POLLEN MORPHOLOGY OF THE TRIBE LOTEAE (LEGUMINOSAE) BY LIGHT AND SCANNING ELECTRON MICROSCOPY

by

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ABSTRACT

Pollen morphology is shown to refute some taxonomic decisions related to the classification of old world Loteae and the genus Lotus. The analysis of data by numerical taxonomic techniques showed a clear taxonomic separation of many higher taxa based on the characters scored. Subgenera Syrmatium, Sympeteria and Acmispon were determined as being palynologically closely related, while subgenus Hosackia, palynologically is separate. Old world Lotus was determined to be stenopalynous while new world Lotus was eurypalynous. The various taxonomic treatments were assessed and relationships of old world Loteae seem to be more clearly defined than the relationships between North American taxa. This is supported by the results of the palynological study. Further taxonomical and biosystematical studies are required to clarify the taxonomy of Tribe Loteae, the genus Lotus sensu lato in particular. Some taxa considered as Lotus sensu stricto may indeed require reclassification into other taxonomic groups in the Leguminosae.

Résumé

La morphologie pollinique révèle ici un désaccord avec certaines décisions taxonomiques concernant la classification des Loteae européo-méditerranéens et du genre Lotus. L'analyse de données par des techniques de taxonomie numérique montre qu'il existe entre plusieurs importants taxa une nette séparation taxonomique basée sur les caractères évalués. Les sous-genres Syrmatium, Sympeteria et Acmispon semblent très voisins d'un point de vue palynologique alors que le sous-genre Hosackia s'avère palynologiquement différent. Le Lotus européo-méditerranéens a été jusqu'ici considéré comme sténopollinique et le Lotus américain, eurypollénique. Suite à de nombreux traitements taxonomiques, la parenté entre les Loteae européo-méditerranéens semble beaucoup mieux définie que celle qui existe entre les taxa nord-américains. Ceci est appuyé par les résultats de l'étude palynologique. D'autres études taxonomiques et biosystématiques s'avèrent nécessaires pour clarifier la taxonomie de la tribu Loteae et plus particulièrement celle du genre Lotus sensu lato. Quelques taxa qui jusqu'ici étaient incorporés au genre Lotus sensu stricto nécessitent vraisemblablement une reclassification vers d'autres groups taxonomiques des Légumineuses.

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CLAIM TO ORIGINAL RESEARCH

This thesis is the result of the author studying Lotus and Loteae pollen and is entirely based upon original observations. The technique of trying to relate numerical taxonomical techniques to Lotus and Loteae was explored for the first time. An attempt was successful in delimiting some of the higher taxa in Loteae or Lotus by pollen morphology. At the level of species some interesting relationships between the taxa were revealed. Scanning electron microscopy was used to study many taxa in a Leguminosae tribe for the first time. In addition, the major treatments of Lotus and Loteae were gathered together and assessed.

TABLE OF CONTENTS

LITERATURE REVIEW

I. PALYNOLOGY AND PLANT TAXONOMY

According to Hyde (1944) who coined the term palynology, it is a science which deals with the study of the walls of pollen grains and spores, but not with their live interior. More recently, however, much interest has been devoted to the study of the physiological processes within these fundamental agents related to sexual and often asexual reproduction in the plant kingdom (Heslop-Harrison, 1975; Linskins, 1963; Stanley and Linskins, 1974).

The origin of the word pollen is from the Latin meaning "fine flour" or "fine meal" (Kremp, 1965; Faegri and Iversen, 1964; Hyde, 1944). Pollen grains are correctly referred to as microspores in Phanerogams and as antherozoides in the Mosses (Jackson, 1928).

Since the invention of the microscope, pollen grains have interested the microscopist, naturalist, botanist and taxonomist. In an excellent review on the early state of the science Von Mohl (1835), reported that Geoffroy had orally presented to the French Academy of Sciences in 1811 his opinion that the form (morphology) of each species was constant. According to Von Mohl (1835) various botanists or naturalists between the years 1711 and 1832 including Gleichen, Link, Brown, Guillemin, Fritzsche, and Lindley, discovered various aspects relating to pollen grain morphology such as exine and intine, nucleus and colpi.

Indeed, Lindley (1830) used pollinia as the basis for his taxonomic treatment of the Orchidaceae. Von Mohl's (1835) paper is still considered to be an important contribution to palynology (Wodehouse, 1935; Erdtman, 1943, 1952; Crompton, 1982). As a result of discovering that many plant taxa can be identified by their pollen grains, the science of pollen analyses was developed by geologists-botanists to explain vascular plant succession in the post-glacial Pleistocene of Europe and North America (Tschudy and Scott, 1969). This resulted from the fact that pollen grains by virtue of their readily preserved walls were discovered in strata of lake bottoms and bogs in north-temperate regions (Erdtman, 1943, 1964).

One major limiting factor in the study of plant succession and climatology was the lack of an adequate pollen taxonomy. This in turn led to the development of many identification keys and descriptions by scientists for use at the regional floristic level. These works usually had a diagnostic key and were illustrated by pen and ink drawings or with photomicrographs. Among the more notable works are those of Erdtman (1943), Ikuse (1956), Faegri and Iversen (1964), Heusser (1971) and McAndrews et al. (1973).

Another point of interest in the study of pollen grains was the very important discovery that certain taxa caused

hayfever. The descriptions of the pollen grains of major importance in North America are presented by Wodehouse (1935, 1971). He also presented the first modern attempt at showing important phylogenetic aspects of pollen symmetry, structure, sculpturing and aperture arrangements of pores and furrows (pori and colpi). Another work describing pollen grains of regional hayfever plants is by Bassett et al. (1978). Regional studies showed that in order for the science of palynology to develop, a more systematic or taxonomic approach to various plant families and genera needed to be developed.

Following the research of Von Mohl (1835) and his contemporaries, Hassall (1842) studied pollen grains and tried to use their structure as a means of erecting a classification to angiosperm taxonomy. Wodehouse (1926, 1930) publishing on the Compositae, attempted to place before botanists the importance of pollen morphology to plant classification. He stated "in some groups of plants these (characters) are so few that little can be told about their phylogeny"; "in other groups, however, the structure of the grain is so remarkably various, offering so many characters of taxonomic value, that any attempt at classification of such groups is apt to lead to error unless

account is taken of the pollen grain structure" (Wodehouse, 1928). Since that statement of Wodehouse, the literature abounds with phylogenetic studies and taxonomic treatments of pollen grains. A complete bibliography of the taxa treated is given by Thanikaimoni (1972, 1973, 1976) and a current bibliography is published annually by the journal Pollen et Spores.

The most important treatise on pollen morphology and plant taxonomy was produced by Erdtman (1952, 1966). This was the only attempt to systematically gather all the data on pollen morphology. He organized this work on the basis of Engler and Prantl's Syllabus der Planzenfamilien, the most celebrated and recognized system of plant classification which was produced from 1889 to 1915. This work allowed botanists to observe pollen grain illustrations and descriptions linked together in a concise systematic treatment. He also cross-indexed families which have similar pollen grains, yet often are not closely related.

II. POLLEN GRAIN MORPHOLOGY

In order to understand the taxonomic implications of the morphology of pollen grain walls, a review of their physiological development, which is influenced by both external and internal processes, is necessary.

In addition, selection pressure and evolution play an important role in the form and function of pollen grains.

These factors therefore, often allow researchers to use morphological features of pollen grain walls to identify trends in the phylogeny of various taxa, or groups of related taxa, which subsequently aid us in understanding taxonomical relationships (Nowicke and Skvarla, 1979).

A. Ontogeny of the exine

The angiosperm pollen grain is commonly comprised of a multilayered or laminated cell wall. This physiological and ontogenetical process has been researched by a number of authors on selected taxa. For the purpose of this review only the common factors as outlined by Dickinson (1976) are considered. In that paper he has presented data showing similarities of exine formation between widely diverging taxa such as Pinus (Gymnospermae:Pinaceae), Cosmos (Angiospermae:Dicotyledoneae : Compositae) and Lilium (Monocotyledoneae : Liliaceae).

