington, ballast just south of US74, bridge over Noth East River, LEONARD, CULWELL & RIPPERTON 1996, 14.ix.1968 (DS,SP); South Carolina : Jasper Co : 0.7 mi. N of Savannah River on US Rt 17A, AHLES 18154 & BELL, 7.ix.1956 (NY); ibidem : 0.7 mi. W of junction of Highway 128 with Highway 170, BELL 4822, 7.ix.1956 (NY); Georgetown Co : sandy hill on marsh, W of Waccamaw River, BOZEMAN & LOGUE 11347, 27.viii.1967

(MEXU); Charleston Co : waste areas near docks in Charleston, BRADLEY & BLAISDELL 3408, 21.viii.1966 (E,TEX); Tennessee : Shelby Co : President's Island, Memphis, DEMAREE 21532, 1.ix.1940 (MO,NY); Olbion Co : on west side of Keelfront Lake, STEYERMARK 297, 5.iv.1931 (MO).

North Central - Illinois : Pulaski Co : Mounds City, shore of Ohio River, EVERS 82236, 19.x.1964 (MO); Missouri : Barry Co : Eagle Rock, BUSH 20, 21.ix.1891 (NY,W); Long Beach, JOOR s/n, 19.vii.1891 (MO); Dunklin Co : Kennett, KELLOGG 15222, 6.viii.1929 (MO); no loc. ment., LATROBE 1832, 1833 (and 1835 ?), date ? (BM); Barry Co : White River, Eagle Rock, MACKENZIE s/n, 21.ix.1896 (MO); Ist Ilouis, MUEHLENBACH 1100, 22.ix.1956 (MO); ibidem, MUEHLENBACH 2266, 6.x.1963 (MO); ibidem, NORTON s/n, 9.vii.1898 (MO); Perniscot Co : 7 mi. S of Portageville, STEYERMARK 8302, 22.viii.1935 (MO); Taney Co : Table Rock, STEYERMARK 19631, 25.viii.1935 (MO); Moniteau Co : 3.5 mi. S of McSirk, STEYERMARK 24807, 16.viii.1937 (MO).

SOUTH AMERICA

Argentina - Province of Formosa, Pilaga Dept - Ruta 86 al Km 93, MOREL 7533, 27.iv.1949 (NY).

Brazil - state of Maranhão, Município of Loreto, EITEN & EITEN 4795, 31.v.1962 (K,MO,NY,SP); ibidem, ibidem, EITEN & EITEN 4798, 31.v.1962 (NY); state of Bahia : Chapadão Ocidental da Bahia, 5 km to the N of Tabocas, which is 10 km of Serra Dourada, HARLEY *et al.* 21975, i.v.1980 (K).

Colombia - Tocaima, "in passins montosis proper Rio Fiuza", ANDRE 1823, 20.ii.1876 (K); Valle : between Cali and Palmira, BARBOSA & FORERO 659, 10.ix.1978 (NY); no local. ment., DAWE 573, 31.iii.1917 (K); Antioquia : Turbo, GENTRY 9454, 21.i.1974 (MO); Cundinamarca : 15 km NW of Guadas on road to Honda, alt. 900 M., GENTRY *et al.* 18126, 5.ii.1977 (MEXU,MO,NY); Cundinamarca : Girardot, roadside to Melgar, alt. 400m., SOEJARTO 362, 2.viii.1963 (K).

Ecuador - no local. ment., DELGADO 20, 1964 (MO); ibidem, DELGADO 29, 1964 (MO); Guayas : Capeira, km 21 Guayaquil to Daule, DODSON & DODSON 11237, 15.ix.1981 (MO); ibidem, ibidem, DODSON & DODSON 11961, 25.x.1981 (MO); Napo : Tago Agrio, DWYER 10281 & DWYER, 27.vii.1972 (MO); El Oro : Chacras, alt. 30 m., PAREDES 1, 20.v.1975 (MO).

Paraguay - Gran Chaco : Santa Elisa , 23° 10'S "in campis humidis", HASSLER 2724, ii.1903 (BM,G,K,NY,P); District of Pilar, Dept of Neembucu : along edge of Rio Neembucu, WALTER 207, i.1975 (NY).

Peru - Dept of Piura : Talara ?, HAUGHT 17, 14.x.1925 (K,NY); Dept of Lima : 20 km NE of Talara, alt. 20 m., HORTON 11589, 10.iv.1939 (G,K).

Venezuela - state of Bolivar : Paviche, NW of El Manteco, edges of El Lago de Guri, DELASCIO & LIESNER 7123, viii.1978 (MO); state of Guarico : Sabana de Altagracia, GUYON 153, ix.1890 (P); Delta Amacuro : mouth of Cano Guiniquina, between Punta Araguabisi and Punta Baja, at Barra Guiniquina, STEYERMARK, LIESNER & DELASCIO 114933, 18.x.1977 (MO); state of Guarico, TRUJILLO 8586, 12.xi.year? (BM); ibidem, Estacion Experimental "Los Llanos", near Calabozo, TRUJILLO 8882, 6.v.1968 (BM).

WEST INDIES

Bahamas - Great Inagua : in wet depression at Horse Pond, about 1 mi. NE of Matthew Town, CORRELL 41860, 5.iii.1974 (FTG); Grand Bahama : in open fields about Freeport industrial area on way to harbour, CORRELL & KRALL 42980, 18.viii.1974 (FTG,LL,NY); Great Inagua : near Matthew Town, GILLIS 11756 & PROCTOR, 20.ii.1973 (MO); Andros : farmland 2 mi. S of San Andros airport, HILL 3434, 13.vii.1975 (FTG,NY); Great Abaco Island : along main road, 2.9 mi. S of Wilson City road, WUNDERLIN et al. 8552, 16.xii.1979 (MO).

Cuba - Habana : low hill, near Laguna Ariguanabo, Caimito, ALAIN 2551, 18.ix.1952 (NY); Santiago de Las Vegas, BAKER 86, 25.ix.1906 (DS,E,MO,NMC,NY,P); Habana ; Cuatro Caminos, BAKER 1907, 23.ix.1904 (NY); Santiago de Cuba, near Aguadores at the rail road track, EKMAN 8954, 19.xi.1917 (BM,NY); lowlands at Central Rio Canto, FARIS s/n, 3.x.1925 (NY); Las Villas Province ; Laguna de Gavilan, vicinity of Soledadd, GONZALES 252, 30.ix.1941 (BM,NY); in deep water Laguna del Ariguanabo, near Caimito, LEON 1680, 10.x.1910 (NY); ibidem, LEON 11464, 20.vii.1923 (NY); Caimito : Serafina, wet banks of Ariguanabo Lagoon, LEON & CAZANAS 5745, 27.xi.1915 (NY).

Dominican Republic - 10 mi. E of Cabo Rojo on the Oviedo Road, LIOGIER 16967, 13.xi.1969 (NY,P); province of San Domingo ; San Francisco de Macoris, station 9082, LIOGIER 9082-4, 22.iv.1978 (NY).

Guadeloupe - St Français, RODRIGUEZ 4196, 20.iii.1936 (P).

Jamaica - St Elizabeth : 0.5 mi. NE of Salt Spring Junction, PROCTOR 32755, 13.xii.1971 (BM,LL,NY).

Marie Galante - vicinity of Pointe de Folle Anse, 2 km SW of St Louis, PROCTOR 20229, 2.xii.1959 (BM).

Porto Rico - Cartagena Lagoon, DANKWORTH s/n, v.1924 (NY); Guavate state Forest, LIOGIER 10419, 14.xii.1963 (NY); on roadside, Toa Baja, LIOGIER & LIOGIER 28640, 19.iv.1979 (NY).

Figure 62 – Distribution map of Sesbania emerus in Central and North America and the West Indies (for the species distribution in South America, see Figure 63).

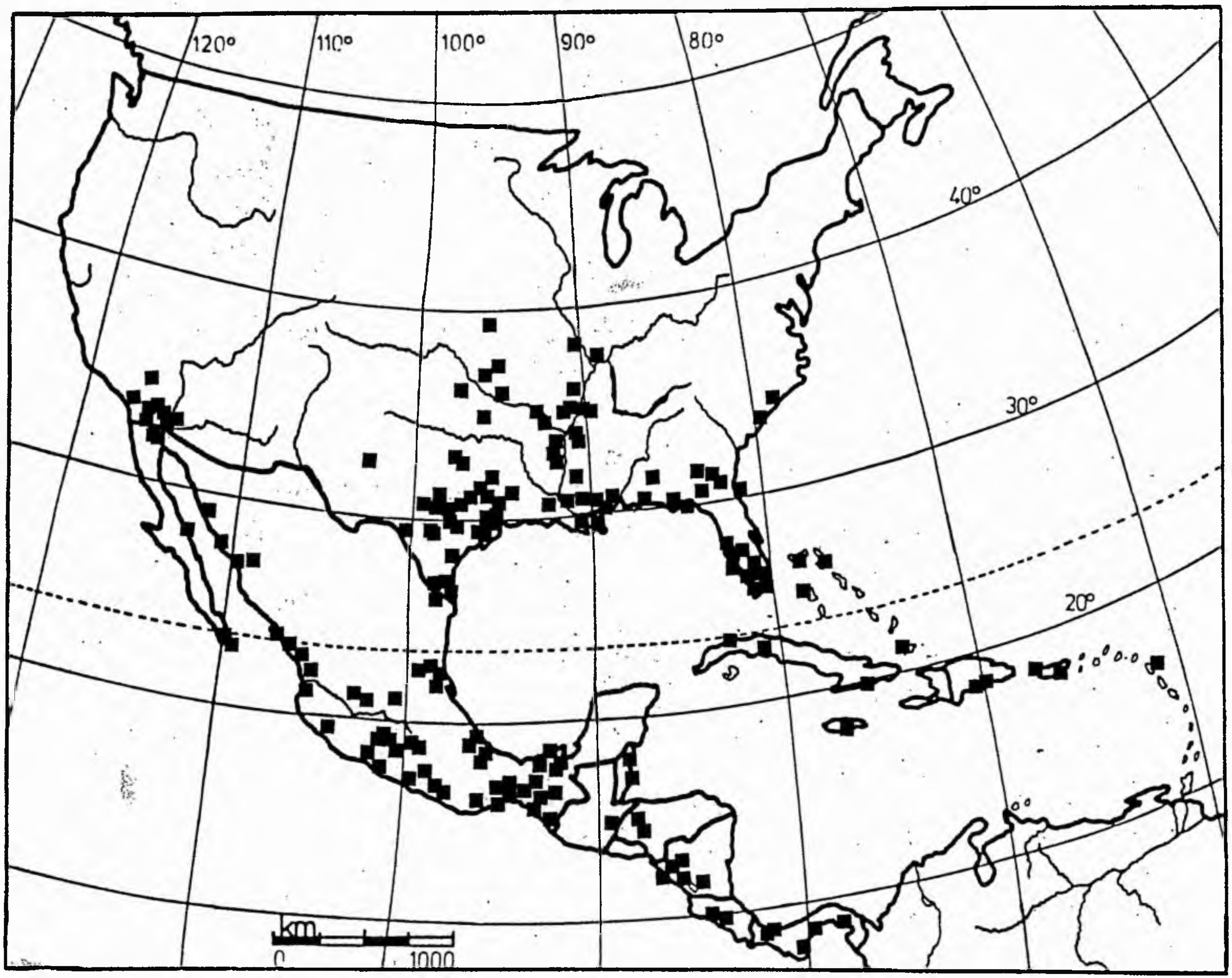

120°
110°
100°
90°
80°
40°
30°
20°
km
0
1000

Figure 63 - Distribution map of *Sesbania* subgen. *Sesbania* in South America.

○ *S. bispinosa*

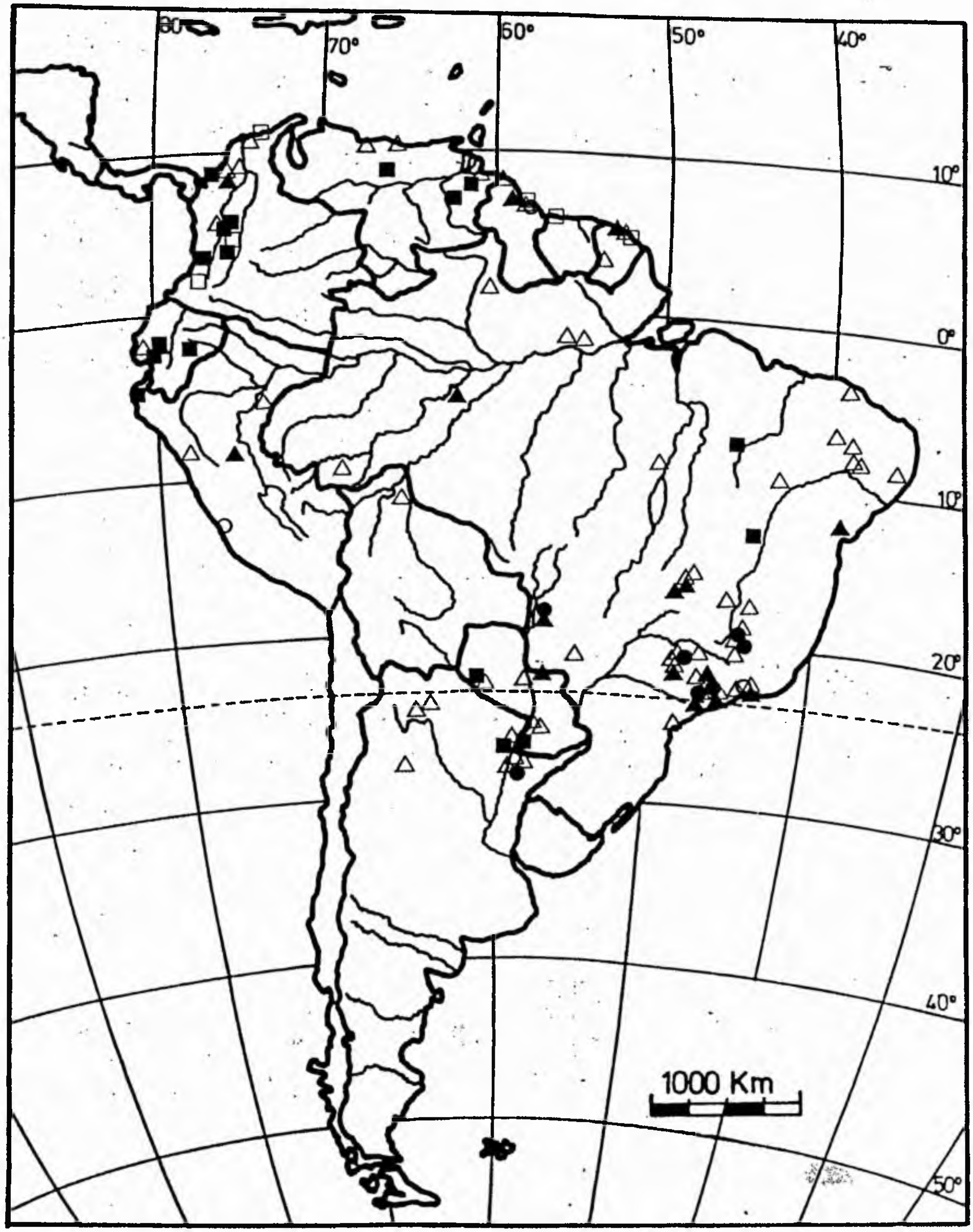
■ *S. emerus*

△ *S. exasperata*

● *S. oligosperma*

□ *S. sericea*

▲ *S. sesban*


80°
70°
60°
50°
40°
10°
0°
10°
20°
30°
40°
50°
1000 Km

(3) . Sesbania exasperata H.B.K.

Nov. Gen. Sp. Pl. 6 : 534, 1824

syn. : Lotus palustris Vell.
Fl. Flum. : 315, 1825, Atlas 7, t. 137, 1835
Sesbania dubia Steud.
Nom. Bot. 2 : 572, 1841. Non S. dubia H.B.K.,
Nov. Gen. Sp. Pl. 7 : 268, t.660, 1825
Emerus exasperatus Kuntze
Rev. Gen. Pl. 1 : 181, 1891
Sesbania paulensis Barb. Rodr.
Plant. Nov. Jard. Bot. Rio de Janeiro,
2 : 13-17, t. 2, 1893

Shrub, woody, to 3 m tall, stem angulous, striate, sometimes with whitish spines in the angles. Leaves 20-30(-40) cm, large, with (15-)20-25(-30) pairs of leaflets; leaflets narrowly elliptic to oblong, mucronate at the apex, 30x5 mm, petiolules 1.5-2.0 mm, stipules linear to lanceolate, acuminate, 5-12 mm, brownish. Racemes (5-)6-12(-18) cm, with 2-6 flowers on relatively thick pedicels of 4.0-7.0 mm; bracts and bractlets linear to narrow-lanceolate. Flowers yellow, 18-30 mm; calyx broad-campanulate, 6.5-8.0(-10.0) mm (including the lobes); the lobes (1.5-)2.5-3.5(-4.0) mm, triangular, acuminate; standard suborbiculate to broad ovate, with long raised appendages at the base of the blade, yellow with dark purple streaks and dots externally; wing and keel petals with an upper basal triangular to linear-triangular, acuminate tooth; wings oblong to obovate, up to 25 mm; keel petals obovate, to 25 mm, the claw 5-9 mm. Staminal sheath 24-26 mm. Pods 250-300 x 4-7 mm, beaked, stipitate, the margins thickened and slightly indented between the seeds. Seeds oblong, 30-40 per pod, 4-5 x 2.0 mm, brown. Figure 64.

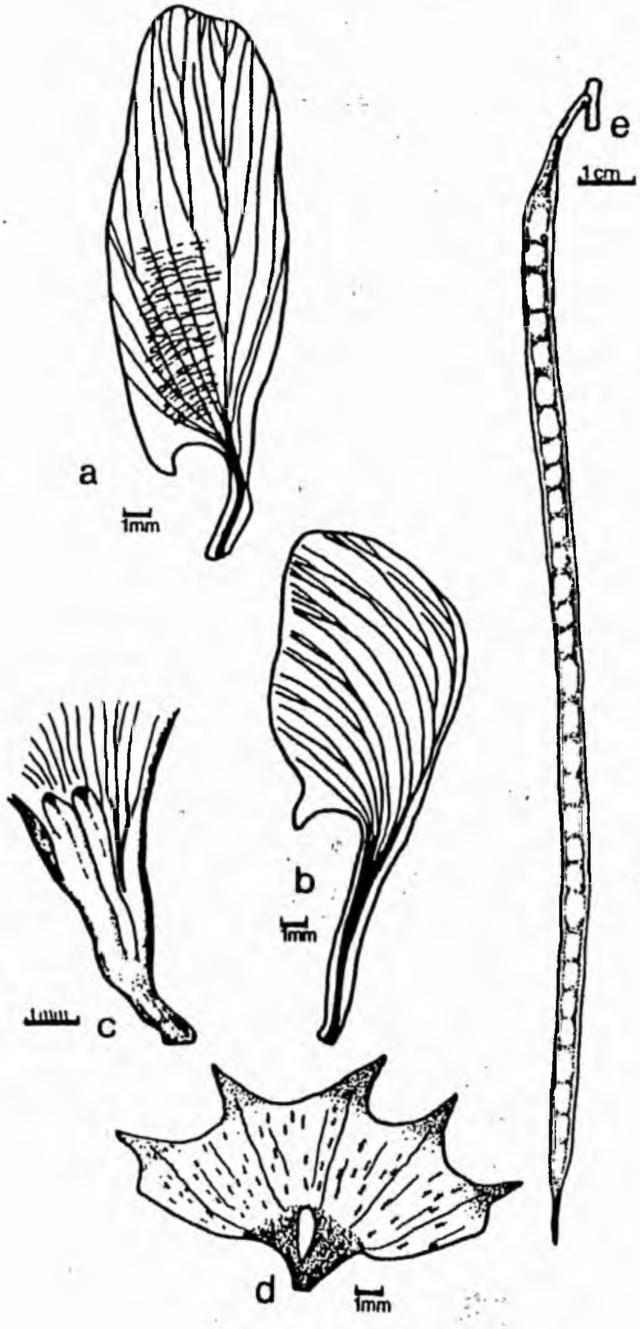


Figure 64 - Sesbania exasperata H.B.K. a - wing petal; b - keel petal; c - detail of the standard claw showing the pair of appendages; d - calyx, flattened out; e - pod.

Type – Venezuela : "locis arenosis apuris", Valles de Aragua, Laguna de Valencia, HUMBOLDT, BONPLAND & KUNTH 811, date ? (P!).

S. exasperata is often found in South America and the West Indies. Apart from the close relationship with *S. oligosperma*, a species which may have derived from the same ancestral stock, *S. exasperata* does not show similarities with any other taxa of subgen. *Sesbania* in the New World.

However, two large-flowered species from Africa, *S. dummeri* Phill. & Hutch. and *S. hepperi* Gillett, both of subgen. *Sesbania*, do resemble *S. exasperata* in habit and other features. Although different from the latter species in several aspects (stipules large and persistent; greater number of flowers per raceme; large, alate to falcate appendages of the standard petal; pod morphology, etc), these African taxa show similar keel and wing petal shapes. In all, similarities between the African species and *S. exasperata* are minimal and scarcely suffice to establish an evolutionary relationship but they do provide a vague and rather inconclusive link between the species of the New and Old World.

Distribution (Figures 63, 65)

CENTRAL AMERICA

El Salvador – South side of Lake Olomega, lat. 13° 17'N, long. 88° 04'W, TUCKER 834, 25.i.1942 (G,LL).

Mexico – state of Guerrero : Acapulco, BOEGE 2446, 10.viii.1972 (MEXU); state of Oaxaca, pueblo of San Mateo del Mar, TELLEZ &

MAGALLANES 161, 20.ix.1976 (BM,MEXU); state ?, Lag. Epatlan, MIRANDA 2486, 11.xii.1942 (MEXU).

Nicaragua - "environs de Grenade", LEVY 3489, i.1870 (P); no local. ment., LEVY s/n, s/d (P); Omotepec, WRIGHT s/n, 1853-56 (NY,P).

NORTH AMERICA

Southeast - Florida : Kissimmee Billy, north of Alligator Alley, CORRELL & POPENOE 47304 & SMILEY, 8.vii.1976 (FTG).

SOUTH AMERICA

Argentina - Corrientes : San Cosme, 25 km E of Corrientes, Ruta 12, AHUMADA 1595, 25.ii.1978 (G); General Paz, Tacuaral, PEDERSEN 7025, 18.v.1964 (K,P); Capital, Paso Pessoa, PEDERSEN 8065, 14.ii.1967 (K,P); Saladas, Estancia La Amistad, SCHWARZ 9668, 11.ii.1950 (K); Formosa : Formosa, JORGENSEN 2723, iii.1918 (MO); Jujuy : Ledesma, camino Ledesma-Caimancito, LEGNAME & VACCA 3062, 20.iii.1963 (NY); Salta : San Martin, Padre Lozano, KRAPOVICKAS & SCHININI 30867, 3.iv.1977 (G); Tucumán: Burroyaes, Rio Nio, VENTURI 10384, 7.iii.1930 (BM,MO,NY).

Bolivia - Cercado : Santa Cruz, playa banado del Piray, STEINBACH 3251, 20.ii.1917 (BM,G,K,MO).

Brazil

North - state of Acre : Rio Branco, ULE 7788, i.1909 (K); state of Amapa : São Joaquim, Rego Furtado, BLACK & LOBATO 50-9413, 16.iv.1950 (NY); state of Amazonas : Paraná do Autaz-Mirim, Fazenda Santa Rosa, BERG, BISBY & MONTEIRO P19776, 27.viii.1973 (MO,NY); Tapeirinha, GINZBERGER s/n, 25.vi.1927 (W), GINZBERGER 715, 10.vii.1927 (W); lago dos Passarinhos, JUNK 37, 19.vii.1974 (NY); without exact location, SPRUCE 1597, vi.1851 (P); "upper Amazon and tributaries", TRAILL 130, 11.xii.1874 (K); state of

Para : Cacanal Grande, "baixia em que entram os canais Fernando Costa e V. C. Miranda", BLACK 52-15410, 5.vii.1952 (NY,P); municipio of Oriximina, Rio Trombetas, "margem esquerda", Lago Iripixi, CID et al. 2416, 12.ix.1980 (NY); região Xambioá, Rio Araguaia, OLIVEIRA 1373, 11.iii.1961 (NY,UB); Santarém, SPRUCE 979, vii.1850 (P), SPRUCE s/n, vii.1850 (BM,E,G,K,NY,P,TCD); territory of Roraima : Fazenda São Marcos, "confluência do Rio Tacutu com Uraricuera", SILVA 280, 9.iv.1964 (UB).

Northeast - state of Bahia : Joazeiro, ZEHNTNER s/n, vii.1912 (M), ZEHNTNER s/n, 1913 ? (M); state of Ceará : no local. ment. ALLEMÃO & CISNEIROS 345, no date (P); município de Maranguape, Lagoa Maracandu, DROUET 2679, 6.xi.1935 (MO,NY); Quixada, DUCKE 1075, 4.vii.1908 (G); state of Pernambuco : "entre Serra Talhada e Petrolina", HERINGER et al. 5, 17.iv.1971 (RB,UB); "entre Bom Nome e Jati", HERINGER et al. 762, 14.v.1971 (UB); no local. ment., MARTIUS s/n, no date (K); Nazaré da Mata, MORAES 1168, 16.v.1954 (NY).

South - state of Paraná : Paranagua, GARDNER 2540, 2541, viii-ix.1839 (BM,FHO,K); state of Santa Catarina ; no local. ment., MUELLER 217, vi.1868 (K).

Southeast - state of Minas Gerais : Belo Horizonte, Jardim Botânico, BARRETO 5660, 24.v.1934 (SP; no local. ment., CLAUSSEN 902, 1838 (P); ibidem, CLAUSSEN s/n, 1840 (NY); between Sítio and Barbacena, GLAZIOU s/n, 22.vi.1879 (P); Serra do Cabral, ca. 5 km of Parada das Batistas, IRWIN et al. 27395, 11.iii.1970 (K,MO,NY, RB); Capinópolis, MACEDO 4067, 15.xii.1955 (MO); Corinto, Fazenda do Diamante, MEXIA 5700, 22.iv.1931 (BM,CAS,G,K,MO,NY,P); no local. ment., St HILAIRE 1568, 1816-21 (P); Lagoa Santa, WARMING s/n, no date (MO,P); state of Rio de Janeiro ; no local. ment., GLAZIOU 12574, ii.1882 (G,K); Baixada do Rio de Janeiro, HOEHNE 85, iii.1916 (SP); Lagoa de Piratininga, RIEDEL 1300, iv.1833 (BM, NY,P,W); state of São Paulo : Taubaté, BRAGA JR s/n, 3.iv.1928 (SP); município of Ituverava, road Franca-Ituverava, 2 km of Ituverava, BUFARAH, PLATES & OLIVEIRA LEITE 281, 22.ix.1977 (UB, UEC); município de Valinhos, LEITÃO FILHO 6748, 5.xii.1977 (UEC); município de Campinas, LEITÃO FILHO *et al*. 7985, 14.vi.1978 (UEC); ibidem, district of Barão Geraldo, LEITAO s/n, 28.iv.1981 (UEC); São Paulo City, Cidade Universitária, MARTINS 2254, 5.viii.1976 (UEC); município of Ribeirão Preto, in swampy riceland on shore of Mogi-Guaçu River, near village of Guatapará, 21°30'S, 48°2'W, NORRIS 268, 26.v.1964 (NY); ibidem, NORRIS 290, 27.v.1964 (NY); município of Matão, Matão, NORRIS 268, 26.v.1964 (NY); no local. ment., St HILAIRE 809, 1816-1821 (P).

West Central - state of Goiás, Federal District : Brasília, cultivated, HERINGER 12831, 8.vii.1973 (UB,UEC); Chapada da Contagem, 30 km NE of Brasília, IRWIN, SOUZA & REIS DOS SANTOS 8466, 19.ix.1965 (NY,UB); state of Mato Grosso do Sul : município of Campo Grande, Anhandui, HATSCHBACH 21830, 12.vii.1969 (NY); município of Bataguassu, Porto XV, HATSCHBACH 23515, 14.ii.1970 (MO); Rio Paraguai, KUNTZE s/n, vii.1892 (NY).

Brazil, locality unknown : GLAZIOU s/n, no date (P); JOBERT 1204 , 1877-1878 (P); POHL s/n, 1836 (K); SPRUCE 1597, vi.1851 (P).

Colombia - Córdoba, 10 km NE of Monteria, ANDERSON 1902, 21.xii.1969 (K); Choco : município of Riosucio, Parque Nacional Los Katyos, LEON 683, 2.xii.1976 (MO); Las Flores, near

Barranquilla, PAUL 884, i.1932 (G); Bolivar, Magangue, PENNELL 3962, 18-19.i.1918 (MO,NY); Magdalena, Isla de Salamanca, ROMERO-CASTANEDA 10433, 26.xi.1966 (MO,NY).

Ecuador - Duran, SCHIMPFF 1113, 20.v.1934 (MO).

French Guyana - Maroni, MELINON 351, 1876 (P); Cayenne, RICHARD s/n, no date (P).

Guyana - Cay, CLAUDE s/n, no date (P); Georgetown, PARKER s/n, no date (K); no local. ment., SCHOMBURGH 1595, vii-x.1843 (P).

Paraguay - Asunción, BALANSA 1379, i.1877 (G,K,P); Madrigan, Aguada del Pescadero, FLOSSDORF 131, 28.xi.1906 (G); "Chaco Septentrionalis", Puerto Talavera, FRIEBRIG 1213, viii.1907 (G); Gran Chaco, Santa Elisa lat. 23°10', HASSLER 2775, ii.1903 (G); Laguna Ypacaray, HASSLER 3948, date ? (G,K,NY,P); Concepción, Paraguay River, HASSLER 7500, ix.1901 (G,NY); ibidem, HASSLER 7620, x.1901 (G); Laguna Ypacaray, HASSLER 11500, i.1913 (E,G,K,MO); Rio Pilcomayo, MORONG 934, 18.ii.1890 (E,K,MO,NY); ibidem, ROJAS 491, vii.1906 (G); Paraguay River, WEDDELL 3190, iv-v.1845 (P), WEDDELL 3260, iv-v.1845 (P).

Peru - Loreto : Maynas, seasonally inundated shrubbery along banks of Rio Amazonas below Tamshiyacu, GENTRY *et al*. 25778, 18.iii.1979 (MO); Lanzal : Chicama, MARTINET 406, no date (P).

Surinam - Nickerie, in *Cyperus articulatus* swamp along Huntley Creek, LANJOUW & LINDEMAN 3107, 5.v.1949 (K,NY); ibidem, on outer side of levee of Nanni creek, LANJOUW & LINDEMAN 3208, 10.v.1949 (K,NY); no local. ment., HARTMANN 761, 1843 (K,P,TCD); Nickerie : Nieuw-Nickerie, bank of Nanni creek, S of town, HEKKING 964, 30.viii.1961 (LL).

Venezuela - Miranda : Rio Chico, ARISTEGUIETA 2720, i.1957 (NY); Delta Amacuro ; along Cano Araguao, lat. 9°05'N, long. 61°6'W STEYERMARK, LIESNER & DELASCIO 114836, 17.x.1977 (MO).

WEST INDIES

Cuba - Yumury, RUGEL 229, 1849 (BM,MO,NY,P).

Dominican Republic - Province of San Domingo : Llano Costero - San Domingo City, eastern bank of Rio Orama, EKMAN 11168, 14.i.1929 (G,K,NY).

Guadeloupe - no local. ment., DUNCHANDING s/n, no date (P); Pointe des Chateaux, GERMAIN s/n, x.1866 (G); ibidem, collector ?, 1848 (TCD).

Jamaica - no local. ment., HOOKER s/n, xii.1874 (P).

Martinique - no local. ment., HAHN 319, no date (P).

Montserrat - region southeast of Silver Hill, PROCTOR 19148, 11.ii.1959 (BM,LL).

Puerto Rico - Mayaguez, Cuesta de las Piedras, SINTENIS 102, 26.x.1884 (G,P); Guanira, SINTENIS 3802, 18.ii.1886 (BM,G,MO,NY,P,W).

St Kitts - no local. ment., BRITTON & COWELL 728, 8.ix-5.x.1901 (NY).

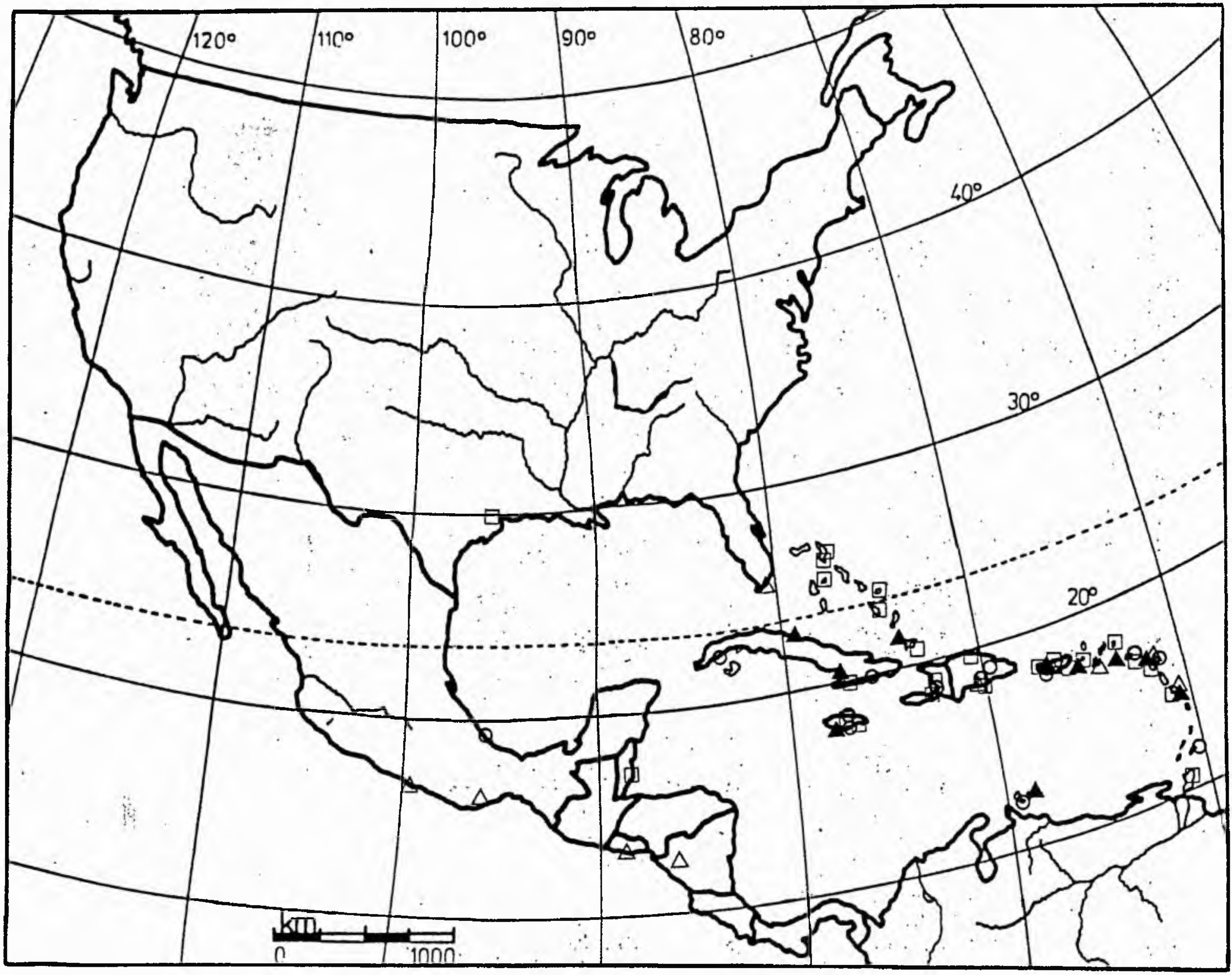
Figure 65 - Distribution map of <u>Sesbania</u> subgen. <u>Sesbania</u> in Central America and West Indies.

○ <u>S. bispinosa</u>

△ <u>S. exasperata</u>

□ <u>S. sericea</u>

▲ <u>S. sesban</u>


120°
110°
100°
90°
80°
40°
30°
20°
km
0
1000

(4) . *Sesbania oligosperma* Taub.

FLORA 72 : 423-424, 1889. Non *S. oligosperma* Glaziou *, BULL. SOC. BOT. FRANCE 53, Mem. 3 : 130, 1906.

Shrub, woody, to 3 m tall, stem angulous, striate, unarmed. Leaves (9-)15-20(-30) cm, narrow to large, with (7-)10-20(-35) pairs of leaflets; leaflets narrow-elliptic to ovate, mucronate, petioles 0.5-0.9 mm; stipules not seen. Racemes 6-18 cm, with 2-4 flowers, pedicels 4-7 mm; bracts and bracteoles not seen but scars of bracteoles seen on pedicels, below the calyx. Flowers yellow, 20-25 mm; calyx campanulate, 5.5-8.5(-10.0) mm (including the lobes), the lobes 2.5-3.5(-4.0) mm, triangular-deltoid; standard suborbiculate to broad-ovate, appendages raised, similar to *S. exasperata*; wing petals obovate, up to 28 mm, with an upper basal narrow-triangular, short acuminate tooth; keel petals obovate to ovate, 25-27 mm, the claw 10-15 mm, with a reduced or absent tooth. Staminal sheath 20-24 mm. Pods 150-200 x 4.0-5.5 mm, beaked, stipitate, constricted-moniliform (by abortion of ovules or seeds) to linear, slightly constricted between the seeds. Seeds oblong, 20-25 per pod, 4-5 x 2.2 mm, brown. Figure 66.

Type - Brazil, state of Sao Paulo : "in humidis Batataes", RIEDEL 2237, v.1834 (B, holotype not seen; phototypes G!, NY!, TEX!, W!; isotype K!).

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* The type of *S. oligosperma* Glaziou, "Brazil, state of Minas Gerais : Carandai, GLAZIOU 14670, i.1882 (P!)", is a *Coursetia* species probably as yet undescribed.

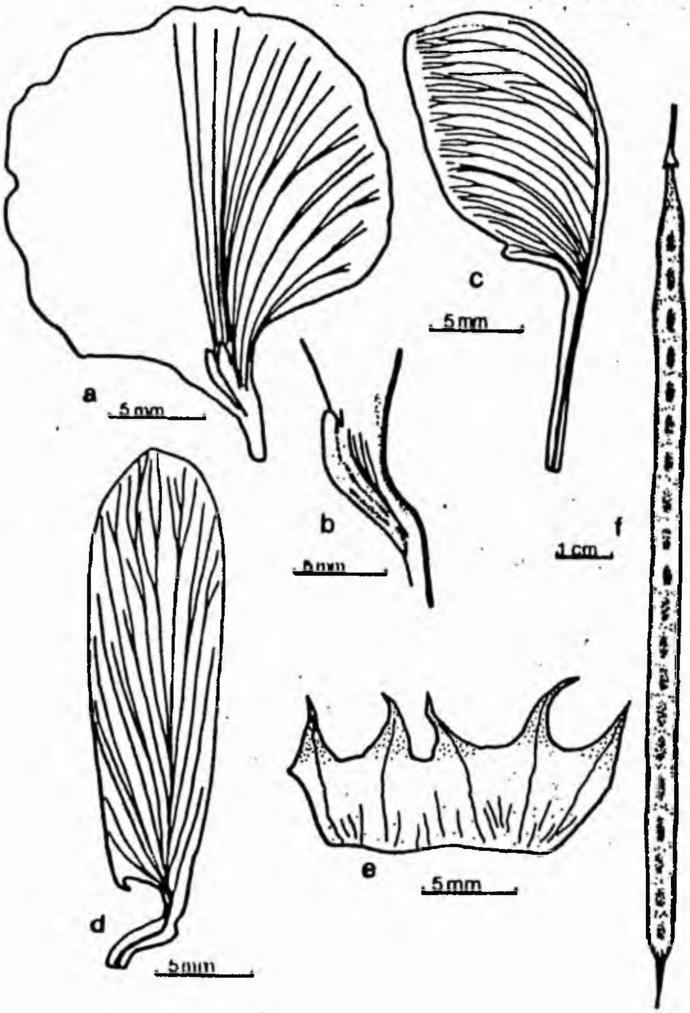

Figure 66 - *Sesbania oligosperma* Taub. a - standard; b - longitudinal section of the standard claw showing the appendage; c - keel petal; d - wing petal; e - calyx, flattened out; f - pod.

S. oligosperma is very close to *S. exasperata* due to corolla colour and size, and to the similarity of pods. However, it is immediately distinguishable from the latter taxon by its narrower wing petals and absence of the teeth in the upper basal angle of the keel petals blade. Furthermore, a reduction of the pod length and, consequently, a decrease of number of seeds makes this species even more distinct from *S. exasperata*.

In the original description of *S. oligosperma* TAUBERT (*loc. cit.*) observed that the ovary of type specimens were pluriovulate although the mature pods showed, by abortion, a very small number of seeds which, together with the constrictions between the seeds gave the fruits a moniliform appearance. Because of this morphological modification, apparently unknown in other Sesbanias, TAUBERT (1889) created a new section for the genus, sect. *Moniligeram*, in which he included his new species. However, the present study has revealed that several specimens of *S. exasperata* show the many-ovules to few-seeded characteristics of *S. oligosperma* although in *S. exasperata* the pods are not constricted. Furthermore, it is possible that the constrictions in the pods of the plants studied by TAUBERT (*loc. cit.*), might have been caused by nematode or beetle infections, since in most materials of this species which have been seen such constrictions are lacking. Therefore, the section *Moniligeram* is here rejected and treated as a synonym of subgen. *Sesbania*.

S. oligosperma has so far been found only in central and southern Brazil, and north-eastern Argentina but it may have a broader distribution. It would be of interest to explore its relationships with *S. exasperata* on reproductive and cytological grounds.

Distribution (Figure 63)

SOUTH AMERICA

Argentina - Province of Corrientes, Dept of Mburucuyá : Estancia Santa Teresa, PEDERSEN 6977, 6.iii.1964 (E,MO,P).

Brazil

Southeast - state of Minas Gerais : Paraopeba, Fazenda do Rasgão, near Horto Florestal de Paraopeba, HERINGER 5139, no date (NY,UB); Sete Lagoas, HERINGER 7232, 26.x.1959 (NY,UB); state of São Paulo: Taubaté, CAMARGO 1, 7.xii.1937 (SP); São Paulo city, EDWALL 2514, iii.1894 (SP).

West Central - state of Mato Grosso do Sul : Fazenda Acurrizal, Rio Paraguai (57°32'W, 17°52'S), PRANCE *et al.* 26079, 7.vi.1979 (NY).

Brazil, without precise locality : collector ?, no date (K).

(5) . *Sesbania bispinosa* (Jacq.) W.F. Wight

U.S. DEPT. AGR. BUR. PL. IND. BULL. 137 : 15, 1909

syn. : *Aeschymonene bispinosa* Jacq.
Ic. Pl. Rar. 3 : 13, t.564, 1793
Aeschynomene sesban Jacq.
Coll. 2 : 283, 1788. Non *A. sesban* L., 1753
Coronilla aculeata Willd.
Sp. Pl. : 1147, 1803, nom. illegit.
Sesban aculeatus (Willd.) Poir.
Lam., Encycl. 7 : 128, 1806, nom. illegit.
Sesbania aculeata (Willd.) Pers.
Syn. Pl. 2 : 316, 1807, nom. illegit.
Emerus aculeatus (Willd.) Horn.
HORT. REG. BOT. HAUN. 2 : 696, 1819
Sesbania muricata Macfad.
Fl. Jam. 1 : 257, 1837

Shrub 2-3 m tall; stem and abaxial face of the leaf rachis usually armed with short prickles. Leaves 15-30 cm, with 20-35 pairs of leaflets; the leaflets linear-oblong, 10-15 x 2-3 mm; petiolules 0.6-1.0 mm; stipules linear-subulate, 3-4 mm. Racemes 3-7 cm with 2-6(-7) flowers; pedicels slender, 10 mm; bracts and bracteoles subulate. Flowers yellow, 10-12(-15) mm; calyx campanulate, 4-5 mm (including the lobes), the lobes 1.0 x 1.5 mm, deltoid, acute; standard suborbicular with raised short, blunt appendages on the claw, mottled with reddish (?) brown externally; wings oblong-lanceolate, 9-12 mm; keel petals upcurved, oblong to oblong-lanceolate, the blade twice the length of the claw. Staminal sheath 9-11 mm. Pods 170-250 x 3-5 mm, beaked, usually slightly constricted between the seeds, the margins relatively thickened. Seeds 35-40(-45) per pod, 3 x 1.5 mm, brown. Figure 67.

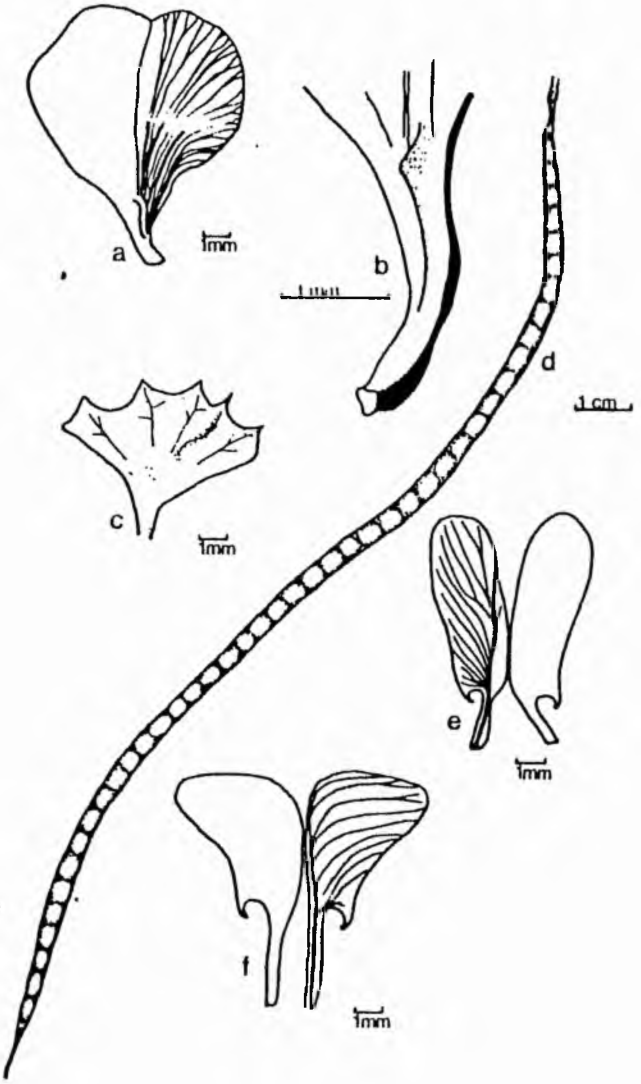

Figure 67 - <u>Sesbania</u> <u>bispinosa</u> (Jacq.) W. F. Wight. a - standard; b - longitudinal section of standard showing the appendage; c - calyx, flattened out; d - pod; e - wing petals; f - keel petals.

Type - Illustration of a plant cultivated in Vienna before 1788, in JACQUIN's "Ic. Pl. Rar.", t.564. GILLETT (1963) mentions that the specimen used in Jacquin's illustration is of an unknown origin (probably Asiatic).

S. bispinosa is native of tropical Africa and Asia, and southern China. In the New World it is found mostly as an introduced weedy species distributed from southern Mexico and the West Indies to northern South America.

GILLETT (1963) recognised two varieties of *S. bispinosa*, var. *bispinosa* and var. *micrantha* (Chiov.) Gill., both distributed in the Old and New World. *S. bispinosa* var. *micrantha* differs from the typical variety in having 1-2-flowered rather than 2-6-flowered racemes and smaller flowers with a shorter filament-sheath. GILLETT (*loc. cit.*) mentioned its occurrence in northern Guyana (collection by GRAHAM 416, 15.v.1960, Georgetown, not seen) where it was found to have yellow standard not mottled with purple. However, a later collection in the same area (GRAHAM 567, 15.vii.1961, not seen) showed the flower also not mottled but the racemes with 4-5 flowers. A variable number of flowers per raceme was also found by GILLETT (1963) in one specimen from India, which was unarmed. Such variations in the differential characters between the varieties, and also the unusual distribution of var. *micrantha* led GILLETT (*loc. cit.*) to consider that this variety was best regarded as an ecotype of *S. bispinosa*. In the present revision only the typical var. *bispinosa* was observed among the

New World specimens, including a single collection from Georgetown, Guyana.

Distribution (Figures 63, 65)

CENTRAL AMERICA

Mexico - Vera Cruz, MULLER 82, 1853 (NY); município of Puente Nacional, VENTURA 7099, 9.x.1972 (LL,SD); no local. ment., collector ? 2043, 2.ii.1896 (NY); ibidem, collector ?, date ? (K).

SOUTH AMERICA

Brazil - Southeast : no local. ment., between São Paulo and Rio de Janeiro, BALL s/n, 1882 (E); state of Rio de Janeiro, GLAZIOU 12553, ii.1882 (K).

Guyana - Georgetown : a piece of saline wasteground just above W. Mark, Georgetown beach, COCHRAM 567, 15.vii.1961 (K).

Peru - Lima, RUIZ & PAVON s/n, no date (K).

WEST INDIES

Antigua - Rock Hill, BOX 950, 6.viii.1937 (BM,MO); near St John, SHAFER 29, 16-17.i.1907 (NY); no local. ment., DUSS 25, xii.1902 (NY).

Barbados - Foster Hall Spring, EGGERS 7129, 22.v.1890 (P); roadside ditch, GOODING 107, i.1940 (BM).

Cuba - Pinar del Rio, near lagoon, CUESTA 666, vi.1913 (NY); no local. ment., WRIGHT s/n, no date (NY).

Curaçao - no local. ment., CURRAN & HAMAN 221, 6.iii.1917 (NY); no local. ment., BOLDINGH 5219, date ? (NY); water course, Mt. Pleasant, BRITTON & SHAFER, 3120, 20-27.iii.1913 (NY); no local. ment., REALINO 23, 1945 (NY).

Dominican Republic - province of Santo Domingo : Valle del Cibao, Navarrete, EKMAN 16124a, 3.xi.1930 (MO,NY); on roadside in a ditch, from Seibo to Miches, LIOGIER 18628, 13-14.vi.1972 (NY); Santo Domingo, near the Botanic Garden, LIOGIER 20238, 20.ix.1973 (NY); near Guerra, LIOGIER & LIOGIER 23993, 8.x.1975 (NY).

Guadeloupe - "Pomle a Pilie", QUENTIN 102h, vii.1935 (P).

Haiti - Port-au-Prince, EKMAN 9631, 25.ii.1928 (NY).

Jamaica - Grant's Pen, Albion Pond, ADAMS 8312, 13.xi.1960 (MO); St Vincent, CALEY s/n, viii.1818 (BM); Parish of St Thomas; roadsides, Holland Bay, BRITTON 4068, 1-13.iii.1909 (NY); St Catherine : Port Esquivel, PROCTOR 28585, 2.iv.1968 (MO); Clarendon: St Jago state, PROCTOR 32976, 15.x.1972 (LL).

Puerto Rico - no local. ment., SHAFER 1975, 13.iii.1913 (MO); Guayanillo, STERUS 5926, 13.xi.1913 (NY).

Without precise locality : RITCHIE 174, no date (NY).

(6) . *Sesbania* *sericea* (Willd.) Link

Enum. Hort. Berol. *2* : 244, 1822

syn. : *Coronilla* *sericea* Willd.
Enum. Pl. Hort. Reg. Bot. Berol. : 773, 1809
Sesbania *pubescens* DC.
Prodr. *2* : 265, 1825
Emerus *pubescens* (DC.) Schumach. & Thonn.
Beskr. Guin. Pl. : 354, 1827
Agati *sericea* Hitch.
Rep. Mo. Bot. Gard. *4* : 75, 1893

Shrub to 3 m tall; stem somewhat angulous but often cylindric, pubescent, usually unarmed or sometimes with minute prickles on the base of the leaf rachis and on the angles of the stem. Leaves 10-25 cm, narrow, with 12-20 pairs of leaflets; leaflets oblong-linear, mucronate, 10-25 x 3-6 mm, glabrous above, sericeo-villous beneath; petiolules 0.5-1.0 mm; stipules subulate, to 5 mm long. Racemes 3-6 cm with 1-4(-6) flowers on slender pedicels; bracts and bracteoles linear to linear-lanceolate, acuminate. Flowers yellow, 9-12(-15) mm; calyx campanulate, 4-5 mm (including the lobes), the lobes 1.0 x 1.5 mm, deltoid, acuminate; standard suborbicular, wider than long, with non-acute raised appendages on the claw, dotted or mottled with black externally; wing and keel petals with an upper basal broad, blunt tooth; wings oblong-lanceolate, up to 8 mm; keel petals upcurved, the blade oblong to obovate, to 8 mm, the claw 5 mm. Staminal sheath 5-7 mm. Pods 170-200(-250) x 3.0-4.0 mm, short-beaked, not constricted between the seeds. Seeds cylindric-oblong, 25-35(-40) per pod, 3.0 x 2.0 mm, brown. Figure 68.

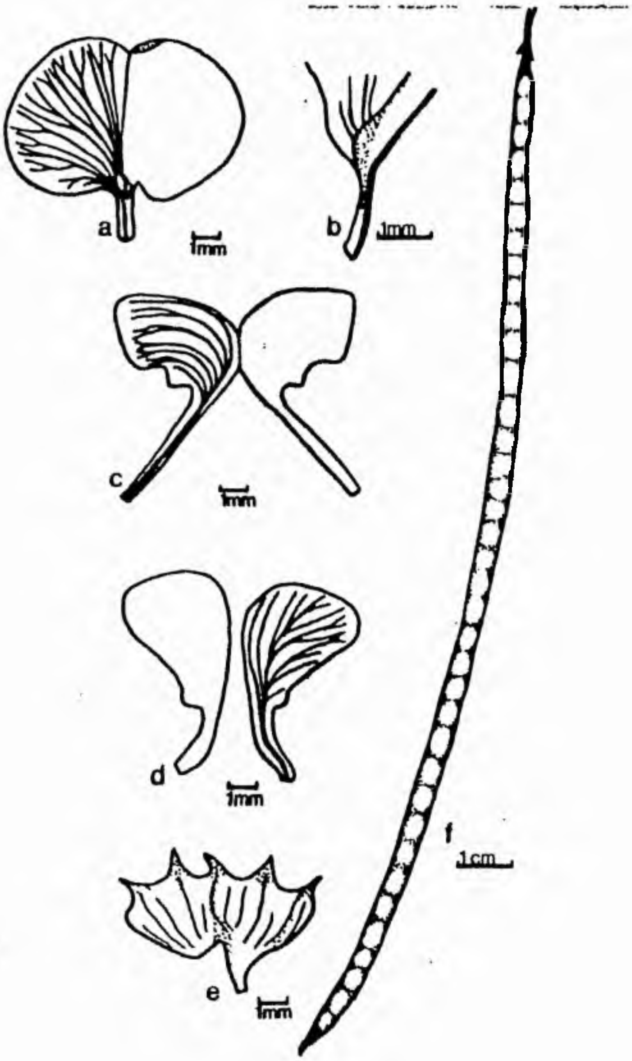

Figure 68 - Sesbania sericea (Willd.) Link. a - standard; b - longitudinal section of the standard base showing the appendage; c - keel petals; d - wing petals; e - calyx, flattened out; f - pod.