Essentially, the process of exine formation is cytoplasmically governed by the microtubules or dictyosome-like structures and their vesicles; subsequently, the vesicles and plasma membrane interact and organize these structures to imprint the protoplast surface. The process is achieved by a layering of the vesicles or by protoplasmic protrusions and is not produced in areas genetically predetermined to be colpi, since a membraneous barrier is

produced beneath the cytoplasm in that position. As the process proceeds, a secondary layer, comprised of deposited carbohydrates, displaces the plasma membrane to form and increase the depth of primordial sexine. This early sexine (exine) is thickened by polymer similar to sporopollenin. According to Dickinson (1976) this may take place on "membrane lamellae, either walls of vesicles or convoluted membrane structures", or it "may be polymerised between cytoplasmic protrusions rather than into them". Therefore, this process has an effect like a negative print of the protrusion arrangements (See Fig. 109).

After the pollen grains are released from the pollen mother cell tetrad callosic wall, the young exine is augmented from without by sporopollenin produced by the nurse cells of the tapetum. Hideux and Ferguson (1976) and Hideux (1979) showed an excellent series of transmission electron photomicrographs of these processes in the Saxifragaceae and Euphorbiaceae. Prior to this consolidation of the theory of exine ontogeny by Dickinson, numerous authors, such as Rowley (1971), Southworth (1971), Heslop-Harrison (1963, 1971), Echlin and Godwin (1968), Skvarla (1966), Skvarla and Turner (1971) and Echlin (1971a,b), surveyed various taxa such as Anthemis, Helleborus, and Zea with the transmission electron microscope. Their studies, aided by high quality photomicrographs of taxa suitable for ontogenetic studies

laid the foundation of basic data for our present day understanding of pollen wall (exine) ontogeny.

Basically, their studies revealed the following steps in ektexine-endexine formation: Callose pattern is determined in the cytoplasm by the generation of vesicles or microtubules in association with quantities of the endoplasmic reticulum; if highly formulated processes are to be developed, a massive protrusion is visible. Microtubules and other cell constituents are beneath the protrusion, but the protrusions are too electron dense to be associated with any particular organelle or part of an organelle; banked arrays of endoplasmic reticulum are formed, coated with ribosomes and producing dictyosome-like vesicles whose destiny are to become the developing pollen walls; at the cell surface, outside the plasma membrane larger bodies appear which stain with lipid stains. These bodies are quickly modified and they permeate between the protrusions and form a layer over the whole surface except for colpus areas; several layers are produced prior to release from the pollen mother cell tetrad; then the pollen wall expands due to unequal morphogenesis between the ektexine and endexine. Laminated areas are produced near colpi and the process is completed.

B. Pollen grain evolution, form and function

The principle given for the many different pollen morphological types is explained by Klacker (1965) who pointed out that at their surfaces, cells interact with their special environments. Pollen grains are cells developed at the anther interface, namely the tapetum. This interface is comprised of sugars and proteins. Rowley (1971) informed us in a review of this subject that the composition of glycocalyx is very important in the synthesis of pollen wall architecture, heteropolar systems, dimorphisms, the cell membrane, colpi forms, etc.... Rowley (1971) summarized the following development: 1) the exine is plastic to allow for alteration of shape; 2) exine modifications require transfer of ions, hence energy is required; 3) margins of germinal apertures expand during development and shrink at maturity; 4) polybasic molecules form an agglutination bridge between negatively charged sites. Many authors previously cited have linked pollen grain morphology to its form and function or evolution. Nowhere is this more evident than when a person examines certain discernible trends associated or correlated to the pollination mode of species; e.g. the viscine threads of Onagraceae pollen, the bladders evident on many Pinaceae pollen, the small size and buoyancy of Urticaceae pollen,

the large production of pollen of chasmogamous flowers and the low pollen production of cleistogamous flowers in the Plantaginaceae (Bassett and Crompton, 1968; Muller, 1979).

According to Heslop-Harrison (1979) "general features" of pollen grains "can now be interpreted as having adaptive significance ..." "...they can be shown to discharge important biological functions." In this sense, the exine is a repository for sphorophytic material. Heslop-Harrison et al. (1975) summarized these functions as follows: 1) the pollen grain wall is adapted to carry physiologically active materials derived from the sporophytic parent (the exine domain) and the gametophyte (the intine domain); 2) the incompatibility system is mediated by the sporophytic proteins contained (conveyed) in the exine cavities; Material of similar origin may also play a role in interspecific compatibility control; 3) intine enzymes function in the penetration of the stigma and in the early growth of the pollen tube and intine proteins may be involved in intra-specific compatibility control; 4) apertures due to the modified structures present in the exine function somewhat like the stomata of a leaf; they are potential outlets for the pollen-tube and as outlets for mobile gametophytic chemicals from the intine domain.

Interestingly, Heslop-Harrison (1974) found that many anomalous monocotyledenous taxa such as Crocus and Canna do not have these proteins. He inferred that some families with reduced exines may not convey tapetal proteins. Therefore, the incompatibility function may be contained in the cytoplasm, the intine, or in the ovary.

Indeed, many legumes such as Trifolium, Lotus and Vicia have non-ornamented (more or less psilate) sculpturing and few cavities (Ferguson and Skvarla, 1981; Gillett et al., 1973). Some species of these genera are well known to have self-incompatability problems (Dobrofsky and Grant, 1980a;b; Townsend, 1971) and sterility complications (Audran and Willemse, 1982).

Wodehouse (1935) made some interesting comparisons between selected taxa of various hayfever plants and used geometry to attempt to explain the various configurations, shapes, colpi and pori arrangements of pollen grains. This led to the trichoclassic system of explaining their various morphologies. However, this system does not take most anomalous pollen shapes into account (see Lesins and Lesins, 1979; Small et al., 1981a), particularly in the genus Medicago. Some of these shapes may be explained as being fixed through speciation, or perhaps due to chromosome loss.

or gain. These pollen grain shapes may be attributed to aneuploidy, or to unreduced or reduced gametes as shown by multiple spindle (microtubule) formation and irregular division of the pollen grains during and after telophase II in the pollen mother cells. These diverse forms may then become fixed characters.

Walker and Doyle (1975) showed a pollen wall pattern evolution and the apparent divergence of exine trends by comparing pteridophytes, gymnosperms and primitive angiosperm spores and pollen grains. These trends are summarized as follows: 1) atectate exine = pteridophytes; 2) atectate-granular-incipient alveolate-alveolate exine = gymnosperms; 3) atectate-granular-incipient columellate-tectate columellate exine = angiosperms.

III. POLLEN GRAIN CLASSIFICATIONS

There are in essence, two main systems of classifying and identifying pollen grains. One is a numerical classification based upon the "NPC" system of Erdtman (1963), or Ikuse (1956), where palynomorphs are categorized on the basis of their pore number, colpi number and position of colpi or pori. The other system is based upon comparing pollen to twenty-two classes of palynomorphs and was devised by Faegri and Iversen (1964). Both systems are complementary and useful to the palynological taxonomist or pollen identifier.

Unfortunately, the keys are only useful for pollen of north-temperate taxa. In addition, the pollen grains of many taxa are very similar in morphology and often are not keyed out to the species level or included in the treatment. Often keys are inadequate, and pollen taxonomies and special keys to many groups are now being produced; e.g." World Pollen Flora" edited by Dr. Swiert Nielsson includes palynological accounts of various families at the taxonomic level.

IV. TAXONOMIC PROBLEMS IN LOTEAE AND REASONS FOR RESEARCH IN THE TRIBE

A. Importance of Loteae

The Loteae is a very important tribe in the Leguminosae because many of the taxa are agriculturally or ecologically significant (Duke, 1981). This significance is due to the desirable characteristics associated mainly with the genera Lotus, Tetragonolobus, and Dorycnium. Some taxa contain pasture and cover plants and supply excellent forage value and browse. Many species of this tribe do not cause bloat in cattle. Allen and Allen (1981) reported that 55 species of Lotus, 5 species of Dorycnium, and 5 species of Tetragonolobus, showed root nodulations indicative of nitrogen fixing ability through associations with various taxa of the bacteria genus Rhizobium.

B. The Taxonomic Problem in Loteae

Since there was no monographic taxonomic treatment of Lotus sensu lato available, it seemed advisable to study the taxonomy-palynology of the species of the Loteae and to investigate the palynology of those taxa which have been shown by various authors to be related at either the specific or generic level to the Loteae or Coronilleae in the Leguminosae.

All taxonomic treatments with the exception of Bentham and Hooker (1865), Taubert (1894), Hutchinson (1964) and Polhill (1981) have been regional in scope and have failed to prove that groupings of taxa, at many levels of the taxonomic hierarchy are cohesive.

All Lotus and Loteae taxonomic treatments, including Brand's 1898 monograph, have been controversial due to attempts by various taxonomists to include or exclude taxa which occur indigenous to North America, or Africa, in their monographs (Greene, 1890; Brand, 1898). Modern authors have tended to ignore this problem (Polhill, 1981; Isley, 1981). It can be observed in Table 1 that not only are tribal differences taxonomically inconsistent, but many generic interpretations of taxa also exist between the authors. In spite of these differences at taxonomic ranks higher than

the species, a considerable proportion of the taxonomy at the level of species is treated remarkably similar and is relatively uncontroversial [e.g. see treatments of Greene (1890), Ottley (1923, 1944), Wiggins (1980) and Isley (1981)]. A comparison of the major treatments at the generic and sub-generic levels is shown in Section VIII (E). The main reason for problems at the higher taxonomic level is the lack of an adequate modern phyletic treatment which is needed to indicate greater taxonomic convergence and dissimilarity of the taxa. In the main, all older and recent treatments have not been phyletic in scope, and tended to group many dissimilar taxa into somewhat artificial subgenera, sections and species groups; therefore, they aided in the identification of taxa, but contributed scant information as to their biosystematical relationships.

Practical considerations may well be the cause for a lack of taxonomic agreement. Several reasons may be advanced for the cause of an inadequate taxonomy of these groups presently under study: 1) taxonomic tradition, e.g. adherence to names complying with the Code of Botanical Nomenclature; the reliance of many taxonomists on the Engler and Prantl system (Taubert,1894); 2) The occurrence of endemic Loteae-like taxa at several "centers of origin" or

"centers of diversity" has caused taxonomists to create many taxonomic categories in Loteae, and especially Lotus, to accommodate these taxa. These centers are the Canary (Atlantic) Islands and North Africa (Monod, 1980), Central Africa (Gillett, 1958); the Mediterranean region of Europe (Ball, 1968) and the Middle East (Heyn, 1966, 1970a,b; Heyn and Herrnstadt, 1967) and the Cordillerian-desert regions of North America including Mexico (Ottley, 1923, 1944). This geographic discontinuity has led initially to the description of many genera such as Hosackia and Pedrosia which subsequently became classified as Lotus taxa (see Table 1). These endemic taxa have been considered as species groups, sections, sub-sections, or sub-genera of the genus Lotus by various authors. Some of these taxonomic complexes may be worthy of generic status (see Appendix I for the taxa treated in this study). It is hoped that evolutionary and taxonomical trends may be shown through pollen morphological studies. Such studies should aid in delimiting these taxa, or groups of taxa, at various taxonomic levels in the tribe Loteae.

Since there is a lack of a comprehensive monograph of the tribe Loteae, I have based this study on the taxonomic treatments of the following authors: Isley (1981), for the

North American taxa; Ball (1968), for European taxa; Heyn (1970b), for the Middle-Eastern taxa; Monod (1980), for Section Pedrosia found mainly in North Africa, Azores, Cape Verde and the Canary Islands, and Gillett (1958), for the Central African taxa. In no sense, except for the practicality of using Ball (1968) for the European elements, are floristic treatments being considered. Neither are floristic synomyms used except rarely for purposes of clarifying nomenclatural problems related to specimen identification (see Appendix I).

TABLE 1. SYSTEMATIC REVIEW OF LOTEAE-CORONILLEAE

Genus	Polhill (1981)	Hutchinson (1964)	Taubert (1894)	Bentham & Hooker (1862-1867)	DeCandolle (1825)
Anthyllis	L	L	L	L	L
Helminthocarpon	Syn.(Lotus)	L	L	L	-
Securigera	Syn.(Coronilla)	L	Syn.(Bonaveria)	L	C
Cytisopis	L	L	L	L	-
Hosackia	Syn.(Lotus)	L	L	L	-
Dorycnium	Syn.(Lotus)	L	L	L	-
Lotus	L	L	L	L	L
Tetragonolobus	Syn.(Lotus)	Syn. (Lotus)		Syn.(Lotus)	C
Hymenocarpus	L	L	Syn.(Circinus)	L	
Hippocrepis	C	C	H-C	H	C
Scorpiurus	C	C	H-C	H	C
Hammatolobium	C	C	H-C	H	
Ornithopus	C	C	H-C	H	C
Coronilla	C	C	H-C	H	C
Gamwellia	Removed	L			
Lyauteya	Syn.(Cytisopsis)	L			
Pseudolotus	Syn.(Lotus)	L			
Kerstania	Syn.(Lotus)	L			
Doryconopus	Syn.(Anthyllis)	L		Syn.(Anthyllis)	
Psysanthyllis	Syn.(Anthyllis)	L		Syn.(Anthyllis)	
Cornicina	Syn.(Anthyllis)	L		Syn.(Anthyllis)	
Artrolobium	Syn.(Coronilla)	C		Syn.(Ornithopus)	
Anopetita	C	C			
Circinus	?	Syn.(Hymenocarpus)	L		
Bonaveria	?	Syn.(Securigera)	L	Syn.(Securigera)	
Benedictella	L	L			

L = Loteae Tribe, C = Coronilleae Tribe,
Removed = placed in Tribe other than L or C,
H-C = Hedysareae-Coronillae,
? = not mentioned, H = Hedysareae

V. TAXONOMY AND PALYNOLOGY OF LOTEAE

In a translation of the classical Greek Herbal of Dioscorides circa 1 A.D., Gunther (1959) pointed out that Dioscorides included a plant now known as Lotus ornithopodioides. (He has in this Herbal a figure of the taxon.) Dioscorides mentioned that the plant was apparently known under several local names. These names were Ammonos, Astrion, Caciatrix, Stilago and Sangrienaria. The plant was "eaten as a pot herb..... grows in tilled places and on hillocks and by the high-waies."

Much later plants of Lotus are mentioned in the Herbal or General History of Plants, better known as Gerard's Herball. Johnston (1633) in that Herball named three Lotus taxa: Lotus trifolia corniculata, horned or codded clover; Lotus quadrifolia, four leafed graffle and Lotus siliquadrata, square crimson velvet pease. Johnson also indicated that the naturalists Camerarius and Clusins called plants Lotus pulcherrima tetragonolobus and Lotus siliquosus rubello flore, respectively. These were apparently known in latin as "psium quadratum". Interestingly, "the inyce given to drinks, cureth young children of the disease called in english the purples".

Tournefort (1719) in his "Institutiones", that important work prior to that of the Species Plantarum by Linnaeus listed 23 taxa of Lotus, 32 taxa of Ononis, 3 taxa

of Securidaca and 2 taxa of Dorycnium. Linnaeus in the Hortus Clifforteanius (1737) listed 4 taxa of Coronilla, 3 of Ornithopus, 1 of Scorparius, 3 of Hippocrepis, 3 of Anthyllis, 3 of Dorycnium, 10 Lotus species plus additional forms and 6 species of Ononis plus some forms. As more specimens were received and studied by Linnaeus, the list of taxa increased and finally Linnaeus (1753) in the Species Plantarum treated over 55 taxa including a current bibliography.

Tournefort (1719) placed the plants he referred to as Lotus, or relatives, in the Class X Sections I to IV, listing various genera within each section. His main taxonomic distinctions were based upon traditional useage, the papilionaceous flowers and number of leaves or leaflets.

However, Linnaeus (1753) in his sexual system, positioned plants now referred to as Loteae in the Diadelphia decandria section based upon their having diadelphous stamens.