Type - Sri Lanka : introduced near Colombo, FERGUSON in THWAITES C.P.3850 (BM!, K!, neotype).

The type of Coronilla sericea Willd. was a plant cultivated at Berlin which has not been preserved. Curiously, GILLETT (1963) selected as a neotype a collection from Sri Lanka, although, in discussion, he argued that S. sericea was probably native only to Africa, and dispersed by Man elsewhere, and furthermore he suggested that seeds of this species which was originally cultivated at Berlin were supplied by Thonning from West Africa.

The first records of S. sericea in the New World already mention that the species was from African or Asiatic origin. This fact supports GILLETT's assertion that the species has been dispersed by Man.

In the New World, S. sericea is mostly found in the West Indies, but there are also some additional records from Central America and northern South America.

The species has been commonly collected in irrigated fields and naturally wet lowland areas and it is notably annual.

Distribution (Figures 63, 65)

CENTRAL AMERICA

Belize - Belize, DIECKMAN 133, 8-15.ii.1970 (MO); Northern River, GENTLE 1368, 15.viii.1934 (LL,MO,NY); no local. ment., LUNDELL 1890, 9.iii.1933 (LL).

NORTH AMERICA

South Plains - Texas : Houston, KUNTZE 23815, viii.1904 (NY).

SOUTH AMERICA

Colombia - Dept of Atlantico : playa de Miramar, Puerto Colombia, DUGAND 5230-A, 2.iii.1960 (NY); ibidem, ibidem, DUGAND 6151, 8.x.1962 (NY); Dept of Santander : Carare, GENTRY & REUTERIA 20131, 2.x.1977 (MO); state of Antioquia ; Puerto Berrio, Magdalena River bridge, NEE & MORI 3816, 28.iii.1971 (MO).

French Guyana - Cayenne, LAGOTZ s/n, 1859 (K).

Guyana - Georgetown, FOREST DEPT FIELD No. F3480, 16.ix.1952 (K); ibidem, in Botanic Garden, HITCHCOCK 16626, 5.xi.1919 (NY); ibidem, JENMAN 4538, x.1888 (K,NY); without precise locality, LEECHMAN s/n, date ? (K); Georgetown, PARKER s/n, 1833 (K).

Suriname - Nickerie : Nieuw-Nickerie, Prins Benhard-polder, ca. 10 km SE of the town, HEKKING 1154, 24.xi.1961 (K,LL,NY).

WEST INDIES

Antigua - Gunthorpes, BOX 1163, 15.x.1937 (MO).

Bahamas - Great Abaco : between cane field and Great Abaco Highway, about 15 mi. SE of Marsh Harbour, CORRELL & MEYER 44690, 15.iii.1975 (FTG); grassy edge of sugar cane field along Great Abaco Highway, about 11 mi. S of Marsh Harbour airport, CORRELL & POPENOE 42685, 7.vii.1974 (FTG,LL,NY); along road to Willson City, 2.4 mi. of junction with main road, WUNDERLIN et al. 8484, 16.xii.1979 (MO); Great Inagua : in open flats and dry depressions about 1 mi.E of Matthew Town, CORRELL 41681, 1.iii.1974 (LL,MO,NY); in and about Horse Pond, just NE of Matthew Town, CORRELL 45816, 31.vii.1975 (FTG,NY); in disturbed saline soil on flats about Morton Salt pans, CORRELL 45862, i.viii.1975 (FTG,NY); in thin soil on rock flats on drainage slope of Marroon Hill, CORRELL 47515, 25.vii.1976 (FTG,MO,NY); Long Island : common in low area on south edge of Clarence Town, along Queen's Highway, CORREL 49121, 18.xi.1977 (FTG,NY); New Providence : in low weedy area where water accumulates near corner of Blue Hill Road and Palmetto Avenue, Nassau, CORRELL 48306, 24.iii.1977 (FTG,NY); in moist and wet soils on flats and in marshes, about Nassau airport, CORRELL 49103, 17.xi.1977 (FTG); near Nassau, HITCHCOCK s/n, xi.1890 (MO); Rum Cay : Port Nelson, BRACE 3932, 4.xii.1905 (NY); in open sandy soil on edge of coppice about Port Nelson, CORRELL & WASSHAUSEN 46738, 14.ii.1976 (FTG,NY).

Guadeloupe - Agronomic Station of Guadeloupe, DASH s/n, 8.iv.1920 (K); Baie Mahanes, DUSS 3012, 1892 (MO; no local. ment., QUESTEL 1479, date ?, 4651, 6.iii.1847; s/n, no date (P).

Cuba - Province of Oriente : Bayate, in the banks of River Jagua, EKMAN 6547, 3.xi.1915 (NY).

Dominican Republic - Villa Mella, LAVASTRE 2329, 5.xi.1966 (NY); near San Cristobal, LIOGIER 17719, 24.xi.1970 (NY); Puerto Plata, LIOGIER 9047-16, 12.xi.1977 (NY); Santo Domingo : "en lugar herboso, cerca de Bani", LIOGIER & LIOGIER 25956, 11.xi.1976 (NY).

Haiti - Guala, AUGUSTO 626, 9.ii.1963 (NY); Massif de la Hatte, Fand-des-Negres at Hab. Buttet, EKMAN 7160, 3.xi.1926 (NY); Port-au-Prince ; Plaine cul-de-sac, in streets, probably recently introduced, EKMAN 9631 , 25.ii.1928 (K); Marfranc, SEIBERT 1746 , 20.ii.1942 (MO,NY).

Jamaica - Ste Catherine ; Caymanas to Port Henderson Flats, ADAMS 6548, 10.iii.1960 (MO); road Kingston to Spanish Town, HARRIS 9051, 3.xi.1905 (NY); Kingston, in the streets, HITCHCOCK s/n, 19.xii.1890 (MO); Kingston ; Port Royal, PROCTOR 31096, 17.xi.1969

(FTG,MO); Ste Catherine : 0.7 mi. NE of Port Henderson, PROCTOR 31508, 1.xi.1970 (LL); Ferry, collector ? 6171, 24.i.1896 (NY).

Martinique - "anses d'Arlet", Trinite, DUSS 1060 , 1879 (NY).

Puerto Rico - Ponce, Hacienda Esperanza, ALAIN 9041, 30.xii.1961 (NY); Laguna Rica, BRITTON & BRITTON 7948, 2.ii.1924 (NY); Eirmada, cultivated ground, BRITTON, BRITTON & BOYNTON 8324, 9.iii.1925 (NY); vicinity of San Juán, BRITTON & COWELL 1465, 11-12.ii.1914 (NY); between Ponce and Santa Isabel, coastal marsh, BRITTON 7 BROWN 5516, 18.iii.1915 (MO); vicinity of Aguirre, BRITTON & EARLE 6484, 1.iii.1922 (NY); Coamo Reservoir, BRITTON, BRITTON & BROWN 5942, 8.ii.1922 (NY); Las Croabas, BURCH 3415, 23.iii.1971 (MO); near Mayaguez, HELLER 4416, 27.i.1900 (E,MO,NY); ibidem, HESS 593, 3.v.1913 (NY); Rio Piedras, Canovanas, JOHNSTON & STEVENSON 1102, 5.xii.1913 (NY); Rio Piedras, Botanic Gardens, LIOGIER 27911, 12.xi.1978 (NY); no local. ment., LIOGIER & JIMENEZ 27415, 19.ii.1978 (NY); Colonia Paraiso, LIOGIER, LIOGIER & MARTORELL 30083, 28.xi.1979 (NY); Bayamon : Santurce, OTERO 220, 25.x.1937 (MO); no precise local., SHAFER, 1975, 13.iii.1913 (NY); "prope Anasco in campis humidis ad Hatillo", SINTENIS 5594, 7.xii.1886 (K,MO,NY,W); highway 2 km near Ponce Salt Industries, SPETZMAN 720, 23.iv.1968 (FTG); Guanica, STEZMAN & COLON 68, 23.ii.1967 (FTG); Boqueron, STEZMAN & COLON 28, 2.ix.1967 (FTG).

San Domingo - Province of Barahoma : Rincon, FUERTES 1396, ix.1911 (E,MO,NY).

St Martin - no local. ment., BOLDINGH 2520, 1906 (NY).

Trinidad - Claxton bay, BRITTON 2924, 12.iv.1921 (NY); ibidem, BROADWAY 7854, 4.ii.1915 (NY); no local. ment., BROADWAY 6935, 10.v.1928 (MO); San Joseph Road, near Evarry, BROADWAY 7053, 27.iii.1929 (MO); near Harmony Hall, via Point a Pierre, BROADWAY 9106, 7.xii.1932 (MO).

Virgin Islands - St Thomas, BRITTON & BRITTON 180, 1-9.iii.1924 (NY).

4.9 - subgenus Daubentonia

subgen. Daubentonia (DC.) Baker
Fl. Trop. Afr. 2 : 133, 1871

Daubentonia DC., Prodr. 2 : 267, 1825; Mem. Leg. 2 : 286, 1826

Sesbania sect. Daubentonia (DC.) Bentham, Gen. Pl. 1 : 502, 1865 - pro majore parte; non Phill. & Hutch. BOTHALIA 1 : 40-56, 1921; sensu Gillett, KEW BULL. 17 : 149, 1963.

Sesbania Scop. sensu S. Watson, BIBL. IND. NORTH AM. BOT. 1 : 258, 1878 - pro minore parte.

Perennial (?) or short-lived shrubs or trees. Racemes 4-10 (-15) flowered. Calyx rounded-campanulate, with short 5 subequal lobes or slightly bilabiate to conspicuously bilabiate (S. macroptera Mich.) and then the upper lip bilabiate, the lower lip with 3 short lobes. Standard without appendages or with small, rounded calli at the base of the claw, orbicular to suborbicular, longer than the other petals. Wing and keel petals without a basal tooth; wing petals oblong, keel lunate to semi-lunate, obtuse. Staminal sheath with a rounded auricle at the base. Pod stipitate, linear, compressed and torulose (S. cavanillesii) or, linear-oblong, 4-angled with thickened margins (S. virgata) or 4-winged, 6-15 cm long. Seeds reniform or oblong-reniform, hilum circular to elliptic, subcentral.

Type species : Sesbania punicea (Cav.) Benth.

The subgenus *Daubentonia* is found exclusively in the New World, with the species showing well delimited distributions, such as *S. drummondii* in North America, *S. cavanillesii* in Central Mexico, and *S. macroptera*, *S. punicea* and *S. virgata* in South America.

The correlated occurrence of pods with thickened margins or 4 wings *and* non-toothed wing and keel petals readily differentiate this subgenus from subgen. *Sesbania* and subgen. *Pterosesbania*, respectively.

No attempt has yet made to check whether reproductive barriers exist between the species of subgen. *Daubentonia* and those of subgen. *Sesbania*. Such experiments would yield data which could enhance the patterns of infrageneric classification proposed for the genus.

(7) *Sesbania cavanillesii* S. Watson

BIBL. IND. NORTH AM. BOT. 1 : 258, 1878; PROC. AM. ACAD. N. S. 9 : 342, 1882.

syn. : *Aeschynomene longifolia* Cav.
Ic. Pl. 4 : 8, t. 315, 1797
Aeschynomene longifolia Ort.
Nov. Rar. Pl. Hort. Matr., Dec. 9 : 700, 1800
Piscidia longifolia (Cav.) Willd.
Sp. Pl. 3 : 920, 1802
Sesbania longifolia (Ort.) DC.
Prodr. 2 : 265-6, 1825
Daubentonia longifolia (Cav.) DC.
Prodr. 2 : 267, 1825
Sesbania mexicana Pollard
BULL. TORREY CLUB 24 : 154, 1897
Daubentonia cavanillesii (S. Watson) Standley
CONTRIB. U.S. NAT. HERB. 23 : 476, 1922
Daubentoniopsis longifolia (Cav.) Rydb.
AM. J. BOT. 10 : 497, t. 35J, 1923

Shrub 2-3(-6) m tall; stem cylindric, glabrous. Leaves 10-15 cm, with (5-)7-10(-12) pairs of leaflets; leaflets oblong-lanceolate to elliptic, acute at each end, mucronulate, 20-30 x 7-10 mm, petiolules 2-2.5 mm; stipules linear-lanceolate, acuminate, glabrous (or sericeous when young), 5-7 mm. Racemes (5-)7-15 cm, with 5-12 flowers on thick pedicels of 15-20 mm; bracts and bracteoles narrow-lanceolate. Flowers yellow, 18-20 (-25) mm; calyx broad-campanulate, 6-8 mm (including the lobes), the lobes 1.0-1.5(-2.0) mm, broad-triangular, acute; standard suborbiculate to oblate, lacking the basal appendages; wing petals oblong to oblong-lanceolate, up to 22 mm, with short claws; keel petals obovate, to 22 mm, the claw 7-8 mm. Pod 100-150 x 0.7-1.0 mm, coriaceous, compressed, linear, torulose, transversely constricted between the seeds. Seeds oblong-reniform, (5-)7-9(-10) per pod, 5-7 x 2.5-3.0 mm, dark-brown. Figure 69.

Type : CAVANILLES s/n, cultivated at Madrid, 1795
(MA, holotype, not seen; phototype E!).

S. cavanillesii has a very confused taxonomic history which also involves S. drummondii, due to the many names differently applied to these species.

CAVANILLES (1797) published Aeschynomene longifolia Cav., a species from Mexico, without a description of its pods. Three years later, ORTEGA (1800) described Aeschynomene longifolia Ort., also said to come from Mexico and which had linear, acute, torulose pods.

DeCANDOLLE (1825) recognised CAVANILLES' and ORTEGA's binomials as applied to different plants, and transferred

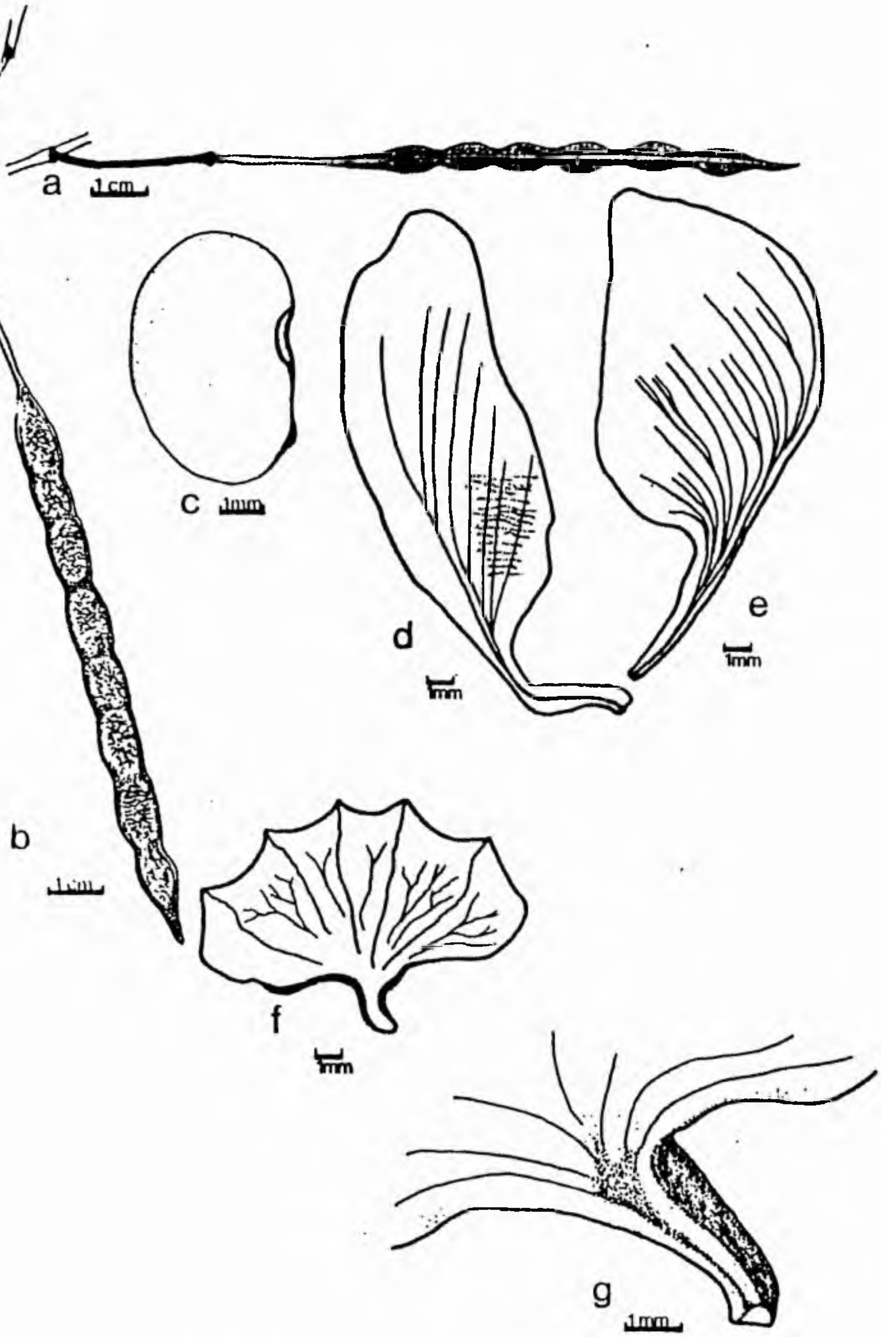

Figure 69 - Sesbania cavanillesii S. Watson. a,b - pod, surface and side view, respectively; c - seed; d - wing petal; f - calyx, flattened out; g - base and claw of standard, showing absence of appendages.

A. longifolia Ort. to *Sesbania*, creating *S. longifolia* (Ort.) DC., and *A. longifolia* Cav. to *Daubentonia*, therefore creating the new combination *D. longifolia* (Cav.) DC. However, for the latter species to belong to *Daubentonia* it should have 4-winged pods, a character which was not available to DeCANDOLLE in CAVANILLES' illustrations*.

Although no types are known for ORTEGA's species, BUNTING & INGRAM (1972), after studying the nomenclatural problems involving *S. cavanillesii* and *S. drummondii*, demonstrated that CAVANILLES and ORTEGA in fact based their new species on plants belonging to the same taxon. Therefore, *A. longifolia* Ort. became not only a homonym but also a synonym of *A. longifolia* Cav. If this resolution is accepted and applied to DeCANDOLLE's (1825) treatment, both his new combinations cited above become synonyms of the same species. This species, however, can not be named *S. longifolia* because the epithet "*longifolia*" has already been used in *Sesbania* (DeCANDOLLE, *loc. cit.*). Therefore, the next name at species rank with description and cited specimens which fit the characters of the Mexican plants in question is *S. cavanillesii* S. Watson.

POLLARD (1897), unlike WATSON (1878, 1880), did not interpret that CAVANILLES' and ORTEGA's binomials were applied to the same plants and, judging in terms of priority, accepted

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* The exsiccata under the cover of *Daubentonia longifolia* (Cav.) DC. in the Herbarium Candolleanum (G-DC!) is, in fact, a true *Sesbania punicea* (Cav.) DC.

the epithet "*longifolia*", as used by CAVANILLES (1797) under synonym of *Daubentonia longifolia* (Cav.) DC., a species with distribution ranging from Mexico and southern Texas along the Gulf coast to western Florida. For the other taxon, based on ORTEGA's *A. longifolia*, POLLARD (*loc. cit.*) created the species *S. mexicana* which, because of its basionym, became another synonym of *S. cavanillesii*. The distribution of *S. mexicana* was mentioned as Mexico, state of Jalisco.

STANDLEY (1922) accepted POLLARD's treatment (*loc. cit.*) with reservation, and questioned whether *A. longifolia* Cav. should not be applied to *S. mexicana* as well, since the latter species resembled CAVANILLES' taxon as much as *Daubentonia longifolia* did.

RYDBERG (1923, 1924) recognised that DeCANDOLLE (1825) was mistaken in his treatments of the binomials published by CAVANILLES and ORTEGA and made an attempt to clarify the situation by transferring both names as synonyms of *Daubentoniopsis longifolia* (Cav.) Rydb.*, a species with linear, compressed, torulose pods from Jalisco, Mexico. In addition, RYDBERG (*loc. cit.*) established a new species, *D. drummondii* based in part on a description by TORREY & GRAY (1838) in "Flora of North America" and *Daubentonia longifolia* DC. Mem. Leg. : 286, "in part, as to description". TORREY & GRAY (*loc. cit.*) did not describe a new taxon but simply tentatively identified a single specimen (DRUMMOND 71, TEXAS) as *D. longifolia* ? DC". By implication, therefore, the type of *D. drummondii* Rydb. must be the specimen

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* RYDBERG (1923, 1924) created *Daubentoniopsis* as a monotypic genus which had intermediate characters between *Sesbania* and *Daubentonia*.

DRUMMOND 71. The species is a taxon with 4-winged pods occurring from Florida to Texas, U.S.A., and San Luis Potosi, Mexico.

In the present work, Daubentoniopsis is rejected and the taxon treated as a synonym of subgen. Daubentonia. The effect of this treatment is that Daubentoniopsis longifolia (Cav.) Rydb. becomes a synonym of S. cavanillesii Watson (as correctly proposed by BUNTING & INGRAM, 1972), which is the valid name for the Mexican species described by CAVANILLES (1797) and Daubentonia drummondii must be transferred to Sesbania (see comments under S. drummondii).

S. cavanillesii is endemic to Mexico, especially in the region of the state of Jalisco, around the humid area of Lake Chapala. Two major characters distinguish it from the other species of Sesbania, viz. its oblong-lanceolate to elliptic and distinctly acuminate leaflets, and the few-seeded, compressed, torulose and conspicuously constricted pods.

Distribution (Figure 71)

CENTRAL AMERICA

Mexico

Jalisco - On the beach of Lake Chapala, BARKLEY, WESTLUND & ROWELL 7612, 12.viii.1947 (MEXU,TEX); Tizapán El Alto, HARO 1691, 20.vi.1970 (MEXU); 33 mi. S of Guadalajara on Highway 15, IRWIN 1305, 26.viii.1957 (NY,TEX); 4 mi. SE of Jocotepec, alt. 5100 ft, roadside, marshly area, JOHNSON 259-68, 10.vii.1968 (MO); ca. 4 mi. S of Jocotepec, JOHNSON 323-73, 5.iii.1973 (MO); Zaplotanejo, Puente Grande, LUNA 9411, 25.iii.1978 (MEXU); Guadalajara, PALMER

237, 17.vii.1886 (BM,K,MEXU,MO,NY,P,W); cerca de ríos, Guadalajara, PRINGLE s/n, 25.vii.1893 (MEXU); by streams near Guadalajara, 5000 ft, PRINGLE 4738, 1.v-9.vii.1894 (E,G,K,NY,P,W); ibidem, PRINGLE 9772, 18.vii.1902 (CAS,MO,NMC,NY); Guadalajara : margen oriental del Lago de Chapala, km 20 de la brecha bombas, ROMERO 63, 25.ii.1976 (MEXU); Tlachichilco del Carmen, Lago de Chapala, ROMERO 92 & ALMÁNZA 22, 12.i.1976 (MEXU); Juanacatlán, RZEDOWSKI 16336, 23.iii.1963 (DS); Cajititlán, ZARATE & SAIZ s/n, 21.xii1978 (MEXU).

Michoacán - Zamora, GREGG 829, 13.v.1849 (MO); Lake Chapala, on hills south of Lake, HITCHCOCK & STANFORD 7171, 16.vii.1940 (DS,MO,NY); vicinity of Zamora, 2 km N of Zamora, on road to La Barca, alt. 1520 m, ILTIS, KOEPPEN & ILTIS 505, 29.vii.1960 (MEXU); north end of Emanuelo Zapata, ca. 10 km E of Jiquilpán, at eastern end of Lago Chapala basin, ILTIS, KOEPPEN & ILTIS 511, 29.vii.1960 (SP); Cerro La Beata, Zamora, PALACIOS s/n, viii.1973 (LL).

Locality not traced : Atecucário ?, ALTAMIRANO s/n, 13.vi.1905 (MEXU); OLIDA s/n, no date (P); "Nueva Espana", PAVON s/n, no date (G); collector ?, no date (P).

(8) *Sesbania drummondii* (Rydb.) Cory

RHODORA **38** : 406, 1936

syn. : *Daubentonia drummondii* Rydb.
AM. J. BOT. **10** : 498, 1923, FL. N. AM. **24** (4) : 207-208, 1924
Daubentonia texana Pierce
TROP. WOODS **72** : 13, 1942

Woody shrub 1.5-3.0 m tall, stems terete. Leaves 10-20 cm, with 10-25 pairs of leaflets; leaflets linear-ablong to oblong, apex rounded and mucronulate, acute to obtuse at the base, 15-35 x 4-7 mm, petiolules 1.0-1.5 mm; stipules lanceolate, 2-4 mm. Racemes 6-10(-12) cm long, with 10-12 flowers on slender pedicels of 8-10 mm; bracts and bracteoles linear-lanceolate. Flowers pale yellow, (9-)10-15(-17) mm; calyx broad-campanulate, 4-6 mm (including the lobes), the lobes 0.5-1.0 x 1.0 mm, broad-triangular, acute; standard suborbiculate to oblate, lacking basal appendages; wing petals narrowly elliptic to oblong, up to 15 mm, short clawed; keel petals ovate to obovate or almost of semi-circular shape, 10-15 mm, the claw 4-5 mm. Pod 40-80 x 10-15 mm, acuminate at both apex and base, the beak up to 10 mm, the wings patent, 3-4 mm wide. Seeds oblong-reniform to quadrate-reniform or, in some cases, quadrate-oblong, 4-7(-8) per pod, 5.0 x 3.0 (-4.5) mm, brown. Figure 70.

Type : U.S.A., Texas : Brazos, DRUMMOND 71, 1834 (NY!, holotype, BM!,FHO!,K!, isotypes).

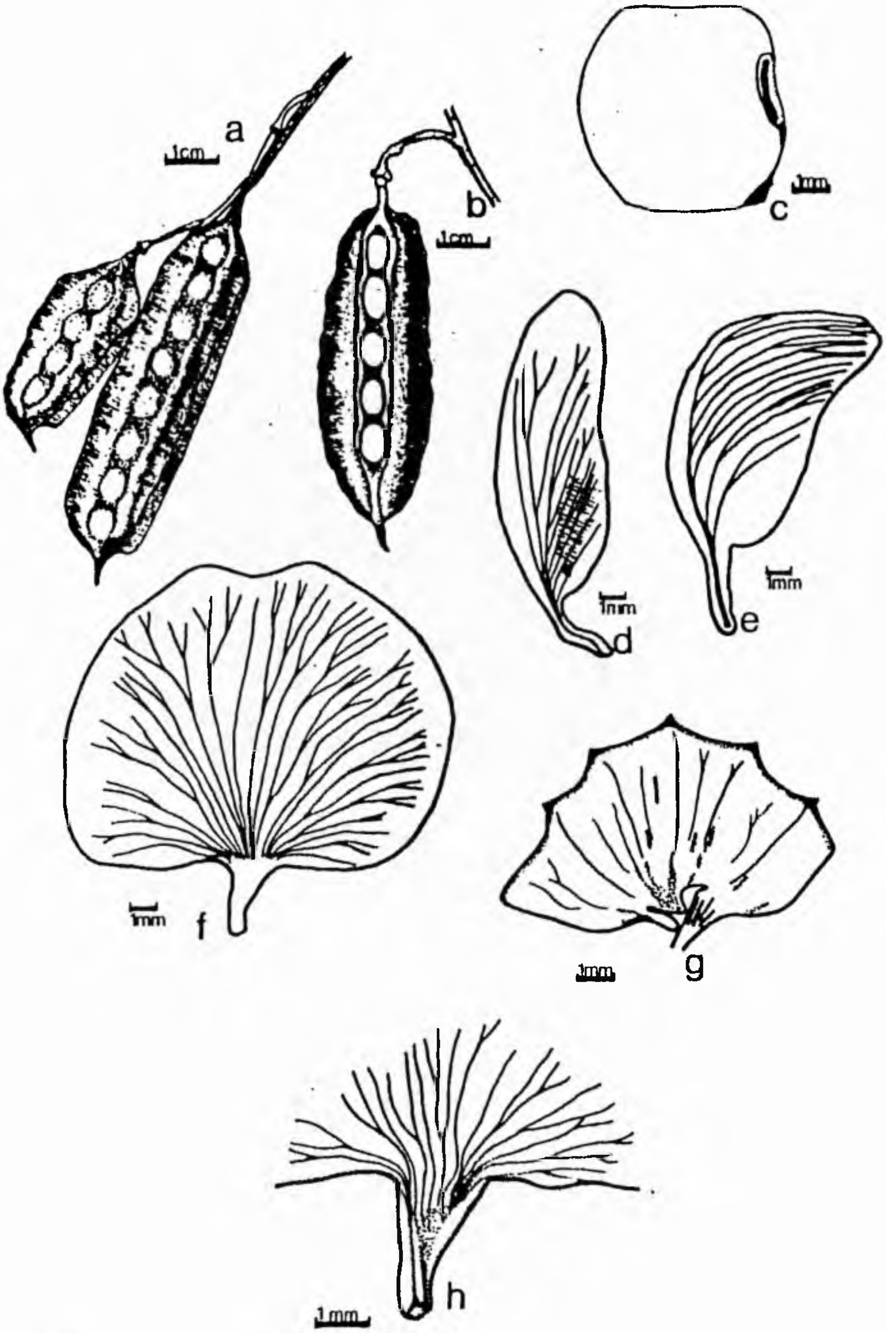


Figure 70 – *Sesbania drummondii* (Rydb.) Cory. a – pods; b – pod, internal view showing the septa between the seeds; c – seed; d – wing petal; e – keel petal; f – standard; g – calyx, flattened out; h – base of the standard showing absence of appendages.

S. drummondii remained virtually undescribed until RYDBERG's treatment of *Sesbania* for *Flora North America*, when it was regarded as a species of *Daubentonia*.

Previously all references to the names of this species were confusing because the plants were considered to be *S. cavanillesii*. Although RYDBERG's separation of *D. drummondii* as distinct species is undoubtedly correct, the species had to be transferred to *Sesbania* when *Daubentonia* was merged into the former taxon. This combination was made by CORY (1936). PIERCE (1942) rejected the name *D. drummondii* Rydb. on the grounds that it was a source of errors and confusion and should be discarded. PIERCE (*loc. cit.*) pointed out that the specific epithet *drummondii* was published without a description by RYDBERG (1923) who stated that it was based on *D. longifolia* ? of TORREY & GRAY (1838) "which was also published without a description". According to PIERCE, the name *drummondii* is either based on TORREY & GRAY or on the DRUMMOND specimen which TORREY & GRAY (1838) cited. However, the latter authors expressed doubts about the identity of the DRUMMOND sheet (p. 293) but in the appendix (p. 687) they removed the question mark by referring the specimen to *D. longifolia* (Cav.) DC. Since this latter name is based on CAVANILLES' plate ("Ic. Pl." *4*, tab. 315), which RYDBERG (1923) cited as the type of *Daubentoniopsis longifolia* (Cav.)Rydb., PIERCE (1942) concluded that the name *drummondii* must become a synonym of *Daubentoniopsis longifolia* (Cav.) Rydb.

PIERCE (1942) further argued that if RYDBERG (1923) based his species on the DRUMMOND sheet cited by TORREY & GRAY (1838), then the application of the name *drummondii* would still be uncertain since the specimen consisted only of the pods whereas the RYDBERG's description includes a reference to the flower. PIERCE (*loc. cit.*) concluded that the DRUMMOND sheet cannot be type specimen. Subsequently, PIERCE (*loc. cit.*) described a new species, *Daubentonia texana*, based on the specimen NOGLE 100 from Texas.

The rejection of *D. drummondii* Rydb. by PIERCE can be faulted on several grounds. Firstly, TORREY & GRAY (1838) did include a description of the DRUMMOND specimen. Therefore *D. drummondii* as published by RYDBERG (1923) did contain a reference to a previously published description. Furthermore, RYDBERG (*loc. cit.*) made it clear that he based *D. drummondii* on the TORREY & GRAY (*loc. cit.*) description and not on *D. longifolia* (Cav.) DC.. In addition, although the DRUMMOND specimen presently lacks flowers, as it did when examined by PIERCE (1942), it is evident from the specimen that it has been damaged and since TORREY & GRAY (1838) reffer to the raceme it clearly did once have flowers.

Thus, although RYDBERG's treatment of *D. drummondii* in 1923 and 1924 is certainly somewhat confused, the view is taken that by reference to the TORREY & GRAY's (1838) description, and by implication *via* these authors to the DRUMMOND sheet, and by his exclusion of the name *D. longifolia* (Cav.) DC, RYDBERG (1923, 1924) satisfied the requirements necessary to validly publish his species.

S. drummondii occurs naturally in southern North America, particularly in the states of the Gulf coast, i.e., Texas to western Florida, extending to the valley of the Mississippi River.

It has certainly been introduced in the Jalisco area of Mexico, from where only one record of the species was studied.

S. drummondii is very close to S. punicea and both may have derived from the same ancestral stock in the early evolutionary radiation of the subgenus Daubentonia. This aspect is discussed later under the study of S. punicea.

Distribution (Figure 71)

CENTRAL AMERICA

Mexico - Reynosa, GREGG 891, iii.1847 (MO); ibidem, GREGG s/n, 21.xii.1847 (MO); Jalisco : 33 mi. S of Guadalajara, IRWIN 1305, 26.viii.1957 (NY,TEX); Tamaulipas : 25 km E of Matamoros sobre el borde del Rio Bravo, MEDRANO 547, vi.1964 (MEXU); en route from San Luis Potosi to San Antonio, PARRY 209, viii.1878 (NY); Tamaulipas : Reynosa, PRINGLE s/n, 7.viii.1888 (MEXU); Chaparral, near Mier ?, WISLIZENUS 368, 31.v.1847 (MO); no local. ment., WISLIZENUS 376, vi.1847 (MO).

NORTH AMERICA

Southeast : Alabama - Mobile Co : Dauphin Island, CRAWFORD 1024, HARVILL & SEGARS, 23.iv.1950 (TEX); Arkansas - Ashley : Sunrise, DEMAREE 13901, 11.x.1936 (CAS,DS,MO); Sunshine, DEMAREE 18563, 9.x.1936 (CAS,MO); Clark Co : Okolona, elev. 310 ft, DEMAREE 20708, 11.x.1939 (CAS,MO); Florida - Madison, BAHENI 293, 4.x.1934 (G); Apalachicola, CURTISS 590, no date (BM,G,MO,NY,W); Pensacola, Ballast Wharf, CURTISS 590, no date (BM,K,MO,NY,P); Louisiana - Bay St Louis, BAHENI 3249, 3.x.1934 (G); New Orleans, COCKS s/n, viii.1898 (NY); Plaquemines Parish : Delta Wildlife Refuge near Pilot town on Mississippi River, EWAN 17473, 21-22.xi.1947

(MO,TEX); St Tammany Parish, EWAN 17796, 19.vi.1948 (BM,G,TEX); St Mary Co : Cotes Blanches, LANGLOIS s/n, 17.vii.1893 (MO); St Martin Parish : 3,6 mi. S of Pierre Pass along road to Morgan City, LASSEIGNE 884, 24.viii.1967 (MEXU); Lake Charles, MACKENZIE 409, viii-ix.1898 (MO,NY); Calcasieu Parish : Lake Charles, PALMER 8527, 12.ix.1915 (CAS,MO); 10 ft high shrub on east bank of Vermillion River about 5 mi. S of Lafayette, PULLIAM III 20, 6.xi.1966 (LL); Point Chevr., THARP s/n, 27.vii.1929 (TEX); Atchefalaya Bay, THARP s/n, 29.vii.1929 (TEX); Calcasieu, ca. 2.5 mi. W of Sulphur, just S of Stegall, THIERET 20589, 21.ix.1965 (LL); Cameron, TRACY 8510, 6.vii.1903 (BM,E,G,MO,NY); <u>Mississippi</u> - Hancock Co : JONES & JONES 14151, 6.vii.1967 (TEX); Jackson Co : roadside ditch, Pascagoula airport road, JONES & JONES 14945, 24.vii.1967 (NY); near Gross Christian, LANGLOIS s/n, vii.1880 (NY); border of Gulf Bay in St Louis, LANGLOIS 33, 13.ix.1883 (NY); Harrison Co : Biloxi, POLLARD 1001, 25.vii.1896 (MO,NY); Bay of St Louis, SARGENT 9697, 13.vii.1968 (MO); Biloxi, TRACY 6342, 23.vi.1899 (BM,E,G,NY); ibidem, TRACY 6904, 15.ix.1899 (BM,E,G,MO,NY).

<u>South plains</u> : <u>Texas</u> - Washington Co : ALBERS 46118, 8.x.1946 (TEX); Liveoak Co : Reynosa, ALBERS 46389, 27.xii.1946 (TEX); Caldwell Co, BARKLEY 1, 13.vii.1943 (MO); Colorado Co : wet places near Eagle Lake, mostly on floating islands, BARKLEY, WARNOCK & THARP A6451, 21.viii.1946 (TEX);

no local. ment., BERLANDIER 3132, no date ? (MO); Castroville, BESCH s/n, 25.vi.1939 (BM); low ground near Medina River banks, camp Cayoca at Castroville, BESCH s/n, 4.vi.1940 (NY);

Harris Co : Humble, 6 mi. N, BOON 159, 2.vii.1943 (TEX); San Jacinto River, N. Humble, 3 mi. N, BOON 375, 8.viii.1946 (TEX); Washington Co, BRACKET s/n, viii.1938 (TEX); Bastrop Co : 6 mi. SE of Bastrop, BUNTE 19, 24.x.1965 (TEX); Columbia, BUSH 220, 28.x.1899 (MO); ibidem, BUSH 1587, 20.x.1900 (MO); Cameron Co : lowd 5 mi. W of Baca Chica, CLOVER 388, 14.viii.1932 (CAS,TEX); Calhoun Co : 2 mi. SW of Green Lake, CORRELL 14148, 25.viii.1946 (LL,NY); Aransas Co : in sandy , open soil of woodlands, in depression, N of Aransas Co airport, CORRELL & CORRELL 18984 (LL); Gonzales Co : along a small stream 7 mi. S of Gonzales, CORRELL & JOHNSTON 17485, 6.vii.1957 (LL); Wilson Co : Sutherland Springs, CORY 45195, 23.vii.1944 (TEX); Harris Co : 5 mi. SE of Genoa, CORY 50704, 11.xi.1945 (CAS,NY); Aransas Co : Aransas Refuge, near Dagger Point, CORY 50205, 26.xi.1945 (NY); Rockwall Co : 1 3/4 mi. S of Rockwall, CORY 52540, 22.x.1946 (NY); Bastrop Co : in pond in pine forest of Bastrop State Park, CRUTCHFIELD 805, 13.ix.1965 (LL); Jasper Co : small creek at Holy Springs, CRUTCHFIELD 2566, 29.iv.1967 (LL); Kleberg Co : Riviera Beach, CRUTCHFIELD 2950, 9.vi.1967 (LL); Sheldon, DEGENER 5166, 5.viii.1933 (NY); Edna, DRUSHEL 503, 504, 23.vii.1913 (MO,P); ibidem, DRUSHEL 2466, 2467, 7.iv.1915 (P); Jackson Co, DRUSHEL 2876, vii.1915 (P); ibidem, DRUSHEL 3550, 25.xii.1917 (P); ibidem, DRUSHEL s/n, xii.1917 (MO); Bastrop Co, DUVAL 30, 19.viii.1919 (TEX); Gregg Co : Langeriene, EGGERT s/n, 28.viii.1898 (MO); Galveston, EIFRIG s/n, 13/vii.1926 (CAS); College Station, ENZIE 48, 16.viii.1953 (NMC); Travis Co : 3 mi. below Austin, FERGUSON 663, 12.x.1907 (TEX); Cameron Co : vicinity of Brownsville, old river channel, Las Palmas Ranch, FERRIS & DUNCAN 3177 (CAS,DS,MO,NY); Houston, FISHER 2273, 18.vi.1912 (MO,NY,W); ibidem, FISHER s/n, 15.x.1932 (BM,DS); Brazoria Co : Brazoria Refuge, Entrance Gate, Hoskins Road, FLEETWOOD s/n, 14.viii.1969 (TEX); Brazos Co : College Station, FRYXELL 1711, 25.x.1970 (NY); Calhoun Co : shrub growing about 100 yards from bay at Port Lavaca, GENTRY 30, 3.viii.1946 (TEX); Brazos Co : about 3 mi. SW of College Station, GOULD 7684, 16.ix.1957 (TEX); Montgomery Co : eastern outskirts of Montgomery, GOULD & MCCULLY 5775, 10.viii.1950 (TEX); Guadeloupe Co : Seguin, GROTH 193, 17.viii.1903 (CAS,NY); no local. ment., HALE s/n, no date (NY); eastern Texas, Houston, HALL 117, 28.vi.1872 (MO,NY); no local. ment., HARVEY 71, 1847 (DS); Rio Grande Valley, Ringold, HAVARD s/n, ix.1884 (NMC,W); Refugio Co : West Steer Pasture, 0.3 mi. NE of gate to Willow Lake Pasture, ca. 8 mi. NE of Refugio, HILL 10521, 16.vii.1981 (NY); ibidem, HILL 10533, 17.vii.1981 (NY); Matagorda Co : west bank of Colorado River, 1/2 mi. from Gulf Beach, HILDEBRAND 22, 25.viii.1954 (TEX); Gonzales Co : in Ottine Park about 80 mi. S of Austin, HINCKLEY 1404, 4.vii.1937 (TEX); Galveston Co, HOOKS s/n, 7.viii.1936 (TEX); Longview, JOHNSON 1758, 7.x.1913 (NY); 0.8 mi.S of Pawelekville, JOHNSON 982, 22.vii.1952 (TEX); Hidalgo Co : sand near Rio Grande, Santa Ana Nat. Wildlife Refuge, JONHSTON s/n, 3.vi.1953 (TEX); Willacy Co : Sanz Ranch, JOHNSTON s/n, 29.vii.1953 (TEX); Kleberg Co : southern part of Santa Gertrudis, JOHNSTON s/n, 6.viii.1953 (TEX); Aransas Co : Goose Island Park State Park, JOHNSTON 541253, 4.viii.1954 (TEX); Jim Wells Co : 5.2 mi. N of Premont, JOHNSTON 541549, 14.ix.1954 (TEX); Nueces Co : NE corner of Laureles Division of King Ranch, JOHNSTON 541707, 17.ix.1954 (TEX);

Harrisburg, JOOR s/n, 28.vii.1875 (NY); ibidem, JOOR s/n, 26.viii.1876 (P); Zapata Co : Dolores Creek, 12 mi. N of San Ignacio, JUAREZ 8, 31.viii.1963 (TEX); Guadeloupe Co : 2 mi. E of Leesville, KELLOGG 33, 15.viii.1940 (TEX); Lee Co : KNOBLOCH s/n, 17.i.1931 (TEX); Herne, LETTERMAN s/n, 1880 (MO); no local. ment., LINDHEIMER 31, 1843 (BM,MO); Hidalgo Co : National Wildlife Refuge, SE of Mission near Anzalduas Park, LONARD 3036, 17.vi.1971 (MEXU); Travis Co : Williamson Creek 2 mi. S of S.E.U. Campus, LYNCH s/n, 1.xi.1954 (TEX); Grimes Co : Plantersville, LYROCK s/n, 13.x.1931 (TEX); Zapata Co : Dolores Creek, 12 mi. N of San Ignacio, MARQUEZ 10, 31.vii.1963 (LL); Burlesson Co, MASSEY 719, 16.vii.1964 (LL); Fayette Co, MATTHES 46, no date (G); Zapata Co : Dolores Creek, 12 mi. N of San Ignacio, MCCART & JUAREZ 8, 31.vii.1963 (LL); Travis Co, McKEE & WESLEY 3917, vii.1911 (TEX); Harris Co : extension of N Burnett past Rollingwood in Lakewood, Baytown, MEARS 707, 13.viii.1966(TEX); Harris Co : 1100 E Canal, Highlands, MEARS 982, 25.ix.1966 (TEX); Bexar Co : Sommerset Road 13 mi. SE of San Antonio, banks of Medina River, METZ 142, 28.viii.1931 (NY); Camp Cayoca, Castroville, METZ 3201, 1.ix.1940 (CAS); Port Arthur, NOGLE 100, vii.1942 (NY, holotype of Daubentonia texana Pierce); Devil's Canyon, NORMANO s/n, 9.xi.1927 (TEX); San Antonio, PALMER 278, 18-27.ix.1880 (K,MO,NY,P,W); Colorado Co : Eagle Lake, PALMER 6586, 19.ix.1914 (MO); Lower Rio Grande, PARRY et al. 251a, no date (NY); Gonzales, PLANK s/n, 22.x.1893 (NY); Caldwell Co : Smith Allen Farm, Luling Oil Field, PLUMMER & BARKLEY 13129, 13.vii.1943 (MO,NY,TEX); Cameron Co : 12 mi. W of Boca Chica, REED 362, 25.x.1947 (CAS,NY); Star Co : Arroyo La Miniti, Roma, REED 4663, 9.xii.1947 (LL); Galveston, REVERCHON

2220, 8.viii.1902 (MO); Sheldon, REVERCHON s/n, 6.ix.1903 (MO); De Witt Co, RIEDEL s/n, 20.vii.1941 (TEX); Fayette Co : Muldoon, RIPPLE 51-906, 2.x.1950 (TEX); McMullen Co : about 10 mi. N of Tilden at San Miguel Creek, ROGERS, ALBERS & WEBSTER 6834, 31.v.1949 (TEX); Austin, SE of City, ROSE & RUSSELL 24118, 14.x.1927 (NY); Webb Co : Rio Grande, near International Bridge, Laredo, RUIZ 19, 11.xi.1961 (TEX); Cameron Co : Brownsville, RUNYON 269, 1923 (TEX); ibidem, RUNYON 1737, 25.v.1937 (P); ibidem, near International Bridge, RUNYON 2416, 25.v.1937 (TEX); Webb Co : Espejo Ranch, 17 mi. SE of Laredo, SALINAS 6, vii.1963 (TEX); San Patricio Co : Welder Refuge, at Coyote Windmill, near water, SANDERSON 104, 2.vi.1965 (NY); ibidem, SCHOTT 100, 1853 (NY); banks of Rio Bravo del Norte near Laredo, SCHOTT s/n, no date (NY); Chambers Co : 17 mi. S of Liberty on Highway 563, SEIGLER & SAUPE 10544, 26.v.1977 (MEXU); Denton Co : 7 mi. E of Denton, SHINNERS 15759, 29.vii.1953 (TEX); Kleberg Co : Kingsville, SINCLAIR s/n, vii-ix.1940 (TEX); Anderson Co : 3 mi E of Palestina, SUEUR & SMITH s/n, 7.vii.1935 (TEX); Harris Co : Sheldon Wildlife Man. Area NE of Houston, TATE 7, 18.viii.1965 (TEX); Victoria Co, Texas Game, FISH & OYSTER COMMISSIONER 214a, 12.xi.1940 (TEX); Hidalgo Co : Penitas Lake, 7 mi. W of Mission, TIDWELL 83, 21.viii.1941 (TEX); Kleberg Co : Riviera, THARP s/n, 7.ix.1929 (TEX); Travis Co : Austin, THARP s/n, 20.vi.1939 (TEX); ibidem, THARP s/n, 4.x.1940 (TEX); no local. ment., THUROW s/n, 1890 (CAS); Hallettsville, TOWSEND s/n, 16.viii.1912 (W); Wharton Co : Pierce, TRACY 7785, 14.ix.1901 (BM,E,NY,TEX); Chambers Co : Trinity River delta, TRAVERSE 818, 15.vii.1958 (TEX); no local.

ment., TRECUL 1064, 1843-50 (P); Galveston Co : Moses Lake, 2 mi. NW of Texas City, TURNER 3149, 8.vii.1953 (TEX); Hidalgo Co : Penitas Lake, 7 mi. W of Mission, UZZELL 31, 21.viii.1941 (TEX); ibidem, Rio Grande Valley, WALKER 17, 30.vii.1942 (NY,TEX); Jefferson Co : 1-10 mi. SW of Port Arthur, WEST 114, 16.vii.1966 (TEX); Goliad, WILLIAMS s/n, 7.x.1926 (MO); Gregg Co, York s/n, vii.1939 (MO,TEX); Williamson Co : Brushy Creek, 0.5 mi. W of Round Rock, YORK 46177, 13.vii.1946 (TEX); Jefferson Co : Beaumont, YOUNG s/n, no date (TEX); Willson Co : Floresville, ZERDA s/n, iv.1930 (TEX); Travis Co : W of Duval, collector ?, 15.xii.1897 (TEX).

Locality not traced : BRAKLEY & PLUMMER 13129, date ? (DS); FISH s/n, 15.x.1932 (DS); HALE s/n, no date (NY); LECONTE s/n, no date (P); WATSON 30, no date (MO).

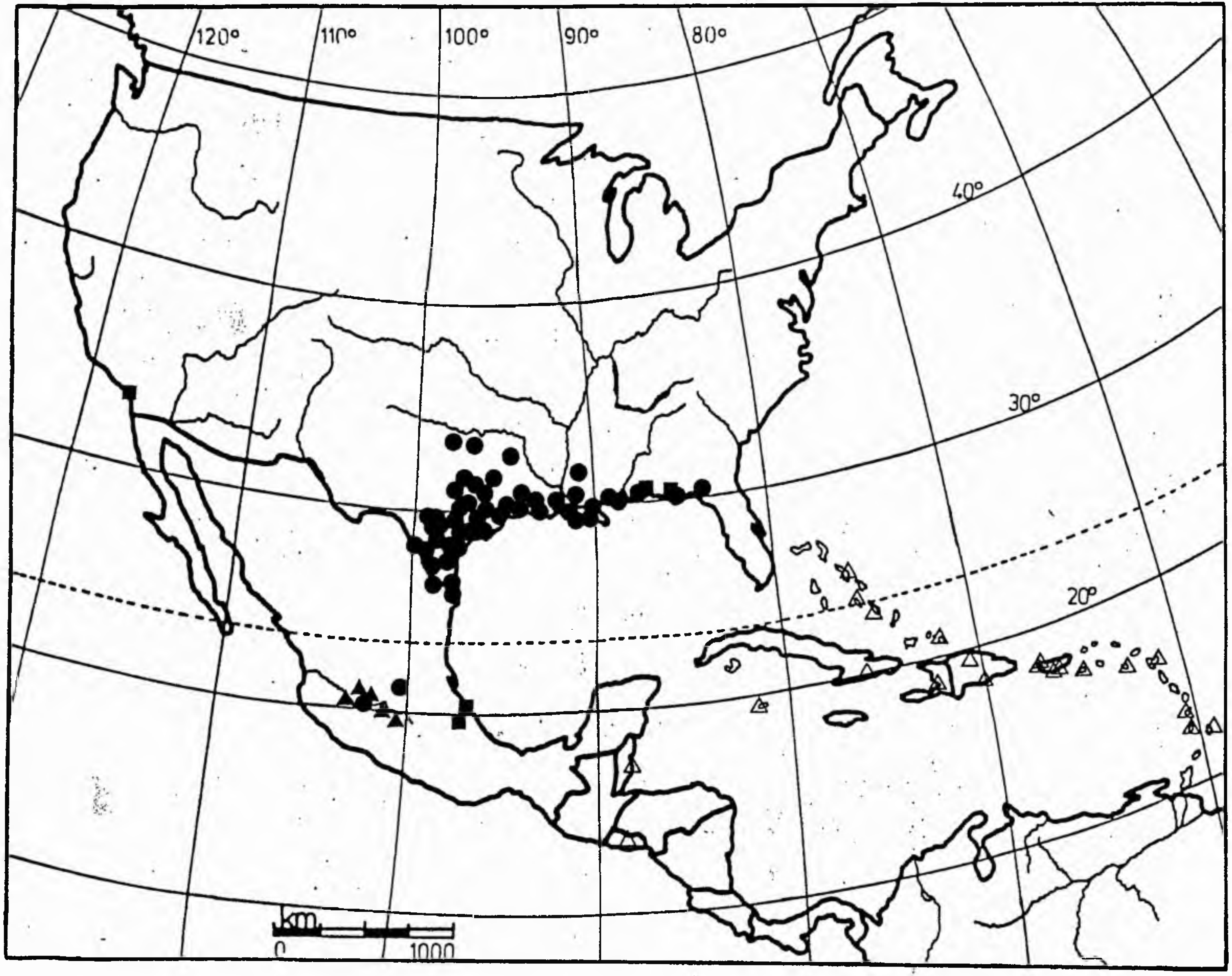
Figure 71 - Distribution map of Sesbania subgen. Daubentonia and subgen. Agati in North and Central America and the West Indies.

▲ S. cavanillesii

● S. drummondii

△ S. virgata

■ S. grandiflora


120°
110°
100°
90°
80°
40°
30°
20°
km
0
1000

(9) . Sesbania macroptera Micheli

MEM. SOC. PHYS. HIST. NAT. GEN. 28 : 14, t.3, 1883

Shrub 2-3(-5) m tall. Leaves 12-15(-17) cm, with 15-20 pairs of leaflets; leaflets 15-20 x 5-6(-7) mm, oblong-lanceolate to oblong-elliptic, mucronulate; petiolule 1.0-1.5 mm; stipules linear-lanceolate, 4-6 mm. Racemes 12-15 cm , with 18-25(-27) flowers on slender pedicels of 3-5 mm; bracts and bracteoles linear-lanceolate. Flowers yellow or the standard pale-yellow and with green streaks (veinlets ?) or faintly mottled, 10-12 mm; calyx campanulate, conspicuously bilabiate, upper lip 4 mm long with 2 short, deltoid lobes, the lower lip 4.5-5.0 mm long with 3 broad-triangular lobes; standard broad-orbiculate, lacking the basal appendages, strongly reflexed; wing petals oblong-falcate, 9-11 mm, short-clawed; keel petals oblong-ovate, upcurved, to 11 mm, the claw 3.0-3.5 mm. Pod 60-70 x 10-15 mm, subtorulose, rounded at the base but the apex acuminate, the beak 10-12 mm; wings striate, folded inward towards the suture (revolute), 4 mm wide. Seeds reniform with the radicular lobe curved, 4-6 per pod, 6-3.5 mm, brown. Figure 73.

Type - Paraguay : Pirayu, "in locis humidis", BALANSA 1377, 1377a, 28.v.1874 (B, holotype , not seen; G!,K!,P!, isotypes; NY!,TEX!, phototypes).

S. macroptera is an endemic species of Paraguay and north-eastern Argentina (Figure 72). It is distinguishable by its small flowers with the standards lacking appendages, pods with four, folded wings, and seeds with a curved radicle.

Distribution (Figure 72)

SOUTH AMERICA

Argentina - Prov. of Corrientes : C. Pellegrini, banado en costa Laguna Iberá, BURKART *et al.* 29909, 5.xi.1973 (MEXU,NY); ibidem, ibidem, GOODAL & TIREL 234, 5.xi.1973 (P); San Martin, col. C. Pellegrini, 8 km N, Ruta 14, KRAPOVICKAS *et al.* 20110, 30.x.1971 UEC); ibidem, ibidem, PEREGO 589, 16.ii.1979 (MEXU); San Martin - La Cruz, SCHININI, CABRAL & VANNI 16891, 14.ii.1979 (MO).

Paraguay - Caacupé a Asunción, BURKART 18359, 12.xi.1950 (MO); "prope Villarica (Pirayu)", HASSLER 8645, i.1905 (G); San Bernardino, HASSLER 1088, ii.1915 (G); Departamento Central : Yaguaron, "orilla del Rio Yaguaron", KRAPOVICKAS, CRISTOBAL & PALACIOS 12308, 1.ii.1966 (G).

Figure 72 - Distribution map of <u>Sesbania</u> subgen. <u>Daubentonia</u> and subgen. <u>Agati</u> in South America.

▲ <u>S. macroptera</u>

■ <u>S. virgata</u>

△ <u>S. grandiflora</u>


80°
70°
60°
50°
40°
10°
0°
10°
20°
30°
40°
50°
1000 Km

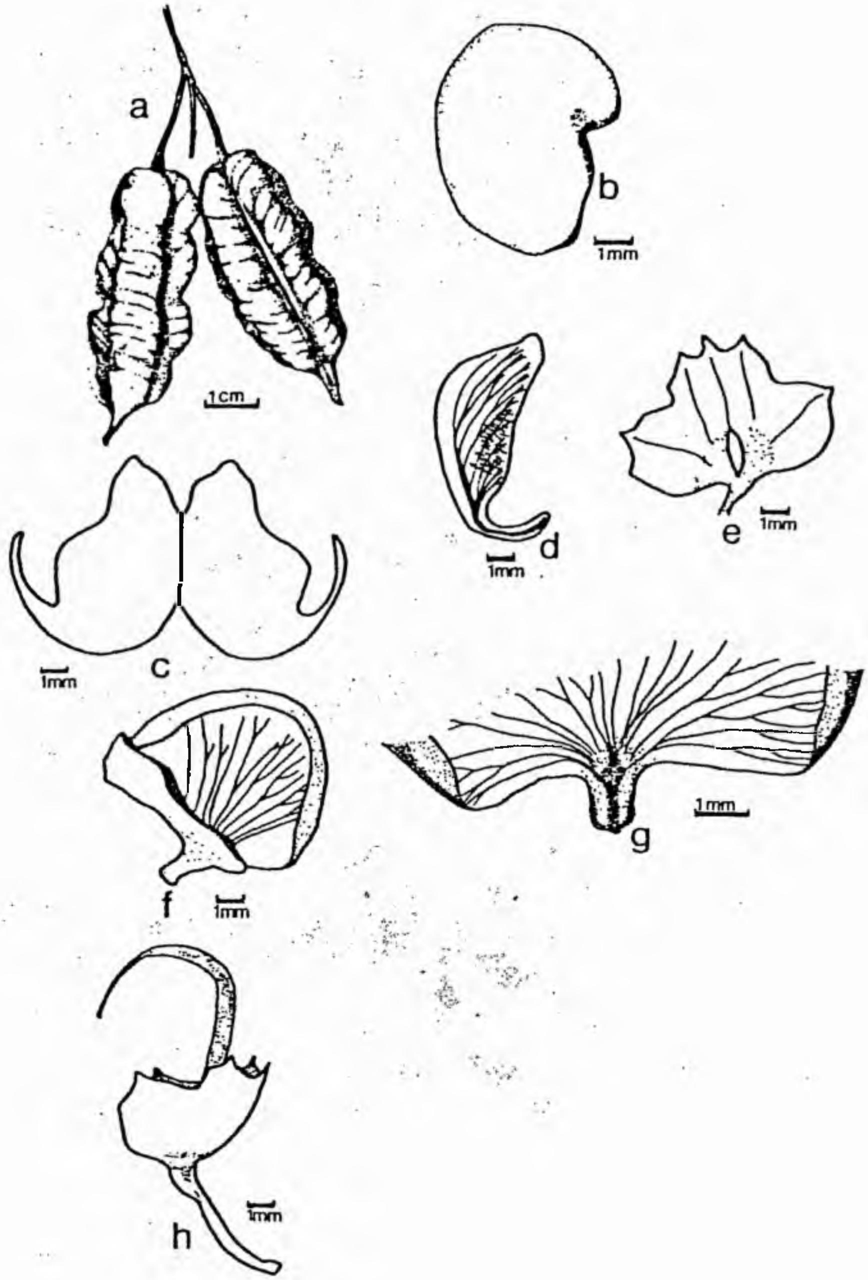


Figure 73 - <u>Sesbania</u> <u>macroptera</u> Mich. a - pods; b - seed; c - keel petals; d - wing petal; e- calyx, flattened out; g - standard base showing absence of appendages; h - calyx and ovary.

(10) . Sesbania punicea (Cav.) Bentham
Fl. Bras. 15 (1) : 43, 1859

syn. : Piscidia punicea Cav.
Ic. Pl. 4 : 8, t. 316, 1797
Aeschynomene miniata Ortega
Nov. Ra. Pl. Hort. Matr., Dec. 8 : 28, 1798
Daubentonia punicea (Cav.) DC.
Prodr. 2 : 267, 1825
Daubentonia tripetii Poiteau
ANN. SOC. HORT. PARIS 27 : 136, 1840
Emerus puniceus (Cav.) O. Kuntze
Rev. Gen. Pl. 1 : 181, 1891
Sesbania tripetii Hort.
Bailey, Stand. Cycl. Hort. : 3157, 1917

Woody shrub 2-3 m, or treelet up to 4 m tall, stem cylindric, smooth or striate. Leaves (7-)10-20(-22) cm, with (5-)7-15(-20) pairs of leaflets; leaflets linear-oblong to ovate-elliptic, mucronulate, (7-)15-25(-30) x (3-)4-7(-8) mm; petiolules 1.5-2.0 mm; stipules lanceolate, acuminate, 4-5 mm. Racemes (5-)7-8(-8.5) cm, with (5-)8-10(-12) flowers on slender pedicels of 15-20(-25) mm; bracts and bracteoles linear-lanceolate. Flowers red, 16-18(-25) mm; calyx broad-campanulate, undulate on the margin, 5-6 mm (including the lobes), lobes 0.8-1.0 x 1.5 mm, broad-triangular, acute, standard sub-orbiculate to large-oblate, with a pair of short appendages on the claw slightly projected upwards; wing petals oblong, up to 2.0 mm, short-clawed; keel petals obovate or almost semi-circular (as in S. drummondii), 15-20 mm, the claw 6-7 mm. Pod (40-)60-120 x 8-20 mm, acuminate at both apex and base, the beak 10-15 mm; the wings 3-5(-7) mm wide. Seeds reniform, 5-9 per pod, 6.0-7.0 x 3.0-4.0 mm, greenish or pale-brown. Figures 74, 75.

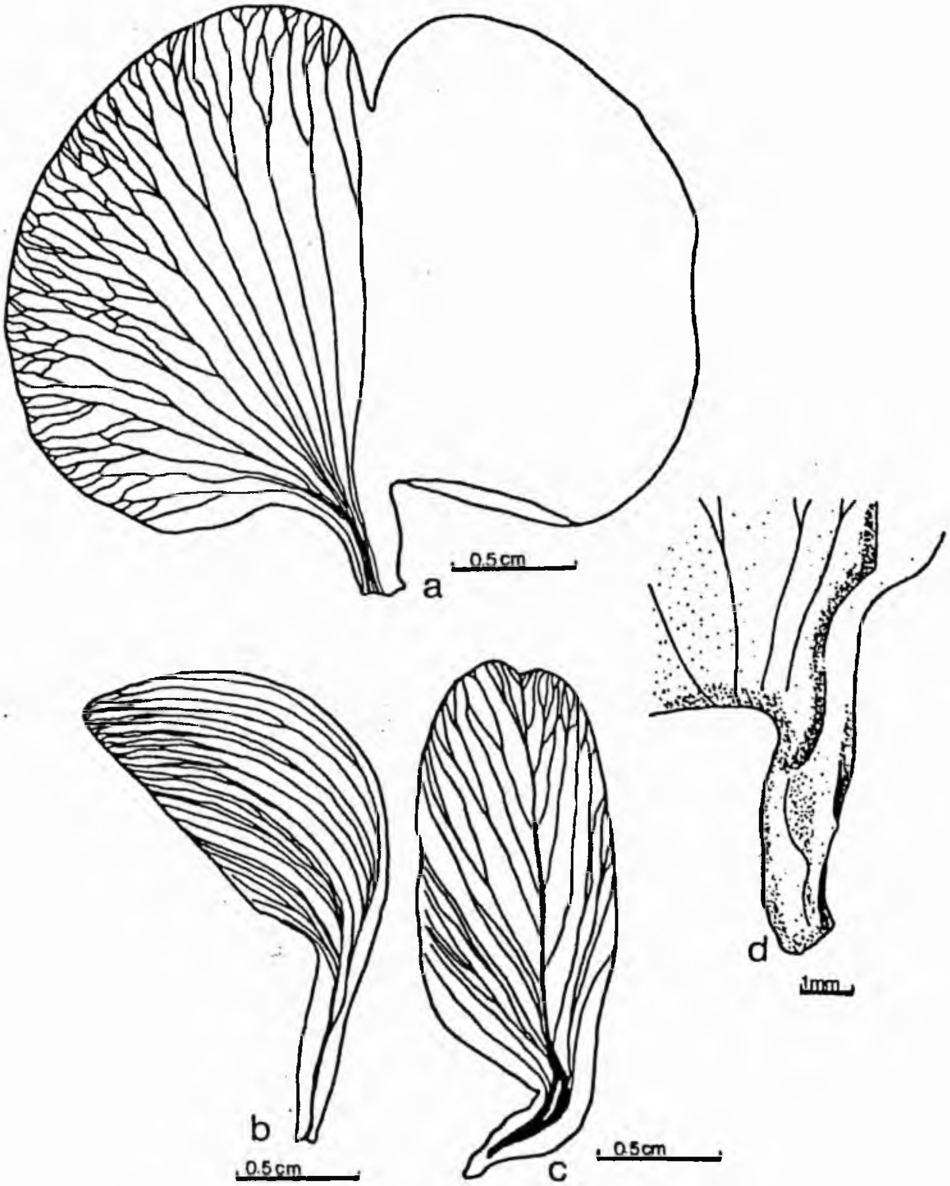


Figure 74 - Sesbania punicea (Cav.) Benth. a - standard; b - keel petal; d - base of the standard showing two small appendages on the claw.

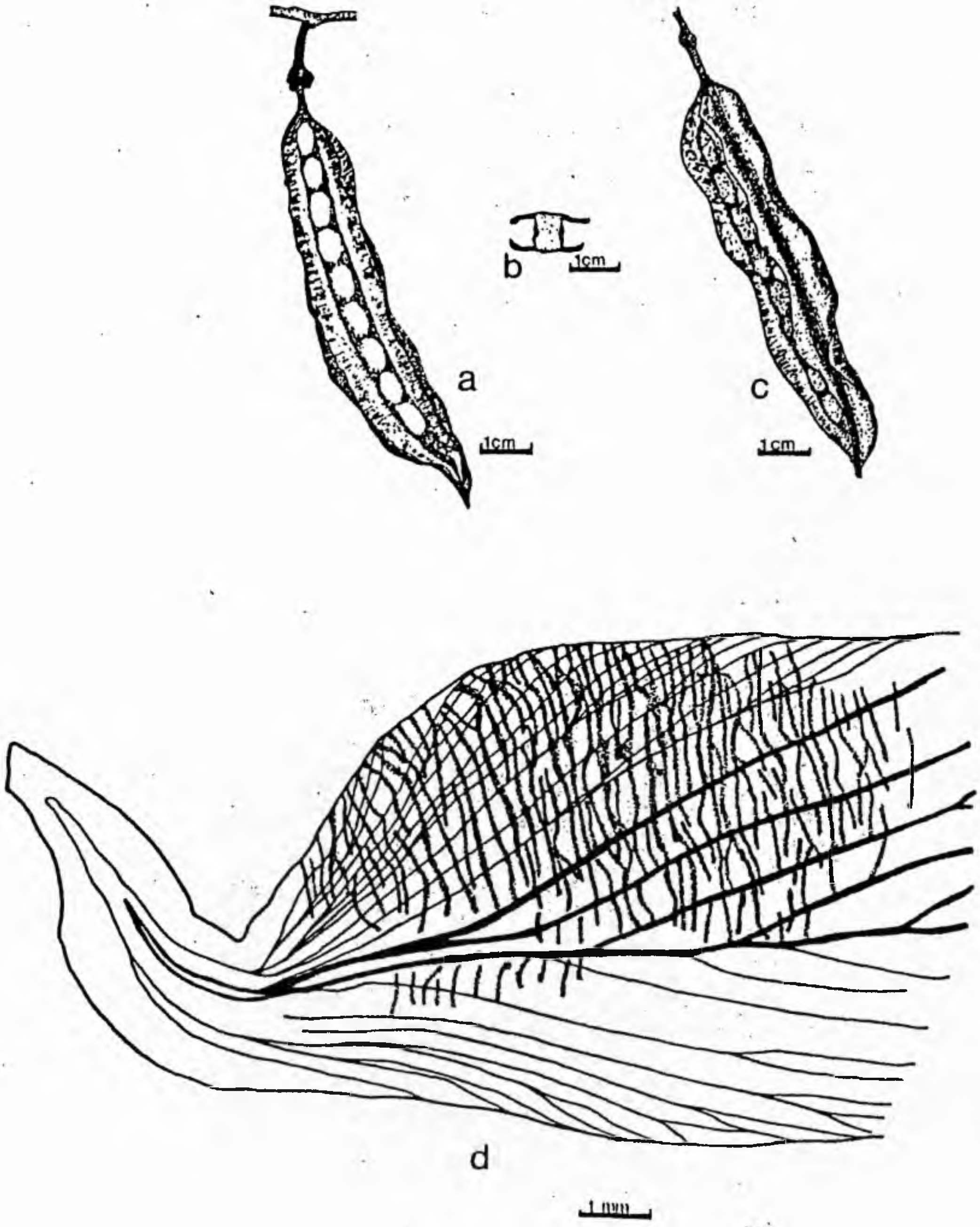


Figure 75 – Sesbania punicea (Cav.) Benth. a – pod; b – transection of pod showing the undulate wings; d – close-up of the upper basal portion of the wing petal showing the lamellate pattern of sculpture.

Type - Argentina ; Buenos Ayres, Colonia del Saevante ?, NEE s/n, 1795 (MA, holotype, not seen; phototypes STA!).

The type specimen of *S. punicea* at Madrid (MA) has a handwritten note which says "*Aeschynomene miniata* Ortega", which indicates that ORTEGA (*loc. cit.*) may have seen CAVANILLES' specimens.

This species has been cultivated for long time as ornamental in the countries of the tropics and subtropics. It has also become weedy in many places where it has been introduced (see section "Economic Uses"). Elsewhere, *S. punicea* occurs naturally in Brazil, Paraguay, Uruguay and Argentina (Figures 76, 77).

In North America (Figure 77), *S. punicea* was introduced not only from South America but also from Africa, according to information in GILLIS 8014 (FTG,MO). These specimens of African origin show a more deeply striate stem which is apparently glabrous when young, narrower leaflets, fruits with longer beak, and smaller seed.

S. punicea and *S. drummondii* are very similar in many many respects but, apart from the obvious differences in flower colour and dimensions, the pods of *S. punicea* are longer and broader, with more seeds and undulate wings (the latter are patent in *S. drummondii*); the seeds are reniform to oblong while in *S. drummondii* they are quadrate-reniform.

Due to the many similarities, it is possible that S. drummondii is, in fact, derived from a S. punicea ancestral stock through reduction of flowers, pods and number of seeds, with subsequent change in petal colour.

The links between the floras of the U.S.A. coastal Gulf of Mexico (the typical distribution locality of S. drummondii, Figure 71) and the Paraná basin (HILL, 1982) already discussed under S. emerus could likewise provide the support for a long-distance dispersal of seeds of S. punicea (or better, of its ancestor) to southern North America by birds. However, BURKART (1967) mentions that seeds of S. punicea are toxic to birds but this toxicity (also present in other species of Sesbania) can be interpreted as a chemical defence recently aquired by Sesbania, and so not necessarily eliminating possible dispersal mechanism, discussed above.

Distribution (Figures 76, 77)

CENTRAL AMERICA

Mexico - Sonora : Agiabampo, PALMER 775, 1890 (BM); no local. ment., PAVON s/n, no date (G).

NORTH AMERICA

California - Berkeley, BRACELIN 1513, 27.vii.1941 (CAS); San Jose, CALIF. HORT. SOC. s/n, 19.vi.1939 (CAS); Holywood, EASTWOOD s/n, viii.1916 (CAS); San Francisco, EASTWOOD s/n, vi.1919 (CAS); Pasadena, EASTWOOD s/n, 19.viii.1924 (CAS); San Diego, Balboa Park, JERABEK s/n, iii.1945 (SD); San Rafael, McCLINTOCK s/n, 25.vi.1961 (CAS); Davis, McCLINTOCK s/n, 16.vi.1969 (CAS); ibidem, McCLINTOCK /n, 24.5.1973 (CAS); Arcadia, Oakhurst Garden, REIDEN-

BACH s/n, 2.vi.1960 (CAS,FTG); Santa Monica, WALTHER 463, 3.viii. 1927 (CAS); Huntingdon's Place, WALTHER s/n, ix.1928 (CAS); no local. ment., WALTHER 305b, x.1929 (CAS); San Diego, WHITMAM 268, 23.vii.1969 (SD).

<u>South Plains</u> - <u>Texas</u> : Panola County, route 79, 4 mi. N of Sabine River bridge, CORRELL, JOHNSTON & EDWIN 22209, 23.v.1959 (LL); Rio Grande City, GRIFFITHS 6468, 27-29.v.1904 (MO); near Port Arthur, NOGLE s/n, viii.1942 (NY); Dallas, REVERCHON s/n, 1877 (MO); Tyler Co : roadside, south edge of Woodville on Beaumont Highway, THARP 50-103, 13.v.1950 (TEX); Hardin Co : 2 mi. N of Silsbee on highway 92, THOMPSON & TURNER 109, 17.v.1958 (TEX); Galveston Co : San Leonard, WALLER & BAULM 3582, 24.iv.1975 (TEX).

<u>Southeast</u> - <u>Alabama</u> : Baldwin, Fish River ca. 9 mi. W of Folly, DAVENSPORT 1906, 24.v.1980 (NY); Mobile Co : Dauphin Island, DERAMUS D231, 3.viii.1964 (MO); Daphine, GRAVES 716, viii.1918 (MO); north side of Dauphin Island, KRAL 35599, 15.vii.1969 (MO,NY); <u>Florida</u> : Lake Co : 4 mi. W of Leesburg, BALTZELL 7113, 16.iii.1975 (BM); Duval Co : 4.3 mi. NE of US route 90 on Fla route 10, BOUFFORD & AHLES 9608, 30.v.1973 (MO); Perdido Bay, BRINKER 70, 21.vi.1941 (MO); Lee Co : Central Sanibel Island, BRUMBACH 8513, 20.iv.1974 (NY); Polk Co : Lakeland, BURCH & FREDRICKS 4190, 11.vii.1971 (CAS,MO); Tampa, BURCH & GIBSON 3811, vii.1970 (CAS); Hillborough Co : crooked Lake Road, Lutz Area , BURCH & MACHEVART 3980, 27.vii.1970 (CAS); Hernando Co : Weeki Wachee, BURCH & WELLS 4113, 22.vi.1971 (CAS,MO); Apalachicola, BUSH 292, 14.viii.1897 (NY); ibidem, CHAPMAN 3787, no date (NY); ibidem, CHAPMAN s/n, no date (NY); Polk Co : 1 mi. N of Providence CORRELL & CORRELL 51720, 27.iv.1981 (FTG); Apalachicola, CURTISS

590, date ? (MO,NY); ibidem, CURTISS 5884, 10.vi.1897 (DS,E,G,MO, NY,P); Alachua Co : Gainnesville, Hogtown Creek, D'ARCY 1658, 28. vi.1967 (LL,SD); Bay Co, DRESS & READ 7679, 25.vi.1959 (E); Hernando Co : SR50, 5 mi. W of US19, GENELLE & FLEMING 728, iv.1971 (FTG); Miami, cultivated at Fairchild Tropical Garden, GILLIS 7563, 12.ii.1969 (FTG); ibidem, ibidem, GILLIS 8014, 8.v.1969 (FTG,MO); Leon Co : 2 i. E of Tallahasee, GODFREY 53361, i.vi.1955 (NY); ibidem, near Northwood Mall, Tallahasee, GODFREY 79005, 14. vii.1981 (FTG); Bradford Co : ca. 2 mi. S of Lawtey, HANSEN & RICHARDSON 5565, 18.v.1979 (DS); Gadsden Co : at the north edge of Quincy, HENDERSON 63-1393, 27.vii.1963 (TEX); Hillsborough Co : immediately south of Riverview, adjacent to US301, ISELY & ISELY 10993, 12.iv.1971 (CAS,NY); Washington Co, ISELY & WEMPLE 9180, 4.ix.1964 (NY); Hillsborough Co, LAKELA & ALMEDA s/n, 24.iv.1967 (BM); no local. ment., LEROY s/n, no date, (NY); Brevard Co : Cocoa, McFARLIN 4931, 22.iv.1931 (CAS); Manatee Co : south of Cates City, ,MOLDENKE 1044, 23.iv.1930 (BM,K,MO,NY,P); New Port Richey, O'NEILL s/n, 23.iv.1927 (MO); Sarasota, RUSBY s/n, 22.iii.1935 (NY); Clay Co : SCHALLERT s/n, 4.v.1941 (NY); Seminole Co, SCHALLERT 6113, 20.iii.1963 (G,P); along Indian River, Coco, SMALL 8724, 9.v.1918 (NY); Pensacola, TRACY 8513, 30.iv.1903 (G, MO,NY); Tamiami Trail, Sarasota Way, collector ? 7168, 14.iv.1926 (NY); <u>Georgia</u> : 10 mi. W of Sylvannia, DUNCAN 5561, 7.vii.1942 (MO); south part of Dublin, DUNCAN 9920, 9.vii.1949 (MO); 2 mi. NW of Jesup, DUNCAN 10913, 21.v.1950 (MO); Grady Co : Coastal Plain Province, 2 mi SW of Wigham, FAIRCLOTH 1380, 24.vii.1964 (MO); Colquit Co : 6.5 mi. W of Lenox, FAIRCLOTH 3367, 11.vii.1966 (MO);

St George, JONES *et al.* 23061, 31.viii.1978 (BM); Pierce Co : banks of stream flowing under College Avenue, S of Blachshear limits, KISER s/n, 23.v.1970 (MO); Dooly Co : 1.5 mi. S of Vienna, LANE Jr 29000, 4.vii.1968 (BM); roadsides on St Simmons Island, MODY s/n, 19.v.1978 (G); ibidem, MOLDENKE & MOLDENKE 29901, 20.v.1975 (LL); Camden Co, SCHALLERT s/n, 24.vii.1940 (DS,MO); Lownsden Co : 8 mi. S of Valdosta, VOLOSEN s/n, 12.v.1970 (MO); *Louisiana* : Jefferson Parish : Central Grande Island, ANDRUS 63, 28.vii.1903 (NY); New Orleans, JOOR s/n, 17.v.1889 (MO); Terrebone Parish, 12-9 mi. SW of Thibodeaux along highway to Morgan City, LASSEIGNE 361, 7.vii.1967 (MEXU); Quachita Parish : edge of woods at Curve Drive, E of LA139 near US80 E of Monroe, THOMAS & THOMAS 275, 20.v.1967 (NY); *Mississippi* : Hancock Co : 6 mi. of Bay St Louis, BRENNER Jr s/n, 27.viii.1940 (MO); Pearl River Co : about 6 mi. NW of Poplarville, DARWIN *et al.* 744, 4.viii.1978 (MO); Harrison Co : Biloxi, DEMAREE 28176A, 16.vii.1949 (TEX); ibidem, DEMAREE 30680, 6.i.1951 (TEX); Santa Rosa, EWAN 18287, 1950 (BM); Pearl River Co : Picayune, JONES 11961 & REYNOLDS, 3.v.1967 (NY,TEX); Forrest Co : Hattiesburg, ROGERS 8514-C, 19.vii.1972 (MO); Petit Bois Island, TRACY 5054, 8.v.1898 (NY); ibidem, TRACY 5354, 8.v.1898 (MO,NY); *North Carolina* : New Hanover Co : Caroline Beach, BRADLEY & STEVENSON 3344, 24.vii.1966 (E,NY,TEX); ibidem, Wilmington, ballast area near North east River, LEONARD & RUSS 2620, 23.vii.1969 (DS,SP); Roanoke Island, The Elizabethan Garden, MEYER 10119, 19.viii.1967 (CAS); Columbus Co : Chadbourne, PRYAH 3096, 1.vi.1965 (NY); *South Carolina* : Hampton Co, AHLES 15756 & BELL, 29.vi.1956 (NY); Clinch Co, RODGERS *et al.* 74192, 4.v.1974 (MO).

Figure 76 - Distribution map of Sesbania punicea in North and Central America.

North America, without precise locality : state ?, Georgetown County, 3 mi. N of Georgetown, US701, ISELY *et al.* 10392, 13.v.1976 (NY); locality ?, SHUTTLEWORTH 131 (772), 12.vi.1867 (NY).

SOUTH AMERICA

Argentina - Province of Jujuy, Jujuy, AHUMADA, VACA & LEGNAMO 2174, 15.x.1961 (DS,K,LL,NY); Buenos Ayres, BADE 79, 6.iii.1945 (G); Province of Misiones : Posadas, BERTONI 792, 6.iii.1945 (NY); Isla de Santiago, ca. La Plata, CABRERA 523, 8.xii.1928 (NY,SP); ibidem, CABRERA 2165, i.v.1932 (NY); Province of Jujuy, dept of Capital : Quebrada de Chyra, CABRERA & RIESLING 20082, 2.xii.1969 (K); Prov. of Misiones, Dept of Leandro : N. Aleman, Guemes, S. José, etc, CABRERA *et al.* 26823, x.1977 (RB); Prov. of Corrientes : "sur tout le cours du Paraná, du 26° au 33° de latitud sud", D'ORBIGNY 148, date ? (P); Prov. of Misiones : Posadas, EKMAN 1766, 2.xii.1907 (MO,NY); on the banks of the river below the town of Buenos Ayres, FOX 1, date ? (K); Prov. of Corrientes : Paso de Los Libres, GOMEZ s/n, 3.xi.1973 (MO); no local. ment., HUGUENIN s/n, 1848 (G); Prov. of Salta, HUMBERT 21103, 1948 (P); Prov. of Corrientes ; Paso de Los Libres, IBARROLA 2079, 12.i.1945 (NY); ibidem, IBARROLA 2158, 21.i.1945 (NY); ibidem ; Montes Caseros, Juan Pujol, 12 km E, IBARROLA 2377, 10.ii.1945 (NY); Prov. of Buenos Ayres : Partido de Anellaneda, Darsena de Inflamables, KRAPOVICKAS 2682, 24.xi.1945 (K,MO,NY); Prov. of Salta : Vaqueros, "orillas Rio Vaqueros", 8 km. N of Salta, KRAPOVICKAS & SCHININI 30380, 21.iii.1977 (G); no local.

ment., KRAPOVICKAS et al. 16993, 3.xii.1970 (MO,P); Prov. of Corrientes : Ituzaingo, Isla Apipe Grande, Puerto Santo Antonio, KRAPOVICKAS et al. 24043, 9.xii.1973 (MO); ibidem, KRAPOVICKAS et al. 24387, 11.xii.1973 (G); Province of Entre Ríos : Concepción del Uruguay, LORENTZ 891, ii.1877 (BM,K,P,W); ibidem, LORENTZ s/n, 1879 (FHO,G,K,W); Prov. of Corrientes, Dept of Paso de los Libres : Estancia "El Recreo", 21 km E of Bonpland, LOURTEIG, SCHININI & MARUNAK 2747, 18.xi.1973 (G,P); Prov. of Misiones : Obera, on the road, ca. 14-15 km. N of Campo Viera, MARUNAK 100, 6.i.1970 (LL,MO); Prov. of Tucumán, : Tucumán, MEYER 3416, 8.xii.1940 (NY); Prov. of Misiones : Pacanguassu, MONTES 27600, no date (NY,SP); Isla Martin Garcia, PALACIOS 47, 20.xii.1946 (P); Prov. of Corrientes : Estancia Gauchos, PEDERSEN 9249, 10.x.1969 (NY,P); Prov. of Misiones : Piray Guazu, QUARIN 263, 7.i.1972 (UB); Prov. of Buenos Ayres : between S. Santiago and Pelo Branco, RODRIGUEZ 597, 2.xii.1944 (BM,NY); ibidem : delta of Rio Paraná, Rio Chaua, SCALA 165, i.1914 (NY); ibidem : Buenos Ayres, SCALA 166, i.1914 (SP); Prov. of Jujuy : Perico del Carmen, SCHIAVONE et al. 11741C, 11.xi.1975 (MO); Prov. of Misiones : Candelaria, road 204, between road 12 and Profundidad, SCHININI 5404, 29.ix.1972 (G); Prov. of Corrientes, Dept of Santo Tomé : road 40 and Arroyo Chimirray, SCHININI & CARNEVALI 10324, 12.xi.1974 (G); Prov. of Entre Rios : Concepcion del Uruguay, SCHULZ 343, 9.I.1945 (NY); Prov. of Buenos Ayres : 1 km S of Punta Alta, SOLOMON & SOLOMON 4017, 7.xii.1978 (MO); Prov. of Corrientes : Arroyo Itambé, TESMERO 206, 15.xii.1944 (NY); Buenos Ayres, TWEEDIE s/n, no date (FHO); Prov. of Tucumán : Rio Sale, Tucumán, VENTURI 7238, 14.i.1928 (MO).

Brazil

South - state of Paraná : Paranaguá, Alexandra, DUSÉN 15477, 1.ix.1914 (G,MO); ibidem, HATSCHBACH 380, 22.ix.1946 (MO,UEC); Rio Negro, SELLOW s/n, no date (W); no local. ment., TWEEDIE s/n, (1775 ?), date ? (BM); state of Rio Grande do Sul : Taím, Pelotas, ARY 123, 29.i.1950 (BM,G,MO); Belem Novo, CASTELLANOS 24472, 18.i.1964 (K); no local. ment., RICHARD s/n, 10.xii.1845 (P); ibidem, FITCH s/n, v.1871 (K); ibidem, GAUDICHAUD B416, no date (P); ibidem, GAUDICHAUD 1533, 1492, 1833 (P); Rio Pelotas, km. 270 of Road BR-116, KRAPOVICKAS & VANNI 36867, 23.ix.1980 (MEXU); Porto Alegre, Jardimn Botânico, KUHLMANN s/n, xi.1936 (RB); ibidem, proximities of the airport, PABST 10148, 25.i.1952 (RB); between Guaiba and Arroio dos Ratos, PEREIRA 6591, 30.x.1961 (RB); no local. ment., PRATES s/n, no date (P); Itapuan, RAMBO 39115, 22.xii.1948 (NY); Pelotas, SACCO 260, 27.xii.1948 (NY); Porto Alegre, TRINTA 1112, 15.i.1966 (NY); without precise locality, SELLOW s/n, 1823 (SP); no local. ment., VIANNA 164, 1941 (RB); state of Santa Catarina : Hansa, EIPPER s/n, 27.x.1932 (SP); Ararangua, Sombrio, REITZ c119, 30.x.1943 (RB); ibidem, REITZ c498, 12.iv.1944 (RB); ibidem, REITZ c908, 23.xii.1944 (RB); Laguna, REITZ & KLEIN 173, 22.xii.1951 (G); Salto de Itajaí de Blumenau, ULE 1017, xi.1888 (P); Laguna. ULE 1422, xii.1889 (P).

South east - state of São Paulo : Cananéia, BUHARAH s/n, 16.v.1978 (UEC); Fazenda Campininha, 25 km NW of Mogi-Guacu, GIBBS & LEITAO FILHO 4263, 17.i.1977 (UB,EUC); Cananéia, GOES 52, 22.ii.1978 (SP); Nova Odessa, Instituto de Zootecnia,, GOMES 4 & MANTOVANI, 20.ix.1978 (SP); São Paulo, HANDRO 35232, 10.ix.1935 (P);

Campinas, district of Barão Geraldo, LEITÃO FILHO & TARODA 2548, 12.viii.1976 (UEC); São Paulo : Botanic Garden, Instituto de Botânica, collector ?, 30.xii.1935 (SP); state of Mato Grosso do Sul : município of Rio Brilhante, Rio das Araras, HATSCHBACH 25248, 26.x.1970 (NY).

Brazil, without precise locality : NADEAUD s/n, no date (P); "in various parts of the Banda Oriental and Rio Grande, along the borders of creeks" FOX s/n, no date (K); FOX s/n, no date (K).

<u>Paraguay</u> - "Adelanas Santa Misiones", HASSLER 496, x.1901 (G); Caaguazu, HASSLER 8864, ii.1905 (BM,G,K,NY,P); Encarnación, HASSLER 1468, ix.1915 (G); ibidem, ROJAS 10834, 17.i.1944 (P); ibidem, SCHROTTKY 19, 9.x.1902 (G).

<u>Uruguay</u> - Playa Real de San Carlos, 7 km N of Puerto Colonia, ARCHER 4955, 17.i.1937 (NY); Department of Colonia, along Arroyo de Pintos, Artilleros, near Puerto Platero, BARTLETT 21189, 17.xii.1943 (NY,P,TEX); Bella Union, CASTELLANOS s/n, 28.i.1948 (P); Montevideo, COURBON s/n, 1856 (P); Colonia Valdense, DUBUGNON 184, xi.1955 (G,K,NY); on the north bank of Uruguay River, above Martin Garcia, FOX s/n, no date (K); no local. ment., FOX s/n, no date ? (BM); Montevideo : Pincon del Cerro, FRUCHARD s/n, x.1871 (P); ibidem, FRUCHARD s/n, 13.x.1874 (P); Department of San José : Barra, HERTER 680, xii.1926 (G); San Javier, HERTER 680a, xi.1927 (G,NY); Department of Cerro Largo : Rio Branco, Rio Yaguarón, HERTER 680b, 29.xi.1947 (MO,NY); Montevideo, Carrasco, OSTEN 4731, 24.ii.1907 (E,G); Paysandu : Chapicuy, "orillas del Rio Uruguay", near Santa Sofia, ROSENGURTT B-4229, 15.xi.1942 (MO,SP); "Banda Oriental", StHILLAIRE 2443, 1816-21 (P); no local. ment., StHILLAIRE 373, no date (P); La Plata, TWEEDIE s/n, no date (E);

Figure 77 - Distribution map of Sesbania puniceá in South America.

Department of Rivera : Cunapiru, WRIGHT s/n, 1928 (BM); Santa Lucia, collector ? 217, iii.1867 (K).

(11) . *Sesbania virgata* (Cav.) Pers.

Syn. Pl. 2 : 316, 1807

syn. : *Aeschynomene virgata* Cav.
Ic. Pl. 3 : 47, t. 293, 1796
Coronilla virgata (Cav.) Willd.
Sp. Pl. 3 : 1148, 1803
Agati virgata (Cav.) Desv.
JOURN. BOT. 2 : 120, 1813
Coursetia ? *virgata* DC.
Prodr. 2 : 264, 1825
Sesbania marginata Benth., *in* Martius
Fl. Bras. 15 (1) : 43, t. 7, 1859
Sesbania tetragona Pamp.
N. GIORN. BOT. ITAL. 14 : 604-6, 1907

Shrub (0.5-)1.0-4.0 m tall. Leaves (7-)10-25(-30) cm, with 8-20(-25) pairs of leaflets; leaflets oblong to elliptic-ovate, mucronulate, 15-25(-30) x 5-7(-10) mm; petiolules 1.5-2.0 mm; stipules lanceolate, acuminate, 3-4(-5.5) mm. Racemes 6.0-8.0 cm, with 10-17(-19) flowers; bracts and bracteoles linear-lanceolate. Flowers yellow or the standard streaked with green, 8-12 mm; calyx campanulate, slightly bilabiate, 4-5 mm (including the lobes), the lobes 1.0-1.2 x 1.0 mm, triangular, acute; standard orbicular to oblate, deeply emarginate, with a pair of short, acute appendages on the claw, strongly reflexed (as in *S. macroptera*); wing petals oblong, up to 10 mm; keel petals obovate, upcurved, to 12 mm, the claw 3-4 mm. Pod 40-70 x 6-10 mm, stipitate, rostrate, subarticulate or with deep lateral constrictions between seeds, subcylindric and then marginate, or 4-winged with the margins shortly expanded simulating wings; the beak (2.5-)5-8 mm. Seeds reniform, 5-9 per pod, 5.0-7.0 x 3.5-4.0 mm, pale-brown. Figure 78.

Type - Argentina, no local. ment., NEE s/n, no date (MA, holotype, not seen; phototypes E!).

CAVANILLES (1796) mentioned that the plants which he used for the description of "*Aeschynomene virgata*" were raised at Madrid Botanic Garden from seeds sent from "Nova-Hispania" (i.e., Mexico) but, the type specimens' labels show that the original collection comes from Argentina, collected by NEE.

The illustration of this species given by CAVANILLES (*loc. cit.*) does not depict very accurately the type specimens as far as the pod morphology is concerned. It shows a compressed but not exactly 4-angled pod as the description mentions. This fact might be the reason why BENTHAM (1859) described his *S. marginata* and ignored completely CAVANILLES' taxon (which, furthermore, was said to come from Mexico, and not South America).

Distribution (Figures 71, 72)

CENTRAL AMERICA

Mexico - no local. ment., HAHN s/n, 1865-66 (P); Veracruz : 24 mi. S of Alvarado on Rt 175 along Rio Papalaopán, OZMENT, ALTIG & ALTIG 456, 20.vi.1964 (MO); no local. ment., PAVON s/n, no date (BM); Veracruz : 1.5 km. S of Tunilla, 11 km. N of Tlacotalpán,

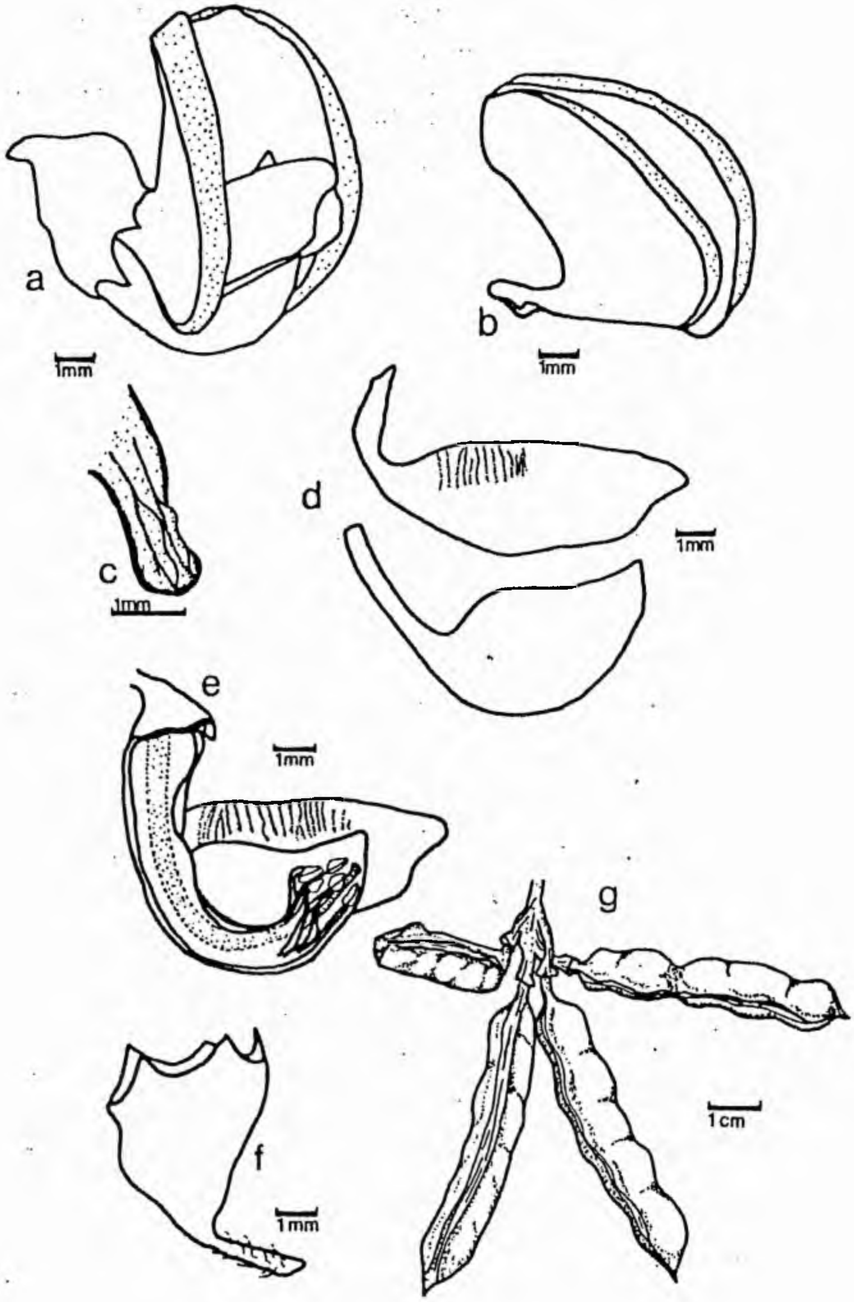


Figure 78 - Sesbania virgata (Cav.) Pers. a - flower; b - standard; c - base of standard showing appendages; d - wing and keel petals; e - partially dissected flower; f - calyx; g - pods.

SOUSA 4435, 27.viii.1974 (CAS); ibidem ; Tlacotalpan, collector ? 132, 20.iv.1866 (P); no local. ment., collector ?, date ? (K); without precise locality, collector ?, date ? (G-DC, holotype of *Coursetia* ? *virgata* (Cav.) DC.); ibidem, ibidem, (FI, holotype of *Sesbania tetragona* Pamp., not seen; phototype E!).

NORTH AMERICA

California - San Diego, McCLINTOCK s/n, 1.ix.1972 (CAS).

Southeast - *Florida* : Gulf Co : 2 mi. NW of Port St Joe, BECKNER 1851, 29.vii.1967 (NY); ibidem, beach of Pensacola Bay, BRINKER 189, 4.vii.1941 (MO); ibidem, Pensacola, GANDER 7639, 15.vi.1939 (SD).

South Plains - *Texas* : no local. ment., DRUMMOND 135, 1836 (BM).

SOUTH AMERICA

Argentina - Ialta : Joaquin V. Gonzáles, AGUILAR 303, 28.i.1945 (NY); Corrientes, Lavalle : Lavalle, "Isla en Rio Paraná", AHUMADA, SCHININI & TRESSENS 3372, 29.ii.1980 (MEXU); ibidem, Esquina : on road 25, ca. 59°15'W, 29°48'S, AHUMADA, SCHININI & TRESSENS 3453, 2.iii.1980 (G); ibidem, San Miguel : 12 km S of Caa-Cati, Road 5, AHUMADA *et al.* 2334, 13.iii.1978 (G); ibidem, San Cosme : 4 km. E of Paso de la Pátria, ARBO *et al.* 724, 20.iii.1974 (G); Corrientes, BONPLAND s/n, date ? (P); Entre Ríos : Paraná River, CABRERA 6490, 23.v.1940 (NY); Corrientes, San Roque : San Roque, Santa Lucia, CRISTOBAL *et al.* 1476, 6.xii.1975 (G); ibidem, Rio Parana, D'ORBIGNY 146, date? (P); Posadas, EKMAN 1765, 21.ii.1907 (MO,NY); Buenos Ayres, FIELDING s/n, no date (P); Entre Rios : El Briete, FRENGUELLI 8, 11.x.1937 (NY); Santiago del Estero, Robles : Beltrán, GARCIA 773, 20.i.1945 (NY); Corrientes, Cosme : Isla Claudia, HUIDOBRO 2014, 16.iv.1945 (NY); Santiago del

Estero, Rio Hondo : Las Fermas, HUIDOBRO 3038, 24.x.1946 (MO); Santa Fe, Las Colonias : Esperanza, HUIDOBRO 3242, 15.xi.1946 (MO); Corrientes : San Cosme, Ensenada, HUIDOTRA 1832, 28.iii.1945 (NY); San Vicente, HUNZIKER 1586, 30.i.1946 (CAS); Corrientes, IBARROLA s/n, viii.1944 (NY); ibidem : pueblo San Luis del Palmar, IBARROLA 838, 23.ix.1944 (NY); ibidem, San Martin : Yopeyu, E of Guarirobi, IBARROLA 1909, 31.xii.1944 (NY); no local. ment., JURGENSEN 125, xi.1894 ? (MO); Chaco, JORGENSEN 2698, ii.1917 (MO); Formosa, JORGENSEN 2944, v.1919 (MO); Buenos Ayres : San Vicente, "en la Laguna S. Vicente", KRAPOVICKAS 2842, 30.i.1946 (K,MO,NY); Corrientes, San Tomé : Santo Tomé, near Uruguay River, KRAPOVICKAS et al. 25315, 13.iv.1974 (G); ibidem, Esquina : islands in front of Esquina, KRAPOVICKAS et al. 26898, 30.x.1974 (G); ibidem, ibidem ; Colonia Libertador, arroyo Barrancas, KRAPOVICKAS et al. 27844, 15.iii.1975 (G); ibidem, Gen. Alvear : road 40 and Aguapey River, LOURTEIG, SCHININI & MARUNAK 2853, 20.xi.1973 (P); Algarrobal ?, LUNA 93, 20.iv.1947 (CAS); Santiago del Estero : Beltran, MALDONADO 481, 29.x.1940 (NY); Salta, Anta: El Quebrachal, alt. 339 m, MALVAREZ 610, 1.ii.1947 (K); Islas Puentes, MEYER 10091, 2.xi.1946 (P); Tucuman, Leales : Arroyo Mixta, MEYER 12758, 19.xi.1947 (NY); Formosa, Pilcomayo : Riacho Negro, MOREL 2881, 19.v.1947 (LL); Salta, Capital : between San Francisco and El Jardin, 1 km. N of Rio Ancho, NOVARA s/n, 14.xi.1981 (MO); Corrientes : Itati, PEDERSEN 7015, 3.iv.1964 (E,K,MO,NY,P); Formosa, Bermejo : Las Lomitas, PIEROTTI 4074, 4.ix.1945 (BM,K); Formosa, Riacho Negro : Clorinda, km 107 of Road 11, REALES 382, 22.iii.1947 (MO); Chaco : Resistencia, ROJAS 11212, 17.vi.1944

(NY); Corrientes, Capital : road to Santa Ana, Laguna Soto, SCHININI 12142, 1.xi.1975 (G); Corrientes, Alvear : 30 km. NE of Alvear, banks of Uruguay River, SCHININI, CABRAL & VANNI 16937, 10.ii.1979 (MO); Corrientes : Montes Caseros, 8 km S of Labougle, borders of Uruguay River, SCHININI, CABRAL & VANNI 17563, 22.ii.1979 (MO); ibidem, Saladas : Laguna Roto, SCHOVARZ 47, 25.x.1944 (NY); Buenos Ayres, TWEEDIE s/n, date ? (K); Santiago del Estero, Capital : Rio Dulce, VENTURI 9796, 22.xi.1929 (BM,MO); Burrojaio : Rio Nio, VENTURI 10384, 7.iii.1930 (BM,NY).

Brazil

South - state of Rio Grande do Sul : Rio Grande, DESLANDES s/n, i.1928 (SP); Uruguaiana, ROSENGURTT, DEL PUERTO & BRESCIA 9440, 17.v.1963 (K); Pelotas, Retiro, SACCO 1014, 11.iii.1958 (SP).

Southeast - state of Minas Gerais : município of Bicas, km. 55 of road Leopoldina to Juiz de Fora, SALGADO & PAULINO 480, 18.v.1978 (UEC); state of Rio de Janeiro : Dutra Raod (BR 116), km 110, ALCÂNTARA, ARAUJO & OLIVEIRA LEITE 201, 26.vi.1977 (UEC); Rio de Janeiro city, grassy shore of Lagoa Rodrigo de Freitas, LEDINGHAM 4430, 15.i.1966 (NY); Restinga de Jacarepaguá, PABST 8251 & SMITH, 29.ix.1964 (NY); Cabo Frio, PEREIRA 10518, 23.i.1967 (K); Itaipu Sands in Cabo Frio, PLOWMAN 2802 & SUCRE 5102, 27.v.1969 (K,RB); no local. ment., RAMBO 46632, date ? (CAS); Cabo Frio, road to Arraial do Cabo, SUCRE 1448, 22.i.1967 (RB,UB); state of São Paulo : São Paulo city, Museu Paulista, HOEHNE s/n, 18.ii.1921 (SP); ibidem, cultivated at Jardim Botânico, MATTOS 15383, 21.xi.1968 (SP); município of Campinas, Fazenda Santa Elisa, TARODA & KINOSHITA 4170, 14.xii.1976 (UEC).

West Central - state of Mato Grosso do Sul : near Corumbá, BOURKE-

BORROWES 13, 6.ix.1928 (K); road Miranda-Corumba, GIBBS, SHEPPERD, ANDRADDE & BUFARAH 5368, 21.vii.1977 (UEC); road Transpantaneira, HERINGER *et al.* 849, 28.i.1979 (NY,UEC); Corumbá,KUNTZE s/n, viii.1892 (NY); ibidem, MOORE 1040, 1891-2 (BM); Distrito Federal: QNL Taguatinga Norte, SILVA 258, 9.iii.1980 (MO).

Paraguay - Asunción : borders of Paraguay River, BALANSA 1378, iv.1874 (G,K,P); Curupayty, Humaitá, Neembucu, BERNARDI 18486, 10.xi.1978 (G); Cordillera : north shore of Lake Ypacarai, about 40 km E of Asunción, CONRAD 2195 & DIETRICH, 15.i.1974 (MO); Lake Ypacarai, FRIEBRIG 338, 28.x.190 (E,G,K); Gran Chaco, KERR s/n, 1890-91 (K); Lake Ypacarai, HASSLER 530, date ? (G); ca. 20°-28° S and 59°-63° W, HASSLER 815, 1885-95 (G,K,NY,P); Gran Chaco, Santa Elisa, HASSLER 2724, ii.1903 (BM,K,NY); Lake Ypacarai, HASSLER 3702, 3703, xii.1898-1900 (K,P); Cordillera de Villa Rica, HASSLER 8590. i.1905 (G,K,NY,P); n the vicinity of Caaguazú, HASSLER 8864, ii.1905 (BM,K,NY); Lake Ypacarai, HASSLER 11757, v.1913 (E,G,K,MO,NY); prope Villarica", JORGENSEN 3610, no date (DS,MO,NY); Concepción de Paraguay, KUNTZE s/n, ix.1892 (NY); ibidem, KUNTZE s/n, no date (NY); Asunción, LINDMAN A1649, 10.vii.1893 (NY); Rio Apa, Coloni Risso, MALME 1106, 30.x.1893 (BM,G); Estancia 14 de Mayo, MALME s/n, 29.iii.1903 (MO); "Central Paraguay", MORONG 64, 621, 1888-1890 (K); San Bernardino, OSTEN 8181, 27.viii.1915 (G); in fields near River Pilcomayo, ROJAS 494, vii.1906 (G); "Central Paraguay" : Trinidad, SPARRE & VERVOOST 108, 14.xi.1950 (TEX); Paraguarí, SPARRE & VERVOOST 577, 25.xi.1950 (K); Sta Trinidad, near Asunción, TEAGUE 660, 24.i.1946 (BM); Pilar, Neembucu department : along edge of Rio Neembucu, WALTER 204, ii.1975 (NY); Puerto Rosario, WOOLSTON 948, 18.iii.1958 (K,NY).

<u>Uruguay</u> - riversides, FOX 254, no date (K); Montevideo, Barra de Santa Lucia, FRUCHARD s/n, i.1872 (P); ibidem, GILBERT 110, iii.1858 (K); Barra : San José, HERTER 679, xii.1926 (G,MO,NY); Montevideo, arenales de Carrasco, ROSENGURTT B-68, 8.ii.1836 (NY); Department of San Jose, collector ?, ii.1926 (G).

4.10 - subgenus Agati*

subgen. Agati (Adans.) Baker
Fl. Br. Ind. 2 : 115, 1876

Agati Adans.
Fam. Pl. 2 : 326, 1763

Small trees, glabrous. Racemes 2-3(-4) flowered; flowers white, pinkish or reddish, 50-85(-100) mm. Calyx campanulate, truncate, slightly bilabiate, the upper lip with 2, the lower with 3 short lobes. Standard without appendages at the base, oval, shorter than the wings. Wing and keel petals lanceolate-lunate, without basal tooth. Staminal sheath 35-60 mm, with long, large, curved, rounded auricles near the base. Pod linear, elongate, compressed, 30-40(-45) cm. Seeds reniform-oblong, hilum circular, central to subterminal.

Type species : Sesbania grandiflora (L.) Pers.

The subgenus Agati is here accepted as comprising two species, S. grandiflora (L.) Pers. and S. formosa (F. Muell.) Burbidge, but also possibly S. tomentosa Hook. & Arn.

S. grandiflora owes its present distribution to Man but it seems to have occurred naturally in India and south-eastern Asia.

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* The description does not include the variations present in S. formosa, which occurs in Australia.

However, its closest related species occurs in Australia (*S. formosa*) and this widely disjunct distribution of the subgenus *Agati* is rather intriguing. No studies on biological interrelationships between these two species have yet been done.

(12) . *Sesbania grandiflora* (L.) Pers.
Syn. Pl. *2* : 316, 1807

syn. : *Robinia grandiflora* L.
Sp. Pl. : 722, 1753
Aeschynomene grandiflora (L.) L.
Sp. Pl. : 1060, 1763 (ed. 2)
Dolichos arboreus Forssk.
Fl. Aegypt.-Arab. : 135, 1775
Aeschynomene coccinea L.f.
Suppl. Pl. : 330, 1781
Coronilla grandiflora (L.) Willd.
Sp. Pl. : 1145, 1802 (ed. 4).
Non *C. grandiflora* Boiss., 1844
Coronilla coccinea (L.f.) Willd.
Sp. Pl. : 1146, 1802 (ed.4)
Sesban grandiflorus (L.) Poir.
Lam., Encycl. *7* : 127, 1806
Sesban coccineus (L.) Poir.
Lam., Encycl. *7* : 127, 1806
Sesbania coccinea (L.) Pers.
Syn. Pl. *2* : 316, 1807
Agati grandiflora (L.) Desv.
J. BOT. *1* : 120, t.4, 1813
Agati coccinea (L.) Desv.
J. BOT. *1* : 120, 1813
Agati grandiflora var. *coccinea* (L.) Wight & Arn., Prodr. Ind. Or. *1* : 216, 1834
Resupinaria grandiflora (L.) Raf.
Sylva Tell. : 116, 1838
Emerus grandiflorus (L.) Kuntze
Rev. Gen. Pl. : 180, 1891

Trees or treelets to 6(-8) m tall. Leaves 25-30 cm, large, with 10-20(-25) pairs of leaflets; leaflets narrowly oblong to oblong, glabrous or puberulent when young, 25-35 x 7-10 mm, petiolules up to 3 mm; stipules triangular to narrow-triangular, to 5 mm, late deciduous. Racemes 10-20 cmm, with 2-4 flowers, pedicels 20 mm, thin; bracts and bracteoles ovate, minute. Flowers white to rosy white or pinkish (or red in some cultivated ornamental varieties, (50-)60-85(-100) mm; calyx 10-18(-25) mm (including the lobes), the lobes broad-triangular, very short, 1-1.5 mm or apparently absent; standard 50-85 x 40 mm; wings 50-85(-90) x 20 mm, the claw 20 mm; keel petals upcurved, 60 mm, the claw 30 mm. Pods with a flat surface or more or less indented between the seeds, margins thickened and raised above the valve surface. Seeds 25-40 per pod, 6-4 mm, brown.