The Leguminosae was first given formal family status in taxonomy by Jussieu in Gen. 345 (1789), and was confirmed by De Candolle in Prod. II 93 (1825) and Bentham and Hooker in Gen. I (1862) 434.

The Loteae were delimited as a tribe in the Leguminosae family by De Candolle in 1825. He used morphological

characters associated with the embryo, legumes (fruits) and the flowers to subdivide the family into 11 tribes.

Bentham and Hooker in their Genera Plantarum 1862-1867 also recognized the Tribe Loteae. They further increased the number of tribes of the Leguminosae to 23. Morphological characteristics selected were similar to those used by former authors. They combined suborders used by DeCandolle (1825) into three suborders namely: Papilionaceae, Caesalpinaceae and Mimoseae. These suborders are often given separate family rank by authors. In the most recent attempt to classify the Leguminosae, Polhill (1981) agrees that the Loteae is a tribe of the Papilionoideae. In his synopsis, he has pointed out many of the problems encountered by taxonomists in revising the groups both at an inter-and infra-group level. In his review it was stated that authors such as Hutchinson (1964), Takhtajan (1969), Yakovlev (1972) and El-Gazzar (1981) gave the subfamily, family rank. It is not suprizing that, with so many difficulties at the rank of family, many taxonomic anomalies should occur at the rank of tribe, genus or species.

Recently, the subfamily Papilionoideae was divided into 31 tribes (Polhill, 1981). The tribe Loteae comprised four genera, which he categorically indicated were closely related to the Tribe Coronilleae. The genus Lotus posed the most difficult generic delimitation. Representative photographs of plants in the Loteae are shown in Figures 118 to 136.

Ferguson and Skvarla (1981) surveyed the pollen morphological and other recent palynological literature available for the Papilionoideae. They included a SEM-TEM study of selected taxa from all of the tribes as delimited by Polhill (1981). They identified certain pollen morphological trends which are: 1) thickening of the endexine, loss of a foot layer and various modifications of the ektexine; 2) a specialization of apertures from colpi to pori and a more elaborate tectum structure; 3) a reduction of the endexine so as to be almost indistinct, the development of a distinct footlayer with long columellae; 4) the loss of the lalongate endoaperture and the occurrence of a distinct colpus membrane, or operculum, or margo. They stressed that their survey was a starting point for the study of Papilionoideae pollen and that considerably more investigative research work is required in particular tribes and genera.

Various authors [for example, Anderson (1961), Autug et al. (1971), Erdtman (1963), Faegri and Iverson (1964), Fisher (1890), Godwin (1975), Hansgrig (1897), Hassall (1842), Ikuse (1956), Nika (1954), Parmentier (1901), Planchais (1964); see Thanikaimoni (1972, 1973, 1976) or the bibliographic annual supplements to Pollen et Spores] studied Loteae-Coronilleae pollen related to regional geological problems, honey plants and taxonomy (identification) of selected taxa.

Gillett et al. (1973) have studied the pollen taxonomy of the North American Trifolium. There has been a trend recently to using numerical taxonomical techniques to study pollen data. A review of some of the methodologies employed are given in Hideux (1977). Small et al. (1981[a]) applied numerical taxonomic methods to the study of Medicago, Trigonella, and Melilotus pollen morphology.

Grunet (1981) supported the phylogenetic approach of Ferguson and Skvarla (1981) in switching from a colpi-pori-based classification to a system based on trends in the endexine-ektexine rather than the "pollen type" approach which is based upon aperture arrangements. Furthermore, he states that "when a great amount of sporopollenin is used to build endexine, this generally seems to be to the detriment of the ektexine and vice versa.... therefore within the

equilibrium of ektexine-endexine the infratectal layer is of great importance."

Stainier and Horvath (1978a,b) and Horvath and Stainier (1979, 1980) discovered in a study of the pollen wall ontogeny of Phasaeolus-Vigna that the aperture type depended upon the exine structure. Compound apertures depended upon a columellae-infratectum; simple apertures depended upon a simpler granular tectum structure. Intermediate structural architecture produced either compound or simple apertures.

Hutchinson (1969) considered the Leguminales (Leguminosae) to have arisen from Magnoliales, Diapensiales, and Rosales. His Leguminales comprised three families:- Caesalpinaceae, Mimosaceae, and Fabaceae (=Papilionaceae). The taxa of Papilionaceae R. Br. are distinguished from those of the other families by possessing luminaceous tannin sacs, having brown aluminous contents, thus separating it from Caesalpinaceae, and those having simple uniseriate trichomes made up of long terminal cells supported by one or several short basal cells unlike either the Caesalpinaceae or the Mimosaceae.

Hutchinson (1964) felt that anther form and dehiscence or indehiscence of fruits had taxonomic value. Glands, stipules and the transverse jointing of fruits also

indicated the climax of fruit (legume) evolution in the family. Interestingly enough, all taxonomists and students of the Leguminosae seem to have difficulty understanding the relationships of the various genera in the tribes Loteae or Coronilleae. Many of the characteristics used to separate plant groups into taxonomical categories "higher" than the genus seem to pose problems as shown in the diagnostic Tribal key of Polhill (1981).

Davis and Heywood (1963), in their important textbook on plant taxonomy, coined the category "dustbin taxa". They state, the taxonomist may be "left with one or several groups of plants that cannot be classified into any of the obvious striking species and which therefore form dustbin species". "Dustbin species may be an unnatural agglomeration which further study may enable us to disentangle." Such is the case, I feel, for many taxa included in the Loteae, the genus Lotus in particular.

Hutchinson (1969) found too many exceptions to allow for adequate key characters to be used in the classification of the tribes in the Papilionoideae. This can be seen by examining both Hutchinson (1969) and Polhill (1981) for their illustrated taxa. They pictured legumes (pods) of the following genera: Psophocarpus, Spatholobus,

Sesbania and Onobrychis which closely resemble the morphology of legumes of genera presently included in the Loteae.

It is also interesting to note that evolution has lead to the production of legumes in Medicago Section Hymenocarpos Seringe, of Tribe Trifolieae that are similar in morphology to the genus Hymenocarpus of the Tribe Loteae. The medicagoid species is Medicago radiata L., which was at one time considered by both Linnaeus and Boissier to be a Trigonella species of the Tribe Trifolieae (Lesins and Lesins, 1979; Small, 1981; Small et al., 1981b). Unfortunately, no author has shown figures of all of the taxa in Loteae for purposes of comparing diagnostic characteristics of legumes, leaves and flowers.

Recent studies in serology, wood anatomy, sieve elements, chemical taxonomy, petal sculpturing, biogeography, and botanical history (Polhill and Raven, 1981) have contributed considerably to the understanding of many groups of the Leguminosae in general, but add little to the understanding of the tribes Loteae-Coronilleae in particular. Bentham and Hooker's (1865) treatment clearly showed a relationship between the tribes Loteae and Galegeae. Further study at the level of traditional

taxonomy, as well as biosystematic studies, phenetic and cladistic analyses of these tribes are required on the world level. The regional taxonomic treatments are not only inadequate but are misleading. Even Polhill's (1981) world treatment of trends in Papilionoideae is weak, in that his major groupings are only useful to determine the following: 1) the Sophoreae; 2) the genistoid alliance ; 3) the tropical tribes; 4) the temperate herbaceous tribes including Galegeae sensu stricto, Hedysareae sensu stricto, Loteae, Vivieae, Trifoleae and relatives.

Papilionoideae pollen grain studies of Ferguson and Skvarla (1981) showed an Old World-New World divergence based upon the former having a thickening of the endexine and loss of foot layer and the latter having a reduction of the endexine and the development of a distinct foot layer and longer columellae. These trends are interesting since cryptic pollen characters are considered to be conservative and probably indicate an Early Tertiary separation and independent evolution of the taxa.