Type - Figure 51 in RHEEDE's "Hortus indicus Malabaricus",
Vol. 1, p. 95, 1678.

The LINN herbarium does not have a specimen of Robinia vesicaria L. but LINNAEUS (1753) actually mentioned the illustration provided by RHEEDE (1678) who described and illustrated a plant of S. grandiflora growing in India. The herbarium of RHEEDE for his "Hortus indicus Malabaricus" is unknown, therefore the illustrations are considered the actual types of his plants.

S. grandiflora is certainly original to the Old World but cultivated throughout the tropics and subtropics. GILLETT (1963), who did not mention the type of this species in his revision of the African and South Arabian species of Sesbania, has suggested that S. grandiflora is a native of Indonesia and it has been cultivated in Africa for more than 160 years. In the New World, S.

grandiflora has also been introduced and cultivated for about the same time in Central America and West Indies.

Distribution (Figures 71, 72)

CENTRAL AMERICA

Belize - St John's College, DIECKMAN 119, 16.iii.1970 (MO); ibidem DWYER, ELIAS & MAXELL 10, 15.iii.1967 (MO).

El Salvador - San Salvador, CALDERON 1336, 1922 (NY).

Mexico - Yucatan, GAUMER 670, date ? (BM,E,MO,NY,OXF); Coba, TELLEZ & CABRERA 1834, 12.iii.1980 (BM); no local. ment., collector ? 558, 1825 (TCD).

Panama - Cocle : Santa Clara, BLUM & TYSON 1883, 8.xii.1965 (MO); Panama City : collected at the Facultad de Ciencias, Universidad de Panama, CARRASQUILLA 259, 8.xi.1972 (MO).

SOUTH AMERICA

Brazil - Southeast : state of Rio de Janeiro - Horto Florestal de Niterói, APPARÍCIO s/n, 27.viii.1963 (RB); state of São Paulo _ cultivated at Fazenda Santa Elisa, Campinas, LEITÃO FILHO 1544, 10.x.1975 (UEC).

Colombia - Department of Santa Marta, "como ornamental en los jardines de la ciudad", BARBOSA 380, xii.1977 (NY); Department of Valle : Palmira, " cerca a la Facultad de Ciencias Agrarias", BARBOSA & FORERO 656, 8.xi.1978 (NY); Department of Girardot, Cundinamarca, DUQUE JARAMILLO 3628, 17.v.1946 (NY); Department of Bolivar : Sahagun, "carretera de Cerete a Shagun", alt. 120 m., GARCIA-BARRIGA 13456, 1.vi.1950 (NY); Departament of Magdalena : Barranquilla, HOLTON s/n, 30.viii.1812 (NY); Departament of

Cordoba : 10 mi. N of Planetarica, PLOWMAN & DAVIS 3732, 22.v.1974 (K,MO,NY).

<u>Guyana</u> - La Bonne Intention, east coast of Georgetown, OMAWALE & PERSAUD 43, 29.i.1970 (NY); Faifield, OMAWALE & PERSAUD 196, 14.vii.1972 (NY); Georgetwon, PARKER s/n, no date (K); no local. ment., PARKER s/n, no date (K).

<u>Surinam</u> - no local. ment., COULON 104, 1841 (NY).

<u>Venezuela</u> - Sta Lucia, CURRAN & HAMAN 1092, 19.vi.1917 (NY); La Vela de Coro, CURRAN & HAMAN 618, 4.x.1917 (NY); Jardin de Crurana, MOCQUERYS s/n, 1893-4 (NY); Maracaibo, MOCQUERYS s/n, 1893-4 (NY).

<u>WEST INDIES</u>

<u>Bahamas</u> - Acklin's Island : Pompey Bay, BRACE 4457, 21.xii.1905-6 (NY); Long Island : Turtle Cove, on the Queen's Highway, CERBIN C102, 13.i.1973 (FTG,NY); Great Exuma Island : along road entrance to Great Cay, in waste places, CORRELL 40719, 6.xii.1973 (FTG); South Caicos Island : along waterfront of Cockburn Town, CORREL 49244, 30.xi.1977 (FTG); Fortune Island : HITCHCOCK s/n, xi.1890 (MO).

<u>Barbados</u> - no local. ment., LANE s/n, 1843 (E).

<u>Cuba</u> - Cieneguito, COMBS 719, 21.ii.1896 (MO,NY); El Palmar, Guantanamo, HIORAM 2295, 26.xii.1918 (NY).

<u>Dominican Republic</u> - Province of Santo Domingo : vicinity of Ciudad Trujillo (=Santo Domingo), ALLARD 14412, 29.xii.1945 (NY); Guayacanes, AUGUSTO 451, xii.1962 (NY); province of Espaillat : Moca, Colonia de Famao, EKMAN 12559, 21.v.1929 (NY); Santo Domingo, JAGER s/n, no date (FHO).

<u>Guadeloupe</u> - no local. ment., collector ? s/n, 1849 (TCD).

Haiti - Port-au-Prince, JAEGEY 93, 1.ii.1828 (NY).

Jamaica - Grand Cayman Island : East End, KINGS 147, no date (MO); ibidem, north side, KINGS 288, 17.vii.1938 (MO).

Martinique - no local. ment., DUSS 1037, 1881 (NY); ibidem, DUSS 1957, 1881-94 (NY).

Montserrat - south of Plymouth, SHAFER 133 and 133A, 21.i.1907 (NY).

Porto Rico - Santure, HELLER & HELLER 592, 20.ii.1899 (NY); Rio Grande, HIORAM s/n, ii.1913 (NY); Vieques Islands : Santa Maria, SHAFER 2654, 2.ii.1914 (NY); Mayaguez, "in hortis", SINTENIS 858, 8.i.1885 (NY,W); N of Mayaguez on new section of Highway 2, a few miles N of Anasco at Km 135.6, SPETZMAN 189 & COLON, 24.i.1967 (FTG); Las Mesas area, 4 mi. SE of Mayaguez, new hilltop roadside of Highway 349, SPETZMAN 530, 4.iii.1968 (FTG); Isabela, UNDERWOOD & GRIGGS 213, 14.vi-22.vii.1901 (NY); Guayama to Cayey, UNDERWOOD & GRIGGS 441, 14.vi-22.vii.1901 (NY); Coama to Ponce, UNDERWOOD & GRIGGS 575, 14.vi-22.vii.1901 (NY).

Trinidad - no local. ment., BROADWAY s/n, 21.iv.1927 (MO,OXF).

St Vincent - no local. ment., WIGHT 902, no date (E).

Virgin Islands - St Croix : near Fredensborg, FOSBERG 54131 and 54132, 24.i.1972 (NY); ibidem, no local. ment., RICKSECKER 299, 29.ii.1896 (MO,NY); ibidem, ibidem, RICKSECKER s/n, no date (E); ibidem, Anna's Hope, THOMPSON 1027, 20.xii.1925 (NY).

5 . TAXONOMIC STUDIES IN THE UNIFOLIOLATE SPECIES OF LUPINUS L. IN BRAZIL

5.1 - Taxonomy of Lupinus L.

5.1.1 - Infrageneric classification

The earliest attempt to classify the unifoliolate species of Lupinus as a separate group within the genus was made by AGARDH (1835) who recognised Lupinus as divided into 'Leaves digitate' ("Foliis digitatis") as against 'Leaves entire' ("Foliis integris"). However, these groupings were not given any formal taxonomic rank. The digitate-leaved species were further subdivided in 12 "tribes", each of which was named after a constituent species, i.e., Albi, Polyphylli, Concinni, etc.

A similiar treatment was used by BENTHAM (1859) who, in his treatment of the genus Lupinus for "Flora Brasiliensis", also recognised the groupings "Simplicifolieae" and "Digitatae", both without any taxonomic rank.

WATSON (1873), in a monograph of the North American lupins, divided the genus into 'segments' without designating their taxonomic category : Lupinus proper (all the perennials and annuals without "petioled cotyledons"), Platycarpos (comprising the annual species with clasping petioles) and Lupinellus (with one species with solitary, axillary flowers).

TAUBERT (1894) recognised the genus as divided in three "sections", i.e., Digitatae Gerontogeae, Digitatae Neogeae and Simplicifolieae, the latter being accepted as circumscribed by BENTHAM (1859). In the Digitatae Neogeae, the segments published by WATSON (1873) were included without taxonomic rank.

Several other studies dealing with regional treatments of the genus have presented different infrageneric classifications for Lupinus. For example, PIPER & ROBINSON (1906) established WATSON's (1873) "segments" Lupinus and Platycarpos as subgenera and named as sections the supraspecific groupings as published by AGARDH (1835), i.e., Sericei, Saxosi, etc. RYDBERG (1917), in his "Flora of the Rocky Mountains and adjacent Plains" recognised 19 sections, some as new taxa.

SMITH (1938-1952) treated the genus in "Species Lupinorum" as divided into many informal groupings all of which he left unnamed. DUNN (1971), in his revision of the unifoliolate species of Lupinus from North America, considered these taxa as belonging to the grouping named "Simplicifolieae" which did not warrant any taxonomic rank. More recently, FALUYI (1980) has accepted WATSON's (1873) 'segments' Eulupinus (as treated by TAUBERT (1894)) and Platycarpos as subgenera of Lupinus.

It can be seen, therefore, that the genus presents some difficulties in its infrageneric classification with an accumulation of informal groupings rather than formal taxa. The present nomenclatural confusion can be attributed to two general causes : (1) the natural variation within the genus is considerable, mainly in the New World, where hybridization is very frequent (DUNN & GILLETT, 1966) but the variation pattern presents few obvious discontinuities; (2) the task of circumscribing species limits and relationships in the New World lupins is still far from complete so that the establishment of natural groupings of species which could be reflected in formal infrageneric categories is scarcely worth attempting at present.

A sensible way of approaching the infrageneric classification of Lupinus at present is the one proposed by DAVIS

& HEYWOOD (1963) for such genera in which the natural subdivisions are "almost impossible to find [with] sufficient discontinuity and correlation of characters". In these cases, DAVIS & HEYWOOD (*loc. cit.*) propose that "if satisfactory natural sections cannot be found ...there seems nothing for it but to rely for identification on an artificial key or on artificial (or partly artificial) groups based on a few technical characters". Furthermore, the same authors (DAVIS & HEYWOOD, *loc. cit.*) say that "in a natural classification it would seem preferable not to give these any formal taxonomic rank, but to treat them as informal groups outside the taxonomic hierarchy". This approach ha been adopted here and, for the purposes of delimitation of the unifoliolate species of *Lupinus*, the informal grouping "Simplicifolieae" *sensu* BENTHAM (1859) is employed without any taxonomic rank.

5.1.2 - Tribal position and generic relationships

The genus *Lupinus* was treated by BENTHAM (1865) as belonging to the large and diversified tribe Genisteae. This tribe was subdivided by HUTCHINSON (1964) into nine tribes based essentially on BENTHAM's (*loc. cit.*) subtribes. As a result of HUTCHINSON's rearrangement of Genisteae *sensu* BENTHAM, *Lupinus* and *Argyrolobium* were treated under the new tribe Lupinieae. However, the classification proposed by HUTCHINSON (*loc. cit.*) has been considered unsatisfactorily artificial and, therefore, rejected by many taxonomists.

The Genisteae *sensu* BENTHAM (1865) was revised by POLHILL (1976) who retained it as a distinct tribe along with three others, i.e., Bossieae (Australia), Liparieae (South Africa) and

Crotalarieae (mostly African but Crotalaria pantropical). The members of Genisteae, as delimited by POLHILL (loc. cit.) occur essentially in Europe and Africa except for Lupinus which is mainly distributed also in the New World.

More recently, BISBY (1981) has accepted the classification of the Genisteae as proposed by POLHILL (1976) but with the amendment that Lupinus should be considered in a subtribe Lupininae on its own with the other members (the "Cytisus-Genista complex") separated in the subtribe Genistinae. This taxonomic isolation of Lupinus from the other genera of Genisteae was recognised on the basis of data from seed-protein serology, pollination biology, and root nodule evidence which reinforce the "clear morphological distinction" between these taxa (BISBY, 1981).

The retention of Lupinus in the Genisteae is certainly supported by much evidence (POLHILL, 1976; BISBY, 1981) but it is also clearly tenuous when this genus is compared in habit and chemical compounds with the members of the Thermopsideae, in which the lupine alkaloids are common (MEARS & MABRY, 1971; POLHILL, 1976; TURNER, 1981).

The genus, therefore, represents a special entity, somewhat intermediate between the Genisteae and the Thermopsidae. However, intermediate taxa between tribes, genera and even species are not uncommon in the Leguminosae (POLHILL, 1981) and Lupinus, therefore, must not be treated as an exception.

Lupinus is here accepted as a member of the Genisteae in which it comes close to Argyrolobium Eckl. & Zeyh. but from which it differs in having the keel strongly adnate at the apex. Outside the limits of the Genisteae, Lupinus closely resembles Thermopsis (Thermopsideae) from which it differs in many morphological and anatomical traits (POLHILL, 1976) but with biochemical links via the alkaloid constituents, as already mentioned above.

The association and resemblance of Lupinus with Crotalaria are mostly derived from the fact that both genera have similarities in their morphological traits as they occur in the tropics and subtropics of South America. DUNN (pers. com., and 1984) has pointed out that some species of Lupinus have had their identity mistakenly confused with Crotalaria and that more evidence from various studies comparing these taxa are needed, particularly in South America. Further links of Genisteae members with the Crotalarieae are given by FERGUSON & SKVARLA (1981) who consider that pollen morphology in both tribes is very similar.

It seems, therefore, that like the rather anomalous position of Sesbania in the Robinieae, Lupinus also presents a similar situation in the Genisteae but for which no data is provided in the present study to either support or reject the isolation of the genus in a separate tribe.

5.2 - The genus Lupinus in Brazil

5.2.1 - Multifoliolate species

In Brazil the genus Lupinus is represented by multifoliolate and unifoliolate species. In the former group there are ca. 16 names published which still need considerable study in order to evaluate their taxonomic validity. A brief taxonomic history and an appraisal of the present taxonomic status of these taxa are given below simply as an attempt to outline the problems present in the genus as a whole and to encourage further studies on this group.

DESROUSSEAUX (1789) was the first author to describe three multifoliolate species from Brazil, all of which have been considered good species. They are L. bracteolaris, L. linearis and L. multiflorus. Subsequently, BENTHAM (1859) in his account of Lupinus for "Flora Brasiliensis" accepted DESROUSSEAUX's taxa as distinct species and described three others : L. comptus, a remarkable taxon with leaves conspicuously 3-foliolate, a unique feature among the multifoliolate species of the genus, L. lanatus, and L. hilarianus. Under L. multiflorus Dsr., BENTHAM (loc. cit.) treated as synonyms L. albescens Hook. & Arn. (Argentina, Paraguay), L. incanus Grah. (Uruguay, Paraguay) and L. aureonitens Gill. (Uruguay), all of which are now accepted as distinct species by DUNN (pers. com.) possibly with additional taxa for this group published by SMITH from Bolivia.

L. hilarianus has recently received a re-evaluation of its taxonomic validity by DUNN & PLANCHUELO (1981), involving the re-establishment of generic limits and relationships of Cytisus and

Lupinus, and, with some reservations, also of *Crotalaria* (DUNN, pers. com.). The valid name available for the plants belonging to this species is *L. gibertianus* C.P. Smith which has a very wide distribution from Peru to Paraguay, Uruguay and northern Argentina, encompassing an extensive and complex array of phenotypic plasticity. The species is possibly a large group of many small ecological races and polyploid series of difficult interpretation (DUNN & PLANCHUELO, 1981; DUNN, 1984).

MICHELI (1900) described *L. czermakii* as a new species from southern Brazil but recently DUNN & PLANCHUELO (DUNN, pers. com.) have recognised this taxon as a variety of *L. bracteolaris*.

After BENTHAM's (1859) broad taxonomic treatment of the Brazilian species of multifoliolate *Lupinus*, the next author to study these taxa in any detail was C.P. SMITH, in his series of "Papers" in "Species Lupinorum", particularly in "Paper Sixteen" ("The digitate-leaved lupines in middle-eastern South America, SMITH, 1940) and later in "Paper Fourty-six" ("Lupinus in Brazil, SMITH, 1945). SMITH (1940) described five new species of multifoliolate *Lupinus* from Brazil, i.e., *L. dusenianus*, *L. paranensis*, *L. regnellianus*, *L. russelianus* and *L. uleanus*. Furthermore, the same author (SMITH, *loc. cit.*) added the new variety *L. hilarianus* var. *reineckianus* C.P. Smith to the list of taxa occurring in Brazil which he later elevated to specific rank (*L. reineckianus*, SMITH, 1945 *).

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*Curiously, DUNN & PLANCHUELO (1981) did include *L. hilarianus* var. *reineckianus* as a synonym of *L. gibertianus* but failed to list *L. reineckianus* in the same category despite the fact that both taxa are based on the same type.

DUNN (pers. com.) regards these five new species published by SMITH (*loc. cit.*) as belonging to the variable group of *L. gibertianus*, therefore not warranting true specific status.

SMITH (1945) brought together all the multifoliolate (in total, 16 native and three non-native) and unifoliolate species in Brazil under a single "Paper" in which he classified all these taxa in eight 'tentative groups'. One group (Group 8) comprised all the unifoliolate species (ca. 20), whereas the multifoliolate ones were divided into seven smaller groups. Of these, the non-native species were either treated in separate groups (*L. luteus*, from Argentina, in Group 4 and *L. paraguariensis*, from Paraguay, in Group 7) or included with the native taxa (*L. bandelierae* in Group 6 along with *L. dusenianus*, *L. paranensis*, etc). It must be stressed that SMITH (1945) was in fact unsure that the "non-native" species occurred in Brazil but, because of "proximities of countries" he considered them as possibly growing naturally in that country.

The groups proposed by SMITH (1945) represent an attempt to isolate clusters of species with some affinities but, due to (a) the many new species described and (b) the inclusion of "non-native" species, the naturalness of these groups is questionable.

PLANCHUELO (*in* DUNN & PLANCHUELO, 1981) recently completed a revision of the whole genus in Argentina, which will obviously include those species which extend into Brazil. Unfortunately, however, this revision has not yet been published except for short treatments of two isolated groups of species (*L. grisebachianus*, *L. subacaulis*, and *L. subinflatus* - PLANCHUELO & DUNN, 1980; and *L. gibertianus* - DUNN & PLANCHUELO, *loc. cit.*).

Most of the exsicatae loaned by these authors have not yet been returned to the institutions concerned. As a consequence, it is difficult to analyse the variation present and the specific limits accepted for the multifoliolate taxa in southern South America.

Furthermore, because of the phenotypic plasticity of some species, for which field studies will be necessary to evaluate the large number of binomials available, the study of the Brazilian multifoliolate taxa was not further attempted in the present work.

5.2.2 Unifoliolate species

5.2.2.1 - Taxonomic history and conspectus.

The earliest citations of unifoliolate species of *Lupinus* refer to the North American taxa *L. villosus* Willd. and *L. diffusus* Nutt. which were first mentioned by WILLDENOW (1802) and NUTTALL (1818), respectively. Subsequently, BENTHAM (1839) was the first author to describe three species from the uplands of central and eastern Brazil : *L. velutinus*, *L. subsessilis* and *L. coriaceus*.

BUNBURY (1841) added *L. nitidissimus*, which he considered as distinct from any species previously published by BENTHAM (1839). However, this taxon is here recognised as synonymous of *L. velutinus*. GARDNER (1843) described *L. arenarius*, *L. attenuatus*, *L. parvifolius* and *L. decurrens*, all four species from the uplands of Minas Gerais state in Brazil. GARDNER (*loc. cit.*) regarded *L. attenuatus* as very close to *L. coriaceus*, earlier published by BENTHAM (1839) and this relationship was to persist until this present work in which *L. attenuatus* Gardn. is treated as a synonym of *L. coriaceus*.

CASARETTO (1843) published L. chrysomelas almost simultaneously with GARDNER's (1843) L. arenarius but, in fact, some 3 months later, so that L. chrysomelas is treated here as a synonym of L. arenarius.

BENTHAM (1859), in his treatment of Lupinus for von MARTIUS' "Flora Brasiliensis" recognised eleven species of unifoliolate Lupinus, i.e., the three he had published previously (BENTHAM, 1839) those treated by GARDNER (1843) and four new species : L. ovalifolius, L. crotalarioides, L. vaginans and L. laevigatus. The species L. nitidissimus Bunb. and L. chrysomelas Casar. were completely ignored in this account. A key to distinguish these eleven species was also provided by BENTHAM (1859) but it presents several inadequacies in the separation of the taxa because of the weak limits between species which were a reflection of the scarcity of specimens available for study.

After a period of about 40 years since BENTHAM's treatment of the Brazilian taxa, GLAZIOU (1906) published the name L. insignis (nomen nudum) as a possible new species of the same group, also from central Brazil (Goias). SMITH (1945) later confirmed the interpretation given by GLAZIOU (loc. cit.) and validated L. insignis. Another distinct species, L. sellowianus, was described by HARMS (1921) which proved to be a remarkable taxon among the unifoliolate group.

The extensive and prolific papers by C.P. SMITH published as "Species Lupinorum" only brought the Brazilian unifoliolate species under revision in the "Signature Thirty, Paper Fourty-six" of this series (SMITH, 1945, pp. 481-501). In this paper, 20 species were listed of which six were described as new. Again, as in BENTHAM's (1859) treatment, SMITH (*loc. cit.*) did not mention *L. chrysomelas* Casar., and *L. nitidissimus* Bunb. was included as the valid epithet for the species *L. vaginans*, earlier described by BENTHAM (*loc. cit.*). Two other taxa were listed by SMITH (1945) as occurring in Brazil : *L. guaraniticus* C.P. SMITH, which is found in Argentina, Paraguay and Brazil, and *L. spectabilis* (Hassl.) C.P. Smith from Paraguay. SMITH (*loc. cit.*) did not see any specimens of the latter taxon from Brazil but, because of the proximity of the two countries, he considered it likely that *L. spectabilis* extended from Paraguay into Brazil. This species, now treated as *L. amabayensis* C.P. Smith by DUNN (pers. com.) and considered to be very close to *L. velutinus* Benth., has not been found among the exsiccatae here studied.

Since the treatment of the unifoliolate *Lupinus* from Brazil provided by SMITH (1945) no other modern taxonomic study has dealt with this group of plants. This situation has been unfortunate because the number of names available is high and the existing treatments unsatisfactory so that attempts to identify new collections have been difficult. Furthermore, the North American unifoliolate species have been revised by DUNN (1971) who suggested that these taxa originated by long-distance dispersal from South America. It is clear that without an adequate knowledge of the taxonomy of the South American group this evolutionary hypothesis cannot be evaluated.

As noted above, the whole genus has recently been revised for Argentina by PLANCHUELO (DUNN, pers. com.) but this study has not been published, so that, as is the case with the multifoliolate species, comparisons between the Brazilian and relatively few Argentinian unifoliolate taxa cannot yet be made.

As a consequence, the taxonomic revision of the Brazilian unifoliolate species presented here must be regarded as an outline treatment only, pending further studies, both in the field, and with regard to the conclusions reached by PLANCHUELO for neighbouring Argentina.

CONSPECTUS

The present revision recognises 13 unifoliolate species of Lupinus in Brazil which can be divided into two distinct subgroups:

One subgroup is characterised by taxa with leaves exstipulate or, if stipules are present, then they are totally fused with the petioles. The species are :

L. ovalifolius Benth.
L. coriaceus Benth.
L. parvifolius Gardn.
L. prouvensalanus Gardn.
L. guaraniticus C.P. Smith

Except for L. guaraniticus, these species are endemic to the the uplands of the state of Minas Gerais, and all are adapted to rocky habitats.

The species of the second subgroup have distinctly stipulate leaves and the stipules, although partially fused with the petioles, have conspicuous free tips. They are :

L. laevigatus Benth.

L. crotalarioides Mart. ex Benth.
L. sellowianus Harms
L. arenarius Gardn.
L. subsessilis Benth.
L. velutinus Benth.
L. insignis Glaziou ex C. P. Smith

These taxa as a whole have wider distribution ranges than the former and although some of them also occur in the same upland sites as the exstipulate species, the typical habitat of the stipulate taxa is the "cerrado" areas, with those in the core region in west-central Brazil showing marked endemism.

5.2.2.2 - Taxonomic parameters

The following general comments on morphological characters of the Brazilian unifoliolate species of Lupinus are based primarily on herbarium material. Nevertheless, many of these observations can be applied to the genus as a whole. It is important to note that a remarkably uniform floral morphology, with differences only in size of petals is a feature of the unifoliolate taxa, and this is also a general characteristic of the multifoliolate species from Brazil (SMITH, 1945; DUNN, 1984). It is therefore necessary to resort to vegetative characters to distinguish Lupinus species, with the risk that these may be subject to phenotypic modification by factors such as, e.g. altitude. Nevertheless, some confidence in the use of vegetative characters can be gained from the fact that in those species which are represented by fairly extensive collections the character correlations remain constant to an acceptable extent.

Habit - All species of unifoliolate Lupinus are perennials, with the habit varying from decumbent (L. ovalifolius) to erect herbs or subshrubs up to 1 m or so tall. The stems sprout from a woody rootstock and may be single or few to several branched.

Vestiture - Traditionally, trichome characters have been used in species delimitation in Lupinus hence its importance in the identification of the unifoliolate taxa. Pubescence may vary on different organs of plants of the same species so that in the descriptions here presented, the general form of pubescence has not been attempted for the species, but rather each part of the plant (stem, petiole, leaf, peduncle, pedicel, calyx) is described. In general, the forms of pubescence found in Lupinus are : hirsute, sericeous, tomentose, velutinous, villous and lanate.

Stipules - Stipules are an important taxonomic character in the Brazilian unifoliolate species of *Lupinus*. They may be absent, as in *L. ovalifolius*, *L. coriaceus*, *L. parvifolius* and *L. prouvensalanus*. When stipules are present, they are *either* totally adnate with the petioles and then without free tips (*L. decurrens* and *L. guaraniticus*) *or* partially adnate with the petiole, that is, the base is adnate to the petiole and usually also extends back along the previous internode, but, from the portion close to the lamina base the tips are free (Figure 79). In this case, the length and shape of the free tips are of useful application at specific level, i.e., the tips may be short and deltoid to narrowly lanceolate (*L. arenarius*, Figure 79d), or long, lanceolate and straight (*L. insignis*, *L. laevigatus*, *L. velutinus*, *L. subsessilis*, Figure 79 a,b,e-h) or long, foliaceous to linear-lanceolate, sometimes curved (*L. sellowianus* and *L. crotalarioides*, Figure 79,c i). In all cases, the stipules are pubescent externally but always glabrous on the inner face.

Leaves - The leaves may be sessile (*L. coriaceus*, *L. parvifolius* and *L. prouvensalanus*), subsessile (*L. ovalifolius*), shortly petiolate (*L. decurrens*), to distinctly petiolate, and sometimes long-petiolate (*L. sellowianus* and *L. crotalarioides*). On the whole, there is great variation in the dimensions of the leaf blade, from 15-17 mm long in *L. ovalifolius* to more than 120 mm in *L. insignis*. The shape is also very variable (elliptical, lanceolate, oblong, oblong-lanceolate, ovate or oblong-ovate).

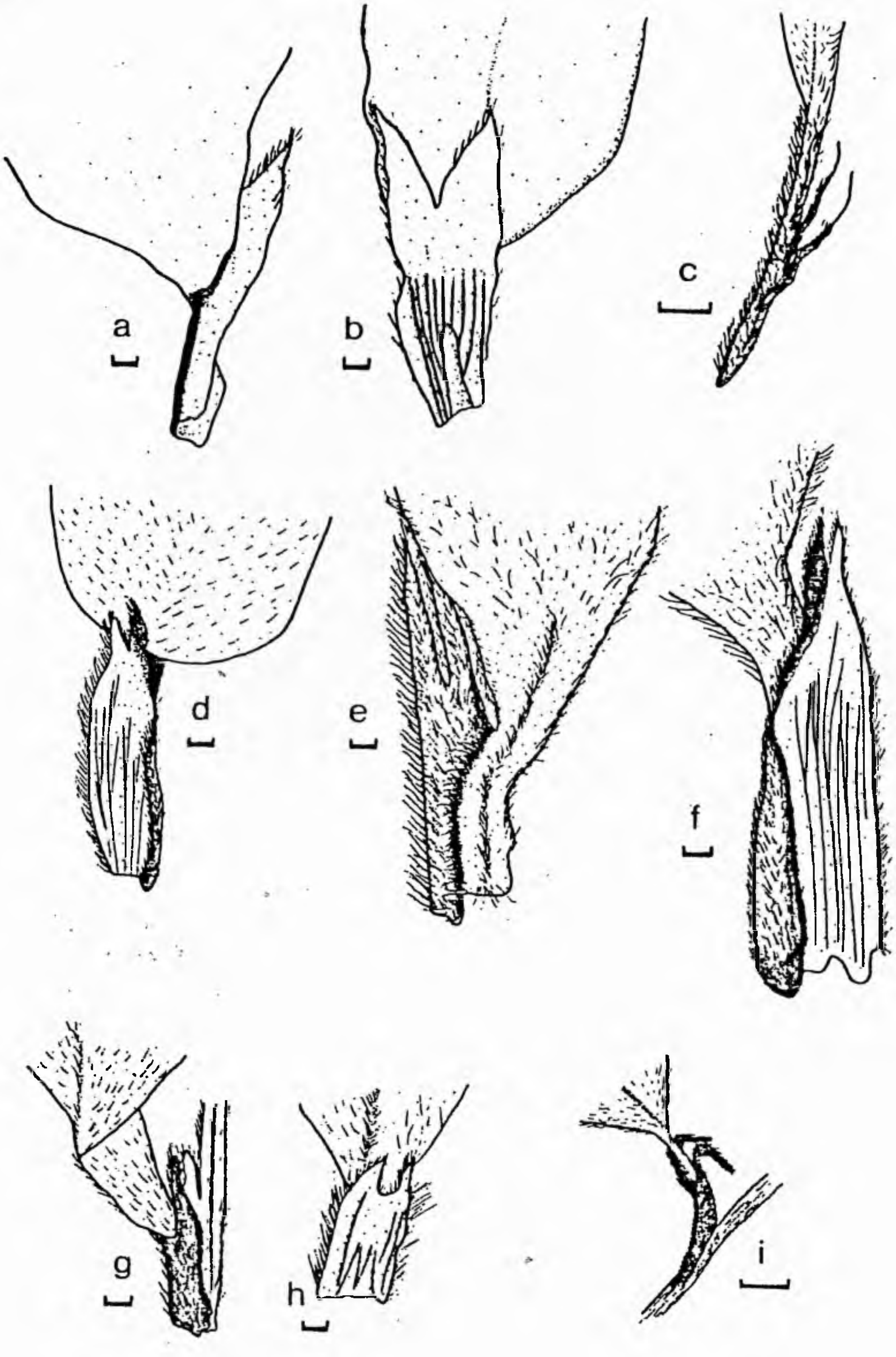


Figure 79 - Stipules of unifoliolate species of Lupinus from Brazil. (a,b) - L. laevigatus; (c) - L. sellowianus; (d) - L. arenarius; (e,f) - L. velutinus; (g,h) - L. subsessilis; (i) - L. crotalarioides. (b,f,h - internal face)
Scale : all = 1 mm, except c,i = 1 cm.

The majority of the species have pubescent leaves and the exceptions to this rule are the subglabrous taxa L. laevigatus and L. coriaceus. In other species the pubescence varies in density according to the species, from hirsute or sericeous, to tomentose or villous. The hairs are always simple. Leaf texture is membranaceous in all species except for L. coriaceus - which is aptly named - with coriaceous leaves.

Despite such variations in leaf characters it is the correlation of their features with the stipules which gives the best and most reliable set of data for the identification of the unifoliolate species. A similar set of character correlations was also used by DUNN (1971) for the species of southeastern North America.

Calyx - The calyx is 2-lipped, with the upper lip deeply divided into two teeth, and the lower lip with three, shorter teeth. Variation in these features, particularly the size of the teeth of the lower lip are of taxonomic value.

Corolla - The corolla is always glabrous, the standard oval to ovate-circular and alxways strongly reflexed. Size of the standard was the only variation found to be of taxonomic value among the unifoliolate species, and this can vary from 8-15 mm.

The wing petals are oblong, oblong-ovate, to oblong-lanceolate with the apex usually curved but often straight. This character presents intraspecific variation and must be used cautiously. The keel petals are usually lanceolate to oblong-lanceolate, with the apex arcuate and beaked.

The corolla shows a large range of colour in the genus, apparently independent of any formal or informal taxonomic groupings (POLHILL, 1976; BISBY, 1981). It is important that the corolla colour of young, unpollinated flowers is annotated since it has been shown (WAINWRIGHT, 1978; BISBY, 1981) that insect-visited flowers of *Lupinus* species change colour after pollination has taken place. Therefore, a blue standard with white spots of an unpollinated flower may change colour to purple with yellow spots (WAINWRIGHT, *loc. cit.*) after being triggered by insects. These colour changes have not been recorded for any unifoliolate species from Brazil but very often a set of exsiccata for a single species (for example, *L. crotalarioides* and *L. velutinus*) may have the corolla variously described as blue, variegated, or purple.

Androecium - The stamens are connate in a closed, glabrous tube; the anthers are alternately long and short, dimorphic, with the short ones sagittate ("horse-shoe shaped", *fide* POLHILL, 1976) and basifixed whilst the long ones are lanceolate and dorsifixed.

Pollen - The pollen grains are treated separately in the section "Palynology".

Pods - It has not been possible to study the pods of all the unifoliolate species due to the lack of material. However, in the taxa with fruiting specimens available (L. *parvifolius*, *L. decurrens*. *L. laevigatus*, *L. coriaceus*, *L. guaraniticus*, *L. sellowianus*, *L. crotalarioides* and *L. velutinus*) the pods are generally rectangular, coriaceus to ligneous, beaked, compressed, 2-valved, densely pubescent, with the seeds separated by transversal septa and varying from 35-50 x 8-10 mm. No variation of taxonomic value was found in the present work.

Seeds - The seeds are treated in a separate section ("Seed morphology").

5.2.2.3 - Palynology

The only palynological records available for the genus *Lupinus* are a few studies which treat with isolated species. The only account given for the Old World taxa is by PLITMANN *et al.* (1980) who mention that pollen grains of *L. pilosus* and *L. palaestinus* are "oval in equatorial view" and with the surface (exine) foveolate. The differences in dimensions observed by these authors were considered to be of no taxonomic value. No indication was provided as to whether the observations and measurements were obtained with fresh or acetolysed grains.

For the New World species, VISHNU-MITTRE & SHARMA (1962) have reported that the acetolysed grains of *L. polyphyllus* (cultivated in India ?) have the exine "faintly reticulate" and with 3-zonicolpate apertures. ADAMS & SMITH (1977) have presented photographs of acetolysed grains of *L. perennis* taken with optical microscope and also SEM. These authors do not give any description of the grains but, from their illustrations it is possible to characterise the pollen of *L. perennis* as triaperturate (colpate ?) and with the exine reticulate.

FERGUSON & SKVARLA (1981), in their revision of pollen grains of the subfamily Papilionoideae, give SEM micrographs of *L. aschenbornii* pollen which has colpate apertures and reticulate exine. Finally, more recently POWELL & JONES (1983) have published SEM micrographs and measurements of pollen grains of *L. benthamii*, a species from California, which has subprolate, 3-colpate grains with reticulate-perforate exine.

It is rather unfortunate that, with the size and diversity of the genus no more palynological data is available. However, from the the albeit sparse data presented above, reticulate exine and colpate apertures seem to be a more or less consistent pattern for the genus and this is certainly the pattern which has also been observed for the unifoliolate species from South and North America for which pollen grains were studied here using SEM microscopy. The study consisted of the SEM observation of the external exine and aperture morphology of 11 unifoliolate species (eight from Brazil, one from Paraguay and two from North America) and one Brazilian multifoliolate taxon (Table 23 and Figures 80, 81, 82).

The pollen grains of the unifoliolate species are subprolate to prolate, tricolpate, the colpus is covered with a membrane (operculum ?) and the exine is uniformly reticulate (Figures 80, 81, 82). It seems that this pattern presents no major differences or variations among the unifoliolate species, either from South or North America <u>or</u> between these taxa and the South American multifoliolate <u>L. gibertianus</u> (Figures 80, 81, 82). Furthermore, this pattern is also very similar with the one described by other authors, as mentioned above (VIHSNU-MITTRE & SHARMA, 1962; ADAMS & SMITH, 1977; FERGUSON & SKVARLA, 1981; POWELL & JONES, 1983).

In conclusion, although the palynological data so far available for the genus <u>Lupinus</u> as a whole is very meagre, it seems that a certain uniformity in pollen grain morphology is observable throughout its species, a pattern also found for other

Table 23 - Collections of *Lupinus* material used for palynological studies.

TAXON	ORIGIN	FIGURE
UNIFOLIOLATE		
L. amabayensis Smith	Paraguay, ROJAS 10347 (G)	82 c,d
L. arenarius Gardn.	Brazil, GARDNER 4500 (E)	81 e,f
L. coriaceus Benth.	Brazil, BARRETO 5445 (SP) VAUTHIER 141 (P) VAUTHIER 142 (P)	81 a,b 81 g,h 81 i
L. crotalarioides Mart. ex Benth.	Brazil, GEHRT 172 (SP) GLAZIOU 20933 (P)	80, d,e,f
L. decurrens Gardn.	Brazil, IRWIN *et al.* 22891 (K,NY)	82 a,b
L. diffusus Nutt.	U.S.A., DUNN 15794 (K)	82 i,j
L. laevigatus Benth.	Brazil, CLAUSSEN 921 (P)	80 j,k,l
L. ovalifolius Benth.	Brazil, StHILAIRE 2167 (P)	80 a,b,c
L. parvifolius Gardn.	Brazil, FOSTER & BARRETO 10845 (SP)	80 g,h,i
L. velutinus Benth.	Brazil, IRWIN *et al.* 19324 (K) RATTER & FONSECA, 2819 (E)	81 c,d 81 j,k
L. villosus Willd.	U.S.A., NUTTAL s/n (K)	82 g,h
MULTIFOLIOLATE		
L. gibertianus Smith	Brazil, CARVALHO 1010 (RB) GINZBERGER 129 (W) OLIVEIRA 102 (UEC)	82 e,f

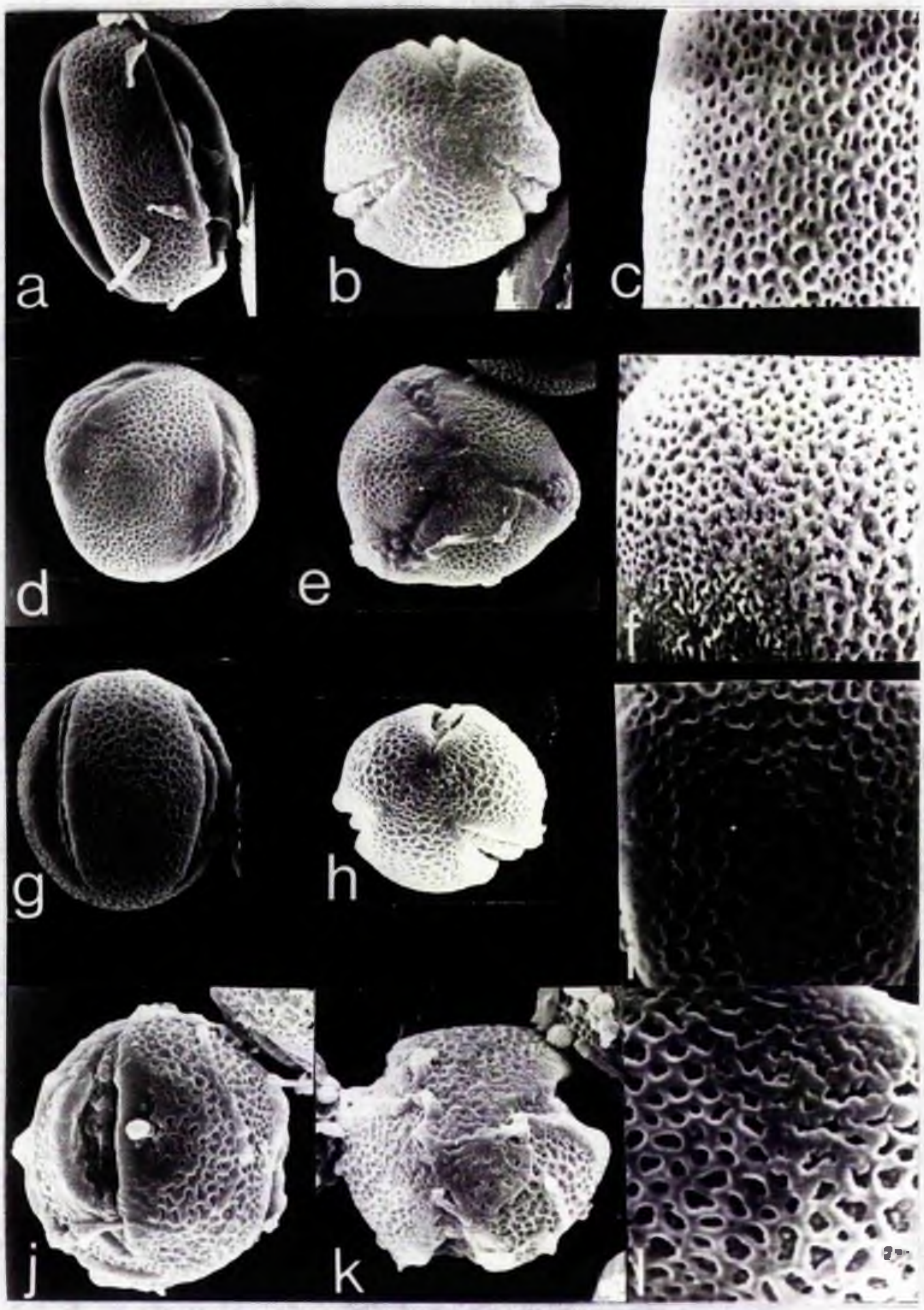


Figure 80 - SEM micrographs of equatorial and polar views and exine ornamentation of pollen grains of unifoliolate species of Lupinus. (a,b,c) - L. ovalifolius; (d,e,f) - L. crotalarioides; (g,h,i) L. parvifolius; (j,k,l) - L. laevigatus. (magnifications : all 500 x; except c,f,i,l , 1750 x).

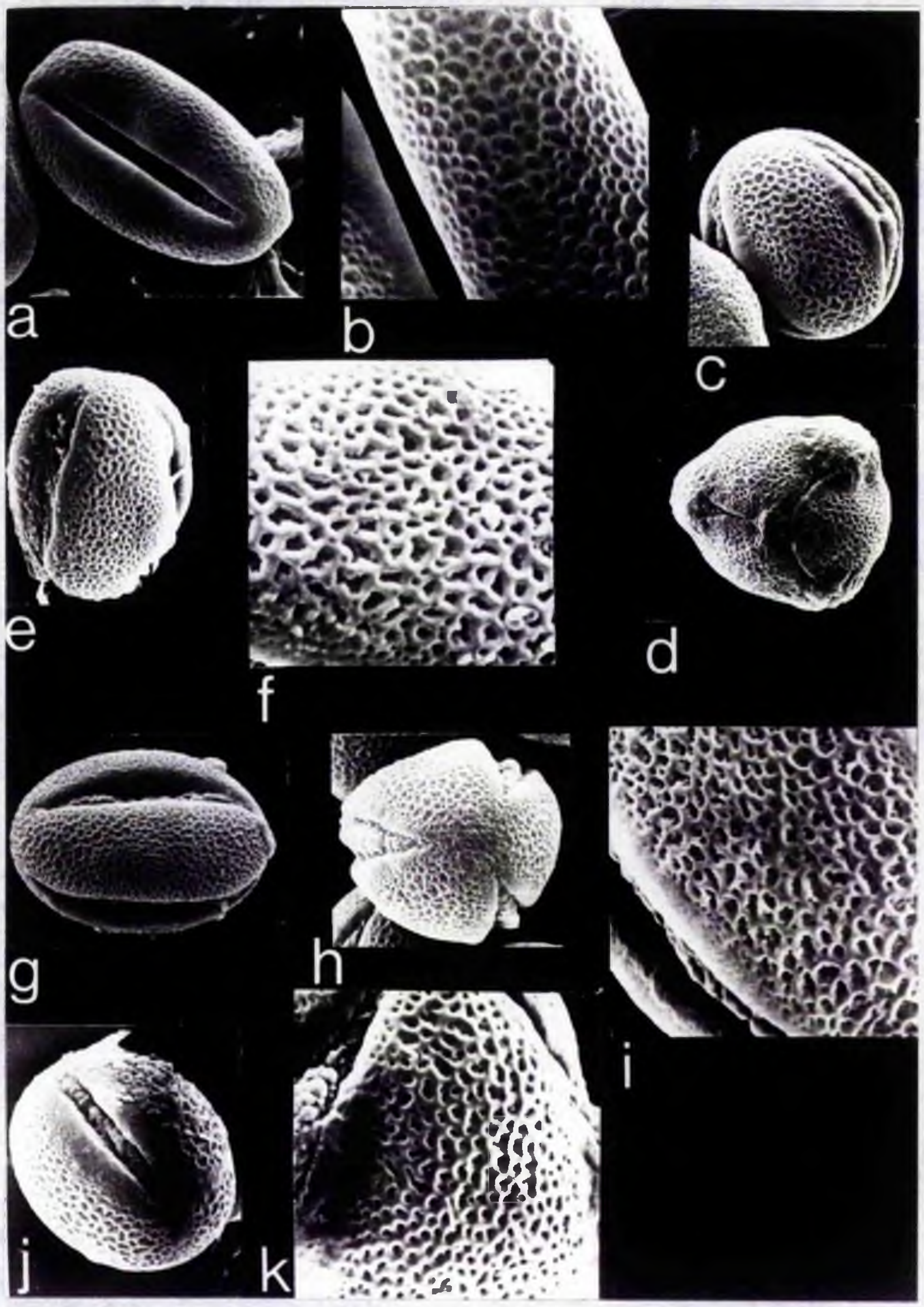


Figure 81 - SEM micrographs of pollen grains of species of Lupinus. (a,b,g,h,i) - L. coriaceus (a,b, grains collapsed); (c,d,j,k) - L. velutinus; (e,f) - L arenarius. (magnifications : all 500 x; except b,f,i,k , 1750 x).

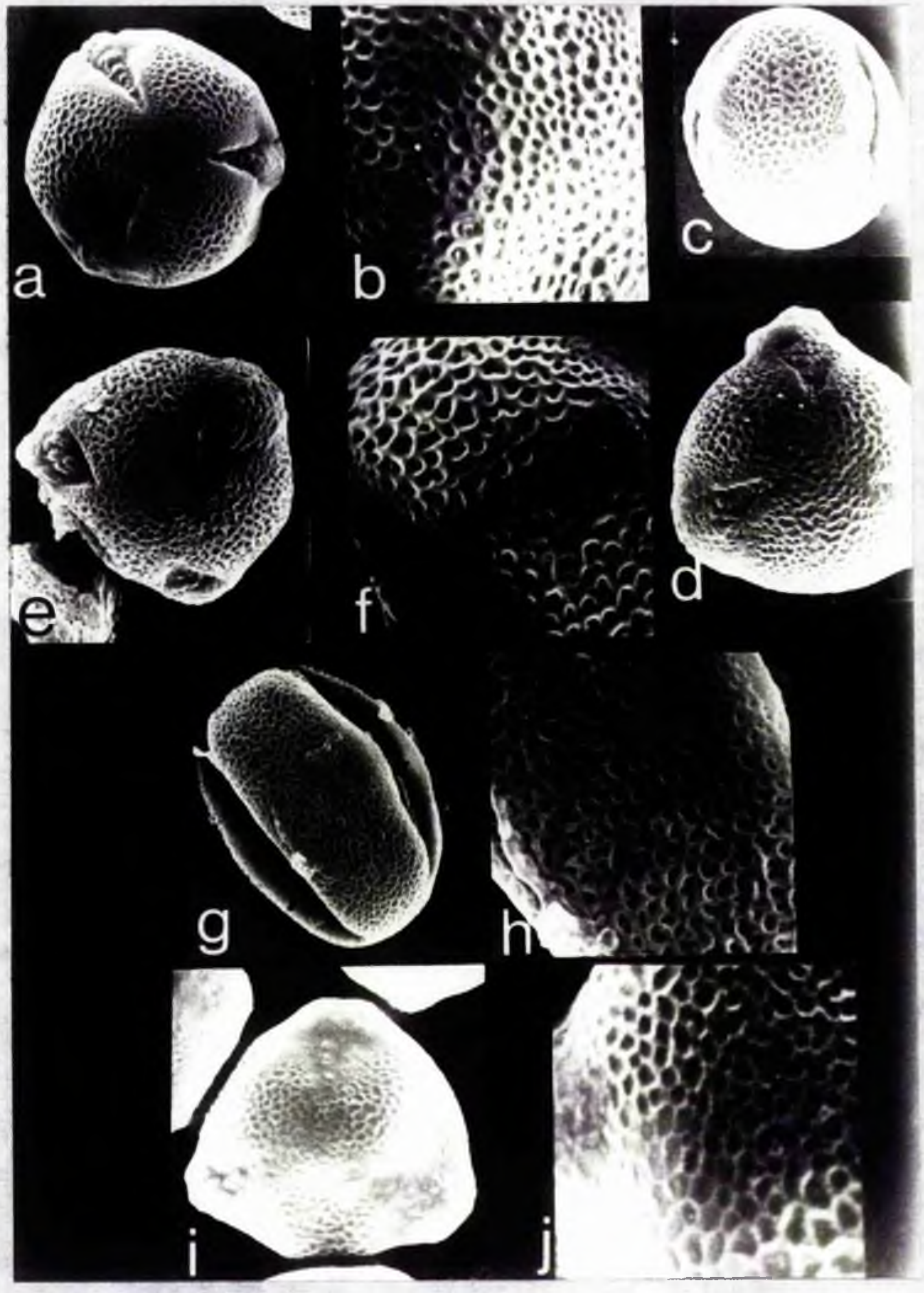


Figure 82 - SEM micrographs of pollen grains of unifoliolate and multifoliolate (e,f) species of <u>Lupinus</u>. (a,b) - <u>L</u>. <u>decurrens</u>; (cd) - <u>L</u> <u>amabayensis</u>; (e,f) - <u>L</u>. <u>gibertianus</u>; (g,h) - <u>L</u>. <u>villosus</u>; (i,j) - <u>L</u>. <u>diffusus</u>. (magnifications : all 500 x, except b,f,h,j; 1750 x).

floral features (section "Taxonomic Parameters"). Therefore, the pollen grain data here presented can be used to confirm the naturalness of the genus but do not have any taxonomic value which can be applied to separate the unifoliolate species from the multifoliolate ones or which can be correlated with any other characters that isolate natural groups within the Brazilian unifoliolate species.

5.2.2.4 - Seed morphology

5.2.2.4.1 - Seed testa

Seed testa pattern has been used in the genus Lupinus by various authors as a taxonomic character to separate major groups of species. The first such application was made by GLADSTONES (1974) who, in a revision of the Old World species of this genus, recognised two distinct groups on the basis of the texture of the testa : the "rough-seeded" and the "smooth-seeded species. The first group comprises about seven taxa which are distributed in North Africa, and the second has five species occurring in the Mediterranean (GLADSTONES, loc. cit.).

HEYN & HERRNSTADT (1977) accepted GLADSTONES' (1974) classification of the genus in the Old World and presented a SEM survey of the seed testa of eight species of this area (Table 24). For comparison, HEYN & HERRNSTADT (loc. cit.) also included six New World species, all of them from Central and North America, except for L. mutabilis, a cultivated species from Peru. The Old World taxa were subdivided in four groups according to the testa pattern (Table 24) : (1) the rough-seeded species, with "protuberances with fascicled cells"; (2) L. angustifolius and L. micranthus, with "rounded protuberances"; (3) L. graecus and L. albus, both with "granulated" seed coat, and (4) L. luteus, in which the testa was characterised by "shallow protuberances".

For the New World species, the testa was said to have several patterns, varying from "irregularly ridged, smooth or granular" (Table 24) but which, in comparison with the Old World taxa, were considered by the authors (HEYN & HERRNSTADT, 1977) as

Table 24 - Patterns of testa surface found in Old and New World multifoliolate species of *Lupinus*. After HEYN & HERRNSTADT (1977) with corresponding terminology by LERSTEN (1981).

OLD WORLD

GROUP	TAXON	TESTA PATTERN	
		HEYN & HERRNSTADT 1977	LERSTEN, 1981
ROUGH-SEEDED	*L. cosentinii* *L. palaestinus* *L. pilosus*	protuberances with fascicled cells	PAPILLOSE
	L. angustifolius *L. micranthus*	rounded protuberances	PAPILLOSE
SMOOTH-SEEDED	*L. graecus* * *L. albus*	granulated	
	L. luteus	shallow protuberances	SIMPLE FOVEOLATE

NEW WORLD

TAXON	ORIGIN	TESTA PATTERN	
		HEYN & HERRNSTADT 1977	LERSTEN, 1981
L. succulentus	U.S.A.	irregular ridged, smooth or granular	PAPILLOSE
L. albicaulis	U.S.A.		LEVIGATE
L. arboreus	U.S.A., Canada		RUGULATE
L. mutabilis	Peru		
L. aschenbornii	Mexico		SIMPLE RETICULATE
L. montanus	Mexico		COMPLEX MULTIRETICULATE

NOTE :

* Elsewhere treated as a synonym of *L. albus* (GLADSTONES, 1974).

having a "relative uniformity" of the seed coat. This statement seems rather incongruent because the seed testa types described for the Old World species are all variations on a basic "protuberance" pattern, which PLITMANN (1981) called "prominent tuberculi", whilst for the New World representatives they seem to vary more strikingly as to the basic form. Apart from this interpretation, HEYN & HERRNSTADT (1977) also encountered problems in describing their results due to the lack of a proper terminology .

LERSTEN (1981), in a comprehensive revision of SEM seed testa study of the Papilionoideae proposed a useful terminology for testa morphology based on the patterns he found throughout the survey in the whole subfamily. Using his newly proposed descriptive terms for the testa sculpturing, LERSTEN (loc. cit.) considered the patterns published for the Old World lupins by HEYN & HERRNSTADT (1977) as basically "multi-foveolate". However, a detailed analysis of HEYN & HERRNSTADT's micrographs and an interpretation of the patterns proposed by LERSTEN (1981) reveal that this group of Old World species has two distinct testa patterns, i.e., papillose and foveolate (Table 24).

Interestingly, the papillose pattern is present in both groups of species, i.e., in the rough-seeded and smooth-seeded taxa, therefore indicating that at least in one character the broad separation of these groups is somewhat dubious (see section "Evolutionary History" below). When the same terminology and concepts are applied to the six New World species studied by HEYN & HERRNSTADT (1977), it becomes evident that there is a striking variation of seed testa among these taxa rather than a "relative uniformity", as indicated by these authors.

Because of this variation shown by a very small sample of the New World species of Lupinus, a survey of this character was made in the present work using seeds of some multifoliolate and unifoliolate species, but with emphasis on the latter. The seeds were obtained from herbarium specimens or through introductions to the University of St Andrews Botanic Garden. Preparation for SEM observations are described in the section "Material and Methods". A list of the species is found in Table 25 and the results in Table 26 and Figures 83 - 85. Unfortunately, it was not possible to study the testa pattern of all the Brazilian and North American unifoliolate species due to the lack of material.

In a first instance, it can be seen (Table 26 and Figures 83,84,85) that the simple-foveolate pattern is a remarkably constant feature of the unifoliolate species but it is also present in some of the Brazilian multifoliolate taxa (L. bracteolaris, L. comptus and L. lanatus, Figure 84 D,E,F). Second, a variety of patterns is found among the multifoliolate species, ranging from levigate (smooth testa) to complex-reticulate (Figure 85). The last observation confirms the morphological variation of seed testa among the New World multifoliolate species and is in further disagreement with the "relative uniformity" initially reported for these taxa by HEYN & HERRNSTADT (1977).

It is interesting to note that whilst the papillose testa pattern is common among the Old World lupins (Table 24), it was only observed in one of the New World taxa studied. In this respect, such testa pattern provides a discontinuous character

Table 25 - Collections of *Lupinus* species studied for seed morphology (* seeds also used for anatomical studies).

TAXON	ORIGIN
UNIFOLIOLATE	
L. arenarius Gardn.	Brazil, CASARETTO 2902 (G) BRADE 20725 (RB)
L. crotalarioides Mart. ex Benth.	Brazil, LIMA 58-2975 (K)
L. decurrens Gardn.	Brazil, GARDNER 4503 (K)
L. guaraniticus Smith*	Paraguay, FRIEBRIG 5681 (G)
L. parvifolius Gardn.*	Brazil, GARDNER 4502 (K) MAGUIRE *et al*. 49175 (SP)
L. sellowianus Harms*	Brazil, STUBBLEBINE *et al*, 591 (UEC)
L. velutinus Benth.*	Brazil, DUARTE 9197 & PEREIRA 10107 (RB)
L. villosus Willd.*	U.S.A, CUSRTISS 4647 (E)
MULTIFOLIOLATE	
L. albifrons Benth.	U.S.A., introd.1
L. alopecuroides Desr.	Ecuador, ASPLUND 7395 (K)
L. angustifolius L.	Italy, cult. BILLOT 2649 (OXF) Scotland, cult. RBG (E)
L. bracteolaris Desr.	Brazil, DESLANDES s/n (SP) RAMBO 49089 (LL)
var. *czermakii**	Brazil, REINECK & CEZERMAK 130 (P)
L. comptus Benth.*	Brazil, BARRETO 5446 (SP)
L. covillei Greene	U.S.A., DRESS 3564 (E)
L. elegans H.B.K.	Mexico, introd.1
L. elongatus Greene	U.S.A., HELLER 9774 (E)
L. excubitus var. *hallii* (Abrams) Smith	U.S.A., BALLS 10094 (E)
L. exochus C.P. Smith	Peru, HUTCHINSON & WRIGHT 7073 (K)
L. hartwegii Lindl.	Mexico, introd.[1]

Table 25, cont.

TAXON	ORIGIN
L. humifusus Benth.	Ecuador, HARTWEG 944 (E)
L. lanatus Benth.*	Brazil, RAMBO 49088 (SP)
L. magdalensis C.P.Smith	Colombia, HANBURY-TRACY 350 (K)
L. multiflorus Desr.	Brazil, HOEHNE & GEHRT 37028 (SP)
L. nootkatensis Sims	Colombia, introd.[1]
L. nubigensis H.B.K.	Peru, MATTHEWS 479 (OXF)
L. paniculatus Desr.	Peru, SAUNDERS 1284 (K)
L. prostratus Agardh	Ecuador, CAZALET & PENNINGTON 5324 (K)
L. pubescens Desr.	Colombia, HARTWEG 945 (OXF)
L. ramosissimus Benth.	Colombia, HARTWEG 952 (OXF) Ecuador, SPRUCE 5806 (OXF)
L. sarmentosus Desr.	Colombia, PENNELL 3061 (K)
L. smithianus Kunth.	Ecuador, ASPLUND 17315 (K)
L. subcarnosus Hook.	Mexico, introd.[1]

Note :

[1] - Introduced to the Univ. of St Andrews Botanic Garden.

Table 26 – Patterns of seed testa surface observed in New World species of *Lupinus*.

TESTA PATTERN	TAXON	FIGURE
SIMPLE FOVEOLATE	UNIFOLIOLATE	
	L. arenarius	84 A
	L. crotalarioides	83 A
	L. decurrens	83 B
	L. guaraniticus	84 B
	L. parvifolius	83 H,G
	L. sellowianus	83 C
	L. velutinus	83 D
	L. villosus	83 F
SIMPLE FOVEOLATE	MULTIFOLIOLATE	
	L. bracteolaris	84 E
	L. comptus	84 D
	L. lanatus	84 F
LEVIGATE	*L. excubitus*	
RUGULATE	*L. covillei*	
RETICULATE SIMPLE RETICULATE	*L. humifusus*	
	L. prostratus	85 F
	L. smithianus	85 G
SIMPLE RETICULATE WITH HEAVY RIDGES	*L. albifrons*	
	L. hartwegii	
	L. nootkatensis	
	L. pubescens	84 D,E
	L. sarmentosus	85 J
	L. ramosissimus	85 K,L
MULTI-RETICULATE WITH HEAVY RIDGES	*L. alveorum*	
	L. elongatus	
	L. exochus	85 B
	L. magdalensis	85 C
	L. paniculatus	85 I
COMPLEX MULTI-RETICULATE	*L. alopecuroides*	85 H
	L. elegans	
	L. subcarnosus	

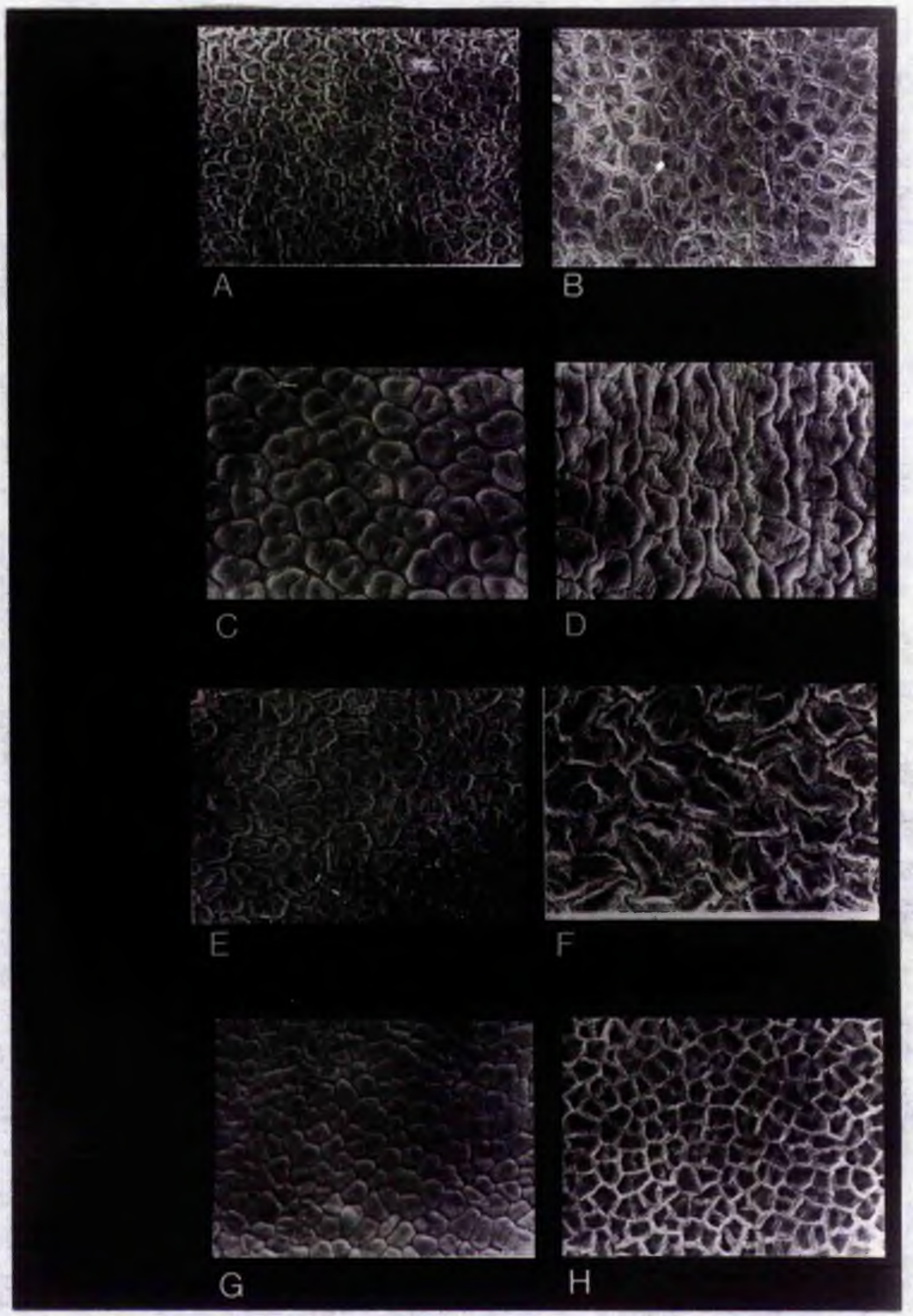


Figure 83 - Seed testa pattern in Brazilian unifoliolate species of Lupinus (all 1750x).

A - L. crotalarioides
B - L. decurrens
C - L. sellowianus
D - L. velutinus
E - L. arenarius
F - L. villosus
G , H - L. parvifolius

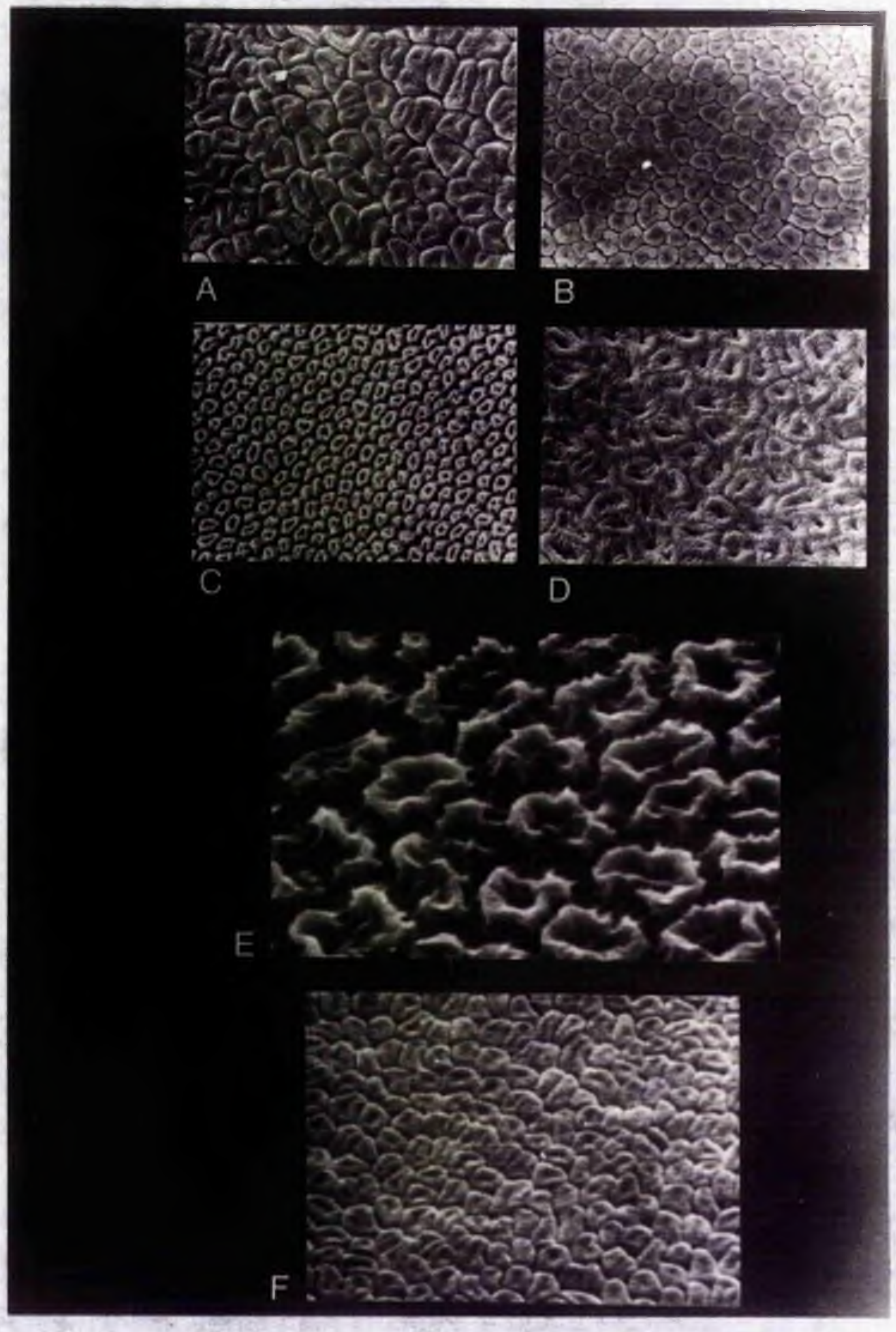


Figure 84 - Seed testa pattern in Brazilian uni- and multifoliolate* species of Lupinus. (all 1750 x; except E, 2500 x).

A - L. arenarius
B - L. guaraniticus
C - L. bracteolaris
D - L. comptus*
E - L. bracteolaris*
F - L. lanatus*

Figure 85 - Seed testa pattern in New World multifoliolate species of *Lupinus* (all 1750 x).

A - *L. nubigensis*

B - *L. exochus*

C - *L. magdalensis*

D , E - *L. pubescens*

F - *L. prostratus*

G - *L. smithianus*

H - *L. alopecuroides*

I - *L. paniculatum*

J - *L. sarmentosus*

K , L - *L. ramosissimus*

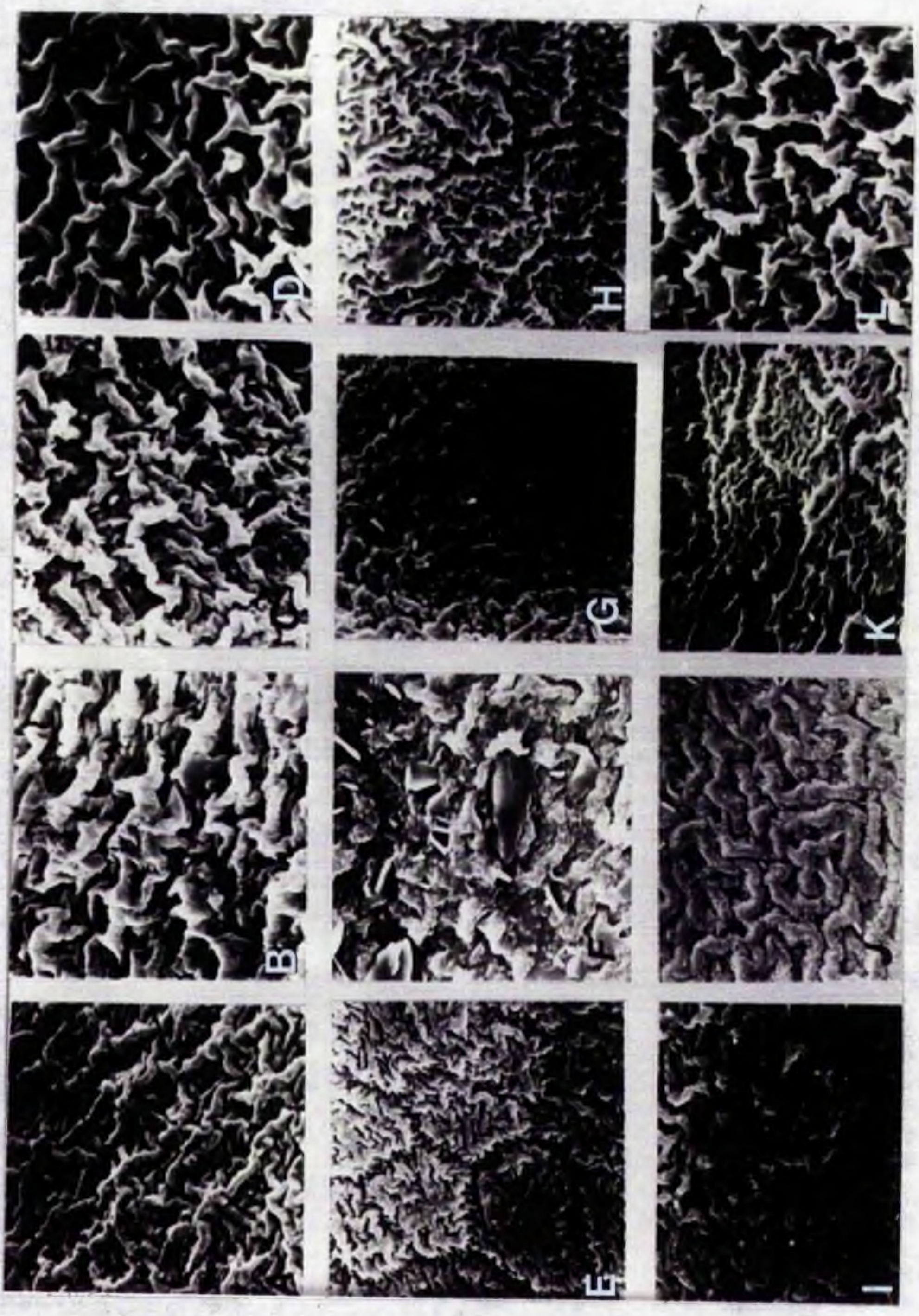


FIGURE 85

between the species of the different centres of diversity of the multifoliolate group. On the other hand, the constancy of the simple-foveolate testae observed in the unifoliolate species (Table 26, Figures 83,84) is certainly a reflection of the naturalness of this group and in fact, almost unique among them. However, it must be noted that this pattern can also be found not only in some of the Brazilian multifoliolate species but also in L. luteus, a taxon of the Old World smooth-seeded group (Table 24). Finaly, the presence of simple-foveolate testa in the North American unifoliolate L. villosus provides additional evidence for the hypothesis proposed by DUNN (1971) that the unifoliolate species of that country are derived through long-distance dispersal from South America.

It was observed that differences in seed maturity may alter the morphological pattern of the testa. This fact is shown in Figure 83 G,H, in which the fully developed seeds of L. parvifolius (Figure 83G) have a pristine foveolate pattern but, in an immature seed (Figure 83 H) the cells may show a "shrinking", causing a collapse of the cell walls. Therefore, care is needed in the interpretation of this phenomenon.

5.2.2.4.2 - Internal structure

The hilar anatomy of the seeds of some Brazilian uni- and multifoliolate species of Lupinus was also studied (Table 25, species marked with an asterisk). The diagrams of the internal structure of the papilionoid seed presented in Figure 17 and 18 (pages 71 and 72) also apply to Lupinus and the structures there represented will be used here.

A summary of the more important features of internal structure of the hilar region in seeds of Brazilian Lupinus is given in Table 27 and the illustrations for this section are found in Figures 86-93, with the captions given on the preceeding page.

The hilum in seeds of Lupinus has the same structure already discussed by POLHILL (1976), GUNN (1981), LERSTEN (1982), LERSTEN & GUNN (1982) and in the present work for Sesbania. However, the aril present in Lupinus is conspicuous and large, both in the unifoliolate (Figure 86,87) and multifoliolate species (Figure 91). The transverse sections of the hilum show that in this structure the epidermis is usually overlayed by the counter-palisade (Figures 88,89,90) which is interrupted in the median line of the hilum by the hilar groove which, in turn, leads to the tracheid bar (Figures 86b,87c,88a,90a,c). The tracheid bar does not show much variation in shape (Table 27) and, as in Sesbania and other legume genera (LERSTEN, 1982) is circular to elliptical. The constituent tracheoids are extremely uniform in pit shape and vesturing (Figures 86 - 92) with only minor differences.

In sagittal sections (Figures 86a, 89a, 91a, 92a) the structure of the tracheid bar and the position of the ovular vascular bundle do not show differences among the species studied here. However, contrary to the situation in Sesbania, where the tracheoids of the tracheid bar are larger than the tracheids of the ovular vascular bundle, in Lupinus it was observed that the latter may be larger, i.e., long and narrower than the tracheoids

Table 27 - Summary of testa internal features of *Lupinus* species.

TAXON	TRACHEID BAR SHAPE	TRACHEOID PIT		SCLEREID		
		SHAPE	VESTURING	SHAPE	SURFACE	FIGURE
UNIFOLIOLATE						
L. arenarius	elliptical	circular to elongated	warty	humeroid	striate	86, 90 c-d 93 b
L. crotalarioides	circular to elliptical	circular	warty	dumbelloid	striate	87 a,b 93 a
L. guaraniticus	circular	circular	warty	humeroid	striate	88 c,d
L. parvifolius	circular to elliptical	circular to elongated	n.v.* warty	humeroid	striate	86 a,b 93 c
L. sellowianus	circular to elliptical	circular to elongated	n.v.* warty	humeroid	striate	87 c,d
L. velutinus	circular to elliptical	circular to ellongated	n.v.* warty	dumbelloid	striate	89 c 93 d
MULTIFOLIOLATE						
L. bracteolaris	circular	circular to ellongated	warty	dumbelloid	striate	92 93 f
L. comptus	elliptical	circular	warty	dumbelloid	striate	90 a,b
L. lanatus	elliptical	circular	warty	dumbelloid	striate	91

Note : * n.v. = non-vestured to warty

Abreviations used for the illustrations of internal seed morphology (Figures 86 to 93).

Ar = aril

Co = cotyledons

Cp = counter-palisade

Ep = epidermis

Hi = hilum

Hg = hilar groove

Hr = hilar rim

Hy = hypodermis

Le = lens

My = micropyle

Pa = palisade

Pr = parenchyma

Sc = sclereids

Te = testa

Tb = tracheid bar

Tp = tracheoid pit

Tr = tracheoid

Vb = ovular vascular bundle

Vs = vesturing

Figure 86 - Internal seed morphology of L. arenarius.

a - longitudinal section through the hilum (25 x)

b - transversal section through the hilum (75 x)

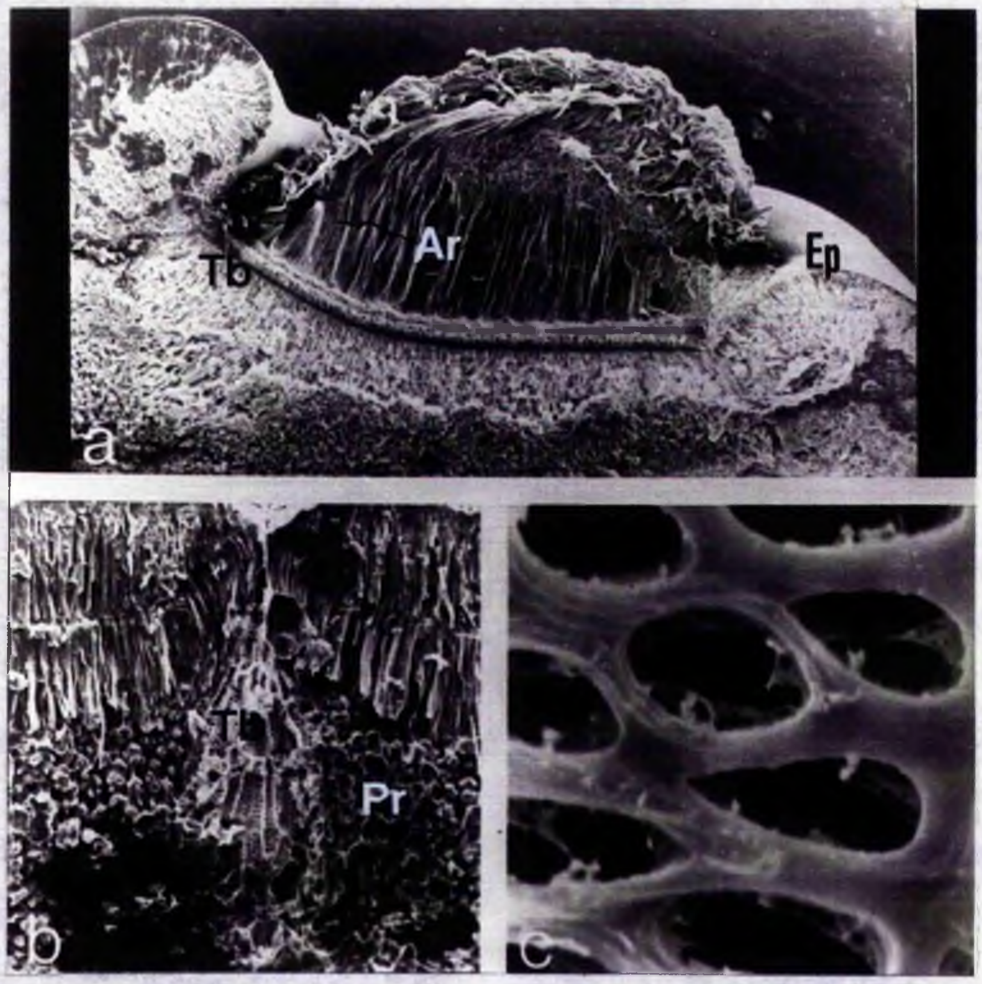
c - tracheoid pits (2500 x)

Figure 87 - Internal seed morphology of (a,b) L. crotalarioides and (c,d) L. sellowianus.

a, c - transversal section through the hilum (75 x)

b, d - tracheoid pits (2500 x)

86



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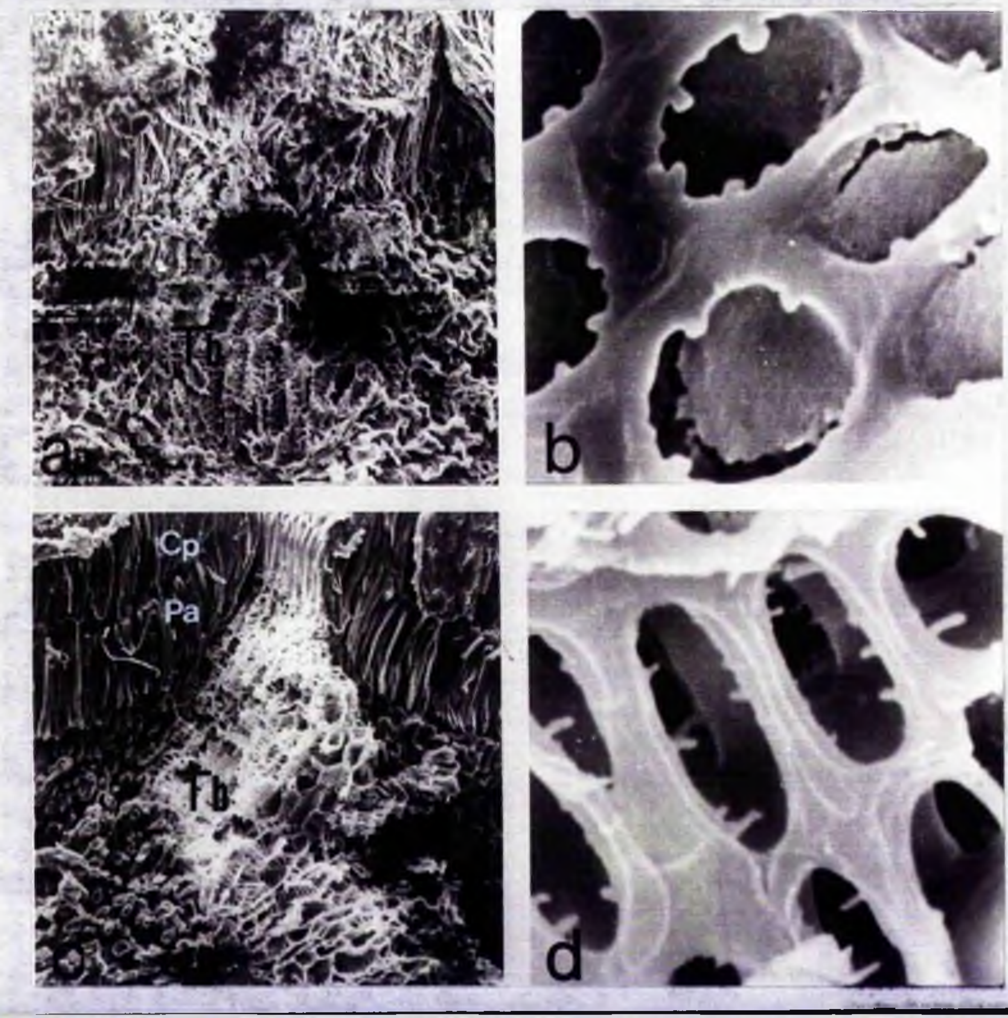


Figure 88 – Internal seed morphology of (a,b) L. parvifolius and (c,d) L. guaraniticus.

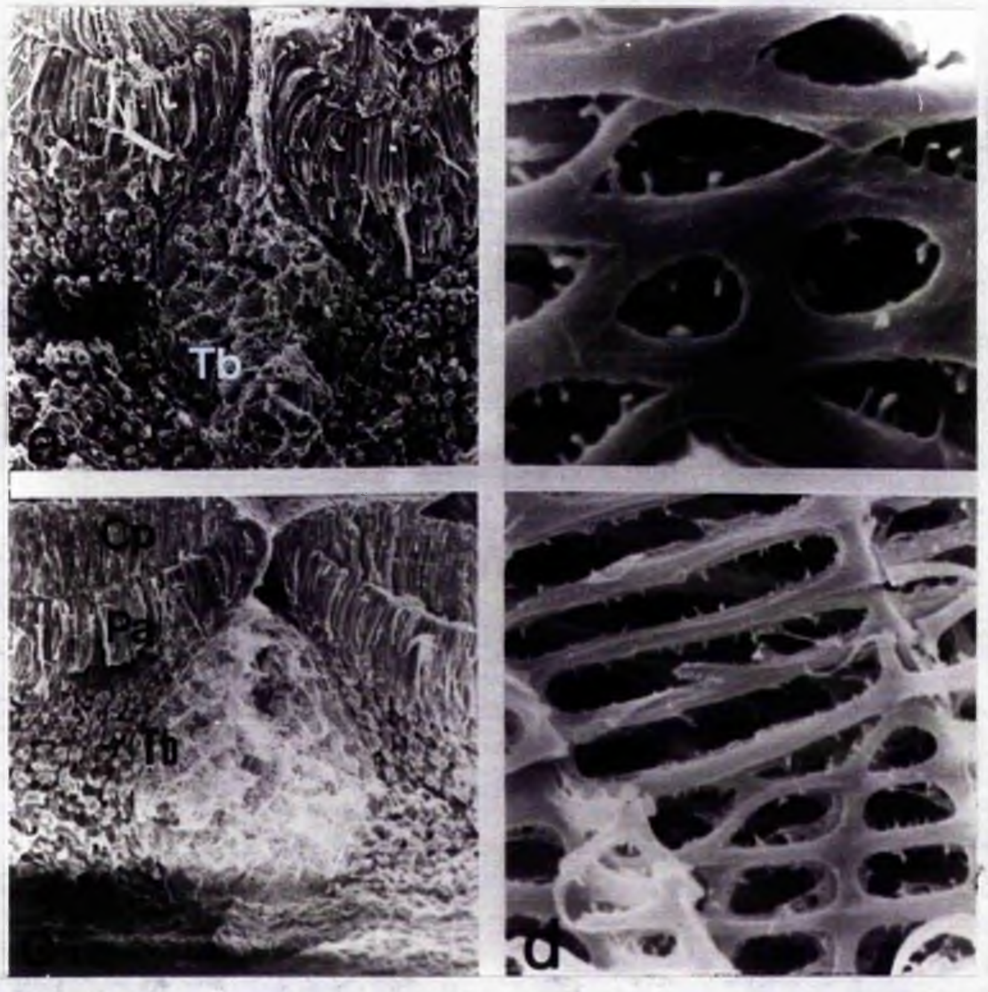
a, c – transversal section through the hilum (75 x)

c, d – tracheoid pits

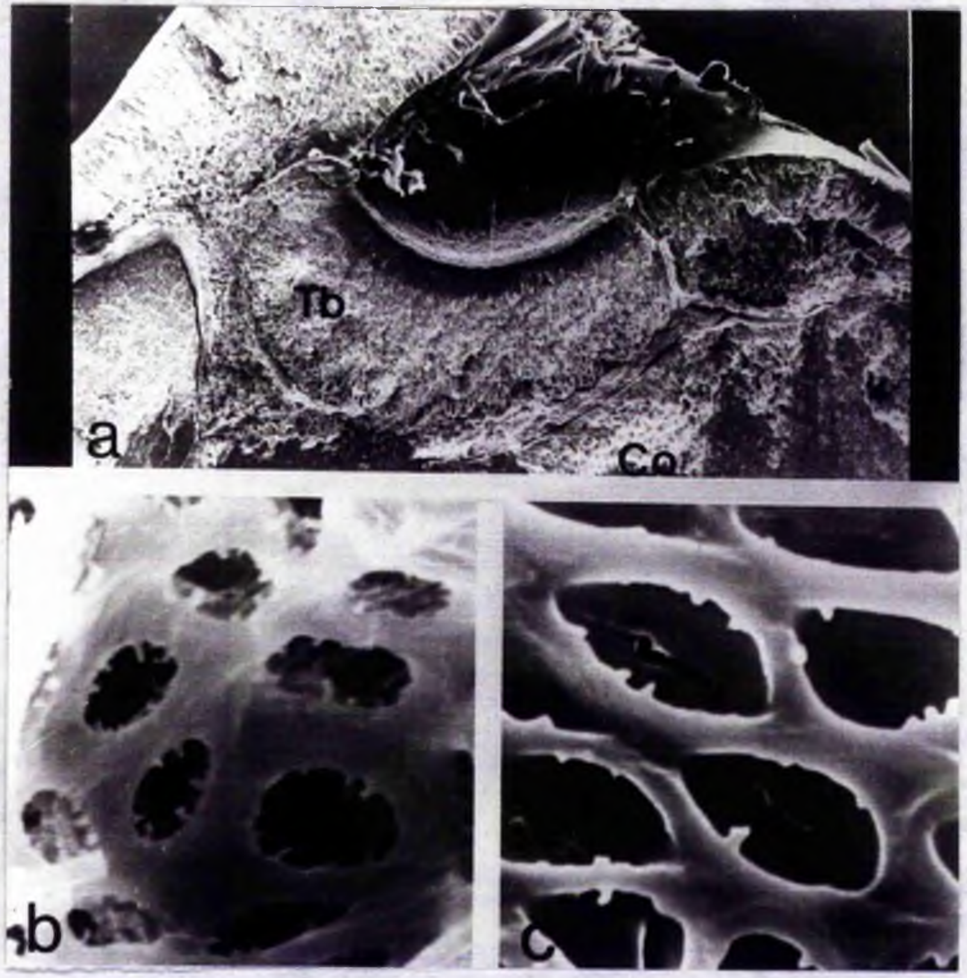
Figure 89 – Internal seed morphology of (a,b) L. villosus and (c) L. velutinus.

a – longitudinal section through the hilum (25 x)

b, c – tracheoid pits (2500 x)



88



89

Figure 90 - Internal seed morphology of a,b) L. comptus and (c,d) L. arenarius.

a, c - transversal section through the hilum (50 x)

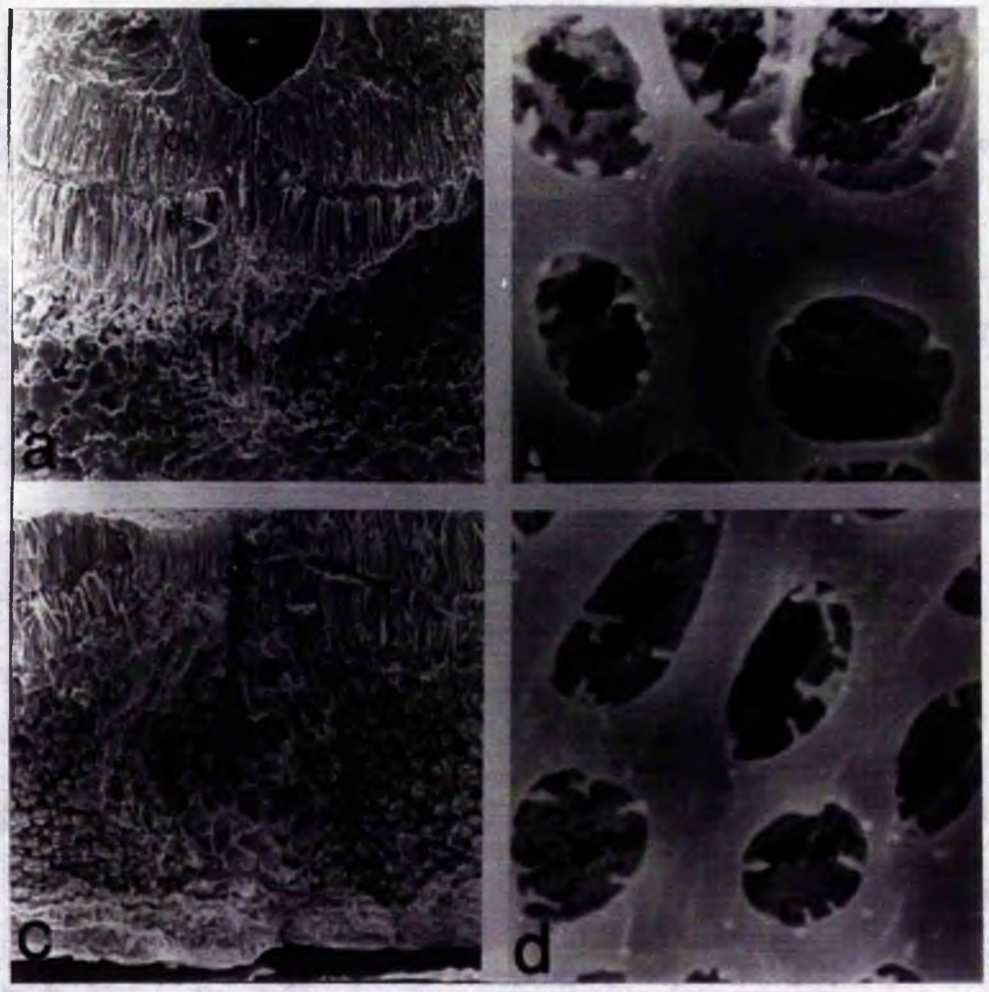
b, d - tracheoid pits (2500 x)

Figure 91 - Internal seed morphology of L. lanatus.

a - longitudinal section through the hilum (25 x)

b - detail of vascular bundle and tracheid bar (100 x)

c - transversal section of the tracheid bar (75 x)



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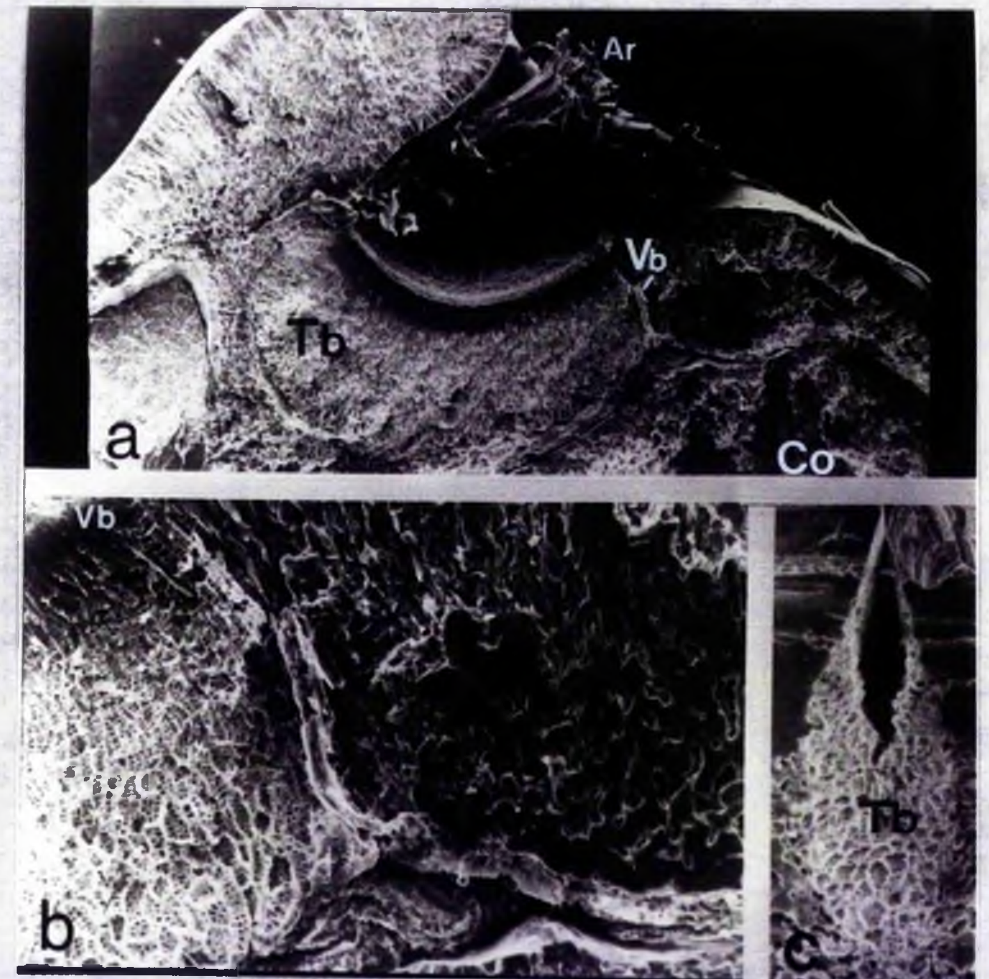

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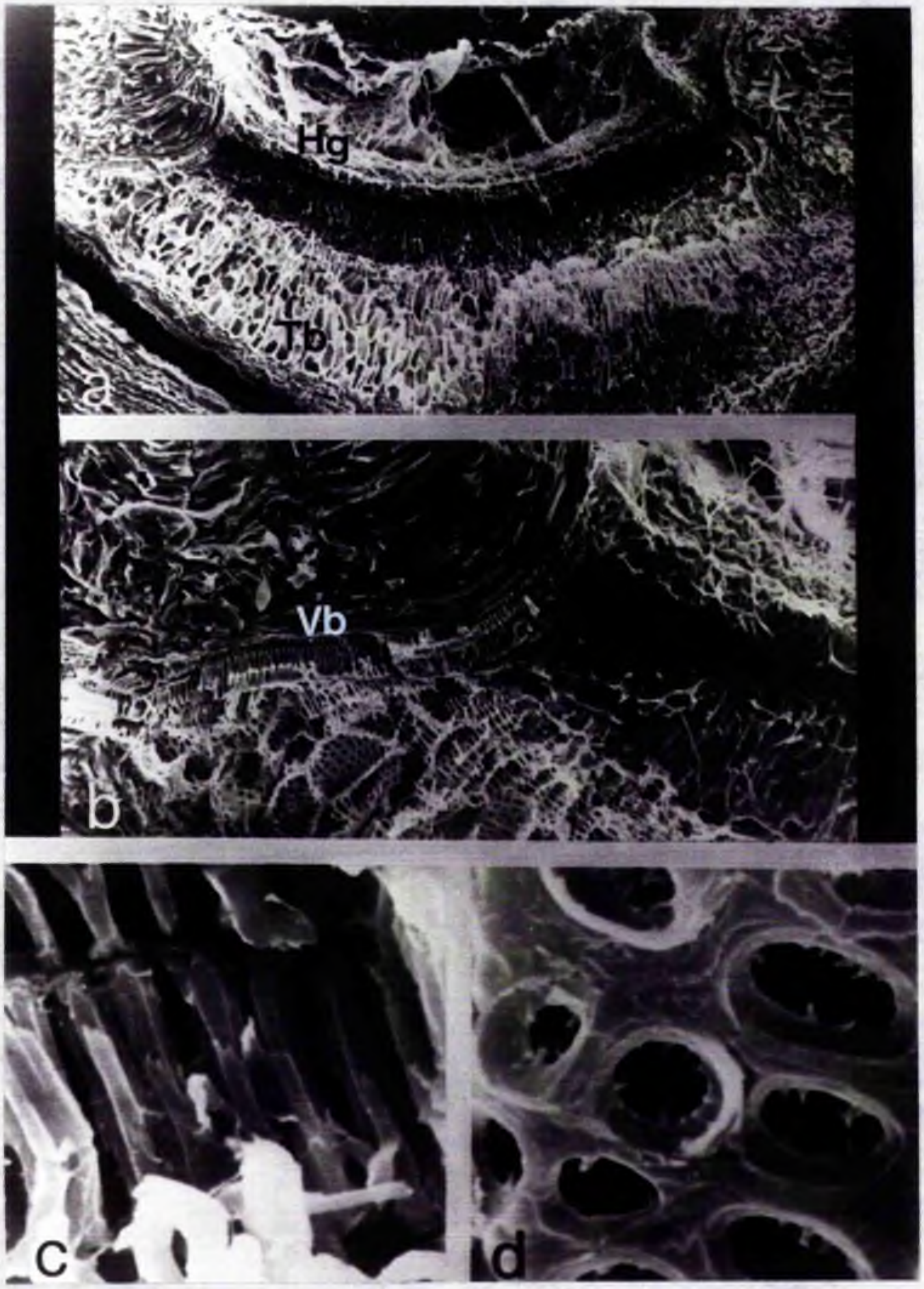


Figure 92 - Internal seed morphology of L. bracteolaris var. czermakii. (a) - longitudinal section through the hilum (50 x); (b) - detail of vascular bundle (175 x); (c) - tracheid of vascular bundle (2500 x); (d) - tracheoid pit (2500 x).

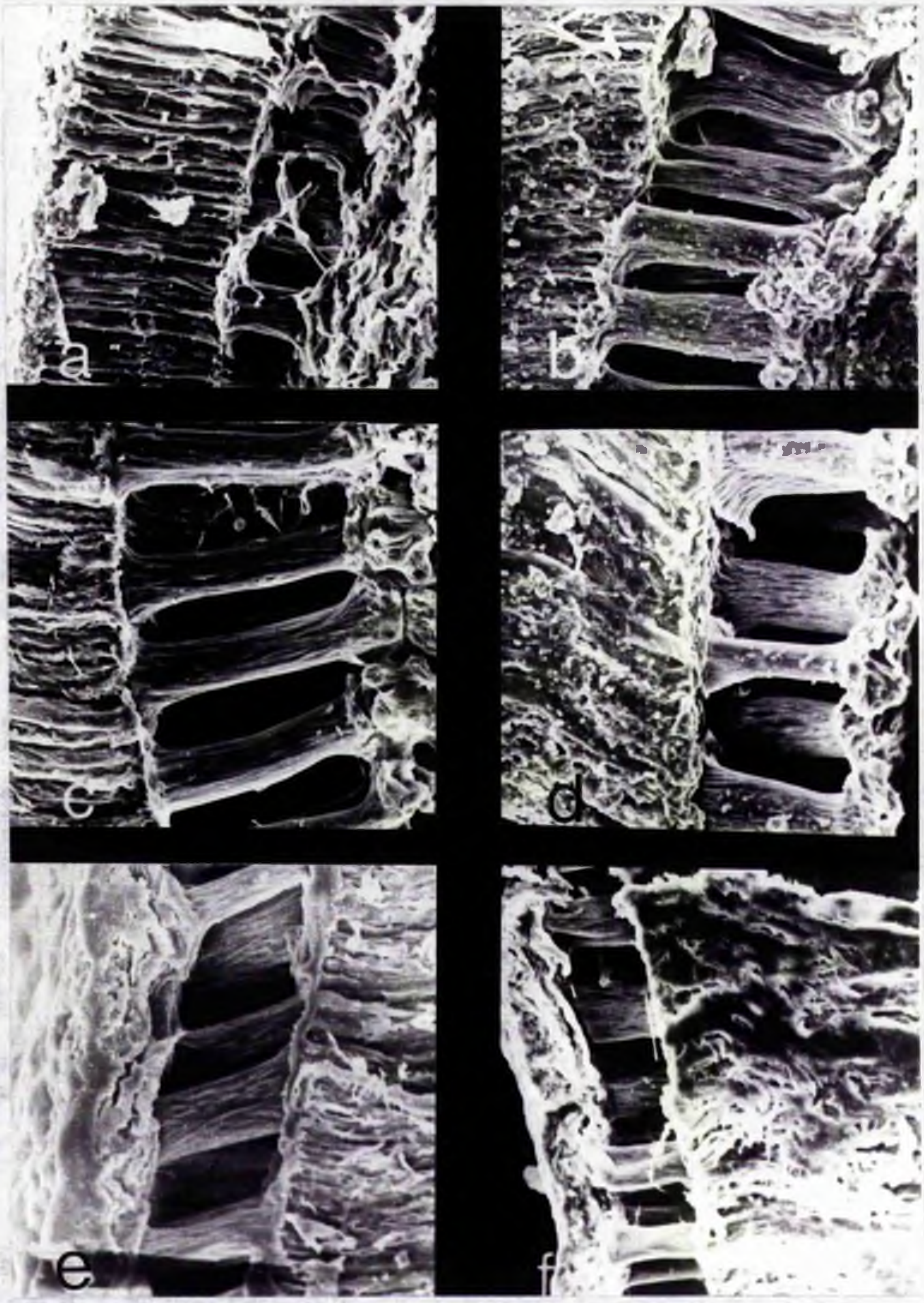


Figure 93 - Transversal section of seed testa showing the hypodermis (macrosclereids). (a) - L. crotalarioides; (b) - L. arenarius; (c) - L. parvifolius; (d) - L. velutinus; (e) - L. comptus (f) - L. bracteolaris. (all 175 x).

(Figures 91b,92b,c). No correlations with any other feature could be found for this characteristic.

Finally, the macrosclereids, which in Sesbania are of some infrageneric taxonomic value are not helpful in Lupinus. The presence of striate, mixed dumbelloid and humeroid macrosclereids in uni- and multifoliolate species makes this character devoid of any taxonomic use for the species studied here.

5.2.2.5 - Evolutionary history

Old World *Lupinus*

As noted above (section "Seed Morphology"), GLADSTONES (1974) divided the Old World annual, multifoliolate species of *Lupinus* into two groups (Table 28) : the "rough-seeded" lupins and the "smooth-seeded" lupins. The latter group has five reasonably distinct species which are essentially Mediterranean (GLADSTONES *loc. cit.*; PLITMANN, 1981, Figure 94) with different chromosome numbers. The rough-seeded species occur in northern Africa and the Middle East and comprise some seven species which difer in chromosome number and with allopatric distributions (Table 28, Figure 94).

These two groups in the Old World seem to be isolated from each other and apparently without any close systematic relationships. The main isolation mechanisms between them is achieved by a breeding system with high levels of automatic self-pollination and strong interspecific cross incompatibility, both in the smooth-seeded (FALUYI, 1980; WILLIAMS, AKHTAR & FALUYI, 1980) and in the rough-seeded taxa (PLITMANN, HEYN & PAZY, 1980; PLITMANN, 1981; PLITMANN & HEYN, 1981; PAZY, 1984). This isolation is supported by the fact that no natural hybrids have yet been found to occurr between these groups of species.

Recently, a further separation of these Old World groups has been provided by studies of leaf flavonoids (WILLIAMS, DEMISSIE & HARBORNE, 1983), as summarised in Table 29. It can be seen that the smooth-seeded species are characterised by a mixture of flavonoid patterns which isolates *L. micranthus* (with flavones, luteolin and apigenin), *L. albus* (with flavonols only) and *L.*

Table 28 - Classification, distribution (after GLADSTONES, 1974) and chromosome numbers of Old World species of *Lupinus*.

TAXON	DISTRIBUTION	N	2N
SEEDS ROUGH (allopatric distributions)			
L. cosentinii Guss.	NW Africa and W Mediterranean		32[1]
L. digitatus Forskal *(including *L. tassilicus* Maire)	Egypt,central and western Sahara, Senegal		36[2]
L. princei Harms	E African highlands		
L. pilosus Murray *	E Mediterranean	21[1]	42[2]
L. palaestinus Boiss.	S Israel and Sinai Peninsula	21[1]	42[2]
L. atlanticus Gladstones	NW Africa, in the High Atlas foothills and Anti Atlas (Morocco)		38[2]
L. somaliensis Baker	Highlands of Somaliland and possibly Ethiopia		
SEEDS SMOOTH (sympatric distributions)			
L. albus L.	Balkan Peninsula	25[2]	48[3] 50[2,3]
L. angustifolius L.	Mediterranean and SW France	20[2]	40[2,3]
L. micranthus Guss.	Mediterranean	26[2]	52[2,3]
L. luteus L.	mainly W Mediterranean	26[2]	52[3]
L. hispanicus Bois. & Reut.	S, central and NW Spain		52[3]

Notes : PLITMANN, HEYN & PAZY (1980) regard *L. tassilicus* as a distinct species and question the specific status of *L. digitatus* which could be included in *L. pilosus*.

1 - after PAZY *et al.*, 1977
2 - ater PLITMANN *et al.*, 1980
3 - after FERNANDES *et al.*, 1977

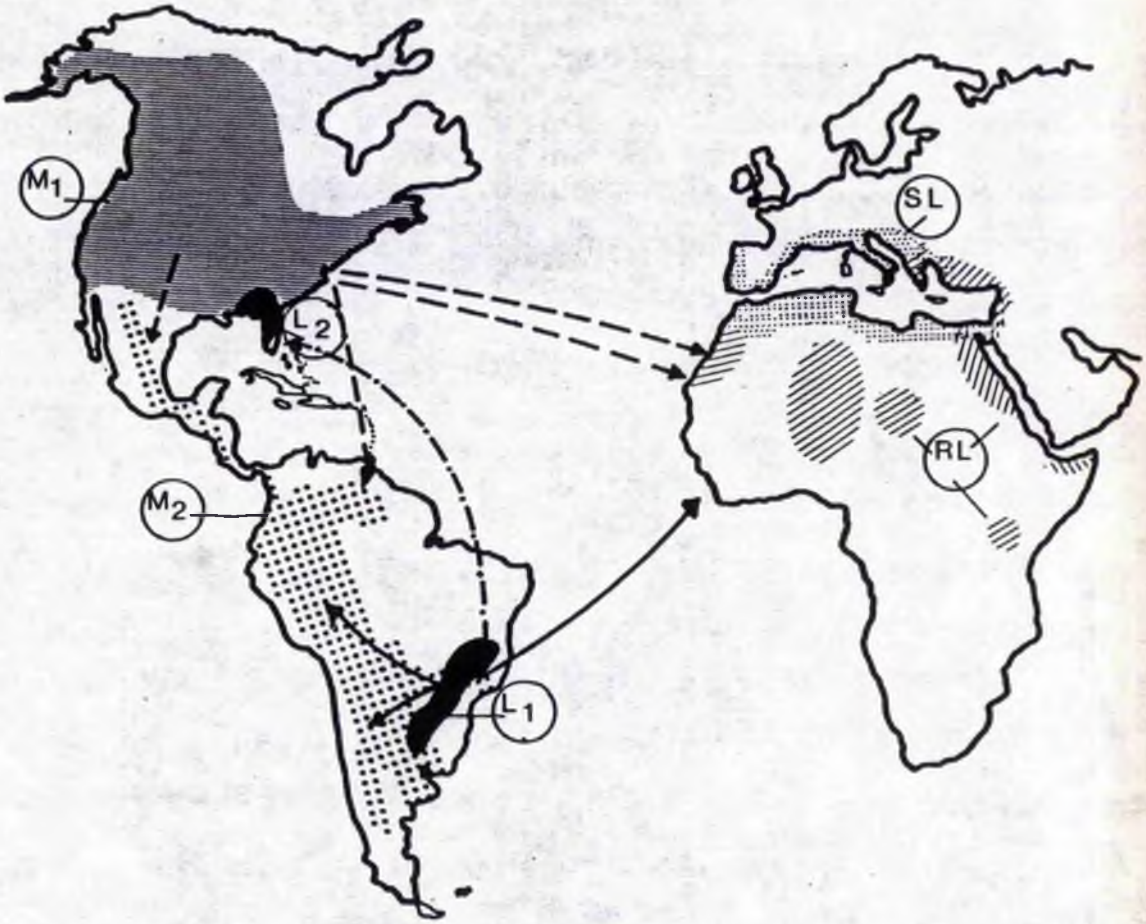


Figure 94 - Evolutionary relationships of the different groups of *Lupinus* L.