Polhill (1981) identified the following important trends in Old World versus New World Papilionoideae:

OLD WORLD	NEW WORLD
1. Nectary - interstaminal disc, pollen (explosive release)	1. Nectaries - retained in hypanthium, pollen (passive release)
2. Flowers - (excl. Indigofereae) clustered on the rachis.	2. Flowers - in a pseudoraceme
3. Seedling leaves - usually unifoliate, opposite	3. Seedling leaves - usually not differentiated, alternate
4. Seeds - containing canavanine	4. Seeds - not containing canavanine (Bell et al., 1978)

METHODOLOGY

VI. MATERIALS AND METHODS

A. Pollen morphology and terminology

The following discussion will explain the various methodologies used to describe pollen grains in taxonomy-morphology.

1) Size is determined for grains possessing regularly distributed and oriented pores and furrows on the basis of a polar-equatorial axis. The polar axis is always positioned in the same direction as the furrows (colpi) regardless of pollen shape. The equatorial axis is at right angles to the polar axis. Therefore, it is possible to assign shape classes based upon the ratio, Polar:Equatorial axis (P:E) (Kremp, 1965).

Erdtman (1952) distinguished the following shape classes:

P.E.			
	2.0	:	perprolate
	1.33-2	:	prolate
	1.14-1.33	:	subprolate
	1-1.14	:	prolate spheroidal
	1.0	:	spheroidal
	1-0.88	:	oblate-spheroidal
	0.88-0.75	:	suboblate
	0.75-0.50	:	oblate
	0.50	:	peroblate

2) Apertures are described using the morphological terminology of Iversen and Troels-Smith (1950): pori, colpi, and colpi transversales. Using their system pori can be distinguished by having a length:breadth < 2; if length:breadth > 2 the aperture is a colpus. If the endexine is thickened underneath a porus or colpus apertures are called costapori or costacolpi. Colpus transversales is a term used to indicate a thinning of the endexine and is usually found only in the complex apertures, e.g. colporate apertures. In Loteae-Coronilleae all apertures are colpi, transversales.

3) Iversen and Troels-Smith (1950) also developed the Polar Area Index (PAI). It is the ratio between the greatest distance of the ends of the colpi and greatest breadth of the pollen grain, which is normally the equatorial axis. It reflects the length that colpi extend into the polar area.

4) Sculpture may be said to be those ornamentations which show only in relief under the microscope.

5) Structure refers to the ornamentation of the wall (exine) when grains are examined in section; therefore structure is always in profile.

For further discussion of pollen terms the reader is referred to Kremp (1965), Praglowski (1970, 1971), Praglowski and Raj (1979), and the glossary in Punt (1962).

B. Light microscopy

Flowers from reliably identified dried herbarium specimens were examined for anthers which were beginning to dehisce using a stereomicroscope and watchmaker forceps. Several florets were removed at that stage of development and material was acetolized according to the procedure of Erdtman (1960) modified in the following manner:

(1) Using a funnel and 40 mesh saran screen, grind the entire flower into a 15 ml centrifuge tube;

(2) Add a 7 cc mixture of freshly made 9:1 acetic anhydride: sulphuric acid;

(3) In a double boiler-waterbath bring tubes to 100°C stirring frequently with a clear glass rod;

(4) Centrifuge in a clinical centrifuge and decant

(5) Wash in 7 cc distilled H_2O and stir contents (Vortex Jr. Mixer), centrifuge and decant;

(6) Wash in 7 cc distilled H_2O, stir, centrifuge and decant;

(7) Wash in 5 cc glacial acetic acid, stir, centrifuge and decant;

(8) Wash in 5 cc 95% ethanol (ETOH) stir, centrifuge and decant;

(9) Wash in 3 cc 100% ETOH stir, centrifuge and decant;

(10) Take a small amount of pollen in a micropipette and mount in glycerine jelly - observe under a compound microscope. If the exine is too dark, bleach pollen using the following procedure:

(a) Reverse procedure until step (7) when pollen is in glacial acetic acid;

(b) Add 1 drop of sodium chlorate to 1 drop hydrochloric acid. Observe pollen and supernatant under a 40X stereomicroscope until exine is golden brown; carry on to step (10);

(11) Wash in 3 cc acetone, stir, centrifuge and decant;

(12) Wash in 3 cc thiophene-free benzene, stir, centrifuge and decant;

(13) In a porcelain spot-plate place (circa) 3 cc of silicone oil, 40,000 viscocity (Dow Corning);

(14) Using a microspatula, or micropipette, remove pollen from benzene and embed in the silicone oil (prepare microscope slide).

Material was also prepared in glycerine jelly for analysis. This involves reversing the above procedures from step (12) through (9). Pollen grains are removed in a micropipette from the 100% ETOH and placed in melted glycerine jelly on a microscope slide. The ETOH is evaporated from the preparation on a alcohol or gas flame. Coverslip and seal the preparation.

In addition, microscope slides of unacetolized pollen were made using melted glycerine jelly to which several crystals of basic fuschin were added. Basic fuschin, when added to achieve the correct optical intensity, stains the cytoplasm of pollen grains pink and the exine dark red clearly showing the sculpturing morphology.

Voucher specimen pollen slides are deposited in the Department of Agriculture, Ottawa (DAO) Permanent Pollen Collection.

C. Pollen grain preparation for scanning electron microscopy (SEM)

(1) Standard aluminum specimen stubs were coated on the top surface with a light application of adhesive. The adhesive is made by removing the glue from cellophane tape using chloroform as a solvent. The chloroform-glue is applied to the stub surface with a toothpick. The chloroform evaporates leaving a sticky stub surface to which the pollen will adhere. (Note: too thick an application will cause the pollen grains to be absorbed into the adhesive.)

(2) Pollen grains were then extracted from flowers having dehiscing anthers using fine watchmaker forceps under a stereomicroscope.

(3) They were dusted onto an aluminum standard specimen stub using a single hair brush.

(4) The pollen and stubs are then stored in "dryerite" desiccant overnight to remove any moisture which may have been absorbed by the pollen grains (e.g. humidity from the ambient air).

(5) The specimen stubs are then coated by two bursts of molten gold in a shadow-caster at 10^0 and 60^0 respectively at 10^{-6} atmosphere while the specimen stub rotates through 180^0. (200nm thickness of gold/specimen)

(6) The specimens are then examined at 30^0-40^0 on a Cambridge Instruments Limited Mark IIa SEM at 10,000 volts on aperture setting No. 2.

(7) Photographs were made using Polaroid Type 42 film 400 ASA or Plus X 135-20 Kodak film.

D. Preparation of pollen for examination of structural detail

The recent technique of Blackmore and Dickinson (1981) was modified to show structural details exhibited in the pollen wall of taxa selected arbitrarily on the basis of their divergent sculpturing morphology as revealed by both interference contrast microscopy and SEM.

The procedure is as follows:

(1) Flowers were selected in an appropriate stage (see former preparation methods);

(2) Flowers were heated in distilled H_2O to which a small quantity of laboratory aerosol was added;

(3) Flowers were placed in a watch-glass and squeezed gently with watchmaker forceps. (The flower structure acts as a bellows, through which pollen grains are expelled into the aerosol-distilled H_2O solution in an almost pure state.)

(4) Swirl the watch-glass (as if panning for gold) to concentrate the pollen grains in the centre, remove pollen by using a micropipette and place in 5 ml centrifuge tube with 4 cc distilled H_2O, stir, centrifuge and decant.

(5) Add 4 cc distilled H_2O, stir, centrifuge and decant.

(6) Add 2 cc of warm 15% aqueous solution of gelatin, stir, centrifuge and decant.

(7) Repeat step (6).

(8) Remove melted gelatin and pollen from centrifuge tube by micropipetting into half of a gelatin capsule.

(9) Allow pollen to precipitate to bottom of gelatin capsule, freeze and store for sectioning.

(10) Place frozen capsule in embedding block of cryostat microtome at -30^0C and trim material for sectioning.

(11) Prior to sectioning, dip block in liquid nitrogen.

(12) Section at half the diameter of the grains to be examined in a cryostat microtome at -30^0C.

(13) Collect sections in a centrifuge tube and dissolve gelatin in boiling water, stir, centrifuge and decant.

(14) Mount on standard SEM stubs.