M - multifoliolate species of (1) North America and (2) Central and South America
L - unifoliolate species of (1) South America and (2) North America
(RL) - "rough-seeded" and (SL) "smooth-seeded" species of the New World

The different routes of migration and/or origin are based on ideias suggested by :
PLITMANN (1981) (— — — →) and DUNN (1971, 1984) (———→, —·—·→)

(—·—·→) long-distance dispersal route of unifoliolate lupins from South to North America.
For explanation of these routes, see text.

Table 29 - Distribution of flavonoids in leaves of Old and New World species of *Lupinus* (after WILLIAMS, DEMISSIE & HARBORNE, 1983).

TAXON	LEAF FLAVONOIDS
OLD WORLD	
Smooth-seeded	
L. micranthus	FLAVONES, LUTEOLIN, APIGENIN
L. albus	FLAVONOLS
L. angustifolius	
L. luteus	FLAVONES AND FLAVONOLS
L. hispanicus	
Rough-seeded	
L. cosentinii	
L. digitatus	
L. princei	FLAVONOLS ABSENT IN ALL
L. pilosus	BUT COMMON OCCURRENCE OF :
L. palaestinus	FLAVONE C-GLYCOSIDES
L. atlanticus	LUTEOLIN AND
	2'-HYDROXYFLAVONE
NEW WORLD 13 species, all from North America	

angustifolius, L. luteus and L. hispanicus, all of which have a mixture of flavonols and flavones.

In the rough-seeded species, however, a remarkable uniformity was observed in the leaf flavonoid pattern (Table 29) which is characterised by the absence of flavonols and a common occurrence of flavone C-glycosides, luteolin and 2'-hydrixyflavvone. These compounds are generally absent in the smooth-seeded group, except for the presence of luteolin in L. micranthus (Table 29). Interestingly, WILLIAMS, DEMISSIE & HARBORNE (1983) have found the same flavonoid patterns of the rough-seeded group are present in 13 multifoliolate species from the New World (all from North America), therefore providing some possible relationships between the species studied.

PLITMANN (1981) has discussed the origin of the Old World lupins with the following assumptions : (1) the genus originated in North America and (2) through migration (island hopping or other means of long-distance dispersal) it reached the Old World during the Miocene (ca. 20 m.y. BP) on a few separate occasions. PLITMANN (loc. cit.)and also DUNN (pers. com.) have suggested that the subsequent evolution of at least some of the Old World lupins has been linked with early agricultural use by Man.

Clearly, the existence of two groups of lupins in the Old World suggests independent introductions and there is further support for these isolated introductions since the smooth-seeded taxa, unlike the rough-seeded group, do not have the same flavonoid constituents found in the New World species. However, seed testa pattern provides a link between the South American multifoliolates and all the unifoliolates since the species with smooth seeds have foveolate testa, a pattern so far only otherwise found in the South America, whereas the rough-seeded group has papillose testa, which has only been found in one species of the New World.

New World Lupinus

The distribution of species of Lupinus in the New World (Figure 94) encompasses multifoliolate species in arctic, subalpine, mediterranean, subtropical and tropical climatic zones, ranging from Alaska in North America extending through Central America and reaching the northern regions of Argentina and Chile, and unifoliolate species centred in Brazil and also in southeastern North America. The variety of habitats in which the species of Lupinus occur in this large distributional range is remarkable and has certainly played a major role in their evolution and has also allowed many species to experience a wide array of microhabitat diversification and adaptation. Thus, whilst ca. 12 species of Lupinus are accepted in the Old World, the number of names available for the New World taxa is so large and so poorly studied that it can be only estimated. Recently, DUNN (1984) has 'guess-estimated' 500-600 taxa warranting naming at specific or infraspecific level. Partly as a consequence of these large numbers very few modern taxonomic revisions are available for the genus in the Americas. Instead, most published works deal more with more or less isolated problems treating with very few species.

Whereas in the Old World all the lupins are annual herbs, the New World taxa comprise a large range of perennial herbs, subshrubs, shrubs or even treelets to annual herbs with chromosome numbers 2n = 24 to 96, but most are associated with 2n = 36-48. Furthermore, individuals of the same species may either have 48 or 96 chromosomes or 24 or 36 (DUNN. 1984) with the basic number being regarded as x = 6. It is clear, therefore, that in the New World, the genus shows polyploidy at multiple levels in a way quite different to the Old World species (Table 28) and unlike the latter, evolution in the New World lupins has been considerably influenced by hybridisation and polyploidy, the former sometimes associated with introgression. These processes have contributed to the taxonomic complexity of the genus *Lupinus* as encountered in North America and South America.

An example of this complexity is reflected in the leaf flavonoid patterns found in 73 taxa of *Lupinus* in North America (NICHOLLS & BOHM, 1983). The variation of pattern was very large and ca. 56 compounds were identified and treated by numerical analyses which, whilst showing some groupings which correlated with morphological features , in general were neither able to confirm earlier taxonomic treatments of these taxa nor provide a new classificatory work (NICHOLLS & BOHM, *loc. cit.*). One interesting pattern which did emerge from NICHOLLS & BOHM's work is that a unique combination of flavonoid constituents was encounterd in the only unifoliolate species from North America which was studied. The detailed comparison of these patterns with the ones found for the Old World species still remains to be made by specialists for a better understanding of the biochemical aspects of these plants.

It is evident that any attempt to outline an evolutionary history for the genus Lupinus must remain a vastly speculative exercise because of the continuing lack of monographic studies on the geographical sub-units of the New World species, lack of detailed cytological data, eg. totally lacking for the unifoliolate taxa, and the very partial scope of the present phytochemical studies.

The hypothesis of a North American origin for the genus proposed by PLITMANN (1981), with sporadic introductions to the Old World, presumably invokes the same explanation for the introduction of the lupins into South America. From the point of view of the continental drift theory, RAVEN & AXELROD (1974) and RAVEN (1983) have repeatedly emphasized the isolation of South America, particularly from North America, and increasingly, from Africa during the Cretaceous, with North and South America only establishing close proximity as recently as the Pliocene. On that basis, therefore, Lupinus could be treated as a recent arrival, from North America in to South America. Whilst this scenario mmay well be readily acceptable for some of the perhaps recently evolved Andean species complexes, it is more problematical as an explanation of the occurrence of the unifoliolate group which occurs, often as restricted endemics, in the Brazilian uplands of Minas Gerais. DUNN (1984) has argued that the unifoliolates in South America are a primitive group and indeed, rather than representing unifoliolate taxa, they are a unifoliate or single-leaved group which gave rise to the multifoliolate lupins. The arguments supporting this hypothesis are (DUNN, 1984) : (1) perennial habit is considered to be primitive and the annual derived and this fits the pattern in Lupinus, where the unifoliolates are all perennials and the annuals have compound leaves; (2) the leaf abscision of all the unifoliolates is at the base or near the base of the petiole and not at the top of the petiole; (3) the laminas of the unifoliolate species have developed "strongly arcing lateral veins", similar to those in Rosales and other primitive orders; (4) most unifoliolate species have stipules, "present in Rosales and other primitive orders" and these persist in the digitate-leaved taxa; (5) there is some indication of a 3 5 lacunar vascular system in the petiole, which is considered to be anatomically primitive; (6) the unifoliolate species are large-flowered and insect-pollinated, in contrast with "small flowered annuals and some high altitude lupins specializing in autoselfing".

An alternative phytogeographical hypothesis, which although equally vague, permits an open mind on this latter theory, would be that Lupinus was sufficiently evolved during the mid - late Cretaceous to permit fragmentation between west Africa - North America - South America. RAVEN (1982) has argued for such an ancient connection in various groups of angiosperms, and this kind of hypothesis would also fit with the generally African origin of leguminous groups favoured by RAVEN & POLHILL (1981).

Certainly, whatever the ancient phytogeographical links may have been they have become obscured by being overlain with recent hybridisation-polyploidy stimulated evolution in North America and Pacific (Andean) South America. In the latter context north and south migration have probably played a part. Whether the picture is further confused by a mixture of primitive South American lupins with North American immigrants must remain an open question at present. In conclusion, it seems that the evolutionary history of the genus Lupinus in the Old and New World is far from clear and still devoid of even the basic taxonomic understanding of the genus which is a prerequisite for such an analysis.

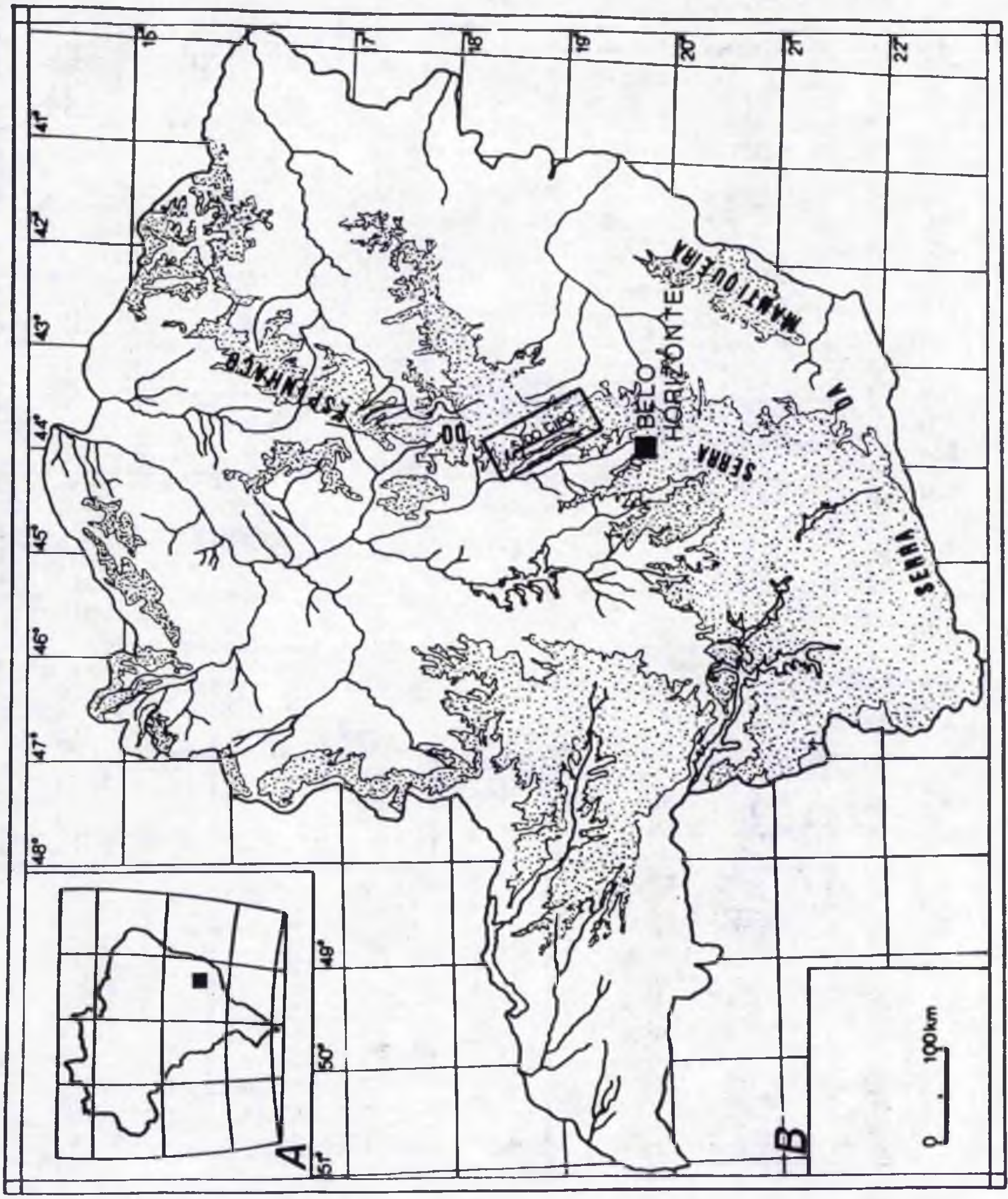
Endemism in the unifoliolate lupins

The main concentration and diversity of the unifoliolate species are found in East Central region of Brazil, particularly along the the extensive range of mountains known as the "Serra do Espinhaço" (Figure 95). The Serra do Espinhaço is ca. 1000 km long and betwenn 50-100 km broad. It has its origins at 20° 35'S, about 100 km south of Belo Horizonte, the state capital of Minas Gerais, and extends northwards into the state of Bahia, where it terminates at around 11° 10'S. The altitude can reach a maximum of 2000 metres, but mostly ranges from 800 to 1200m, similar to the adjacent chain of mountains located further south of Serra do Espinhaco, called Serra da Mantiqueira (Figure 95), where some lupins also occur.

At about 110 km NW of Belo Horizonte a subunit of the Serra do Espinhaco called "Serra do Cipó" occurs (Figure 95). This area probably has the richest endemic flora in Brazil (JOLY, 1970; SENDULSKY & BURMAN, 1978).

SENDULSKY & BURMAN (1978), in a paper which they present new, endemic species of Gramineae from Serra do Cipó, have provided an excellent description of this region's habitat, as follows :

Figure 95 - Location of "campos rupestres" in the Serra do Espinhaco and Serra do Cipó areas in the state of Minas rais, Brazil. In A, the plot represents Belo Horizonte and the shaded area in B shows altitude above 800 m


ESPINHAÇO
DO
Serra do Cipó
BELO HORIZONTE
SERRA
DA
MANTIQUEIRA
SERRA
15°
17°
18°
19°
20°
21°
22°
41°
42°
43°
44°
45°
46°
47°
48°
49°
50°
51°
A
B
0
100km

"The geological structure of the Serra do Espinhaço is far from uniform, and involves four groups of rocks : the two oldest formations are composed of phyllites and quartzites, with some mica-schist and gneiss, while above these appear glacial conglomerates, clays and calcareous rocks. The lower formations have undergone extensive metamorphosis and folding, and may safely be regarded as Devonian. The characteristic surface morphology of the Serra do Cipó depends on two factors : the displacement of the quartzite bedrock, and different rates of erosion. The watercourses cut with relative rapidity into the schists and phyllites, forming depressions, while on the other hand the more resistant itabirite (granular quartz and haematite) and itacolomite (micaceous quartz) persist to form striking crests protruding through the thin soil. The result is a strongly accidented region of deep valleys, jagged outcrops, and extensive areas of open, rocky pasture".

This typical high rocky pasture is named in Portuguese as "campos rupestres" and is characterised in its herbaceous elements by the occurrence of families such as Poaceae, Eriocaulaceae, Xyridaceae and Cyperaceae, whilst trees and shrubs, although sparse, are represented by the Leguminosae, Melastomataceae, Compositae, Velloziaceae and Vochysiaceae (JOLY, 1970; SENDULSKY & BURMAN, 1978).

On the flanks of the Serra, the high rocky pasture of the "campos rupestres" is substituted by an upland form of "cerrado" vegetation, which itself gives way to typical "cerrado" at lower altitudes. Thus, the "campos rupestres" in Brazil are isolated as 'islands' of high altitude in an extensive cerrado area (Figure 96). The "cerrados" present a range of forms, from "campo limpo" (open grassland with scattered shrubs) to "cerrado *sensu strictu*" (rather closed shrub-savanna) forms (COUTINHO, 1978). It is not surprising, therefore, that once the ecological adaptations occur which allowed species of the "campos rupestres" to occupy "cerrado" habitats, these taxa tend to have very wide distributions in the "cerrados" areas of Brazil. Furthermore, the "cerrados" represent another habitat in which the lupins may evolve in isolation from the "campos rupestres", therefore permitting further speciation to occur. In this case, the central core of the "cerrados" in Brazil (Figure 96) represents one such area where endemic species of unifoliolate *Lupinus* have also been found (*L. subsessilis* and *L. insignis* are two typical examples).

The phytogeographical scenario described above is well supported by the distribution of the unifoliolate species of *Lupinus* in Brazil. Most of the taxa are well represented in the Serra do Espinhaco area (*L. decurrens*, *L. laevigatus* are endemics) but some not only occur in this region but are also found in "cerrados" of west central and southern Brazil (*L. arenarius*, *L. crotalarioides* and *L. velutinus*). Furthermore, at least three of the unifoliolate species (*L. velutinus*, *L. sellowianus* and *L. guaraniticus*) have wider distribution ranges and extend southwards to Argentina and Paraguay (SMITH, 1945; DUNN, pers. com.)

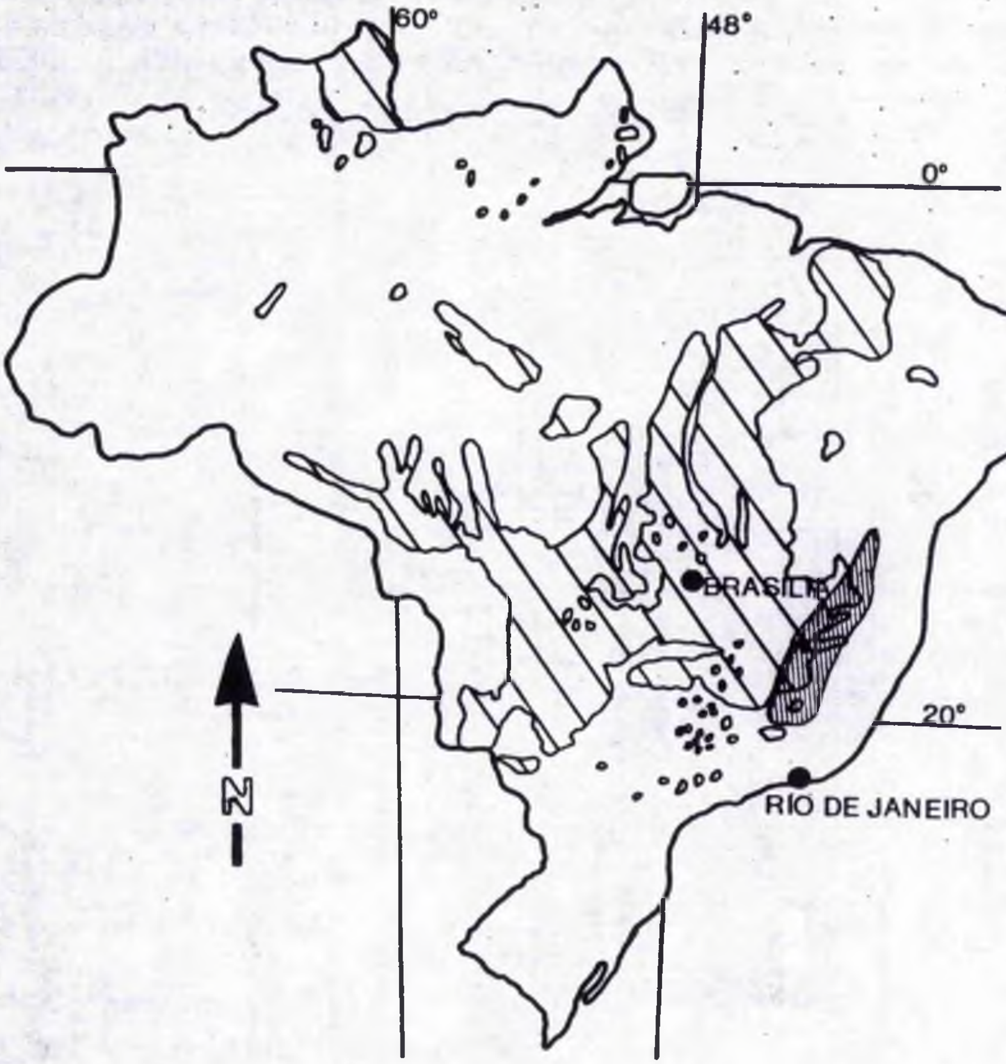


Figure 96 - Distribution of "cerrado" vegetation in Brazil (after CAMARGO et al, 1972). The shaded area represents the complex of mountains comprising the Serra do Espinhaço (Figura 95).

5.2.2.6 - Formal taxonomy of the unifoliolate taxa

Lupinus L. Sp. Pl. 2 : 721, 1753.

Unifoliolate species, "section" Simplicifoliae (sensu BENTHAM, Fl. Bras. 15 (1) : 10, 1859).

Herbs, subshrubs or shrubs; stems single or branching, erect or rarely decumbent (L. ovalifolius), hirsute to densely villous-lanate. Stipules absent or, if present, completely fused with the petioles or partially fused and then with conspicuous shortly deltoid to long-lanceolate, acuminate free tips, pubescent externally, glabrous within. Leaves unifoliolate, sessile to petiolate, linear to lanceolate or ovate to ovate-lanceolate, glabrous to densely villous, membranaceous to coriaceous. Racemes terminal, usually multi-flowered, inflorescence, lax or subverticillate; bracts lanceolate to oblong-lanceolate, deciduous. Calyx pubescent externally, glabrous within; deeply 2-lipped, lower lip shortly trifid to tridentate, upper lip bifid; bracteoles 2, usually lanceolate. Corolla blue to purple or the standard with a central white to deep purple spot; glabrous; standard ovate to ovate-circular, strongly reflexed over the upper lip of the calyx; wing petals oblong to oblong-lanceolate, the tips adnate at the apex which is either straight or arcuate, with a short claw; keel petals oblong-lanceolate to lanceolate, often arcuate. Stamens 10, monadelphous, the filaments unequal, glabrous; the anthers dimorphic, the lowermost linear, the uppermost sagittate. Ovary pubescent; style curved upward; stigma capitate; ovules 3-6 (-9). Pods oblong, beaked, hirsute-sericeous to densely villous. Seeds prolate to cylindric-reniform.

Key to the Brazilian unifoliolate species of Lupinus

1 . Stipules absent or, if present, totally adnate with the petioles and without free tips ---------------------------- 2

1' . Stipules present, partially adnate with the petiole and with free tips -- 7

2 . Leaves sessile or subsessile; petioles up to 1 mm ------- 3

2' . Leaves distinctly petiolate; petioles more than 1 mm ----- 6

3 . Leaves ovate; plants decumbent --------- (1) L. ovalifolius

3' . Leaves linear to oblong-lanceolate; plants erect ------- 4

4 . Leaves glabrous to subglabrous, with the margins ciliate, lamina linear to linear-lanceolate, coriaceous --- (6) L. coriaceus

4' . Leaves sericeo-villous to lanate-tomentose, lamina oblong-elliptic to oblong-lanceolate; membranaceous ------------ 5

5 . Standard 12-15 mm; leaf base amplexicaul, sericeo villous --- (2) L. parvifolius

5' . Standard 8-10 mm; leaf base not amplexicaul, lanate-tomentose ------------------------------------ (3) L. prouvensalanus

6 . Leaves 20-35(-45) x 7-14 mm, decurrent, with venation inconspicuous; stems unbranched; standard 8 - 10 mm -- (4) L. decurrens

6' . Leaves 70-110 x 9-15 mm, loose, with venation inconspicuous; stems branched; standard 12 - 15 mm ---- (7) L. guaraniticus

7 . Leaves and stipules glabrous (margins sparsely ciliate)--- (5) L. laevigatus

7' . Leaves and stipules pubescent ---------------------------- 8

8 . Petioles 20 - 50 (-65) mm; stipules with free tips linear to narrowly lanceolate; wing and keel petals with acute apex --- 9

8' . Petioles 8-15 mm; stipules with free tips lanceolate; wing and keel petals with obtuse apex ------------------------- 10

9 . Leaves lanate, apex acute; calyx also lanate,8 - 10 mm, lower lip with subequal teeth 1.5 - 3.0 mm -- (8) L. sellowianus

9' . Leaves sericeous to villous, apex obtuse; calyx hispid-sericeous, lower lip with unequal teeth, median tooth 0.8 - 1.9 mm ------------------------------ (9) L. crotalarioides

10 . Wing petals with apex straight; leaves with a conspicuous cordate base ---------------------------- (10) L. arenarius

10'. Wing petals with apex arcuate; leaves with attenuate base -- 11

11 . Plants sericeous; stipules 7 - 11 mm with free tips 3 - 5 mm -- (12) L. subessilis

11'. Plants densely villous to appressed villous; stipules 13 - 25 mm with free tips 8 - 13 mm ------------------- 12

12 . Internode 20 - 35 mm; lower lip of the calyx distinctly tridentate; leaves lax, less than 120 mm ---- (11) L. velutinus

12'. Internode 9 - 13 mm; lower lip of the calyx shortly trifid; leaves congested, more than 120 mm ------ (13) L. insignis

(1) . *Lupinus ovalifolius* Bentham

Fl. Bras. 15 (1) : 11, 1859

Herbs decumbent, stem long-hirsute to hirsute-sericeous; internodes 5.0 - 7.0 mm. Leaves (12-) 15 - 17 x 9-12 mm, sessile, to subsessile, with the petiole ca. 1 mm; ovate-circular to ovate-elliptic, rounded at the apex, hirsute on both faces and densely hirsute on the margins. Peduncles 60 - 80 mm, erect, hirsute-sericeous. Racemes 100 - 120 mm; flowers lax; bracts lanceolate to oblong-lanceolate, 4.5 - 5.0 x 2.0 mm, tardily caducous (or persistent ?); pedicels (2.0-) 3.0 - 4.0 mm, dense hirsute. Calyx hirsute-sericeous; lower lip lanceolate, 10 - 11 mm, tridentate, the median tooth ca. 1.0 x 0.5 - 0.7 mm, the two lateral teeth shorter, diverging; upper lip oblong-lanceolate, 5.5 - 6.5 mm, bifid, the teeth 1.0 - 1.5 mm ; bracteoles lanceolate, 3.0 x 0.7 mm. Standard (8.0-) 10.0 - 11.0 mm, oblong-ovate; wing petals oblong , subarcuate, 8.0 - 3.5 - 4.0 mm, the claw 1.5 - 2.0 mm; keel petals oblong-lanceolate, arcuate, 7.0 x 2.0 mm, the claw 1.0 - 1.5 mm. Ovules 3-4. Pods and seeds not seen. Figure 97.

Type - Brazil, Minas Gerais : no locality mentioned,
St HILAIRE 2167, 1816 (P!).

BENTHAM (1859) mentions the locality "campis herbidis Serra da Tapa" for the type but there is no such indication on the holotype at Paris. Furthermore, it has not been possible to trace such a locality in the state of Minas Gerais.

Figure 97 - Lupinus ovalifolius Benth. a - habit; b - flower and bract; c - gynoecium and androecium; d - wing petal; e - calyx and bracteoles; f - keel petal (scale: a = 1 cm, the others = 1 mm).

L. ovalifolius is only known from its type, a situation that reflects the need for better and intensive collections and sampling of the vegetation of Serra do Espinhaço area. Nevertheless, this species is very distinct among the others of the unifoliolate group due to its small, ovate leaves.

(2) . Lupinus parvifolius Gardner
Hook. Ic. Pl. 6(1), t. 521, 1843

Shrubs 1.5 - 2.0 m tall; stems woody, simple or few branched, sericeo-villous; internodes 3.0 - 4.0 mm. Leaves 17.0 - 23.0 x 8.0 - 17.0 mm, sessile, the base amplexicaul, oblong-elliptic to elliptic-ovate with the apex acute, sericeo-villous on both faces. Peduncles 3.0 - 10.0 mm. Racemes 30.0 - 70.0 mm, flowers congested; bracts ovate-lanceolate, 5.0 - 6.0 x 3.0 mm, caducous; pedicels 3.0 - 6.0 mm, densely sericeo-villous. Calyx appressed sericeous; lower lip lanceolate, 10.0 - 14.0 mm, shortly trifid to tridentate, the median tooth ca. 2.5 - 3.0 x 0.5 - 0.6 mm, the two lateral teeth shorter, 2.0 - 2.5 x 0.3 mm; upper lip lanceolate to oblong-lanceolate, 10.0 - 11.0 mm, bifid, the teeth 4.5 x 1.0 - 1.5 mm. Standard 12.0 - 15.0 mm, ovate-circular; wing petals oblong-ovate, straight to subarcuate at the tip, 12.0 - 17.0 x 6.0 -8.0 mm, the claw 2.5 mm; keel petals lanceolate, strongly arcuate at the tip, 8.0 - 10.0 x 3.5 - 4.5 mm, the claw 3.0 - 3.5 mm. Ovules 3. Pods 40.0 x 10.0 mm, erect to suberect, sericeo-villous. Seeds subcircular to cylindric-reniform, slightly compressed, 6.0 x 5.0 mm, brownish. Figure 98.

Type - Brazil, Minas Gerais : "in narrow rocky valleys, near Cidade Diamantina", GARDNER 4502, viii.1840 (K!, holotype; BM!,E!,G!,P!,TCD!, isotypes; NY! phototype of holotype; G!,NY!,TEX!, phototype of isotype at B).

L. parvifolius is easily recognisable by the distinct amplexicaul leaves, few-flowered, congested racemes, and also by the deeply bifid upper lip of the calyx. It has been found only in the Serra da Diamantina area of the Serra do Espinhaço, and in the Serra do Cipó.

Distribution (Figure 98a)

Brazil - state of Minas Gerais: Serra do Cipó, município of Jaboticatubas, km 131, Palácio, FOSTER & BARRETO 10845, 13.vii.1940 (SP,UB); município of Diamantina, Conselheiro da Mata, HATSCHBACH 30227, 12.viii.1972 (NY); ca. 26 km SW of Diamantina, on road to Gouveia, elev. 1300 m, IRWIN et al. 22413, 22.i.1969 (NY); road between Diamantina and Gouveia, MAGUIRRE, MAGALHÃES & MAGUIRRE 49175, 12. viii.1960 (K,NY,SP).

No locality mentioned : GARDNER 4512, no date (FHO).

Figure 98 - Lupinus parvifolius Gardn. a - distribution; b - part of the stem showing shape and insertion of the leaves (pubescence ommited in the upper leaves); c - pods; d - keel petal; e - wing petal; f - calyx and bracteoles, flattened out (pubescence partially omitted) (scale : b,c = 1 cm; d,e,f = 1 mm).

(3) . Lupinus prouvensalanus C. P. Smith

Sp. Lup. : 492, 1945

syn. : L. subsessilis var. lanata Bentham, in Martius

Fl. Bras. 15(1) : 13, 1859

Herbs up to 0.25 m tall, stems erect, lanate-tomentose; internodes 3.5 mm. Leaves 50.0 - 58.0 x 12.0 - 17.0 mm, subsessile oblong to lanceolate, the apex acute to obtuse-cuspidate, mucronate, the abaxial face sericeo-tomentose with the mid-vein proeminent, the adaxial face lanate-tomentose, the margins tomentose-villous. Peduncle 55.0 mm, erect, lanate-tomentose. Raceme 110.0 mm, flowers lax; bracts lanceolate-acuminate, (5.0-) 7.0 - 8.0 x 0.8 - 1.2 mm, tardiky deciduous; pedicels 2.0 - 3.0 mm. Calyx lanate-tomentose, lower lip oblong-lanceolate, tridentate, 9.0 - 11.0 x 3.0 - 4.0 mm, the median tooth 1.0 x 0.5 mm, the two lateral teeth shorter, straight or diverging, upper lip oblong-ovate, bifid, 6.0 - 7.0 x 2.5 3.0 mm, the teeth 1.0 -1.5 mm; bracteoles lanceolate, 2.0 - 3.0 x 0.5 - 0.8 mm. Standard 8.0 - 10.0 mm, ovate circular; wing and petals oblong-lanceolate, with the apex straight or slightly arcuate, 7.0 - 10.0 x 3.0 - 4.0 mm, the claw 0.6 - 0.8 mm; keel petals lanceolate, strongly arcuate, 5.5 - 7.0 x 2.5 - 3.0 mm, the claw 1.5 - 2.0 mm. Ovules 3. Pods and seeds not seen. Figure 99.

Type - Brazil, state of Minas Gerais : without precise locality, St HILAIRE 2996, no date (P!, holotype).

Figure 99 - Lupinus prouvensalanus C.P. Smith. a - habit, pubescence omitted in some leaves and upper raceme (ab - abaxial face; ad - adaxial face); b - wing petal (sculpturing omitted); c - keel petal; d - flower and bract; e - calyx, pubescence omitted (br - bract; bt - bracteole) (scale : a = 1 cm; the others = 1 mm).

The type specimen was identified and named by BENTHAM (1859) as *L. subsessilis* var. *lanata* Benth. However, the same author had earlier described *L. subsessilis* (BENTHAM, 1839) as stipulate and petiolate, both features not found in the specimen St HILAIRE 2996. Because of this difference, BENTHAM (1859) had to give two entries for *L. subsessilis* in his key.

SMITH (1945), who studied the types of *L. subsessilis* and *L. subsessilis* var. *lanata* created the new species *L. prouvensalanus* for the specimen St HILAIRE 2996. Curiously, SMITH (*loc. cit.*), unlike BENTHAM, failed to match the characters of his description of *L. prouvensalanus* since this sessile, exstipulate species with subsessile leaves was treated as petiolate in his key.

(4) . Lupinus decurrens Gardner

Hook. Ic. Pl. 6 (1), t. 521, 1843

Herbs to subshrubs, erect, 0.3 - 0.5 m tall; stems sericeous; internodes 10.0 - 12.0 mm. Stipules totally adnate with the petiole, without free tips. Leaves 20.0 - 35.0 (-45.0) x 7.0 - 14.0 mm, lanceolate, acute at the apex, decurrent, short-mucronate, sericeo-lanate to sericeo-tomentose on both faces, mid-vein prominent on the abaxial face; petioles 0.5 - 8.0 mm. Peduncle 20.0 - 36.0 mm, erect, sericeous. Racemes 60.0 - 110.0 mm; flowers lax; bracts lanceolate, 6.0 - 7.0 x 1.0 - 1.5 mm, sericeo-tomentose, caducous; pedicels (2.5-)5.0 - 8.0(-10.0)mm, sericeous. Calyx densely sericeous to sub-tomentose; lower lip oblong-lanceolate, tridentate, 4.5 - 6.0 mm, the median tooth 1.5 - 2.0 x 0.3 - 0.5 mm, the two lateral teeth much shorter; upper lip oblong to oblong-lanceolate, 2.0 - 3.5 x 1.0 - 1.5 mm, bifid, the teeth 1.5 - 2.0 mm; bracteoles lanceolate, acuminate, 1.0 - 1.5 x 0.3 - 0.5 mm. Standard 8.0 - 10.0 mm, oval-ovate; wing petals oblong-ovate, straight., 7.0 -9.0 x 3.0 - 4.0 mm, the claw 0.6 - 1.0 mm; keel petals lanceolate,arcuate, 7.0 - 9.0 x 2.5 - 3.5 mm, the claw 1.5 - 2.6 mm. Ovules 4-5. Pods 40.0 - 50.0 - 8.0 - 10.0 mm, sericeo-villous. Seeds suborbicular, compressed, 3.0 - 4.0 x 3.0 mm. Figure 100.

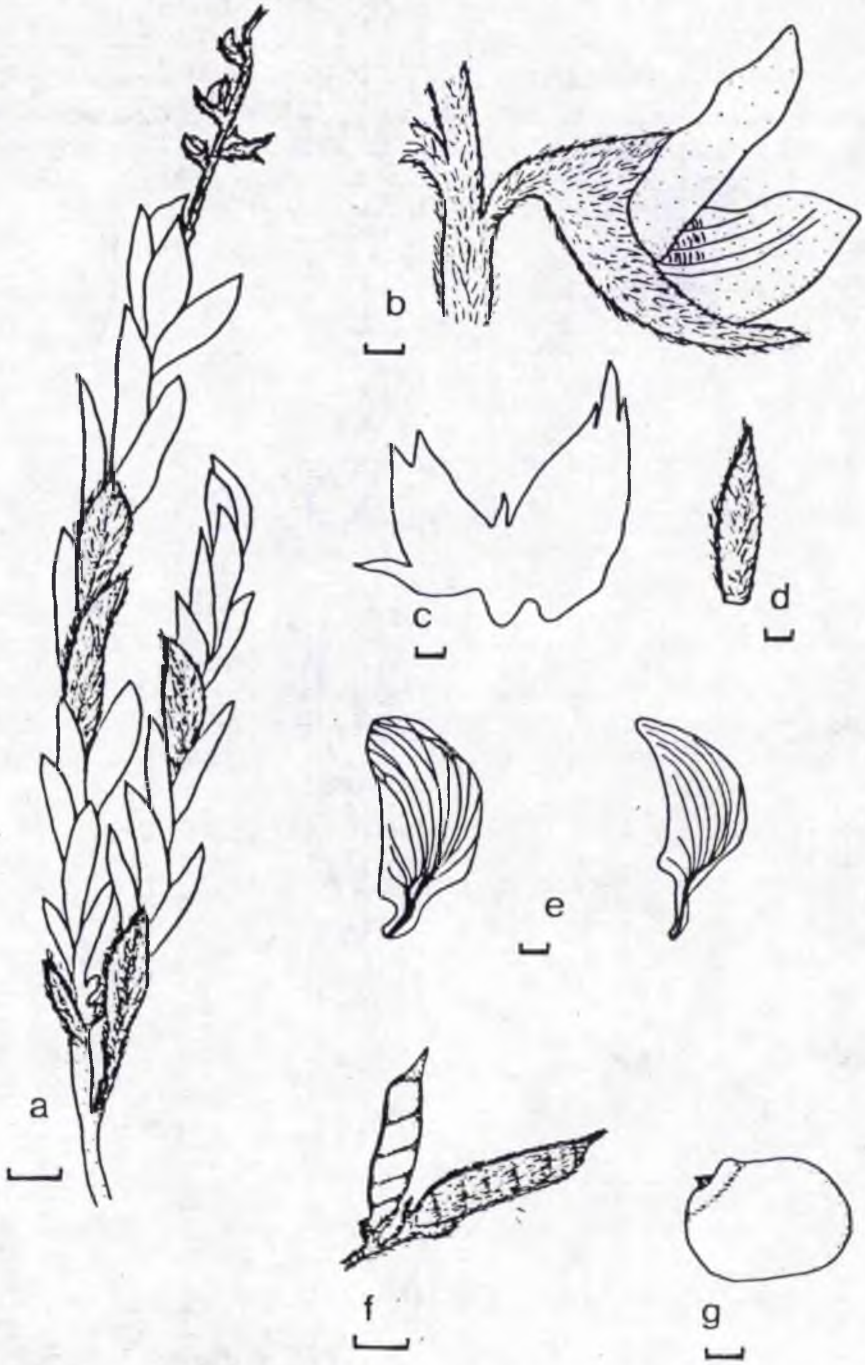


Figure 100 - Lupinus decurrens Gardn. a - habit (pubescence omitted in most leaves); b - flower, bract absent; c - calyx and bracteoles (pubescence omitted); d - bract; e - wing and keel petals; f - pods (pubescence omitted in one); g - seed (scale : a,f = 1 cm; the others = 1 mm).

Type - Brazil, state of Minas Gerais : "in elevated mountain campos, near the capital of Diamond District" (*fide* GARDNER, 1843), Diamantina, GARDNER 4503, viii.1840 (K!, holotype; BM!, isotype; photo of isotype at B : G!, GH!, TEX!).

L. decurrens was originally described by GARDNER (1843) as having sessile leaves and the stipules were not mentioned. However, BENTHAM (1859) recognised the leaves of *L. decurrens* as subsessile or with short petioles and described its petioles as 'obsolete'. The presence or absence of stipules in the unifoliolate species of *Lupinus* was regarded by BENTHAM (*loc. cit.*) only by the presence or absence of the conspicuous free tips, when the latter were not visible, then the plants were considered to be exstipulate, regardless the fact that the stipules could be totally fused with the petioles. Therefore, *L. decurrens* was treated by BENTHAM (*loc. cit.*) as exstipulate, along with *L. parvifolius* , *L. ovalifolius*, etc.

SMITH (1945) described *L. decurrens* as petiolate and stipulate in which case the stipules were fused with the petioles but these charcters are totally confused in his identification key, where *L. decurrens* is treated as having no stipules ("stipulae nullae") and sessile leaves ("folia sessiles, petioli nulli").

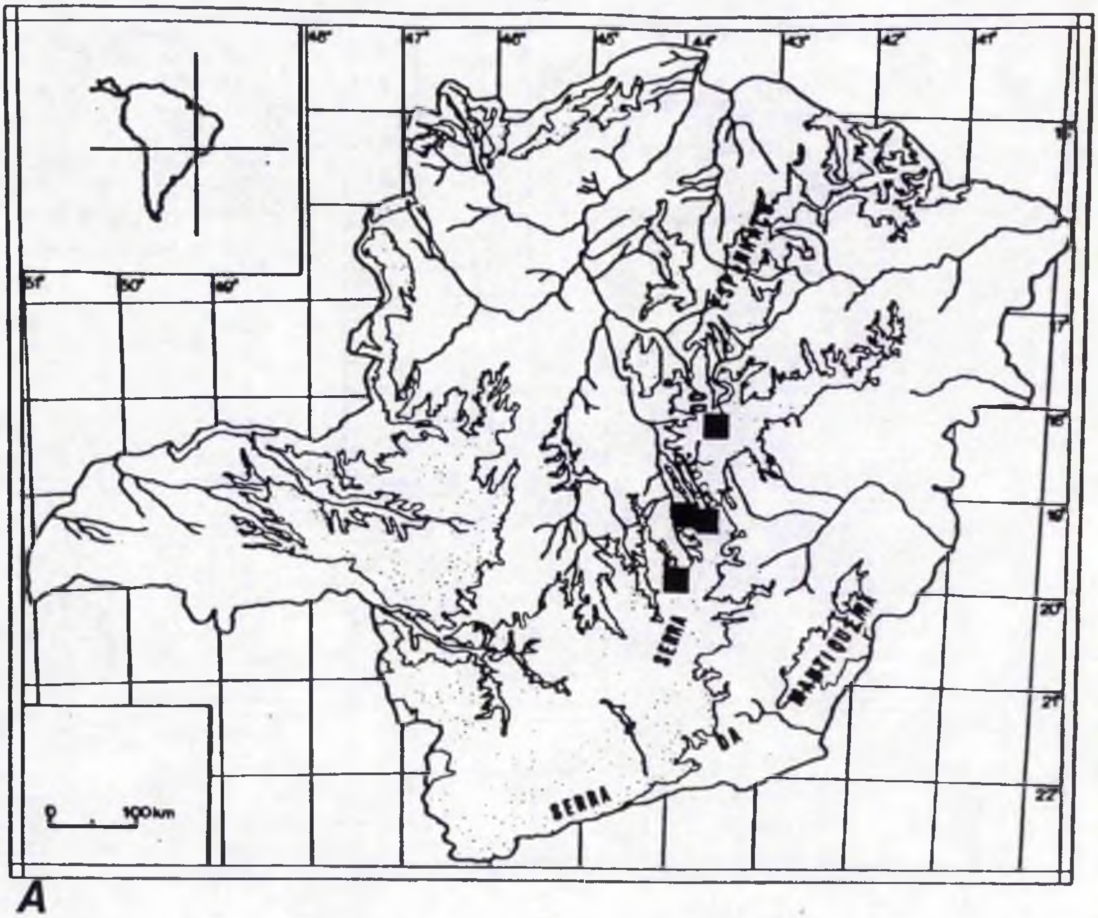
L. decurrens is apparently endemic to the Serra do Espinhaço area and its decurrent, sericeo-lanate leaves are a distinct character among the unifoliolate taxa.

Figure 101 - Distribution map of unifoliolate *Lupinus* in Brazil, state of Minas Gerais.

A - ■ *L. coriaceus*

B - ▲ *L. decurrens*

● *L. laevigatus*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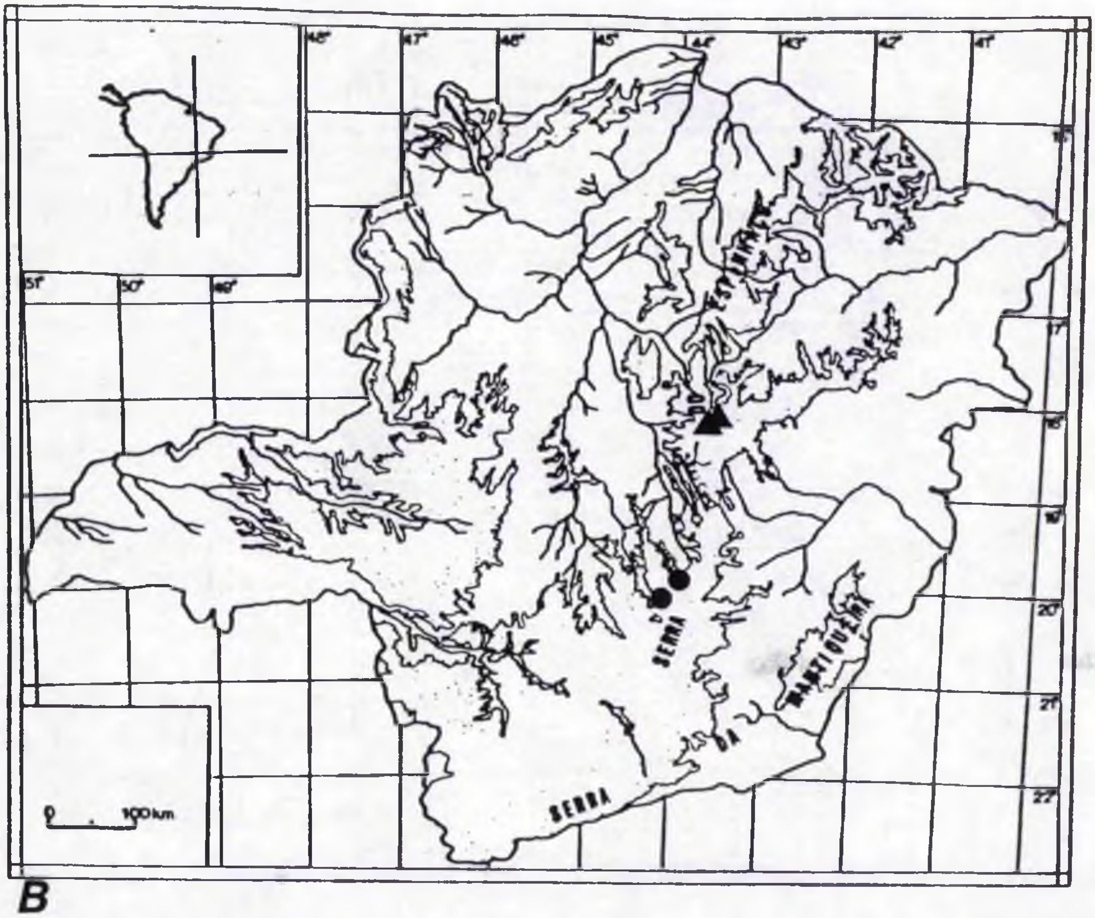
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B

Distribution (Figure 101 B)

Brazil

Southeast : state of Minas Gerais, Serra do Espinhaço : ca 15 km NE of Diamantina, road to Mendanha, elev. 1275 m, IRWIN *et al.* 22891, 30.i.1969 (K,NY); ibidem, "estrada Diamantina a Corinto até 10 km", SHEPHERD *et al.* 3866, 1.xii.1976 (UEC); state of Rio de Janeiro : "in locis ... montis altis Tijuca", RIEDEL 605, no date (K); ibidem, RIEDEL 1276, xii. 1827 (K,P).

Without precise locality : RIEDEL s/n, no date (FHO); WEDDELL 1831, viii. ? 1844 (P).

(5) . *Lupinus laevigatus* Bentham, *in* Martius
Fl. Bras. *15* (1) : 13, 1859

Shrubs erect, up to 1.0 m tall; stems braching, sericeous, hairs reddish-brown; internodes 5.0 - 7.0 mm. Stipules foliaceus, lanceolate (falcate-lanceolate, *fide* BENTHAM) and clasping the stem, subglabrous, withthe margins long-ciliate, 17.0 - 26.0 mm, the free tips lanceolate, acuminate, 7.0 - 12.0 x 3.0 - 6.0 mm, adnate/free length ratio 1.1-1.4. Leaves 37.0 - 60.0 x 16.0 - 26.0 mm, ovate-lanceolate to oblong-ovate, apex obtuse, mucronate, base cordate, glabrous and smooth ("laevigatus") to sparsely ciliate, mid- and secondary veins conspicuous on the adaxial face; petioles 6.0 - 8.0 mm. Peduncle 16.0 - 25.0 mm, erect, sericeous. Racemes 57-85 mm, flowers sub-opposite at the base but becoming alternate and lax towards the apex; bracts foliaceous, ovate-lanceolate to lanceolate, 6.0 -8.0 x 1.5 - 2.0 mm, caducous; pedicels 4.0 - 6.0 mm, sericeo-hirsute. Calyx sub-glabrous to

sparsely sericeous; lower lip oblong, tridentate, 6.0 - 9.0 x 1.5 - 3.0 mm, the median tooth 0.5 - 0.7 x 0.4 -0.5 mm, the two lateral teeth much shorter; upper lip oblong-lanceolate, 3.5 - 5.0 x 2.0 - 2.5 mm, bifid, the teeth 1.5 - 2.0 (-4.0) mm. Standard 9.0 - 12.0 mm, ovate-circular; wing petals oblong, slightly arcuate, 7.0 -8.0 x 3.5 - 4.5 mm, the claw 1.0 - 1.5 mm; keel petals lanceolate-acuminate, arcuate, 5.5 - 6.5 x 2.0 - 3.5 mm, the claw 1.5 - 2.0 mm. Ovules 3-4. Pods immature, 45.0 - 55.0 x 8.0 - 10.0 mm, densely sericeo-tomentose. Seeds not seen .
Figure 102.

Type - Brazil, state of Minas Gerais : without precise locality, CLAUSSEN 921, 1838 (P!, holotype).

L. laevigatus was regarded by BENTHAM (1859) as a species close to *L. velutinus* because of leaf and stipule morphology, but differing from it in the lack of pubescence in both of these organs. Indeed, this resemblance is remarkable but the subglabrous to sparsely ciliate leaves and the longer pedicels readily distinguish *L. laevigatus* from *L. velutinus*. BENTHAM (*loc. cit.*) also mentioned that the flowers of *L. laevigatus* were very similar to those of *L. decurrens* but, as this study has shown, floral morphology is of little taxonomic value within *Lupinus* due to its uniformity throghout the genus.

L. laevigatus has so far been found only in the state of Minas Gerais.

Distribution (Figure 101 B)

Brazil - state of Minas Gerais : município of Santa Luzia, Fazenda da Chicaca, alt. 1100 m, ASSIS 211, 13.xi..1945 (GH); município of

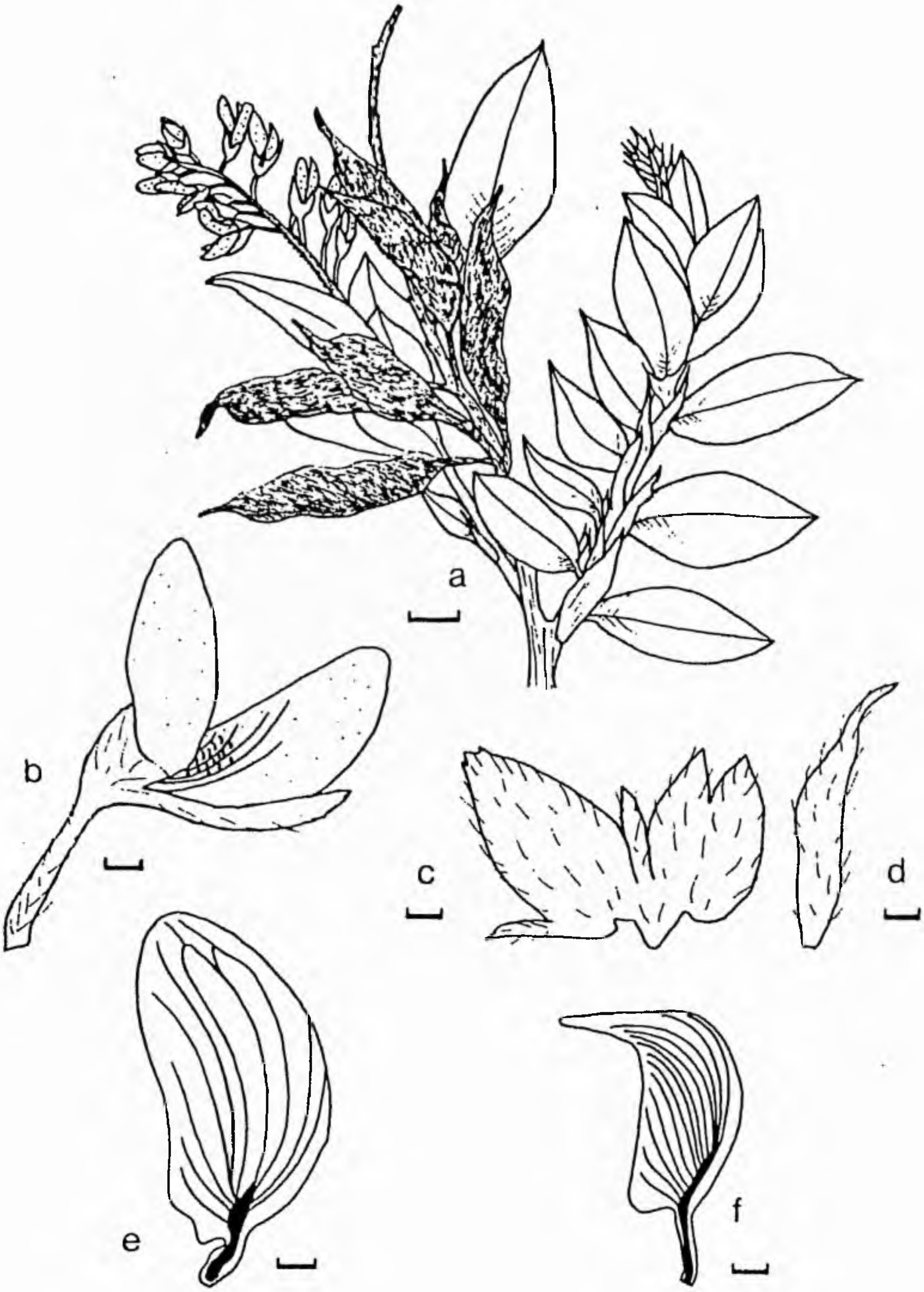


Figure 102 - Lupinus laevigatus Benth. a - habit (pods immature); b - flower; c - calyx, flattened out; d - bract; e - wing petal; f - keel petal (scale : a = 1 cm; the others = 1 mm).

Betim, Barreiros, slopes of Serra da Mutuca, alt. 1000-1200 m, WILLIAMS & ASSIS 7275, 3.vi.1945 (GH).