E. Photomicrography of pollen grains

Pollen grains were examined using a Reichert Zetopan Research Microscope under Nomarski interference contrast microscopy. Photomicrographs were taken under Köhler illumination to obtain the maximum resolution and contrast. Films used were Panatomic X (ASA 25) and Plus X (ASA 125) using a Carl Zeiss Jena camera and automatic exposure device. Prints were prepared using high quality Kodak print paper and to each photomicrograph a micrometer bar was added to show appropriate pollen size of that figured taxon.

F. Specimens examined

Pollen grains examined for this study were obtained from herbarium specimens borrowed from herbaria on loan from the following institutions: Department of Agriculture, Ottawa, Canada (DAO); Hebrew University, Jerusalem (HUJ); Royal Botanical Gardens, Surrey, England (KEW); McGill Unversity Herbarium, Macdonald College, Ste. Anne de Bellevue, Quebec, Canada, (MTMG); and University of California, Berkley, California, U.S.A. (UCB). Acronyms are from Holmgren et al. (1981).

G. Numerical taxonomy

The characters studied were assessed and their character states are given in Appendix II. They were scored in ordered series. The states were either continuous, ordered

multi-state or two state. All states were evaluated by myself to insure realiability.

The figures included in the analysis are the result of scoring at least 20 individual pollen grains per OTU (Operational Taxonomic Units = taxa). A list of the data are presented in Appendix II. The flow chart for numerical taxonomy as outlined by Sneath and Sokal (1973) was followed. i.e.

1) Select specimens
2) Discover and record data
3) Code characters and OTU's
4) Calculate
5) Extract data per taxon
6) Identify specimens.

The numerical analysis was carried out using programs and computation facilities provided by the Engineering and Statistical Research Institute and the Data Processing Division, Financial and Administration Branch, Agriculture Canada, according to the following methods. Agglomerative cluster analysis was executed using the Gower (1971) similarity coefficient for "mixed data". This coefficient corresponds to the complement of a manhattan metric standardized by range. Absence, therefore, contributed equally to presence. Sorting algorithms such as single

linkage (nearest neighbour), unweighted centroid (median), unweighted pair group using arithmetic averages (WPGMA), incremental sums of squares (Burr, 1970) with flexible sorting of $\alpha = 0.625$ and $B = 0.5$ where $\alpha = (1-B)$ (Lance and Williams, 1967). These methods and their properties are discussed by Jardine and Sibson (1971a, 1971b), Williams et al. (1971), Sneath and Sokal (1973) and Clifford and Stephenson (1975). Ordination of the OTU's was computed by principle co-ordinate analysis (Gower, 1966) and by use of the minimum spanning tree (MST).

The programme uses the following coefficients; Jaccard, simplematching, Dice (=Burt), 1st Kulczynski, 2nd Kulczynski, Ochai, Correlation ratio (Sorgenfrei), Simpson, Braun-Blanquet, Fager, Rogers and Tanimoto, method coefficient, Hamann, Yule, Phi, Preston (the value of DIS which satisfies, where DIS is the dissimilarity coefficient), Sokal (average taxonomic linkage). According to Lefkovitch (1976) the programme also allows for mixed data, it admits five types of characters viz: dichotomies, alternatives, multistate unordered, multistate ordered and quantitative, in any combination.

VII. RESULTS

A. Pollen descriptions based upon light microscopy

LOTEAE

Anthyllis montana L. in Sp. Pl. 719 (1753)

Grains spheroidal P:E 1.00, 25.5-31.0 µm (ave. 28.5 µm); tricolporate, tetracolporate and pentacolporate, mainly tetracolporate; PAI 0.822, pores vestibulate; ektexine and endexine 1.0 um thick; psilate sculpturing.

Anthyllis vulneraria L. in Sp. Pl. 719 (1753)

Grains prolate P:E 0.875, width 31-39 µm x length 34-47 µm (ave. 35 x 40 µm); tricolporate; PAI 0.650, pores vestibulate; ektexine and endexine 1.5 µm thick; psilate sculpturing.

Anthyllis vulneraria L. ssp. praepropera (Kerner) Bornon in Bot. Jahrb. 59: 483 (1925)

Grains prolate P:E 0.857, 27-31 x 29.3-34.2 µm (ave. 29.3 x 34.2 µm); tricolporate; PAI 0.650 pori vestibulate; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Cytisopsis dorycniifolia Jaub. et Spach in Illustr. 1:155 (1842)

Grains prolate P:E 1:091, 34.2 x 37.3 µm (32.0-37.0 x 34.4-39.5 µm); tricolporate; PAI 0.484, pores vestibulate; ektexine and endexine 1.0 µm thick; verrucate sculpturing at upper ends of colpi; psilate elsewhere.

Dorycnium hirsutum (L.) Ser. in DC. Prod. 2:208 (1825)

Grains prolate P:E 1.239, 26.0 x 32.2 µm (24.0-28.0 x 30.6-34.4 µm) tricolporate; PAI 0.643, pores non-vestibulate; ektexine and endexine 1.0 µm thick; sculpturing rugulate.

Dorycnium rectum (L.) Ser. in DC. Prod. 2:208 (1825)

Grains prolate P:E 1.345, 17.7 x 23.8 µm (16.5-18.0 x 23.0-25.5 µm) tricolporate; PAI 0.482, pores non-vestibulate; ektexine and endexine 1.0 µm thick; sculpturing rugulate.

Dorycnium axilliflorum Hub.-Mor. in Feddes Rep. 46:138 (1939)

Grains prolate P:E 1.165, 26 x 30 µm (25.5-28.5 x 29-33 µm) tricolporate; PAI 0.456, pores non-vestibulate; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Dorycnium amani Zohary in Pal. J. Bot. Jer. Ser. 2:165, f. 16-18 (1941)

Grains prolate P:E 1.095, 26.0 x 30.0 µm (25.5-28.5 x 29.0-33.0 µm) tricolporate; PAI 0.456, pores non-vestibulate; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Dorycnium pentaphyllum Scop. in Fl. Carn. 1(2):87 (1772)

Grains prolate P:E 1.207, 21.3 x 25.7 µm (19.0-23.0 x 24.0-28.0 µm), tricolporate; PAI 0.336, pores non-vestibulate; ektexine and endexine 1.0 µm thick; rugulate sculpturing.

Dorycnium pentaphyllum Scop. in Fl. Carn. 2(2):87 (1772)

Grains prolate to oblate P:E 1.039, 23.1 x 24.0 µm (22.0-25.5 x 23.0-25.5 µm) ; tricolporate; PAI 0.500, pores non-vestibulate; ektexine and endexine 1.0 µm thick; rugulate sculpturing.

Dorycnium pentaphyllum Scop.

Grains prolate P:E 1.239, 26.0 x 32.2 µm (24.0-28.0 x 30.6-34.4 µm) ; tricolporate; PAI 0.643, pores non-vestibulate, circular, colpi serrate; ektexine and endexine 1.0 µm thick; regulate sculpturing.

Hymenocarpus circinnatus (L.) Savi. in Fl. Pis 2:205 (1798)

Grains spheroidal P:E 1.000, 26.8 µm (24.2-28.1 µm), 6-colporate; PAI 0.522, with compressed polar ends, pores not distinctive; ektexine and endexine 1.5 µm thick; psilate sculpturing.

LOTUS AEGEUS GROUP

Lotus macrotrichus Boiss. in Ann. Sci. Nat. Ser. 4(2):250 (1854)

Grains prolate P:E 1.391, 10.5 x 14.6 μm (9.0-11.5 x 12.8-15.3 μm), tricolporate; PAI 0.443, pores lalongate ora; ektexine and endexine 0.5 μm thick; rugulate sculpturing.

LOTUS ANGUSTISSIMUS GROUP

Lotus angustissimus L. in Sp. Pl. 774 (1753)

Grains prolate P:E 1.255, 10.0 x 13.7 μm (9.0-12.0 x 11.5 17.0 μm); tricolporate; PAI 0.660; pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus palustris Willd. in Sp. Pl. 3:1394 (1802)

Grains prolate P:E 1.560, 9.0 x 14.0 μm (8.0-10.0 x 13.0-15.0 μm); tricolporate; PAI 0.426, pores lalongate ora; ektexine and endexine 0.5 μm thick; psilate sculpturing.