(6) . Lupinus coriaceus Bentham

ANN. NAT. HIST. 3 : 430, 1839

syn. : L. attenuatus Gardner

Hook. Ic. Pl. 2, t. 511, 1843. Sensu BENTHAM, Fl.
in Martius
Bras. 15 (1) : 14, 1859, pro majore parte; also sensu SMITH, Sp. Lup. : 486, 1945, pro majore parte

L. schwackeanus C. P. Smith

Sp. Lup. : 492, 1945

Herbs to subshrubs , erect, 0.10 - 0.30 m tall; stems hirsute to lanate; internodes (2.0-) 4.0 - 7.0 mm. Leaves (20.0-)35.0 - 45.0(-80.0) x (2.0-)3.0 - 8.0 (-10.0) mm, linear to oblong-linear or oblong , coriaceous, apex acute, short mucronate, base amplexicaul, glabrous and then the margins ciliate or sub-sericeous with much longer hairs at the margins, veins and veinlets prominent. Peduncles 12.0 - 27.0 (-35.0) mm, erect, hirsute. Racemes 50.0 - 60.0 (-80.0) mm; flowers lax; bracts lanceolate-acuminate, 2.0 x 1.5 mm, caducous; pedicels 2.5 - 5.0 mm, dense hirsute-sericeous. Calyx hirsute-sericeous to sericeo-villous; lower lip oblong to oblong-lanceolate, shortly trifid to deeply tridentate, the teeth subequal and then the median tooth ca. 1.0 x 0.2 mm, the two lateral shorter, or the teeth equal, all ca. 1.5 x 0.3 mm; upper lip oblong-lanceolate, (5.0–) 7.0 - 10.0 x 3.0 - 4.5 mm, bifid, the teeth 0.5 - 3.5 mm; bracteoles lanceolate, acuminate, (1.5–) 3.0 - 4.0 x 0.5 - 1.0 mm. Standard 8.0 - 13.0 mm, oval-ovate; wing petals oblong-ovate, apex straight, 8.0 - 13.0 x 4.5 - 6.0 mm, the claw 1.0 - 2.0 mm; keel petals lanceolate, strongly arcuate at the apex, 8.0 - 10.0 x 3.0 - 4.0 mm, the claw 2.0 - 2.5 mm. Ovules 3. Pods 35.0 - 40.0 x 8.0 mm, subglabrous to sparsely hirsute. Seeds subcircular, compressed, 3.0 x 2.5 mm. Figure 103.

Type - Brazil, state of Minas Gerais : "near Tejuco, and in Serra do Frio", VAUTHIER 141 and 142, 1833 (M, holotype, not seen; G!,GH!,P!, isotypes).

In the original description of *L. attenuatus*, GARDNER (1843) mentioned that this taxon was very close to *L. coriaceus* and that it was perhaps "only a villous variety" of the latter taxon. However, GARDNER (*loc. cit.*) who did not see the type of *L. coriaceus* was not able to compare these taxa in detail.

BENTHAM (1859) also maintained *L. attenuatus* Gardn. as a distinct species but not without reservations since he also considered that this species was perhaps a variety of *L. coriaceus* as GARDNER (1843) had previously observed. in his key, BENTHAM (*loc. cit.*) differentiated *L. attenuatus* from *L. coriaceus* as having oblong leaves. A detailed analysis of leaf shape in all specimens available for study has shown that *L. attenuatus* can certainly be included in *L. coriaceus*. Many specimens received on loan which were identified as *L. attenuatus* actually belong to *L.*

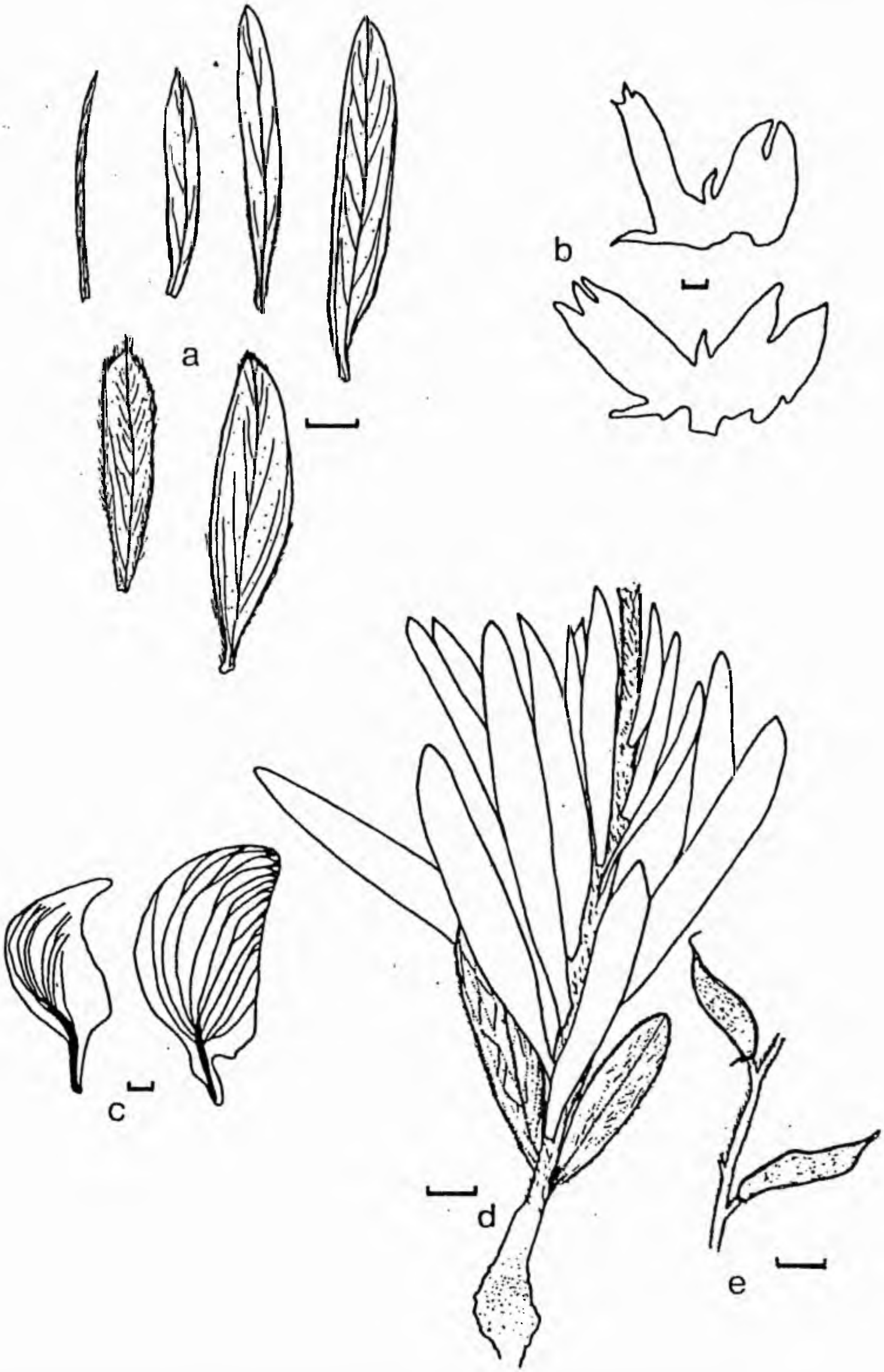


Figure 103 - Lupinus coriaceus Benth. a - leaf shape and pubescence variation; b - calyx outline variations; c - keel and wing petals; d - stem, showing insertion of sessile leaves (pubescence and venation omitted in the upper leaves); e - pods. (scale : a,d,e = 1 cm; b,c = 1 mm).

guaraniticus (Hassl.) Smith, a species that resembles L. coriaceus in the shape. However, the strigose to sericeo-tomentose leaves and the several-branched stems in the former taxon clearly distinguish it from L. coriaceus.

L. aliattenuatus C. P. Smith, a species which, according to SMITH (1945) is close to L. attenuatus could not be compared with L. coriaceus due to the lack of material available for study. It is treated as a dubious species in the present work.

SMITH (1945) recognised L. schwackeanus as distinct from L. coriaceus on the simple basis that the leaf shape in the former taxon is "suboblong-linear" whilst in the latter it is "linear". This contrast at specific level is here rejected and the suboblong leaves of "L. schwackeanus" are considered to be another variation within the expression of leaf shape found in L. coriaceus.

L. coriaceus is a species of common occurrence in the region of Serra do Espinhaço , particularly in the area of Serra do Cipó. It is reacognisable by the glabrous to subglabrous, thick, coriaceous, sessile, linear to linear-lanceolate leaves (Figure 103) with prominent veins and veinlets. The variation of leaf shape found in this species is probably caused by the effects of altitude and light, a phenomenon which is common to plants of high altitudes.

Distribution (Figure 101 A)

Brazil - state of Minas Gerais : Serra do Cipó, km 128, municipio of Santa Luzia, Palácio, BARRETO 5444, 2.ix.1933 (UB); ibidem, "km 139 da estrada do Pilar", município of Santa Luzia, BARRETO 5445, 24.viii.1933 (SP); ibidem, km 116, município of Santa Luzia, BARRETO 54549, 13.viii.1933 (SP); ibidem, km 132, alt. 1150 m, DUARTE 2059, 4.xii.1949 (UB); ibidem, Conceição do Mato Dentro, FERREIRA 1575 _et al._, 6.x.1980 (RB); Serra da Mendanha, GARDNER 4501 , vii.1840 (K, holotype of _L._ _attenuatus_ Gardn.); ibidem ; cerrado on outcrops with adjacent campo, ca. 10 km SW of Diamantina, alt. 1350 m, IRWIN _et al._ 22437, 22.i.1969 (UB); ibidem, município of Jaboticatubas, "km 140 ao longo da rodovia Lagoa Santa - Conceição do Mato Dentro - Diamantina", JOLY & MULLER s/n, 10.ix.1972 (UEC); "in campis graminosis subhumidis prope Cachoeira do Campo", RIEDEL 604, date ? (K); "Bandeirinhas", RIEDEL 1313, xii.1824 (K); no local. ment., SCHWACKE 11790, viii. 1825 (P, holotype of _L._ _schwackeanus_ C.P. Smith); município of Jaboticatubas, "km 127 da rodovia Lagoa Santa - Conceição do Mato Dentro - Diamantina", SEMIR, SAZIMA & CASSIA s/n, 23.vii.1972 (E,UEC); ibidem, ibidem, SEMIR, SAZIMA & KINOSHITA s/n, 7.ix.1974 (UEC); ibidem, "km 114", SEMIR, SAZIMA & KINOSHITA s/n, 8.ix.1974 (UEC).

(7) . *Lupinus guaraniticus* (Hassler) C.P. Smith
Sp. Lup. : 325, 1943.

syn. : *L. attenuatus* Gardn. var. *guaraniticus* Hassler
FEDDE, REPERT. 16 : 158, 1919.

L. succisaefolius Mart. ex C.P. Smith
Sp. Lup. : 493, 1945

Herbs, subshrubs or shrubs 0.3 - 0.7 m tall, stem several branched, sericeous; internodes 20.0 - 50.0 mm. Leaves 70.0. - 110.0 x 9.0 - 15.0 (-20.0), lanceolate-elliptic to lanceolate-oblong, membranaceous, the adaxial face minutely appressed strigose to sericeo-tomentose with venation inconspicuous, the abaxial face densely sericeous to sericeo-villous with the mid-vein conspicuous, the base attenuate with the blade expanding along the mid-vein down the node; petioles (2.0-) 5.0- 8.0 (-10.0) mm. Peduncle (25.0-) 30.0 - 60.0 (-70.0) mm erect, sericeous to hirsute-sericeous. Racemes 70.0 - 150.0 mm, flowers lax, bracts ovate-lanceolate, attenuate at the apex, early deciduous, sericeous, 3.0 - 6.0 x 2.5 - 3.5 mm; pedicels 2.0 - 3.2 mm, densely hirsute-sericeous. Calyx sericeo-tomentose; lower lip lanceolate, tridentate, 11.5 - 17.0 x 2.5 - 5.5 mm; the median tooth 1.0 - 1.5 x 07 - 1.0 mm, the two lateral teeth much shorter; upper lip oblong-lanceolate, 7.0 - 12.0 (-13.5) x 3.0 - 4.0 mm, bifid, the teeth 2.0 - 3.0 (-3.5) mm; bracteoles lanceolate, acuminate, 1.5 - 2.0 x 0.5 - 0.7 mm. Standard 12.0 - 16.0 mm, ovate to ovate-circular; wing petals oblong, straight to arcuate, 13.0 - 17.0 x 5.0 - 6.5 mm, the claw 1.0 - 1.5 mm; keel petals lanceolate, arcuate to strongly arcuate, 6.0 - 8.0 x 4.0 - 5.0 mm, acute at the tip. Ovules 5-8 (-9). Pods 50.0 - 65.0 (-70.0) x 10.0 - 12.0 mm, densely lanate-sericeaous. Seeds cylindric-reniform, slightly compressed, 5.5 - 6.5 x 4.0 mm, brown. Figure 104.

Type - Paraguay : in fields, Alto Paraná, FRIEBRIG 5681, no date (G!, holotype).

The name L. attenuatus var. guaraniticus was applied to plants formerly recognised as belonging to L. attenuatus but from which they differed by having larger, pubescent leaves and calyx (HASSLER, 1919). However, SMITH (1943) elevated this variety to specific rank and this taxonomic decision is accepted here.

The holotype of L. succisaefolius Mart. ex Smith. (the epithet originally a nomen nudum on a herbarium specimen), is also a typical specimen of L. guaraniticus that was formerly identified by BENTHAM (1859) as L. attenuatus. Therefore, it also must be treated as a synonym of L. guaraniticus.

This species occurs in "cerrado" and "campo rupestre" areas of east-central Brazil, extending to grassy areas of slopes of Paraguay and Argentina. In the latter regions the plants have a much more branched caudex which bears several stems.

Distribution (Figure 105)

Brazil

South - state of Paraná : município of Castro, Carambei, HATSCHBACH 35482, 14.x.1974 (UEC); state of Rio Grande do Sul :

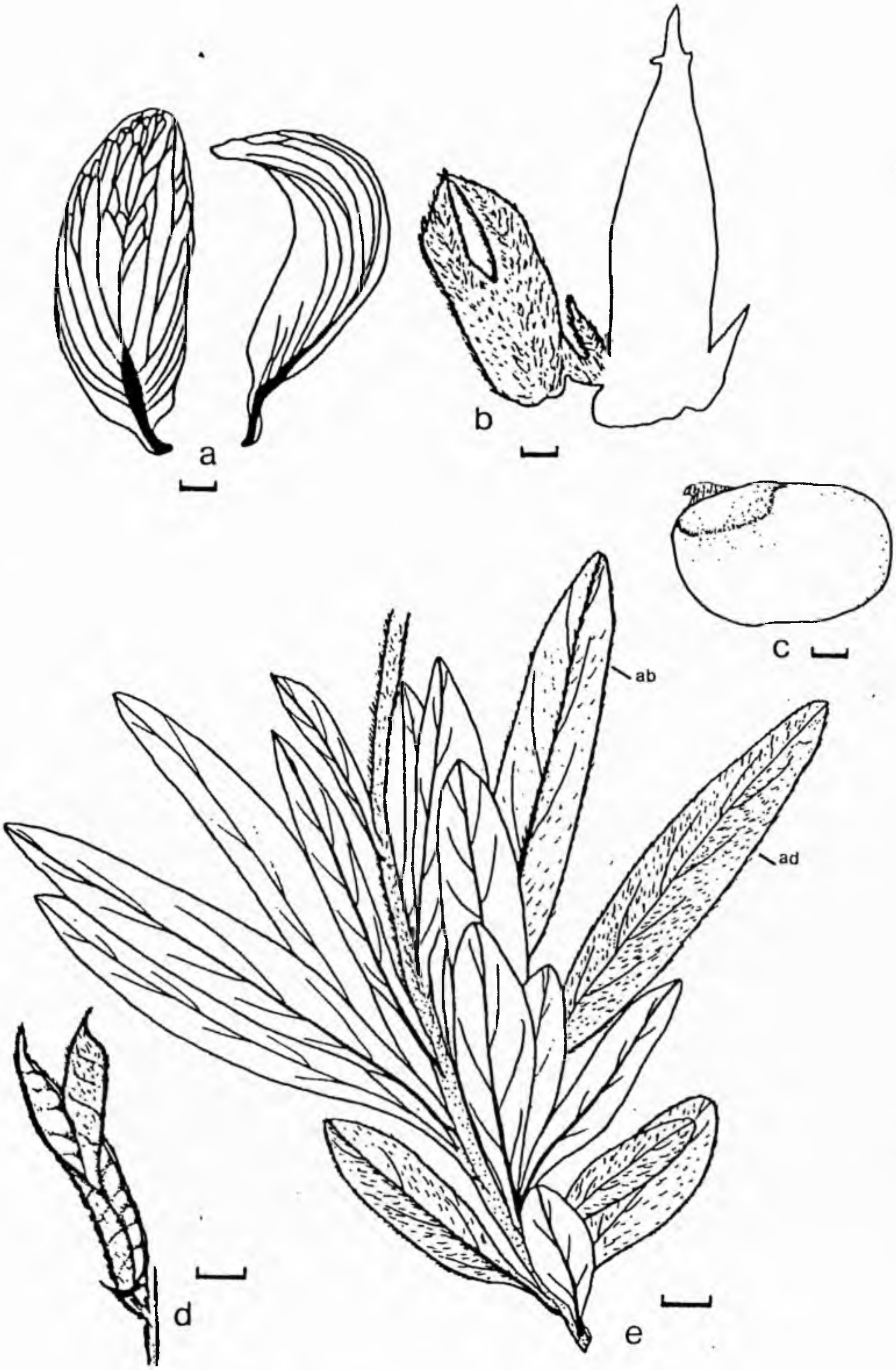


Figure 104 - <u>Lupinus guaraniticus</u> (Hassler) C.P. Smith. a - wing and keel petals; b - calyx, flattened out (pubescence omitted in the lower lip); c - seed; d - pod, open; e - habit, raceme excluded (pubescence showed on adaxial (ad) and abaxial (ab) faces).

(scale : a,b,c = 1 mm; d,e = 1 cm).

Figure 105 - Distribution map of unifoliolate species of Lupinus in Brazil.

● L. guaraniticus

△ L. arenarius

○ L. crotalarioides

▼ L. sellowianus

município of Santo Ângelo, São João Velho, PEDERSEN 11949, 8.xi.1977 (A).

Southeast - state of Minas Gerais : "campis altis ad Pires et Villa Rica", MARTIUS s/n, no date (M°, holotype of L. succisaefolius Mart. ex Smith); state of São Paulo : Jaraguaiba, WEIR 360, 1861-2 (BM,K); Morungava, "prope Itararé, campo cerrado", DUSEN 17399, 5.xii.1915 (G).

(8) . Lupinus sellowianus Harms
FEDDE, REPERT. 18 : 5, 1921

Herbs, erect, up to 0.4 m tall, stems sparsely lanate, hairs very long and whitish; internodes very short at the base of the stem but 15.0 -35.0 mm long at the upper portions. Stipules foliaceous, lanceolate, acuminate, 24.0 - 48.0 mm; the free tips subulate; the base attenuate, 15-25 mm; adnate/free length ratio 0.9 - 1.9. Leaves 90.0 - 150.0 x 12.0 - 20.0 mm, oblong-lanceolate to lanceolate, with the apex acute, short-mucronate, lanate on both faces; petioles 20.0 - 65.0 mm. Peduncle 24.0 - 65.0 mm, lanate. Racemes 100.0 - 230.0 mm, flowers suverticillate or more often lax; bracts lanceolate, with attenuate tips, 7.5 - 12.0 x 2.0 - 2.9 mm, deciduous; pedicels 1.5 - 2.0 mm, densely lanate. Calyx densely lanate; lower lip lanceolate, tridentate, 8.0 - 10.0 x 3.5 - 5.0 mm, the teeth subequal, 1.5 - 3.0 x 1.0 - 1.5 mm; upper lip oblong-lanceolate, 5.0 - 8.0 x 3.5 4.5 mm, bifid, the teeth 2.5 -5.0 mm. Standard 10.0 - 15.0 ovate to oval; wing petals narrowly oblong, the apex pointed, straight, 9.5 - 12.0 x 3.0 - 5.0 mm, the claw 1.5 - 2.0 mm; keel petals lanceolate-oblonge, shortly arcuate, 7.0 - 8.5 x 3.0 - 4.0 mm, the claw 2.0 - 2.5 mm. Ovules 4-5. Pods dense lanate, 40.0 - 50.0 x 10.0 - 13.0 mm. Seeds reniform-cylindric,slightly compressed, 5.0 x 3.5 mm. Figure 106.

Syntypes : Brazil : without precise locality, SELLOW 4866 (B, probably lost, not seen); state of Paraná : Vila Velha, "in campo arenoso", DUSÉN 7261, 26.ii.1908 (photo of isosyntype at B : G!, TEX!).

HARMS (1921) did not designate a holotype for L. sellowianus but instead he only cited SELLOW 4866 and DUSÉN 7261 which are, then, syntypes for this taxon. The specimen SELLOW is probably no longer extant and, so far, all the attempts to locate an exsicata of DUSÉN 7261 have been unsuccessful.

The shapes of leaves and stipules of L. sellowianus are very close to the North American unifoliolate L. villosus Willd. It is possible that in bearing such resemblances, L. sellowianus could have provided the "single, recent source " of lupins introduced in North America through long-distance dispersal (DUNN, 1971). Such an introduction was subsequently followed by speciation process that originated the closely related assemblage of unifoliolate species of Lupinus in that area.

Interestingly, the pubescence of L. sellowianus is very similar to the South American multifoliolate species L. lanatus and L. multiflorus

Distribution (Figure 105)

Brazil

South - state of Paraná : Jaraguaiva, DUSÉN 10548, 26.x.1910 (G).

Figure 106 - Lupinus sellowianus Harms. a - habit (pubescence shown in one leaf); b - calyx and bract; c - wing petal; d - keel petal; e - pod (scale : a,e = 1 cm; the others = 1 mm).

Southeast - state of Minas Gerais : Poços de Caldas, Campo do Saco, GABRIELLI et al. 314, 16.x.1980 (UEC); ibidem, ibidem, STUBBLEBINE et al. 591, 2.xii.1980 (UEC); no local. ment., St HILAIRE 1551, date ? (P); state of São Paulo : São José dos Campos. LOEFGREN 319, 5.ix.1909 (RB); without precise locality, WEIR 361, 1861-2 (K).

(9) . Lupinus crotalarioides Mart. ex Benth. , in Martius
Fl. Bras. 15 (1) : 11, 1859

Herbs, erect, up to 0.5 m tall; stems branching, woody, hispid, hairs transparent; internodes (8.0-) 12.0 - 25.0 (-32.0) mm. Stipules foliaceous, lanceolate to triangular, hispid, (20.0-) 35.0 - 45.0 mm, the free tips linear-lanceolate spreading outwards, 8.0 - 15.0 mm, adnate/free length ratio 0.8 - 3.4. Leaves 40.0 - 100.0 x 24.0 - 35.0 mm, oval to ovate-lanceolate, with the apex obtuse, mucronate, base truncate, sericeous to sericeo-villous; petioles 15.0 - 30.0 mm. Peduncle 20.0 - 45.0 , hispid. Racemes 100.0 - 195.0 mm, flowers lax to congested, bracts subulate, 5.0 - 6.0 x 1.5 - 2.5 mm, tardily caducous; pedicels 3.0 - 4.0 mm, hispid. Calyx hispid-sericeous; lower lip lanceolate, tridentate, 6.5 - 8.0 x 2.3 - 4.0 mm, the median tooth 0.8 - 1.9 x 02. - 03 mm, the two lateral teeth shorter; upper lip oblong-lanceolate, 5.0 - 6.5 x 2.3 - 3.2 mm, bifid, the teeth 0.6 - 2.0 mm. Standard 9.0 - 12.0 mm, oval,; wing petals oblong, apex straight to slightly arcuate, 10.0 - 13.0 x 4.5 - 5.0 mm, the claw 1.3 - 1.8 mm; keel petals lanceolate-acuminate, arcuate, 6.0 - 7.8 x 2.5 - 3.0 mm, the claw 1.8 - 2.4 mm. Ovules (3-) 4-5. Pods 45.0

- 55.0 x 9.0 - 13.0 mm. Seeds cylindric-reniform, compressed, 4.0 - 5.0 x 3.0 - 3.5 mm.

Figure 107.

Type - Brazil, state of Bahia : "campis ad Sincora, in editis apricis, Bahiensis mediterran", MARTIUS 1987, date ? (M!, holotype; E!,GH!,NY!,TEX!, phototypes).

Distribution (Figure 105)

Brazil

Southeast - state of Minas gerais : Lavras, DORSETT, SHAMEL & POPENOE 197B, 19.i.1914 (GH); Belo Horizonte, B. Preto, GEHRT 172, 16.iv.1919 (SP); Morro das Pedras, ca. 50 Km NE of Patrocínio, elev. 1000m, IRWIN *et al.* 25708, 29.i.1970 (K); no local. ment., St HILAIRE 553, 1816 - 21 (P); Lagoa Santa, WARMING s/n, no date (GH,P); ibidem, WARMING 2876, no date (G); Serra da Mutuca, about 8 km beeyond Lagoa Seca, municipio of Belo Horizonte, alt. 1100 m, WILLIAMS & ASSIS 6265, 25.iii.1945 (GH).

West Central - Federal District ; cemitério do Plano Piloto, BELEM 1944, 10.xii.1965 (UB); Brasília, Horto do Guará, HERINGER 7852, 7.i.1961 (UB); Parque Nacional do Gama, HERINGER 10796, 20.ix.1965 (UB); Brasília, "em frente ao BGP", HERINGER 10985 , 4.ii.1966 (UB); Cidade Satélite do Gama, HERINGER 15516, 5.v.1976 (NY,UB,UEC); ca. 1 km W of Sobradinho, elev. 1100 m, IRWIN, SOUZA & SANTOS 11065, 5.xii.1965 (GH,UB); cerrado, Chapada da Contagem, ca. 10 km E of Brasília, elev. 1000 m, IRWIN, SOUZA & SANTOS 11354, 17.xii.1965 (GH,UB); Brasília, LIMA 58-2975, 1.iv.1958 (K); Granja Rui Malta, córrego Sobradinho, PIRES, SILVA & SOUZA 9463, 26.iv.1963 (UB);

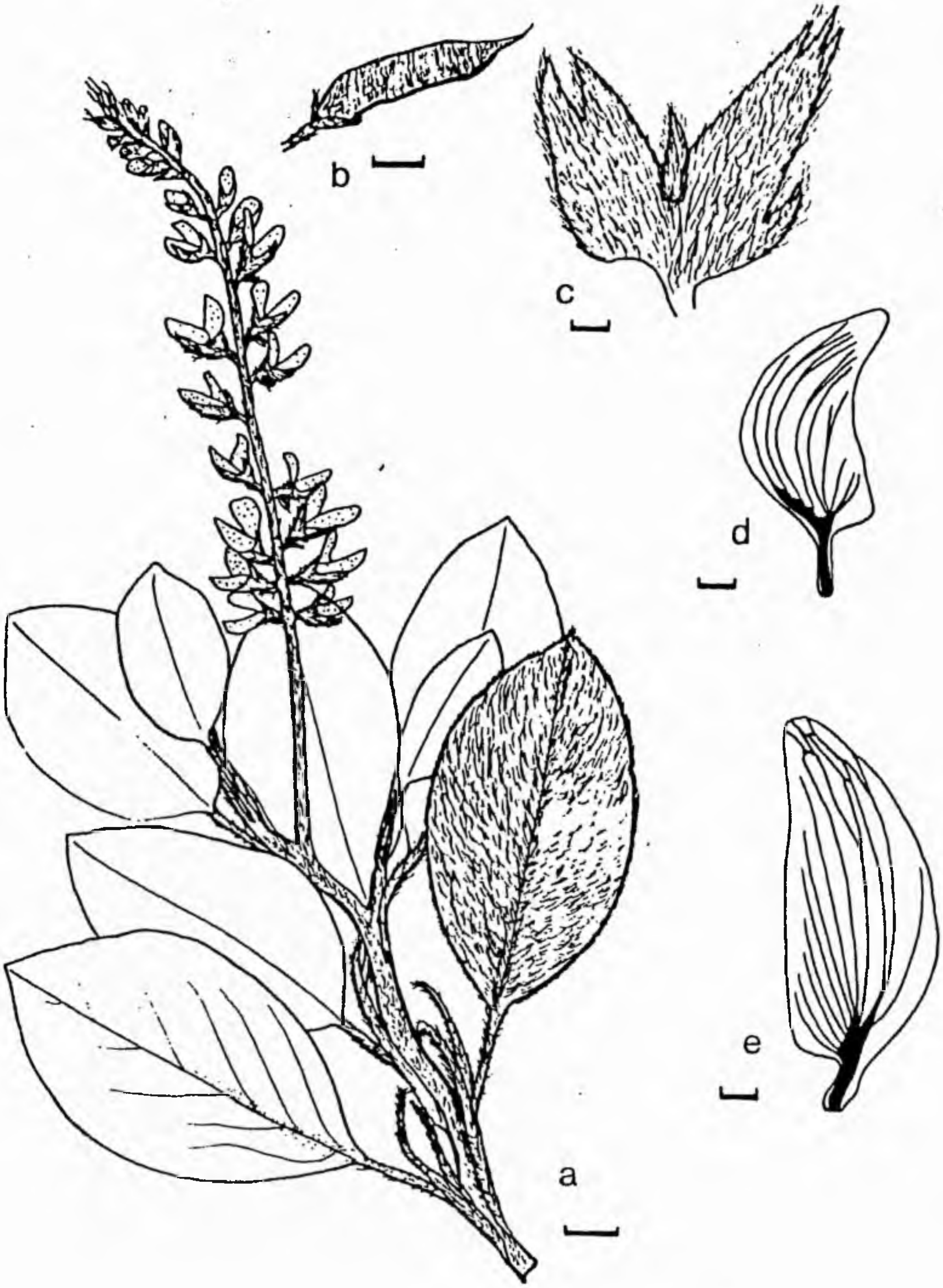


Figure 107 - <u>Lupinus crotalarioides</u> Mart. ex Benth. a - habit (pubescence and venation omitted in all but two basal leaves); b - pod; c - calyx, flattened out; d - keel petal; e - wing petal (scale : a,b = 1 cm; the others = 1 mm).

state of Goias : no local. ment., BURCHELL 736 A, no date (K); Chapada dos Veadeiros, 1 km W of Veadeiros, IRWINN et al. 12749; 13.ii.1966 (K,UB).

(10) . Lupinus arenarius Gardner
Hook. Ic. Pl. 2, t. 511, 1843

syn. : L. chrysomelas Casar.
Nov. Stirp. Bras. Dec. 6 : 52, 1843

L. vaginans Benth., in Martius
Fl. Bras. 15 (1) : 12, 1859

L. luetzelburgianus C.P. Smith
Sp. Lup. : 490, 1945

Herbs or shrubs, erect, 0.5-1.8 m tall; stems several branched, sericeo-villous; internodes 7.0 - 13.0 (-17.0) mm. Stipules clasping the stem, densely sericeous, 13.0 - 20.0 (-23.0) mm; the free tips lanceolate to deltoid, (1.2-) 3.0 - 5.0 (-8.0) x 1.0 - 2.0 mm, adnate/free length ratio 1.3-3.5. Leaves (40.0-) 55.0 - 85.0 (-90.0) x (20.0-) 25.0 - 35.0 mm, elliptic to oblong-elliptic or more often oblong-ovate, acute at the apex, short-mucronate, base cordate, sericeo-villous to villous-tomentose on both faces, veins conspicuous; petioles 8.0 - 13.0 (-18.0) mm. Peduncle 19.0- 47.0 (-53.0) mm. erect, sericeo-tomentose-villous. Racemes 95.0 - 180.0 (195.0) mm, flowers lax to congested; bracts lanceolate, 4.0 - 6.0 mm, sericeeo-villous, promptly caducous; pedicels conspicuously short, up to 3.0 mm long, sericeous. Calyx densely sericeous to sericeo-tomentose or sericeo-villous; lower lip oblong to oblong-lanceolate, tridentate, 7.0 - 9.0 (-12.0) mm, the median tooth 1.0 - 2.0 x 0.3 - 0.6 mm, the two lateral teeth half as long and wide; upper lip oblong-lanceolate, 7.0 - 9.0 x 3.0 - 4.0 mm. bifid, the teeth 0.5 - 4.0 mm; bracteoles lanceolate, 1.0 - 1.5 x 0.2 - 0.4 mm. Standard 12.0 - 18.0 mm, ovate-circular; wing petals oblong-ovate , 12.0 - 14.0 - 5.0 - 7.0 mm, apex straight, the claw 1.5 - 2.0 mm; keel petals lanceolate arcuate, 11.0 - 13.0 x 3.0 - 4.5 mm, the claw 1.5 - 2.5 mm. Ovules 5 - 7 (-8). Pods 45.0 - 60.0 x 15.0 - 18.0 mm, densely sericeo-villous. Seeds subcircular, compressed, 4.5 - 5.5 x 3.5 - 4.0 mm. Figure 108.

Type - Brazil, state of Minas Gerais : Diamantina, "in elevated sandy campos; on a mountain tract to the north of the Diamond District" (*fide* GARDNER, 1843), GARDNER 4500, vii.1840 (K!,holotype; BM!,E!,G!,P!, TCD!, isotypes; G!,TEX, photo of isotype at B).

L.arenarius pre-dates *L. chrysomelas* Casar. by three months; the former was published in January 1843 and the latter in April of the same year so that priority must be given to GARDNER's binomial.

This species and its allied taxa, which are now included as synonyms, have been the cause of confusing taxonomic interpretations of the limits of some unifoliolate, stipulate lupins of Brazil. GARDNER (1843) originally described *L. arenarius* as exstipulate (although his illustration of this species and also the types show plants distinctly stipulate and with oblong-elliptic leaves obtuse both at apex and base. The same

Figure 108 - Lupinus arenarius Gardn. a - habit (pubescence shown in one leaf and parts of the raceme); b - pod; c - wing petal; d - keel petal; e - calyx, flattened out (pubescence shown on the upper lip only) (scale : a,b = 1 cm; the others = 1 mm).

author (GARDNER, *loc. cit.*) also regarded *L. arenarius* as being close to *L. velutinus* from which it differed in the shape of leaves (oblong-ellitic, acute at the apex and with an obtuse base in the latter, according to BENTHAM, 1839), absence of stipules and also by the lower lip of the calyx being trifid (this, in *L. velutinus* was mentioned by BENTHAM as "subintegrous").

CASARETTO (1843), to whom the description of *L. arenarius* might not have been available, described *L. chrysomelas* as ovate to ovate-oblong leaves with conspicuous, petiole-adnate stipules.

BENTHAM (1859), in his treatment of *Lupinus* in "Flora Brasiliensis" did not mention *L. chrysomelas* Casar. but correctly recognised *L. arenarius* as having (short)stipulate, ovate, acute leaves but still considered this species close to *L. velutinus* (long stipulate, ovate-oblong leaves), as GARDNER (1843) had previously suggested. However, BENTHAM ((*loc. cit.*) also described a new species with the same characteristics as *L. arenarius* but under the name of *L. vaginans*; the former was said to have "short petioles, whilst the latter had a "dilatate petiole". In the course of the present study, these differences were found to be scarcely tenable and do not warrant segregate taxa. *L. chrysomelas* and *L. vaginans* have accordingly been treated as synonyms of *L. arenarius*.

Nevertheless, the variations among exsiccata examined certainly make *L. arenarius* distinct from *L. velutinus* on the basis of the stipule features such as length of the free tips and degree of adnation to the petiole.

L. luetzelburgianus is yet another of the many species created by SMITH in the course of publication of "Species Lupinorum". The type of this taxon was formerly identified by HARMS as *L. vaginans* and it was found that the measurements given by SMITH (1945) present an enormous difference with those actually shown by this specimen.

L. arenarius often occcurs in cerrado and campo rupestre areas of east-central and western regions of Brazil.

Distribution (Figure 105)

Brazil

Northeast - state of Bahia : estrada Ituaçu-Barra da Estiva, 8 km from Barra da Estiva, Morro do Ouro, campo rupestre, GIULLIETTI *et al*. SPF 18199, 19.iii.1981 (K,STA); Itubira, LUETZELBURG 213, vii.1913 (M!, holotype of *L. luetzelburgianus* C.P. Smith). *Southeast* - state of Minas Gerais : município de Belo Horizonte, Serra do Taquaril, BARRETO 5450, 18.i.1933 (SP); ibidem, ibidem, BARRETO 5451, 24.ii.1933 (SP); ibidem, ibidem, BARRETO 5453, 21.iii.1933 (SP); ibidem, ibidem 5454, 21.vii.1933 (SP); Serra do Curral, BARRETO 5622, 4.i.1934 (SP; ibidem, Serra da Mutuca, BARRETO 10848, 28.vii.1980 (UB), CASARETO 2902, iv.1852 (G, holotype of *L. chrysomelas* Casar., also phototype, TEX); ibidem, CLAUSSEN 80, vi.1839 (G); "in Prov. Minarum campis Caxoeiras do Campo"(*fide* BENTHAM), CLAUSSEN s/n, no date , MART. HERB. FL. BRASIL NO. 1139 - type of *L. vaginans* Benth.,K, holotype; BM,G,M,P, isotypes; photo of isotype at B : G,NY,TEX); without precise locality, CLAUSSEN 917, 1838 (P); IBIDEM, CLAUSSEN 1769, 1841 (P); ibidem, CLAUSSEN 2217, 1840 (BM); ibidem, CLAUSSEN s/n, 1840 (K); município of Belo Horizonte, Morro Velho, GEHRT 18, 15.xii, 1918 (SP); ibidem, ibidem, GEHRT 3252, 15.xii.1918 (BM);

Morro das Pedras, ca. 26 Km NE of Patrocínio, IRWIN *et al*. 25567, 29.i.1970 (K); "in saxosis Serra do Caraça", RIEDEL 603, date ? (K - syntype of *L. vaginans*); ibidem. RIEDEL 1481, ii, 1825 (BM,K,P,W); Belo Horizonte : Lagoa Seca, SCHWACKE s/n, 6.ii.1900 (SP); no local ment., SELLOW s/n, no date (K); município of Nova Lima, Serra da Mutuca, WILLIAMS 5075 , ii.1945 (GH); state of Rio de Janerio : "entre Macieira e Agulhas Negras", alt. 2000-2500 m, BOCKERMANN 39, ?iii.1951 (SP); ibidem, Campo Feio, GLAZIOU 4787, 24.i.1873 (P); ibidem, alt. 2000-2300 m, SMITH 1730, 17.i.1929 (GH); ibidem, TAMANDARE & BRADE 6404, 4.vi.1913 (SP); state of São Paulo : Serra da Bocaina, Morro da Boa Vista, alt. 1800 m , BRADE 20725, 26.iv.1951 (RB); ibidem, GLAZIOU S/N, 8.iv.1879 (G,P); ibidem, alt. 1650, HOEHENE 6153, 20.x.1966 (SP).

West Central - state of Goiás : Serra dos Cristais, 17°´S, 48°W, rocky hillside, ca. 3 3km E of Cristalina, elev. 1250 m, IRWIN *et al*. 13471, 4.iii.1966 (UB).

Without precise locality - "MGF et APP, 10429, 2.xii.1952 (RB).

(11) . Lupinus velutinus Bentham

ANN. NAT. HIST. 3 : 430, 1839

syn. : L. nitidissimus Bunb.
PROC. LINN. SOC. 1 : 109, 1841

L. glaziouanus C.P. Smith
Sp. Lup. : 488, 1945

Subshrubs or shrubs, erect, 0.4 - 2.0 m tall; stems appressed-lanate to villous-lanate; internodes (10.0-) 20.0 - 35.0 (-40.0) mm. Stipules lanate to villous, 13.0 - 23.0 mm, the free tips lanceolate, 8.0 - 13.0 x 3.0 - 4.5 mm, adnate/free length ratio 1.5 - 2.6. Leaves 60.0 - 120.0 x 25.0 - 70.0 mm; petioles 12.0 - 14.0 mm. Peduncle 15.0 - 60.0 mm, erect, densely-villous. Racemes 165.0 - 350.0 mm, flowers usually lax but sometimes subverticillate and congested; bracts lanceolate-triangular, with acuminate tips, 6.0 - 18.0 mm, sericeo-villous, tardily caducous; pedicels sericeo-villous, 2.0 - 5.0 mm. Calyx densely villous; lower lip lanceolate, 10.0 - 16.0 mm, the median tooth 0.3 - 0.6 x 0.5 - 0.8 mm, the two lateral teeth shorter; upper lip oblong-lanceolate, 6.5 - 9.0 x 3.0 - 4.5 mm, bifid, the teeth 1.2 - 3.5 mm; bracteoles lanceolate, 2.5 - 3.5 x 1.0 - 1.3 mm. Standard 12.0 - 15.0 mm, ovate-circular; wing petals oblong-ovate, 10.0 - 15.0 x 3.8 - 6.5 mm, the claw 0.9 - 2.3 mm; keel petals lanceolate, arcuate, 10.0 - 12.5 x 3.8 - 4.5 mm, the claw 2.0 - 2.5 mm. Ovules 4 - 6. Pods 35.0 - 50.0 x 8.0 x 10.0 mm, densely villous. Seeds subcircular, 6.5 - 7.0 x 3.6 - 5.0 mm. Figure 109.

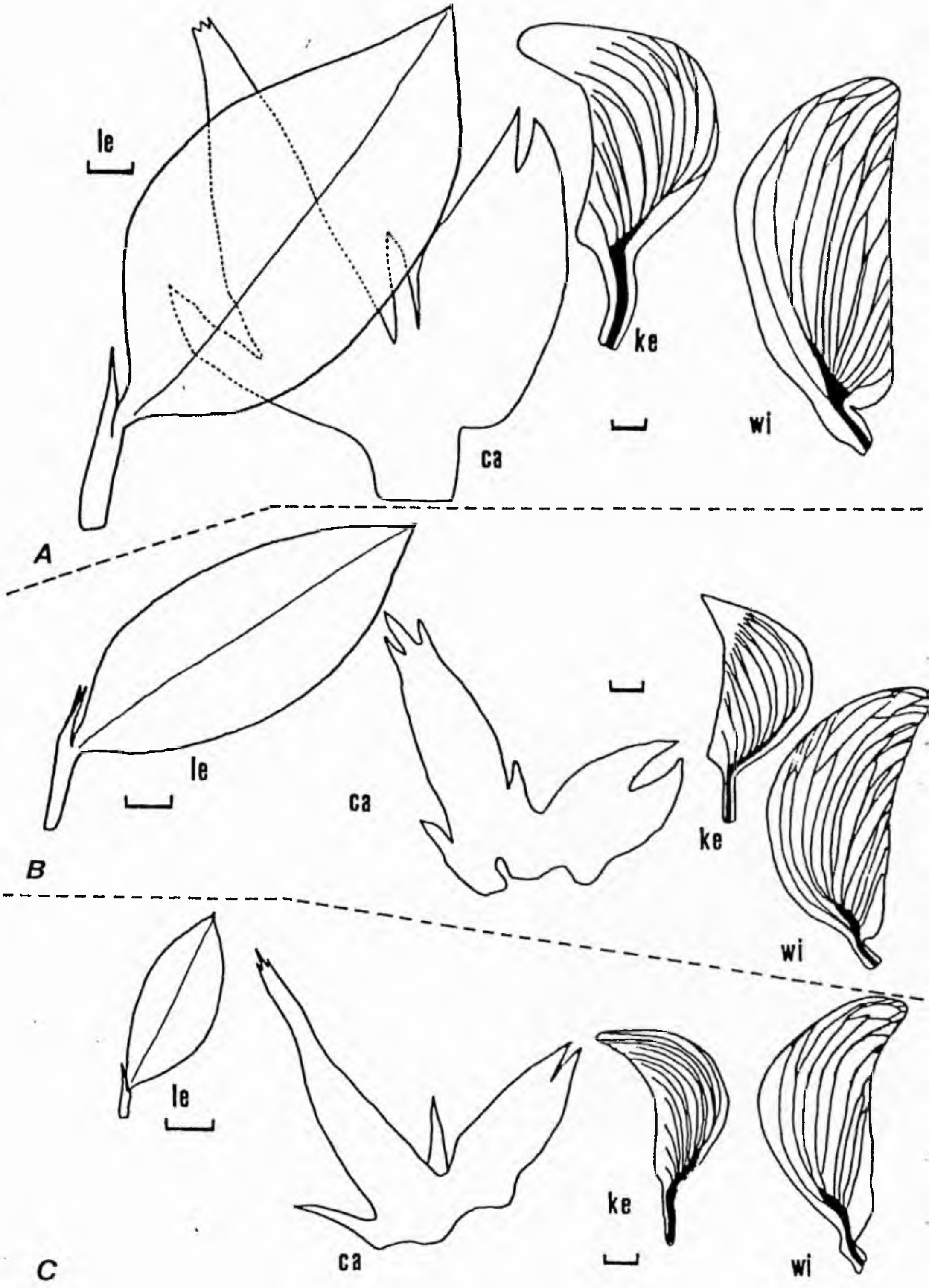


Figure 109 - Leaf (le) and calyx (ca) outlines and keel (ke) and wing (wi) petals of : A - L. insignis; B - L. velutinus and C - L. subsessilis (scale : 1 cm; the others = 1 mm).

Type - Brazil : "on the Rio São Francisco", POHL s/n, no date (K ? holotype, not traced).

In the original description of _L._ _velutinus_ BENTHAM (1839) cited POHL ("on the Rio São Francisco") as the only specimen studied by him, so that this material should be regarded the holotype of that species. Unfortunately, this specimen has not been traced for this study.

However, BENTHAM (1859), in his account of _Lupinus_ for "Flora Brasiliensis", included with some reservations the species _Crotalaria_ _coerulea_ Vell. as a possible synonym of _L._ _velutinus_, a situation that could invalidate the latter taxon since VELLOZO's species was published earlier in 1825. Type specimens for VELLOZO's "Flora Fluminensis" have never been traced, and it is therefore necessary to rely on the descriptions and illustrations in this work.

The interpretation of the illustration published by VELLOZO (1825), here reproduced in Figure 110, shows that the habit of the plant does indeed resemble that of a lupin, although in the description, VELLOZO (_loc._ _cit._) mentions that only the abaxial face of the leaves is tomentose. No such pattern of vestiture distribution has yet been found in a unifoliolate _Lupinus_ species. The details of the dissected flower in VELLOZO's illustration do not clearly depict a typical _Lupinus_ structure for this organ. The stamens are shown to be of the same length, and the anthers monomorphic, both features not present in _Lupinus_ but usually in _Crotalaria_ (HUTCHINSON, 1964). The calyx is not shown to be clearly 'bifid' in the upper lip or 'tridentate' in the lower lip;

Figure 110 - Illustration of Crotallaria caerulea Vellozo in "Flora Fluminensis", Vol. 7, plate 107. Photograph donated by the Library of the Royal Botanic Gardens, Kew. (ca. 80 reduction).

but rather with somewhat entire, separate lips. In all, therefore, the general pattern of VELLOZO's illustration has very little in common with *L. velutinus* and could well represent a species of *Crotalaria* or closely-related genus. Thus, there seem to be no good grounds for rejecting *L. velutinus* Benth. in favour of the VELLOZO's (1825) epithet.

The features of stipules partially adanate with the petioles with lanceolate free tips *and* leaves ovate- to oblong-lanceolate with the base attenuate, clearly isolate a group of three species which resemble each other in the above characters but which can be separated in other respects. These taxa are *L. velutinus*, *L. subsessilis* and *L. insignis* and together they form a group which is virtually endemic to the central core of 'cerrados' area in Brazil (state of Goias), the only exception being *L. velutinus* which extends from this area E into Bahia and SE into Minas Gerais and São Paulo (Figure 109).

A survey of the variation presented by these three taxa gives a distinct pattern in which the smallest values are presented in *L. subsessilis* whilst the largest ones are found in plants of *L. insignis* (Figure 109). The mean values, however, are most common to specimens of *L. velutinus*. In other words, the largest leaves and stipules are present in *L. insignis*, the smallest in *L. subsessilis* and the intermediate in *L. velutinus* (Figure 109). In parallel the leaf vestiture also shows a pattern which is reflected in the density of hairs increasing from the smallest to the largest leaved taxon, i.e., *L. subsessilis* is distinctly sericeous, *L. velutinus* sericeo-villous and *L. insignis* denselly appressed villous-sericeous.

The above features and also the apparent endemism shown by these taxa seem to indicate that this trio of related species have undergone secondary evolution in the cerrado area, otuwith the (original ?) campo rupestre habitat. Clearly, cytological studies, which might reveal further insights into the relationships of these taxa, are urgently needed for the unifoliolate lupins in Brazil.

L. amabayensis C.P. Smith, formerly *L. velutinus* var. *spectabilis* Hassler, a species from Paraguay, is very close to *L. velutinus*. However, it has distinct soft tangled hairs on both faces of the leaves which promptly distinguishes it from the sericeo-villous leaves of *L. velutinus*.

Distribution (Figure 111)

Brazil

Northeast - state of Bahia : Morro do Chapéu, DUARTE 9197 & PEREIRA 10107, 26.ix.1965 (RB).

Southeast - state of Minas Gerais : among brushwood on the mountains between Capão and Villa Rica, BUNBURY s/n, vi.1834 (CGE, holotype of *L. nitidissimus* Bunb.); "in campis Minas", RIEDEL 616, xi.1834 (NY,TEX, photos); state of Rio de Janeiro : Itatiaia, Campo Feio, GLAZIOU 4787, iii.1872 (P); no local. ment., GLAZIOU 6507, ii.1874 (K,P); Itatiaia, "nos campos", GLAZIOU 8643^{a}, 24.xi.1876 (P); no local. ment., St HILAIRE 345, date ? (P).

West Central - Federal District : município of Planaltina, near São Gabriel de Goias, on highway GO-12, elev. ca. 1200 m, ANDERSON 11437, 19.ii.1975 (NY); Brasília, Fazenda Água Limpa, CESAR 47, 22.i.1980 (UB); ibidem, CESAR 359, 4.iii.1980 (E); ibidem, between University and Lake, CLAYTON 4923, 3.iii.1965 (NY,UB); ibidem, "area do Zoobotânico", DUARTE 10123, 10.i.1967 (RB); without precise locality, FONSECA 849, 3.vii.1968 (UB); Brasília, AsaNorte, HANDRO 115, 15.i.1965 (SP); ibidem, HERINGER 6754, 21.iii.1959 (UB); ibidem, Horto do Guará, HERINGER 7875, 25.i.1961 (SP,UB); ibidem, ibidem, HERINGER 8847, 15.i.1962 (UB); ibidem, Chapada da Contagem, HERINGER 12771, 4.iii.1973 (UB); ibidem, Parque do Guará, Plano Piloto, HERINGER 13888, 22.vi.1974 (UB); ibidem, west margin of Lago Paranoá, elev. 975 m, IORWIN *et al.* 13890, 11.iii.1966 (NY,UB); ca. 15 km E of Sobradinho, elev. 1115 m, IRWIN, SOUZA & SANTOS 9029, 7.xi.1965 (UB); summit of Chapada da Contagem, elev. 1100 m, IRWIN, SOUZA & SANTOS 11639, 14.i.1966 (NY,UB); 2 km E of Lago Paranoá, IRWIN *et al.* 26633, 26.i.1970 (NY); gallery forest, ca. 10 km E of Lago Paranoá, near DF-6, elev. ca. 1000 m, IRWIN *et al* 26545, 23.ii.1970 (NY); Brasília, Fazenda Água Limpa, OLIVEIRA s/n, v.1980 (UB); ibidem, Catetinho, cerrado, PEREIRA 9018, 20.iii.1964 (NY,RB); ibidem, Parque Nacional de Brasília, PHILCOX & ONISHI 4313, 13.ii.1968 (E,P); ibidem, campo cerrado between University of Brasília and Lake Paranoá, alt. ca. 1050 m, PHILCOX & ONISHI 4863, 2.v.1968 (K,NY,UB); ibidem, Catetinho, PIRES, SILVA & SOUZA 9038, 12.iv.1963 (UB); ibidem, Fazenda Água Limpa, near Vargem Bonita, ca. 18 km SSW of Brasília TV tower, RATTER & FONSECA 2819, 24.iii.1976 (E,K,UEC); state of Goiás : "entre as Brancas et Cocal", GLAZIOU 20930, 25.i.1895 (G,P, isotypes of *L. glaziouanus* C. Smith); Chico Costa, GLAZIOU 20932, 1896 (G,K,P); 63 km W of Rio Verde on road to Caiaponha, IRWIN 2564, 3.ii.1959 (K,NY,TEX);

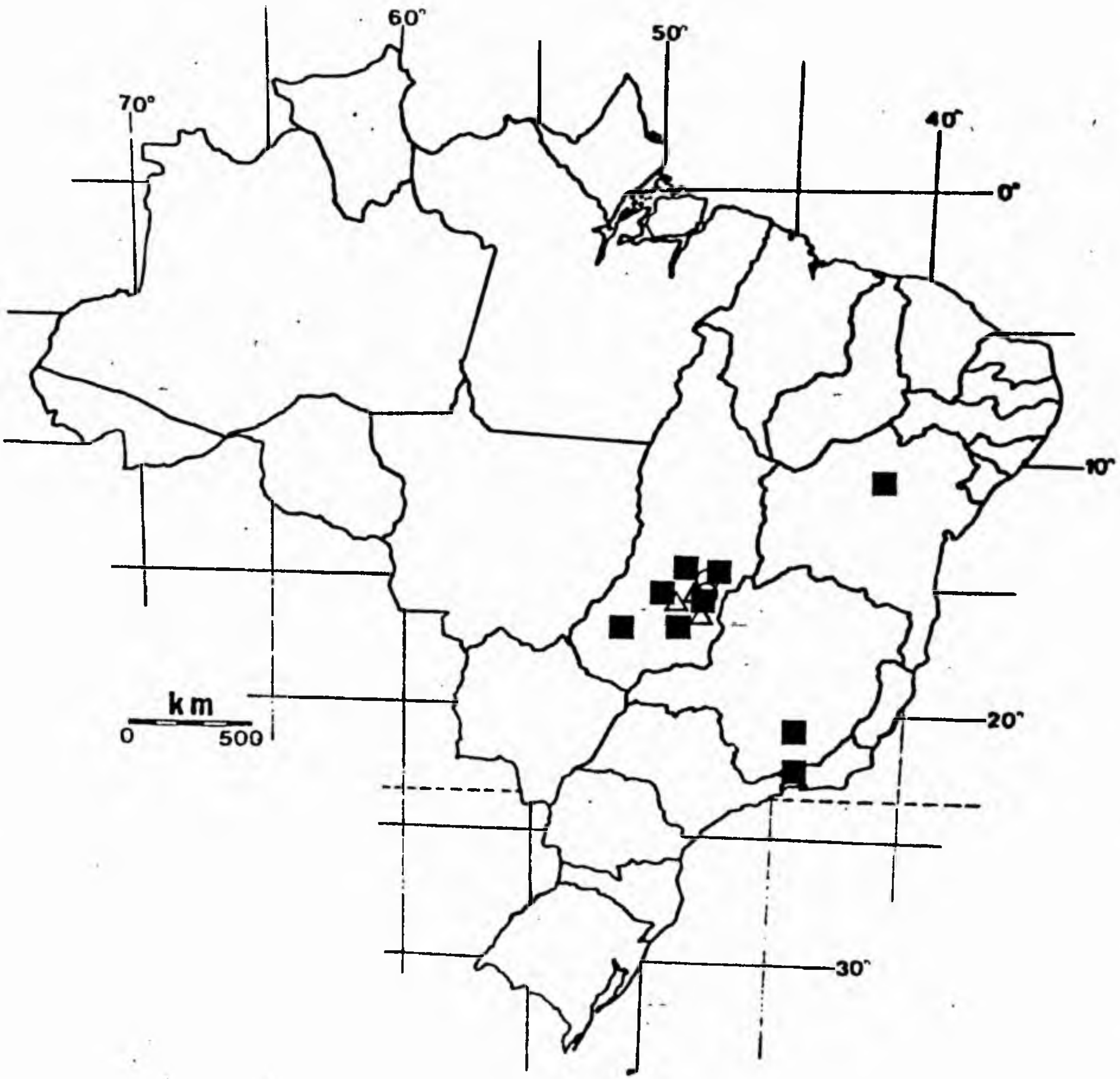


Figure 111 - Distribution map of unifoliolate species of *Lupinus* in Brazil.