Lotus parviflorus Desf. in Fl. Atl. 2:206 (1799)

Grains prolate P:E 1.381, 12.6 x 17.4 μm (11.5-13.0 x 16.6-17.9 μm); tricolporate; PAI 0.589, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus subbiflorus Lag. in Varied. Ci. Lit. Art. (Madrid) 2(4):213 (1805)

Grains prolate P:E 1.515, 12.2 x 18.6 µm (11.5-12.8 x 17.0-21.0 µm) ; tricolporate; PAI. 0.398, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

Lotus corniculatus L. in Sp. Pl. 775 (1753)

Grains prolate P:E 1.191, 12.6 x 19.1 µm (11.5-14.0 x 17.8-21.7 µm) tricolporate; PAI 0.243; pores lalongate ora; ektexine and endexine 0.7 µm thick; micro-rugulate sculpturing.

Lotus tenuis Waldst. et Kit. ex Willd. in Enum. Pl. Hort. Berol. 797 (1809)

Grains prolate P:E 1.181, 13.8 x 16.3 µm (12.8-14.6 x 15.3-17.9 µm) tricolporate; PAI 0.492, pore lalongate ora; ektexine and endexine 1.0 µm; psilate sculpturing.

Lotus uliginosus Schk. in Bot. Handb. 2:412 (1808)

Grains prolate P:E 1.602, 12.8 x 20.5 µm (11.0-14.0 x 19.0-21.0 µm) tricolporate; PAI 0.357, pore lalongate ora; ektexine and endexine 1.0 µm thick; rugulate sculpturing.

LOTUS NAMULENSIS GROUP

Lotus discolor E. Mey. in Comm. Pl. Afr. Austr. 92 (1835)

Grains prolate P:E 1.235, 20.4 x 25.2 µm (19.1-21.7 x 23.0-26.8 µm), tricolporate; PAI 0.378, pore lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

Lotus goetzei Harms in Bot. Jahrb. 30:324 (1901)

Grains prolate to spheroidal P:E 1.059, 22.2 x 23.5 µm (20.4-23.0 x 21.7-24.2 µm), tricolporate; PAI 0.335, pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Lotus namulensis Brand in Bot. Jahbr. 25:213 (1898)

Grains prolate P:E 1.147, 19.8 x 22.7 µm (19.1-20.4 x 21.7-23.0 µm), tricolporate; PAI 0.250, pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

LOTUS CRETICUS GROUP

Lotus collinus (Boiss.) Heldr. in Herb. Grace. Norm. No. 1320 (1896)

Grains prolate P:E 1.500, 12.0 x 18.0 µm (11.0-13.0 x 16.0-20.0 µm), tricolporate; PAI 0.695, pore lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Lotus creticus L. in Sp. Pl. 776 (1753)

Grains prolate P:E 1.403, 12.8 x 16.6 µm (11.0-14.0 x 15.0-18.0 µm), tricolporate; PAI 0.703, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

Lotus cytisoides L. in Sp. Pl. 776 (1753)

Grains prolate P:E 1.450, 10.0 x 14.9 µm (9.0-11.5 x 14.0-16.6 µm), tricolporate; PAI 0.557, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

SECTION KROKERIA

Lotus edulis L. in Sp. Pl. 774 (1753)

Grains prolate P:E 1.475, 12.5 x 18.9 µm (11.5-14.0 x 17.9-20.4 µm), tricolporate; PAI 0.226, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

SECTION ERYTHROLOTUS

LOTUS AUSTRALIS GROUP

Lotus australis Andr. in Bot. Rep. 624 (1797)

Grains prolate P:E 1.221, 16.[illegible] x 19.9 µm (15.3-17.9 x 17.9-21.7 µm), tricolporate; PAI 0.464, pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Lotus coccineus Schlecht. non Vell. (1825), in Linnaea 21: 452 (1848)

Grains prolate to spheroidal P:E 1.066, 18.2 x 19.5 µm (18.0-19.1 x 18.0-21.7 µm), tricolporate; PAI 0.355, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

LOTUS GEBELIA GROUP

Lotus conimbricensis Brot. in Phyt. Lusit. Fasc. 1 No. 28 (1801)

Grains prolate P:E 1.225, 15.0 x 18.5 µm (14.0-18.0 x 17.0-20.0 µm), tricolporate; PAI 0.715; pores lalongate ora; ektexine and endexine 1.0 µm thick, psilate sculpturing.

Lotus gebelia Venten. in Hort. Cels. 57 (1801)

Grains prolate P:E 1.330, 16.0 x 21.0 µm (15.0-17.0 x 10.0-22.0 µm), tricolporate; PAI 0.700, pore lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

Lotus lanuginosus Venten. in Jard. Malm. 92 (1805)

Grains prolate P:E 1.244, 15.6 x 19.4 µm (14.0-17.0 x 18.0-20.5 µm), tricolporate; PAI 0.482; pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

LOTUS ORNITHOPODIOIDES GROUP

Lotus halophilus Boiss. et Spruner in Boiss., Diagn. Fl. Ord. Nov. 1(2):37 (1843)

Grains prolate P:E 1.360, 13.0 x 18.2 µm (12.0-14.0 x 17.0-19.0 µm) tricolporate; PAI 0.457; pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Lotus ornithopodioides L. in Sp. Pl. 775 (1753)

Grains prolate P:E 1.437, 12.6 x 18.1 µm (11.5-14.0 x 16.6-19.1 µm), tricolporate; PAI 0.602, pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Lotus peregrinus L. non Burm. f. (1768) in Sp. Pl. 774 (1753)

Grains prolate P:E 1.355, 16.9 x 22.9 µm (15.3-17.9 x 19.1-25.5 µm), tricolporate; PAI 0.570, pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

LOTUS WEILLERI GROUP

Lotus weilleri Maire in Bull. Soc. Hist. Nat. Afr. Nord. 19:40 (1928)

Grains prolate P:E 1.531, 9.8 x 15.0 µm (8.0-11.0 x 14.0-16.0 µm), tricolporate; PAI 0.222, pores lalongate ora; ektexine and endexine 0.5 µm thick; sculpturing psilate.

SUBGENUS PEDROSIA

Lotus glaucus Dryand. ex Ait. non Sieber ex Reichb. (1832) in Hort. Kew. 1(3):92 (1789)

Grains prolate P:E 1.209, 16.3 x 19.7 µm (15.3-17.9 x 18.0-21.7 µm), tricolporate; PAI 0.309, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

Lotus jacobaeus L. in Sp. Pl. 775 (1753)

Grains prolate P:E 1.881, 8.4 x 15.8 µm (8.0-8.9 x 15.0-16.7 µm), tricolporate; PAI 0.314, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

SUBGENUS HOSACKIA

Lotus angustifolius Moq. et Sesse ex G. Don in Gen. Syst. 2:200 (1832)

Grains spheroidal P:E 1.089, 22.3 µm (17.9-25.5 µm) tricolporate; PAI 0.333, pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Lotus aboriginus Jepson in Fl. Calif. 2:315 (1936)

Grains prolate P:E: 1.354, 16.4 x 22.2 µm (15.0-17.0 x 20.0-24.0 µm), tricolporate; PAI 706, pore lalongate ora; ektexine and endexine 1.0 µm thick; sculpturing rugulate.

Lotus chihuahuanus (Wats.) Greene in Pittonia 2:146 (1890)

Grains prolate, spheroidal, to oblate P:E 1.050, 23.2 x 23.5 μm (21.7-24.2 x 23.0-24.0 μm), tricolporate; PAI 0.417, pores lalongate to circular ora; ektexine and endexine 1.5 μm thick; microreticulate sculpturing.

Lotus formosissimus Greene in Pittonia 2:147 (1890)

Grains prolate P:E 1.040, to spheroidal, 23.5 x 24.7 μm (21.7-24.2 x 23.0-26.8 μm), tricolporate; PAI 0.557, pores lalongate to circular ora; ektexine and endexine 1.5 μm thick; rugulate sculpturing.