△ *L. subsessilis*

○ *L. insignis*

■ *L. velutinus*

Chapada da Contagem, 20 km E of Brasília, IRWIN & SODERSTROM 5057, 13.viii.1964 (NY); 20 km NW of Corumbá de Goiás, near Pico dos Pirineus, IRWIN, MAXELL & WASSHAUSEN 19324, 27.i.1968 (G,K,NY,UB); municipio of Niquelândia, Jacuba, MACEDO 4427, 24.ii.1956 (K,NY); municipio of Alto Paraíso de Goiás, Chapada dos Veadeiros, 43 km N of Alto Paraíso, MARTINELLI 3791 & JOUVIN, 24.i.1978 (RB); Cristalina, road BR-7, km 620, PEREIRA 7343, 27.iii.1963 (NY). Without precise locality : "Brasil Australis", St HILAIRE 1462, date ? (P).

(12) . *Lupinus subsessilis* Bentham

ANN, NAT. HIST. 3 : 430, 1839

Herbs to subshrubs, erect, up to 1 m tall; stems unbranched or with several branches, hirsute-sericeous; internodes 15.0 - 30.0 mm. Stipules sericeous; the free tips lanceolate, acuminate, 3.0 - 5.0 x 1.5 - 2.3 mm, adnate/free length ratio 1.0 - 1.3. Leaves 45.0 - 65.0 x 9.0 - 25.0 mm, elliptic-lanceolate to elliptic-ovate, appressed sericeous on both faces; petioles 6.0 - 7.0 mm. Peduncle 20.0- 35.0 mm, erect, appressed-sericeous. Racemes 100.0 - 150.0 mm, flowers lax; bracts lanceolate-subulate, early caducous, 5.0 - 6.0 mm; pedicels sericeo-villous, 4.0 mm. Calyx densely sericeous to sericeo-villous; lower lip lanceolate-linear, 13.0 - 16.0 mm, the median tooth 0.6 - 0.8 x 0.2 - 0.3 mm, the two lateral teeth much shorter; upper lip oblong-lanceolate, 10.0 - 11.0 x 3.5 - 5.0 mm, bifid, the teeth 2.0 - 4.5 mm.

Standard 14.0 - 16.0 mm, ovate-circular; wing petals ovate-oblong to oblong-lanceolate, 7.0 - 8.0 x 3.0 - 3.8 mm, the claw 1.0 - 1.5 mm; keel petals lanceolate, arcuate, 6.5 - 7.5 - 2.5 - 3.0 mm, the claw 1.5 - 2.0 mm. Ovules 4 - 6. Pods 50.0 x 8.0 - 10.0 mm, densely sericeo-villous. Seeds immature, cyllindric-reniform to subcircular, 6.0 - 7.5 x 3.5 - 4.2 mm. Figure 109.

Type - Brazil : Serra dos Cristais, POHL 721, 20.xii.1818 (K!, holotype).

Although there is no indication on the holotype that the "Serra dos Cristais" mentioned by POHL is located in the state of Goiás (west central region of Brazil), it seems likely that this is the area referred to. Certainly, no other locality or region in Brazil with the same name has been found. However, SMITH (1945) has cited the state of Minas Gerais as the area where the holotype was collected but his citation must be interpreted as erroneous.

L. subsessilis represents one of the extremes of the phenotypic plasticity of the L. velutinus group which also comprises L. velutinus and L.. insignis. The plants of L. subsessilis differ from the those of the central species, L. velutinus in being relatively smaller and showing reduction in leaf and stipule sizes. Furthermore, instead of having the densely villous type of pubescence found in L. velutinus and L. insignis, the vestiture consists of sparser sericeous hairs.

This species has so far only been found in the central core region of "cerrados" in Brazil, where it can be considered endemic.

Distribution (Figure 111)

Brazil

West Central - Federal District : Brasília, Horto do Guará, HERINGER 11041, 27.ii.1966 (UB), state of Goiás : Serra dos Cristais, ca. 5 km S of Cristalina, elev. 1175 m, IRWIN *et al.* 10007, 6.ix.1965 (GH,SP,UB); ibidem, ca. 3 km E of Cristalina, elev. 1250 m, IRWIN *et al.* 13471, 4.iii.1966 (GH,K).

(13) . *Lupinus insignis* C.P. Smith

Sp. Lup. : 489, 1945

Herbs to subshrubs up to 0.75 m tall; stems several branched, densely appressed sericeo-villous. Stipules lanate-villous, 23.0 - 25.0 mm; internodes 9.0 - 13.0 mm. Stipules lanate-villous, 23.0 - 25.0 mm; the free tips lanceolate, acuminate, 9.0 - 12.0 x 3.0 - 5.0 mm, adnate/free length ratio 1.3 - 2.1. Leaves 126.0 - 130.0 x 30.0 - 56.0 mm, ovate-lanceolate, large, densely appressed villous-sericeous; petioles 13.0 - 15.0 mm. peduncles 15.0 - 45.0 mm, erect, densely villous-lanate. Racemes 160.0 - 370.0 mm, flowers congested; bracts ovate-lanceolate, with acuminate tips, denselly villous, 12.0 - 15.0 x 2.5 - 3.9 mm, tardily caducous; pedicels villous, 10.0 - 20.0 mm. Calyx densely appressed sericeo-villous; lower lip lanceolate, 12.0 - 14.0 (-16.0) mm, the teeth subequal, 0.2 - 0.4 x 0.3 mm;

upper lip oblong-lanceolate, 10.0 - 12.0 x 3.5 - 4.0 mm, the teeth 2.5 - 4.0 mm; bracteoles lanceolate, 3.5 - 4.5 x 1.0 - 1.5 mm. Standard 12.0 - 17.0 mm, ovate-circular; wing petals oblong, straight to arcuate at the tip, 11.0 - 12.0 x 4.0 - 5.0 mm, the claw 1.0 - 1.5 mm; keel petals lanceolate, arcuate, 10.0 - 11.0 x 3.5 - 4.8 mm, the claw 1.5 mm. Ovules 4 - 6. Pods and seeds not seen. Figure 109.

Type - Brazil, state of Goiás : "entre Engenho e Jatobá", GLAZIOU 20931, 21.i.1891 (P!, holotype, G!,K!, isotypes)

The typification of this species has a somewhat confusing history because of wrong citations of collection numbers and specimens by GLAZIOU (1906, MEM. SOC. BOT. FRANCE *1* (3) : 129). GLAZIOU (*loc. cit.*) published *L. insignis* as a *nomen nudum* but the specimen GLAZIOU s/n (Goiás, "entre Rio dos Couros e Piçarão") as mistakenly cited as the collection numbered 20931. However, this number actually refers to the specimen (Goias, "entre Engenho e Jatobá"), as the exsiccatae at Paris confirms. Nevertheless, SMITH (1945), who had seen both specimens made the correction and mentioned as the the holotype of *L. insignis* the specimen (Goiás, "entre Engenho e Jatobá"). However, SMITH (*loc. cit.*) cited as the synonym of his new species the combination "*L. velutinus* var. *insignis* Glaziou" which, in fact, was never published by GLAZIOU. Although it is a wrong citation, it does not affect the status of the species *L insignis*.

This species is readily distinguished from *L. velutinus*, the central species of the "*L. velutinus* group" by having larger leaves, denser and thicker pubescence and more compacted racemes. The floral morphology is very similar to that of *L. velutinus* (Figure 109). Unfortunately, due to lack of material, the seed testa pattern could not be studied.

Distribution (Figure 111)

Brazil

West Central - state of Goiás : Chapada dos Veadeiros, 9 km by road S of Teresina, elev. 1100 m, ANDERSON 7467, 19.iii.1973 (NY,UB); "entre Rio dos Couros et Rio Piçarão", GLAZIOU s/n, 18.i.1895 (P); summit of Chapada da Contagem, ca. 10 km E of Brasília, elev. 1250 m, IRWIN, SOUZA & SANTOS 8252, 13.ix.1965 (NY,UB).

5.2.2.7 - Doubtful species

Lupinus aliattenuatus C.P. Smith
Sp . Lup. : 485, 1945

The holotype of *L aliattenuatus* was lost in the Berlin fire and attempts to find an isotype have been unsuccessful. As many other of SMITH's species, *L. aliattenuatus* was based on a single specimen and the characters which differentiate it from "*L. attenuatus*" are very weak.

The leaves were described as linear-oblong and acute mucronulate, which in fact are the characteristics of *L. coriaceus* leaves. SMITH (1945) also mentioned that the upper lip of the calyx was "probabiliter bifidum" but this character is of little assistance because all known species of Lupinus have the upper lip bifid.

Therefore, although it is possible to demote L. aliattenuatus into the limits of L. coriaceus following the data provided by SMITH's (1945) description, the author reluctantly keeps it as a distinct taxon until it is certain that no collections are available for detailed study.

5.3 - Numerical taxonomy

The 13 unifoliolate species of Lupinus recognised for Brazil in this work together with two of the unifoliolate species from southeastern North America (L. diffusus Nutt. and L. villous Willd.) and eight multifoliolate taxa from Brazil (Figure 112) were studied for their taxonomic affinities using numerical methods for clustering analyses. The data matrix was obtained with the measurements and calculations (ratios) presented in Table 30, which comprise a set of macro-morphological characters (leaf, stipules, calyx, etc).

Several clustering methods were applied to the data to generate hierarchical dendrograms using the CLUSTAN package (WISHART, 1978). However, due to the nature of some of these methods, in which "obviously inappropriate" groupings were generated, the results presented here are limited to two dendrograms derived from the CENTROID (Figure 112 A) and WARD's methods (Figure 112 B), both methods considered to be the most reliable for hierarchical group analysis (DUNN & EVERITT, 1982).

In a first analysis, because of the presence of two distinct group of OTUs (uni x multifoliolate), these units would be expected to isolate distinctly, if these character states were enough to separate them. This was not the case with the CENTROID method, in which a series of rather indiscriminate "chainings" at very low coefficient levels linked the OTUs apparently at random (Figure 112 A). In WARD's technique, however, a distinct subunit is separated from the other groupings in the dendrogram tree which

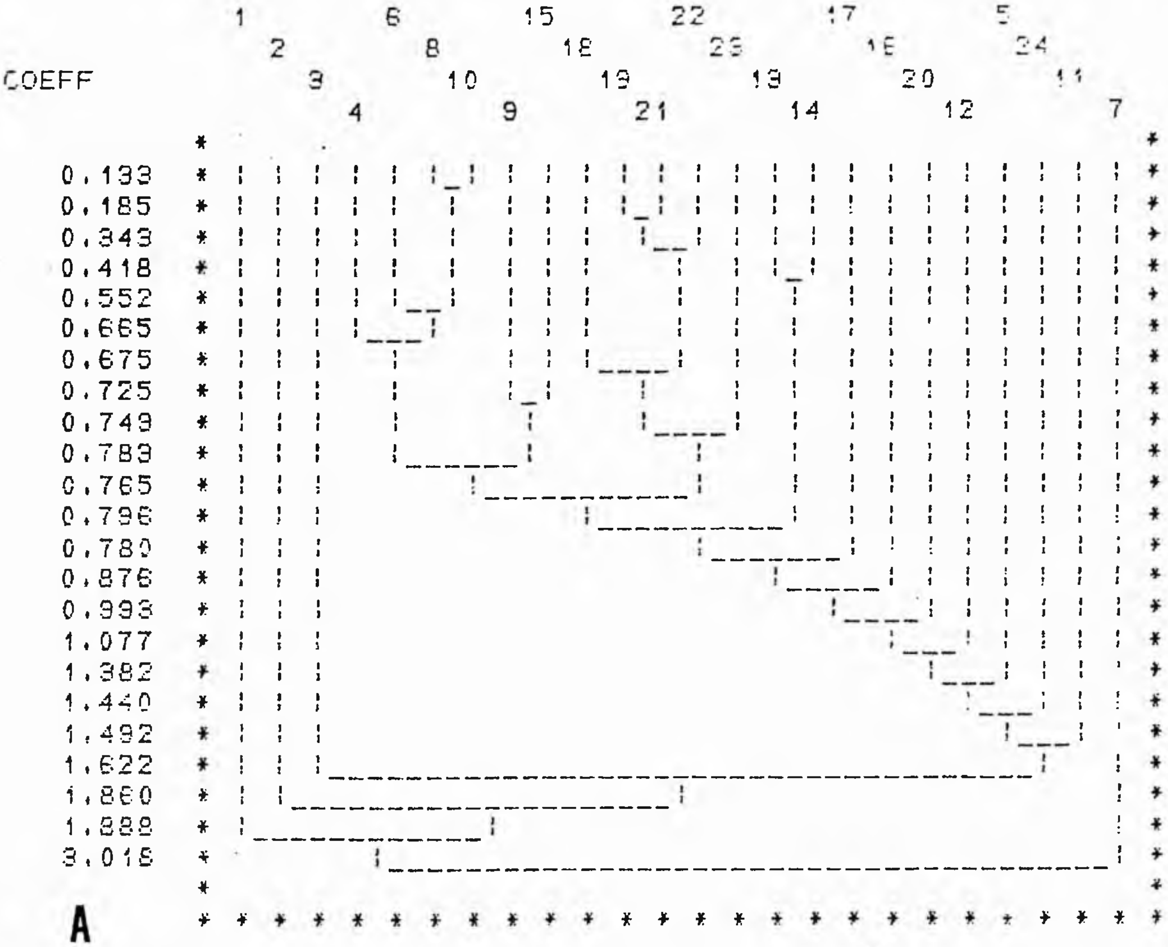
Table 30 - List of variables used in the numerical analysis of *Lupinus*.

BINARY : Leaves petiolate/sessile
unifoliolate/multifoliolate
"leaflets" 3 or less/ "leaflets" more than 3

NUMERICAL : internode length
leaf length/width ratio
leaf/petiole length ratio
total stipule length
adnate/free stipule length
leaf/free stipule length ratio
inflorescence length
inflorescence/leaf length ratio
peduncle length
pedicel length
bract length
corolla length
corolla/free stipule length ratio
upper/lower lip length ratio
upper/lower lip width ratio
upper lip teeth length
inflorescence/peduncle length ratio

Figure 112 - Dendrograms of CENTROID (A) and WARD's (B) methods of hierarchical clustering analyses produced by CLUSTAN (WISHART, 1978) for *Lupinus* species.

OTUs :	UNIFOLIOLATE SPECIES	MULTIFOLIOLATE SPECIES
	1 - *L. amabayensis*	17 - *L. comptus*
	2 - *L. coriaceus*	18 - *L. gibertianus*
	3 - *L. ovalifolius*	19 - *L. regnellianus*
	4 - *L. parvifolius*	20 - *L. paranensis*
	5 - *L. prouvensalanus*	21 - *L. russelianus*
	6 - *L. decurrens*	22 - *L. dussenianus*
	7 - *L. guaraniticus*	23 - *L. bracteolaris*
	8 - *L. laevigatus*	24 - *L. lanatus*
	9 - *L. sellowianus*	
	10 - *L. crotalarioides*	
	11 - *L. arenarius*	
	12 - *L. subsessilis*	
	13 - *L. velutinus*	
	14 - *L. insignis*	
	15 - *L. diffusus*	
	16 - *L. villosus*	


COEFF
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2
3
4
6
8
10
9
15
18
19
21
22
23
13
14
17
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20
12
5
24
11
7
0,133
0,185
0,343
0,418
0,552
0,665
0,675
0,725
0,749
0,783
0,765
0,796
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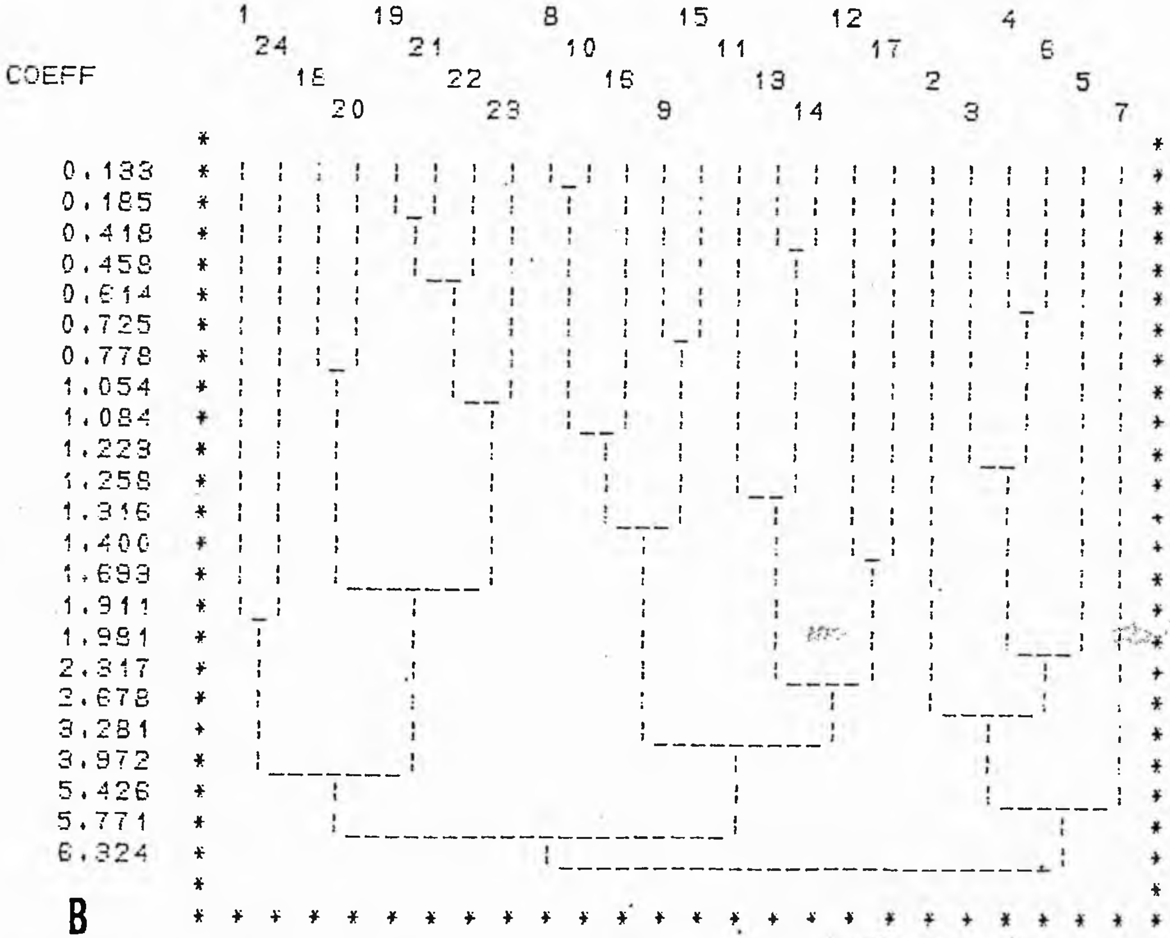
1,622
1,860
1,888
3,015

A


COEFF
1
24
18
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16
9
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11
13
14
12
17
2
3
4
6
5
7
0,133
0,185
0,418
0,458
0,614
0,725
0,778
1,054
1,084
1,229
1,258
1,316
1,400
1,693
1,911
1,991
2,317
2,678
3,281
3,972
5,426
5,771
6,324

B

comprise the multifoliolate species, i.e., OTUs 18-24 (Figure 112 B) and, intriguingly one unifoliolate (L. amabayensis, OTU 1). The latter association is not very clear and must be interpreted as an anomaly caused by the method.

A step further would be to observe the formation of natural subgroupings within the unifoliolate OTUs such as stipulate x exstipulate, petiolate x sessile, etc. For CENTROID, these subgroupings did not occur at all (Figure 112 A), whilst for WARD's method (Figure 112 B) the separation of exstipulate species (OTUs 2,3,4,5) against stipulate (OTUs 8-16) was achieved in reasonably low coefficient levels. Furthermore, WARD's analysis groups in isolation the OTUs 12, 13, and 14 which are the trio of "cerrado" rather than "campo rupestre" unifoliolate species in Brazil.

Interestingly, the North American unifoliolate species (OTUs 15 and 16) tended to link together and, also, with OTU 9 (L. sellowianus) which, as has been pointed out before, is very similar in leaf shape with the former taxa. Once again, it may be possible that the ancestral group (or even an early form of L. sellowianus) represents the source of introduction of the unifoliolate species from Brazil which, according to DUNN (1971) gave origin, through long-distance dispersal, to the North American unifoliolate taxa.

In conclusion, it can be observed that the application of numerical taxonomy to a subgroup of New World Lupinus has provided few insights into the relationships of the taxa. WARD's method of the CLUSTAN package did produce a clustering which confirmed parallel "human" taxonomic ideas in (a) isolating the North and

South American unifoliolate species together, (b) clustering the Brazilian unifoliolate L. sellowianus close to North American group, and (c) clustering together the cerrado unifoliolate species. However, in an exercise which simply feeds to the computer the same characters which the taxonomist has been assessing visually perhaps few revelations should be expected. Numerical taxonomic insights into Lupinus are only likely to be achieved when it is possible to utilise greater quantities of data, including chemical parameters for large number of species.

6 . REFERENCES

ADAMS, M. W. & PIPOLY III, J. J. 1980 - Biological structure and distribution of economic legumes. *In* SUMMERFIELD, R. J. & BUNTING, A. H. (eds) *Advances in legume science*. HMSO (Kew, U.K.).

ADAMS, R. J. & SMITH, M. V. 1977 - Scanning electron and light microscope studies of pollens of some leguminosae. JOURN. APIC. RES. *16* (1) : 99-106.

ADANSON, M. 1763 - *Familles des plantes*. 2 Vols. (Paris).

AGARDH, J. G. 1835 - *Synopsis generis Lupini*. Lundae (Berlin).

ALLEN, O. N. & ALLEN, E. K. 1981 - *The Leguminosae : a source book of characteristics, uses and nodulation*. Macmillan Publishers (London, U.K.).

ARROYO, M. T. K. 1981 - Breeding systems and pollination biology in Leguminosae. *In* POLHILL, R. M. & RAVEN, P. H. (eds) *Advances in legume systematics*, Vol. 1. HMSO (Kew, U.K.).

AUBLET, J. B. C. P. 1775 - *Histoire des plantes de la Guiane Française*... (London, Paris).

BAKER, E. G. 1871 - *Sesbania*. *In* OLIVER, D. (ed.) *Flora of Tropical Africa* Vol. 2. L. Reeve & Co. (London, U.K.).

BAKER, E. G. 1876 - Leguminosae. *In* HOOKER, J. D. (ed.) *Flora of British India*. Vol. 2. L. Reeve & Co. (London, U.K.).

BAQUAR, S. R. & AKHTAR, S. 1968 - Cytogenetical studies of the genus *Sesbania* from W. Pakistan. CYTOLOGIA *33* : 427-438.

BENTHAM, G. 1839 - Enumeration of plants collected by Mr. Schomburgh, Britsh Guyana. ANN. NAT. HIST. *3* : 427-438.

BENTHAM, G. 1859 - Papilionaceae. *In* MARTIUS, C. F. P. (ed.) *Flora Brasiliensis* *15* (1). (Munich).

BENTHAM, G. 1865 - *Sesbania*. *In* BENTHAM, G. & HOOKER, J. D. *Genera Plantarum*, Vol. 1, part 2. L. Reeve & Co. (London, U.K.).

BERGE SEN, F. J. 1982 - *Root nodules of legumes : structure and functions* . Research Studies Press (Chichester, U.K.).

BIR & SINDHU 1966 - *In* LOVE, A. (ed.) IOPB chromosome number report number reports VI. TAXON *15* : 117.

BISBY, F. A. 1981 - Genisteae (Adans.) Benth. In POLHILL, R. M. & RAVEN, P. H. (eds) Advances in legume systematics, Vol. 1. HMSO (Kew, U.K.).

BRISCOE, C. F. & ANDREWS, W. B. 1938 - Inoculation of sesban. J. AMER. SOC. AGRON. 30 : 135-138.

BUNBURY, C. 1841 - Remarks on certain plants of Brazil, with descriptions of some which appear to be new. PROC. LINN. SOC. LONDON 1 : 108-110.

BUNTING, G. S. & INGRAM, J. 1972 - La confusion de tipificación y de nomenclatura de dos especies americanos del género Sesbania (Leguminosae) : S. cavanillesii y S. drummondii. BOL. SOC. BOT. MÉX. 32 : 57-70.

BURBIDGE, N. T. 1960 - The phytogeography of the Australian region. AUSTR. J. BOT. 8 : 75-211.

________________ 1965 - The Australian species of Sesbania Scopoli (Leguminosae). AUSTR. J. BOT. 13 : 103-141.

BURKART, A. 1952 - Las leguminosas argentinas silvestres y cultivadas. ACME (Buenos Ayres, Argentina).

________________ 1969 - Leguminosas nuevas o críticas, VII. Un nuevo género de "Papilionoideae-Galegeae" del Ecuador. DARWINIANA 15 (3/4) : 523-530.

CAMARGO, A. PAES DE; ALFONSI, R. R.; PINTO, H. S. & CHIARINI, J. V. 1977 - Zoneamento da aptidão climática para culturas comerciais em áreas de cerrado. In FERRI, M. G. (ed.), IV Simpósio sobre o cerrado - bases para utilização agrícola . EDUSP (São Paulo, Brazil).

CANDOLLE, A. P. De 1825 (-1827) - Memoires sur la famille des Leguminéuses. (Paris).

________________ 1825 - Prodromus... Vol. 2. (Paris).

CASARETTO, J. 1843 - Novarum stirpium Brasiliensium. Decades, Decas VI, April. J. Ferrandi (Genoa, Italy).

CASTRONOVA, A. 1945 - Estudio cariologico de doce especies de leguminosas argentinas. DARWINIA 7 : 38-58.

CAVANILLES, A. J. 1797 - Icones et descriptiones plantarum...Vol. 4, part 1. (Madrid).

CHATEL, D. L. & ROWLAND, I. C. 1982 - NItrogen fixation and inoculation by lupins. JOURN. AGRIC. WESTERN AUSTR. No. 3 : 92-95.

CIVITA, V. (ed.) 1976 - Brasil por estados (maps). Editôra Abril S.A. (São Paulo, Brazil).

CONEY, P. J. 1982 - Plate tectonic constraints on the biogeography of middle America and the Caribbean region. ANN. MISS. BOT. GDN *69* : 432-443.

COOK, C. D. K.; GUT, B. J.; RIX, E. M.; SCHNELLER, J. & SEITZ, M. 1974 - *Water plants of the World*. Dr. W. Junk. b.v. Publishers (The Hague, Holland).

CORBY, H. D. L. 1981 - The systematic value of leguminous root nodules. *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*. Vol. 2. HMSO (Kew, U.K.).

---------------- ; POLHILL, R. M. & SPRENT, J. I. 1983 - Taxonomy. *In* BROUGHTON, W. J. (ed.) *Nitrogen fixation*. Vol. 3. *Legumes*. Clarendon Press (Oxford, U.K.).

CORNER, E. J. H. 1951 - The leguminous seeds. PHYTOMORPHOLOGY *1* : 117-150.

________________ 1976 - *The seeds of dicotyledons*. 2 Vols. Cambridge University Press (Cambridge, U.K.).

COVAS, G. & SCHNACK, B. - 1946 - Numero de chromosomas en antófitas de la region de Cuyo (Republica Argentina). REV. ARGENT. AGRON. *13* : 153-166.

COZZO, D. 1948 - Estudio anatomico sobre la posicion sistemática de algunos géneros argentinos de leguminosas papilionoideas. LILLOA *16* : 97-124.

DANA, S. K. & DATTA, R. M. 1961 - Comparative cytological studies of the pollen and pollen tubes in diploid and tetraploid species of *Sesbania*. NEW PHYTOL. *60* : 295-311.

DATE, R. A. & HALLIDAY, J. 1980 - Relationships between *Rhizobium* and tropical forage legumes. *In* SUMMERFIELD, R. J. & BUNTING, A. H. (eds), *Advances in legume science* HMSO (Kew, U.K.).

DATTA, R. M. & SEN, S. K. 1960 - Interspecific hybridization between *Sesbania aculeata* Pers. (4n race) and *S. speciosa* Taube. ex Engler (2n race) and cause of failure of viable seed formation. DER ZUCHTER *30* :265-269.

DAVIS, P. H. & HEYWOOD, V. H. 1963 - *Principles of angiosperm taxonomy*. Oliver & Boyd (Edinburgh, U.K.).

DESROUSSEAUX, L. 1792 - *Lupinus bracteolaris*, *L. linearis*. ENCYCL. METH. *3*(2) : 622-3, 625.

DESVAUX, N. A. 1813 - *Glottidium*. JOURN. BOT. Vol. 2, part 1 : 119 (Paris).

DON, G. 1832 - *A general history of the dychlamydeous plants* ... Vol. 2. (London, U.K.).

DUKE, J. A. & POLHILL, R. M. 1981 - Seedlings of Leguminosae. *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*, Vol. 2. HMSO (Kew, U.K.).

DUNN, D. B. 1971 - A case of long range dispersal and "rapid speciation" in *Lupinus*. TRANS. MISS. ACAD. SCI. *5* : 26-38.

----------- 1980 - *Lupinus*, in *Flora of Panama*. ANN. MISS. BOT. GDN *67* : 719-724.

----------- 1984 - Cytotaxonomy and distribution of the New World lupin species. Paper presented at the 3rd International Lupine Conference, La Rochelle, France. (mimeograph.).

----------- & PLANCHUELO, A. M. 1981 - *Lupinus heptaphyllus* (Vel.) Hassl. vs. *L. hilarianus* Benth. TAXON *30* : 464-470.

DUNN, G. & EVERITT, B. S. 1982 - *An introduction to mathematical taxonomy*. Cambridge Univ. Press (Cambridge, U.K.).

ELLIOTT, S. 1822 - *A sketch of the botany of South Carolina and Georgia*. (Charleston, U.S.A.).

ERDTMAN, G. 1969 - *Handbook of palynology*. Munksgaard (Copenhagen, Denmark).

EWAN, J. 1967 - Introduction to a fac-simile edition of RAFINESQUE *Flora Ludoviciana*.

FALUYI, M. 1980- *Studies on the breeding system in lupin species*. Ph.D. Thesis, University of Reading (U.K.).

FARR, E. R.; LEUSSINK, J. A. & STAFLEU, F. A. 1979- *Index Nominum Genericorum (Plantarum)*. 3 vols. Bohn, Scheltena & Holkema (Utrecht, The Netherlands).

FERGUSON, I. K. & SKVARLA, J. J. 1981 - Pollen morphology of the subfamily Papilionoideae (Leguminosae). *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*. Vol. 2. HMSO (Kew, U.K.).

FERNANDES, A.; SANTOS, M. F. & QUEIROS, M. 1977 - Contribution à la connaissance cytotaxonomique des Spermatophyta du Portugal. BOL. SOC. BROT. Ser. 2, *51* : 137-186.

FERRI, M. G. 1960 - Nota preliminar sobre a vegetação do cerrado em Campo Mourão (Paraná). BOL. FAC. FIL. CIÊNC. LETR. USP No. 247, Botânica *17* : 109-115.

FRAHM-LELIVELD, J. A. 1953 - Some chromosome numbers in tropical leguminous plants. EUPHYTICA *2* : 46-48.

GARDNER, G. 1843 - *Lupinus arenarius*, *L. attenuatus*, *L. parvifolius*, *L. decurrens*. *In* HOOK. Ic. Pl. 2, plates 511, 521.

GEESINK, R. 1981 - Tephrosieae. In POLHILL, R. M. & RAVEN, P. H. (eds), Advances in legume systematics, Vol. 1. HMSO (Kew, U.K.).

GENTRY, A. H. 1982 - Neotropical floristic diversity : phytogeographical connections between Central and South America, pleistocene climatic fluctuations, or an accident of the Andean orogeny ? ANN. MISS. BOT. GDN 69 : 557-593.

GIBBS, P. E. & INGRAM, R. 1982 - Chromosome numbers of some Brazilian flowering plants. NOTES RBG EDINB. 40 : 399-407.

GILL, L. S.; OLABANJI, G. O. & HUSAINI, S. W. H. 1980 - Studies on the structural variation and distribution of stomata in some Nigerian legumes. LEGUME RESEARCH 3 : 78-84.

------------;--------------- & ---------------- 1982 - Studies on the structural variation and distribution of stomata in some Nigerian legumes. WILLDENOWIA 12 : 87-94.

GILLETT, J. B. 1963 - Sesbania in Africa (excluding Madagascar) and southern Arabia. KEW BULL. 17 : 91-159.

GLADSTONES, J. S. 1970 - Lupins as crop plants. I.A.B. FIELD CROP ABSTR. 23 : 123-148.

---------------- 1974 - Lupins of the Mediterranean region and Africa. WESTERN AUSTR. DEPT. AGR. TECH. BULL. 26 1-48.

---------------- 1980 - Recent developments in the understanding, improvement and uses of Lupinus. In SUMMERFIELD, R. J. & BUNTING, A. H. (eds), Advances in legume science. HMSO (Kew, U.K.).

---------------- 1982a - Lupins - the genetic resource. JOURN. AGRIC. WESTERN AUSTR. No. 3 : 67-69.

---------------- 1982b - Breeding the first modern crop lupins. JOURN. AGRIC. WESTERN AUSTR. No. 3 : 70-72.

GLAZIOU, A. F. M. 1906 - Plantae Brasiliae centralis a Glaziou lectae. MEM. SOC. BOT. FRANCE 3 : 130.

GOEDERT, W. J. & BLUMENSCHEIN, A. 1977 - Pesquisa agropecuária nos cerrados. In FERRI, M. G. (ed), IV Simpósio sobre o cerrado - bases para utilização agropecuária. EDUSP (São Paulo, Brazil).

GOOD, R. 1974 - The geography of the flowering plants. Longman (London, U.K.).

GOODLAND, R. & POLLARD, R. 1973 - The Brazilian cerrado vegetation - a fertility gradient. J. ECOL. 61 : 219-224.

GOLDBLATT, P. 1981a - Index to plant chromosome numbers 1975-1978. Monographs in Systematic Botany from the Missouri Bot. Gdn, Vol.5.

GOLDBLATT, P. 1981b - Cytology and the phylogeny of Leguminosae. *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*, Vol. 2. HMSO (Kew, U.K.).

GRANT, V. 1971 - *Plant speciation*. Columbia University Press (New York, U.S.A.).

GUNN, C. R. 1972 - Seed characteristics. *In* C. H. HASEN (ed.), *Alfalfa science and technology*. Agronomy Series No. 15, American Society of Agronomy (Madison, U.S.A.).

---------- 1981 - Seeds of Leguminosae. *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*. Vol. 2. HMSO (Kew, U.K.).

HANNA, P. J. 1984 - Anatomical features of the seed coat of *Acacia kempeana* Mueller which relate to increased germination rate induced by heat treatment. NNEW PHYTOL. *96* : 23-29.

HAQUE, A. 1946 - Chromosome numbers in *Sesbania* CUR. SC. *15* : 78.

HARMS, H. 1921 - Uber einige brasilianische *Lupinus*. Arten mit. einfachen Blattern. FEDDE, REPERT. *17* : 5.

-------- 1923 - *Sesbania brenningii* Harms. *In* "Leguminosae Americanae novae". II. FEDDE, REPERT. *19* :68-69.

HAWKES, J. G. 1983 - *The diversity of crop plants*. Harvard University Press (Cambridge, U.S.A.).

HEYN, C. C. & HERRNSTADT, I. 1977 - Seed coat of Old World *Lupinus* species. BOT. NOTISER *130* : 427-435.

HILL, S. R. 1982 - Distributional and nomenclatural notes on the flora of the Texas coastal bend. SIDA : 309-326.

HOEFLICH, E. R. C.; PEREIRA, J.; DUQUE, F. F. & TOLLINI, H. 1970 - Sistema de produção agrícola no cerrado.*In* FERRI, M. G. *IV Simpósio sobre o cerrado - bases para utilização agropecuária*. EDUSP (São Paulo, Brazil).

HOLM, L.; PANCHO, J. V.; HERBERGER, J. P. & PLUCKNETT, D. L. 1979 - *A geographical atlas of world weeds*. John Willey & Sons (New York, U.S.A.).

HOMEM DE MELO, F. B. 1982 - A produção de biomassa e o crescimento da área cultivada no Brasil. REV. BRAS. TECNOL., BRASÍLIA *13* : 3-19.

HONDELMANN, W. 1984 - The lupin - ancient and modern crop plant. THEOR. APPL. GEN. *68* (1/2) : 1-9.

HUTCHINSON, J. 1964 - *The genera of flowering plants* (Angiospermae). Vol. 1, Dicotyledones. Clarendon Press (Oxford, U.K.).

ISELY, D. 1982 - The leguminosae and Homo sapiens. ECON. BOT. 36 : 46-70.

JACOB, K. T. 1941 - Cytological studies in the genus Sesbania. BIBL. GENET. 13 : 225-297.

JACQUIN, N. J. von 1781 - 1793 - Icones plantarum rariorum. 3 Vols. C. F. Wappler (Wiena).

JANZEN, D. H. 1983 - Sesbania emerus (Guanacastillo, Pata de Garza). In JANZEN, D. H. (ed.), Costa Rican Natural History. The University of Chicago Press (Chicago, U.S.A.).

JOHNSON, C. D. 1981 - Seed beetle host specificity and the systematics of the Leguminosae. In POLHILL, R. M. & RAVEN, P. H. (eds), Advances in legume systematics, Vol. 2. HMSO (Kew, U.K.).

JOLY, A. B. 1970 - Conheça a vegetação brasileira. EDUSP (São Paulo, Brazil).

KANNABIRAN, B. & KRISHNAMURTHY, K. H. 1974 - Morphology of foliar epidermis and taxonomy of the genus Crotalaria. PHYTOMORPHOLOGY 24 : 61-68.

LEELAVATHI, P.; RAMAYYA, N. & PRABHAKAR, M. 1980 - Foliar stomatal distribution patterns in Leguminosae and their taxonomic significance. PHYTOMORPHOLOGY 30 (2/3) : 195-204.

LEITAO FILHO, H. F.; ARANHA, C. & BACCHI, O. 1975 - Plantas invasoras de culturas no Estado de São Paulo. Vol. 2. HUCITEC (São Paulo, Brazil).

LEEPIK, E. E. 1966 - Floral evolution and pollination in the Leguminosae. ANN. BOT. FEN. 3 : 229-308.

LERSTEN, N. R. 1981 - Testa topography in Leguminosae, subfamily Papilionoideae. PROC. IOWA ACAD. SCI. 88 : 180-191.

LERSTEN, N. R. 1982 - Tracheid bar and vestured pits in legume seeds (Leguminosae : Papilionoideae). AMER. J. BOT. 69 : 98-107.

LERSTEN, N. R. & GUNN, C. R. 1982 - Testa characters in tribe Vicieae, with notes about tribes Abreae, Cicereae, and Trifolieae (Fabaceae). U. S. Department of Agriculture, Tech. Bull. No. 1667.

LIEUX, M. H. 1982 - An atlas of pollen of trees, shrubs, and woody vines of Louisiana and other south-eastern states, Part IV. Sapotaceae to Fabaceae. POLLEN ET SPORES 24 : 331-368.

LINNAEUS, C. 1753 - Species plantarum . Fac-simile edition (London).

LUBIS, S. H. A.; OKADA, H. & SASTRAPRADJA, S. 1981 - On the cytology of four species of Sesbania. ANN. BOGOR. 7 : 115-127.

MACBRIDE, J. F. 1943 - Leguminosae. In Flora of Peru. PUBL. FIELD MUS., BOT. 13 (3,1).

MEARS, J. A. & MABRY, T. J. 1971 - Alkaloids in the Leguminosae. In HARBORNE, J. B.; BOULTER, D. & TURNER, B. L. (eds), Chemotaxonomy of the Leguminosae. Academic Press (London, U.K.).

MERRILL, E. D. 1949 - Index Rafinesquianus. The Arnold Arboretum of Harvard University (Jamaica Plain, U.S.A.).

MERRILL, E. D. & HU, S-Y 1949 - Work and publications of Henry Muhlenberg, with special attention to unrecorded or incorrectly recorded binomials. BARTONIA 25 : 1-66.

METCALFE, C. R. & CHALK, L. 1950 - Anatomy of the Dicotyledons. Clarendon Press, 2 vols (Oxford, U.K.).

MIEGE, J. 1960- Troisieme liste de nombres chromosomique d'especes d'Afrique occidentale. ANN. FAC. SCI. UNIV. DAKAR 5 : 75-86.

MILLER, P. 1759- The gardeners dictionary... 7th ed. (London, U.K.).

----------- 1768 - The gardeners dictionary... 8th ed. (London, U.K.).

MILLER, P. H. 1967 - Crotalaria seed morphology, anatomy and identification. U.S. Dept. Agric. TECH. BULL. No. 1373.

MUHLENBERG, G. H. E. 1813 - Catalogus plantarum Americae septentrionalis... (Lancaster, U.S.A.).

NICHOLLS, K. W. & BOHM, B. A. 1983 - Flavonoids and affinities of some North American lupines. CAN. J. BOT. 61 : 708-730.

NICOLSON, D. H. 1975 - Paratautonyms, a comment on proposal 146. TAXON 24 : 389-390.

NULSEN, R. A. 1982 - Water use by lupins - their pottential effect on soil salinity. JOUR. AGRIC. WESTERN AUSTR. No. 3 : 91.

NUTTALL, A. 1818 - The genera of North American plants... 2 Vols. (Philadelphia, U.S.A.).

PASCHOAL, A. D. 1983 - O ônus do modelo da agricultura industrial. REV. BRAS. TECNOL., BRASÍLIA 14 : 17-40.

PAWAR, S.M.S. & BORGAONKER, D. S. 1956 - Chromosome numbers of Sesbania cinerascens. CUR. SCI. 27 : 241.

PAZY, B. 1984 - Insect induced self-pollination. PL. SYST. EVOL. *144* : 315-320.

PAZY, B.; HEYN, C. C.; HERRNSTADT, I. & PLITMANN, U. 1977 - Studies in populations of the Old World *Lupinus* species. I. Chromosomes of the East Mediterranean lupines. ISR. J. BOT. *26* : 115-127.

PERSOON, C. H. 1807 - *Synopsis plantarum*... Vol.2. (Paris).

PHILLIPS, E. P. & HUTCHINSON, J. 1921 - A revision of the African species of *Sesbania*. BOTHALIA *1* : 40-56.

PIMENTEL, M. F.; CHRISTOFIDIS, D. & PEREIRA, F.S.S. 1977 - Recursos hídricos no cerrado. *In* FERRI, M. G. (ed.), *IV Simpósio sobre o cerrado - bases para utilização agropecuária*. EDUSP (São Paulo, Brazil).

PIPER, C. V. & ROBINSON, B. L. 1906 - *Lupinus*, in *Flora of Washington*. CONTR. U. S. NAT. HERB. *11* : 350-358.

PLANCHUELO, A. M. & DUNN, D. B. 1980 - Clarification of *lupinus grisebachianus*, *L. subacaulis* and *L. subinflatus* (Leguminosae). BRITTONIA *32* : 387-391.

PLITMANN, U. 1981 - Evolutionary history of the Old World lupines. TAXON *30* : 430-437.

—————— & HEYN, C. C. 1981 - Genetic relationships between *Lupinus pilosus* and *L. palaestinus* (Fabaceae). PL. SYST. EVOL. *137* : 39-4.

PLUMIER, C. 1703 - *Nova plantarum Americanarum Genera*...*Catalogus Plantarum Ameicanarum*. *apud* J. BOUDOT (Paris).

————— 1757 - *Plantarum Americanarum fasciculus primus* (-*decimus*)...Ed. J. Burman (Amsterdam, Holland).

POLHILL, R. M. 1976 - Genisteae (Adans.) Benth. and related tribes (Leguminosae). BOT. SYST. *1* : 143-368.

——————— 1981 - Papilionoideae. *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*. Vol. 1. HMSO (Kew, U.K.).

——————— & RAVEN, P. H. (eds) 1981 - *Advances in legume systematics*. 2 Vols. HMSO (Kew, U.K.).

———————; RAVEN, P. H. & STIRTON, C. H. 1981 - Evolution and systematics of the Leguminosae. *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*, Vol. 1. HMSO (Kew, U.K.).

——————— & SOUSA, M. 1981 - Robinieae (Benth.) Hutch. *In* POLHILL, R. M. & RAVEN, P. H. (eds), *Advances in legume systematics*, Vol. 1. HMSO (Kew, U.K.).

POLHILL, R. M. & STEARN, W. T. 1976 - Linnaeus's notes on Plumier drawings with special reference to Mimosa latisiliqua. TAXON 25 : 71-77.

POWELL, E. A. & JONES, C. E. 1983 - Floral mutualism in Lupinus benthamii (Fabaceae) and Delphiniunm parryi (Ranunculaceae). In JONES, C. E. & LITTLE, R. J. (eds), Handbook of experimental pollination biology. Scientific and Academic Editions (NEW YORK U.S.A.).

PRAKASH, N. & HERR, J. M. 1979 - An embryological sudy of Glottidium vesicarium (Jacqu.) Mohr. through the use of clearing technique. PHYTOMORPHOLOGY 29 : 71-77.

RACHIE, K. O. et al. 1979 - Tropical legumes : resources for the future. Report of an Ad Hoc Panel of the Advisory Commitee on Technology Innovation, Board on Science and Technology for International Development, Commision on International Relations and National Research Council National Academy of Sciences (Washington, D.C., U.S.A.).

RAFINESQUE-SCHMALTZ, C. S. 1967 (fac-simile), original date 1817 - Florula Ludoviciana or A flora of the state of Louisiana. Hafner Publishing Co. (New York, U.S.A.).

RAO, Y. S. 1946 - Chromosome numbers in Sesbania. CUR. SC. 15:78.

RATTER, J. A.; ASKEW, G. P.; MONTGOMERY, R. F.; & GIFFORD, D. R. 1977 - Observações adicionais sobre o cerradão de solos mesotróficos no Brasil Central. In FERRI, M. G. (ed.) IV Simpósio sobre o cerrado - bases para a utilização agropecuária. EDUSP (São Paulo, Brazil).

RAVEN, P. H. 1982 - Plate tectonics and southern hemisphere biogeography. In LARSEN, K. & HOLM-NIELSEN, L. B. (eds) Tropical botany. Academic Press (London, U.K.).

-------------- 1983 - The migration and evolution of floras in the southern hemisphere. BOTHALIA 14 : 325-328.

-------------- & AXELROD, D. L. 1974 - Angiosperm biogeography and past continental movements. ANN. MISS. BOT. GDN 61 : 539-673.

-------------- & AXELROD, D. L. 1978 - Origin and relationships of the California flora. UNIV. CALIF. PUBL. BOT. 72 : 1-134.

-------------- & POLHILL, R. M. 1981 - Biogeography of the Leguminosae. In POLHILL, R. M. & RAVEN, P. H. (eds), Advances in legume systematics, Vol. 1. HMSO (Kew, U.K.).

RAU, M. A. 1951 - The endosperm in some of the Papilionaceae. PHYTOMORPHOLOGY 1 : 153-158.

RAU, M. A. 1953 - Some observations on the endosperm in Papilionaceae. PHYTOMORPHOLOGY 3 : 209-222.

RHEEDE, H. A. van 1678 (-1703) - Hortus indicus malabaricus... 12 Vols. IDC microf.

RICKETT, H. W. & STAFLEU, F.A. 1959 - Nomina generica conservanda et rejicienda spematophytorum III. TAXON 8 : 282-314.

ROCHA, G. L. et al. 1979 - Coleta, identificação e distribuição de leguminosas forrageiras tropicais brasileiras - Brasil Central , Fase I. B. INDUSTR. anim., NOVA ODESSA, SP 36 : 255-324.

ROLSTON, M. P. 1978 - Water impermeable seed dormancy. BOT. REV. 44 : 365-396.

RYDBERG, P. A. 1917 - Flora of the Rocky Mountains and adjacent plains. (New York, U.S.A.).

-------------- 1923 - Genera of North American Fabaceae. I. Tribe Galegeae. AM. J. BOT. 10 : 485-498.

-------------- 1924 - Fabaceae, Galegeae. NORTH AMER. FLORA 24 (4) : 202-249.

SAINT-MARTIN, M. 1976 - Quelque types stomatiques chez les Papilionacées. COMPT. REND. ACAD. SC. PARIS, t. 282, Ser. D: 1503-1506.

SAMPATH, S. 1947 - Chromosome numbers in Sesbania. CUR. SI.16 : 30-31.

SCHENCK, H. 1889 - Ueber das Äerenchym, ein dem Kork homologues Genebe bei Sumpfpflanzen. JAHRB. WISS. BOT. 20 : 557-559.

SCOTT, D. H. & WAGER, H. 1888 - On the floating roots ofSesbania aculeata Pers. ANN. BOT. 1 : 301-314.

SCOPOLI, G. A. 1777 - Introductio ad historiam...(Pragae).

SENDULSKY, T. & BURMAN, A. G. 1978 - Paspalum species of the Serra do Cipó (1) : a contribution to the study of the Brazilian Poaceae. REVTA brasil. BOT. 1 : 1-15.

SENN, H. A. 1938 - Chromosome number relationships in the Leguminosae. BIBL. GENET. 12 : 175-336.

SHAH, G. L. & GOPAL, B. V. 1969 - Development of stomata in some Papilionaceae. CAN. J. BOT. 47 : 387-393.

SHETLER, S. G. & SKOG, L. E. 1978 - A provisional checklist of species for Flora North America (revised). Monographs in Systematic Botany, Missouri Botanical Gardens, Vol. 1 . Miss. Bot. Gdn (St Louis, U.S.A.).

SMITH, C. P. 1938 -1952 - Species Lupinorum . (Saratoga, U.S.A.).

SMITH, D. L. 1981 - Cotyledons of the Leguminosae. In POLHILL, R. M. & RAVEN, P. H. (eds), Advances in legume systematics, Vol. 2. HMSO (Kew, U.K.).

------------ 1983 - Cotyledon anatomy in the Leguminosae. BOT. J. LINN. SOC. 86 : 325-355.

SOLBRIG, O. T. 1970 - Plant biosystematics. The Macmillan Co. (New York, U.S.A.).

------------- 1972 - New approaches to the study of disjunctions with special emphasis on the American amphitropical desert disjunctions. In VALENTINE, D. H. (ed.), Taxonomy, phytogeography and evolution. Academic Press (London, U.K.).

SOUSA, M. & SOUSA, M. P. 1981 - New World Lonchocarpinae. In POLHILL, R. M. & RAVEN, P. H. (eds), Advances in legume systematics, Vol. 1. HMSO (Kew, U.K.).

STABER, M. J. 1909 - Notes on the anatomy of Sesban macrocarpa Muhl. BULL. TORREY BOT. CLUB 36 : 625-633.

STAFLEU, F. A. 1967 - Taxonomic literature. International Bureau for Plant Taxonomy and Nomenclature. (Utrecht, Holland).

-------------(ed.) 1983 - International Code of Botanical Nomenclature. Bohn, Schetelma & Holkema (Utrecht, Holland).

STEBBINS, G. L. 1950 - Variation and evolution in plants. Columbia University Press (New York, U.S.A.).

STEBBINS, G. L. 1971 - Chromosomal evolution in higher plants. Edward Arnold Ltd. (London, U.K.).

STIRTON, C. H. 1981 - Petal sculpturing in Papilionoid legumes. in POLHILL, R. M. & RAVEN, P. H. (eds), Advances in legume systematics, Vol. 2. HMSO (Kew, U.K.).

TAUBERT, A. 1894 - Lupinus. In ENGLER, H. G. A. & PRANTL, K. A. E. (eds) Die Naturlichen Pflanzenfamilien. 1(3) : 231.

---------- 1894 - Sesbania. In ENGLER, H. G. A. & PRANTL,K. A. E. (eds) Die Naturlichen Pflanzenfamilien 1(3) : 277-278.

TERREL, E. E. 1977 - The name for tomato. TAXON 26 : 129-148.

THORNE, R. F. 1973 - Floristics relationships between tropical Africa and tropical America. In MEGGERS, B. J. A. et al. (eds), TropiCal forest ecosystems in Africa and South America : a comparative review. Smithsonian Institution Press (Washington, D.C., U.S.A.).

TJIO, J. H. 1948 - The somatic chromosomes of some tropical plants. HEREDITAS 34 : 135-146.

TURNER, B. L. 1955 - Chromosome numbers in the genus Sesbania (Leguminosae) : evidence for a conservative treatment. RHODORA 57 : 213-218.

TURNER, B. L. 1959 - The legumes of Texas. Univerity of Texas Press (Austin, U.S.A.).

------------- 1981 - Thermopsidae. In POLHILL, R. M. & RAVEN, P. H. (eds), Advances in legumes systematics, Vol. 1. HMSO (Kew, U.K.).

UPPAL, H. L. 1955 - Green manuring with special reference to Sesbania aculeata for treatment of alkaline soils. IND. JOURN. AGRIC. SCI. 25 : 211-235.

URBAN, I. 1919 - Sertum Antillanum. FEDDE, REPERT. 16 : 149-150.

VELLOZO, J. M. C. 1825 - Flora Fluminensis. Vol. 7. (Rio de Janeiro, Brazil).

VISHNU-MITTRE & SHARMA, B. D. 1962 - Studies od Indian pollen grains. 1. Leguminosae. POLLEN ET SPORES 4 : 5-45.

WAINWRIGHT, C. M. 1978 - The floral biology and pollination ecology of two desert lupines. BULL. TORREY BOT. CLUB 107 : 24-38.

WATSON, S. 1873 - Revisions of the extra-tropical North American species of the genera Lupinus, Potentilla and Oenothera. PROC. AMER. ACAD. 8 : 517-618.

----------- 1878 - Bibliographical Index to North American Botany... Part I. Polypetalae. Smithsonian Institution (Washington, D.C., U.S.A.).

WHITE, P. S. 1981 - Sesbania, in Flora of Panama. ANN. MISS. BOT. GDN 67 : 760-765.

WILLDENOW, C. L. 1803 - Species Plantarum... 4th ed. Vol. 3, part 2. (Berlin).

WILLIAMS, C. A.; DEMISSIE, A. & HARBORNE, J. B. 1983 - Flavonoids as taxonomic markers in Old World Lupinus species. BIOCH. SYST. ECOL. 11 : 221-231.

WILLIAMS, W. 1984 - Lupins in crop production. OUTLOOK AGRIC. 3 : 69-76.

WILLIAMS, W.; AKHTAR, M. A. & FALUYI, M. 1980 - Cross compatibility between European and American lupinus species. BOT. J. LINN. SOC. 81 : 225-232.

WILLSON, M. F. 1983 - Plant reproductive ecology. J. Wiley & Sons (New York, U.S.A.).

WIHSHART, D. 1978 - CLUSTAN : cluster analysis package. Program Library Unit, Edinburgh University (Edinburgh, U.K.).