Lotus oblongifolius (Benth.) Greene in Pittonia 2:146 (1890) var. cupreus Ottley

Grains prolate P:E 1.162, 23.5 x 27.3 μm (23.0-24.2 x 26.8-28.1 μm), tricolporate; PAI 0.500, pores lalongate to circular ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus oblongifolius (Benth.) Greene var. nevadensis (Gray) Munz

Grains prolate P:E 1.288, 18.4 x 23.7 μm (17.9-19.1 x 20.4-25.5 μm), tricolporate; PAI 0.534, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus oblongifolius (Benth.) Greene var. torreyi Ottley

Grains prolate P:E 1.222, 19.8 x 24.2 μm (19.1-20.4 x 23.0-25.5 μm), tricolporate; PAI 0.586, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus pinnatus Hook. in Curtis Bot. Mag. 56:2913 (1829)

Grains prolate to spheroidal P:E 1.079, 18.4 x 18.7 μm (17.0-21.0 x 17.0-21.0 μm), tricolporate; PAI 0.579, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus stipularis (Benth.) Greene in Pittonia 2:147 (1890)

Grains prolate to spheroidal P:E 1.095, 20.1 x 22.0 μm (19.0-21.7 x 20.4-23.0 μm), tricolporate; PAI 0.537, pores circular ora; ektexine and endexine 1.5 μm thick; rugulate sculpturing.

Lotus yollabolliensis Munz in Aliso 3:117 (1955)

Grains prolate P:E: 1.153, 24.2 x 27.9 μm (23.0-25.5 x 26.8-28.1 μm), tricolporate; PAI 0.500, pores circular ora; ektexine and endexine 2.0 μm thick; psilate sculpturing.

SUBGENUS ACMISPON

Lotus denticulatus (Drew) Greene in Pittonia 2:139 (1890)

Grains prolate to square in equatoriel view, to square in polar view P:E 1.053, 22.5 x 23.5 μm (20.4-25.5 x 20.4-25.5 μm), tricolporate and tetracolporate; PAI 0.335, pores circular to lalongate ora; ektexine and endexine 0.5 μm thick; psilate sculpturing.

Lotus humistratus Greene in Pittonia 2:139 (1890)

Grains prolate P:E 1.117, 24.0 x 26.8 μm (23.0-25.5 x 25.5-28.1 μm), tetracolporate; PAI 0.392, pores lalongate ora; ektexine and endexine 1.5 μm thick; striate sculpturing.

Lotus micranthus Benth. in Trans. Linn. Soc. 17:367 (1837)

Grains spheroidal in equatorial view P:E 1.021, square in polar view, 21.3 μm (19.1-23.0 μm), tetracolporate; P.A.I. 0.455, pores lalongate ora; ektexine and endexine 2.0 μm thick; psilate sculpturing.

Lotus purshianus (Benth.) Clements et Clements in Rocky Mt. Flowers: 183 (1914)

Grains spheroidal, oblate or square in equatorial view; 23.4 μm (17.4-26.4 μm); tetracolporate; PAI 0.460, pores lalongate ora; ektexine and endexine 1.0 μm thick; rugulate sculpturing.

Lotus purshianus (Benth.) Clements et Clements var. helleri (Britt.) Isley in Brittonia 30:468 (1978)

Grains spheroidal or square in equatorial view P:E 1.000, 20.6 μm (18.0-23.0 μm), tetracolporate; PAI 0.510, pores lalongate ora; ektexine and endexine 1.0 μm thick; rugulate sculpturing.

Lotus salsuginosus Greene in Pittonia 2:140 (1890)

Grains spheroidal or square in equatorial view P:E 1.083, 25.0 x 26.0 μm (24.0-25.5 x 25.5-26.8 μm), tetracolporate; PAI 0.451, pores lalongate ora; ektexine and endexine 1.0 μm thick; rugulate sculpturing.

Lotus salsuginosus Greene var. brevivexillus Ottley in Univ. Calif. Publ. Bot. 10:217 (1923). Grains prolate to retangular in equatorial view P:E 1.204, 19.1 x 23.0 μm (17.9-20.4 x 21.7-24.2 μm), tetracolporate; PAI 0.546, pores circular ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus wrangelianus Fisch. et Meyer in Index Sec. Sem. Hort. Petrop. 2:41 (1836)

Grains prolate to rectangular in equatorial view P:E 1.306, 17.0-22.2 μm (15.0-18.0 x 18.0-24.0 μm), 90% tetracolporate, 10% tricolporate; PAI 0.647, pores circular ora; ektexine and endexine 1.0 μm thick; rugulate sculpturing.

SUBGENUS SIMPETERIA

Lotus argyraeus Greene in Pittonia 2:144 (1890) var. multicaules (Ottley) Isley in Mem. N.Y. Bot. Gard. 25:237 (1981)

Grains prolate to square in equatorial view P:E 1.022, 26.3 x 27.1 μm (24.2-28.1 x 24.2-28.1 μm), tetracolporate; PAI 0.455, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus bryantii (Brandg.) Ottley in Brittonia 5:98 (1944)

Grains oblate to spheroidal in equatorial view P:E 0.902, 30.1 x 27.2 μm (26.8-33.2 x 24.2-31.9 μm), 96% tetracolporate, 4% stephanocolporate; PAI 0.6252, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus cedrosensis Greene in Pittonia 2:144 (1890)

Grains spheroidal P:E 1.000, 29.1 μm (26.8-31.9 μm), 40% tricolporate, 60% tetracolporate; PAI 0.552, pores lalongate ora; ektexine and endexine 1.0 μm thick; verrucate sculpturing on polar ends.

Lotus grandiflorus (Benth.) Greene in Pittonia 2:145 (1890)

Grains prolate, spheroidal, rectangular to square in equatorial view P:E 1.113, 29.3 x 31.0 μm (28.1 - 35.7 x 28.1-35.7 μm), tetracolporate; PAI 0.610, pores lalongate to circular ora; ektexine and endexine 1.5 μm thick; rugulate sculpturing. Note - 50% aberrant grains.

Lotus greenii (Woot. and Standl.) Ottley ex Kearney and Peebles in Jour. Wash. Acad. Sci. 29:483 (1939)

Grains spheroidal to square in equatorial view P:E 1.242, 26.6 μm (24.2-28.1 μm), tetracolporate; PAI 0.502, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing. Note - circa 50% aberrant grains.

Lotus mearnsii (Britton) Greene non de Wild (1925) in Pittonia 2:144 (1890)

Grains spheroidal to square in equatorial view P:E 1.000, 25.1 μm (23.0-26.8 μm), 95% tetracolporate, 5% stephanocolporate; PAI 0.400, pores lalongate ora; ektexine and endexine 1.5 μm thick; rugulate sculpturing.

Lotus oroboides (Humboldt, Bonpland, et Kunth) Ottley ex Kearney et Peebles in Jour. Wash. Acad. Sci. 29:483 (1939)

Grains spheroidal to square in equatorial and polar view P:E 1.000, 29.0 μm (26.8-30.6 μm), tetracolporate; PAI 0.500, pores lalongate ora; ektexine and endexine 1.5 μm thick; sculpturing rugulate. Note - circa 30% aberrant pollen.

Lotus oroboides (Humboldt, Bonpland et Kunth) Ottley ex Kearney var. nummaralis (Jones) Isley in Mem. N.Y. Bot. Gard. 25:242 (1981)

Grains prolate, spheroidal, oblate to square in equatorial view, P:E 0.990, 28.5 x 28.9 µm (23.0-30.0 x 23.0-30.6 µm), tetracolporate; PAI 0.553, pores lalongate ora; ektexine and endexine 1.5 µm thick; rugulate sculpturing. Note - colpi very wide, containing verrucate ornaments.

Lotus plebeius (Brandg.) Barnaby in prep. 1981

Grains prolate, spherodial or oblate in equatorial view P:E 1.008, 26.2 x 26.4 µm, (24.2-28.1 x 25.5-28.1µm), 56% stephanocolporate, 50% tetracolporate; PAI 0.454, pores lalongate ora; ektexine and endexine 1.5 µm thick; psilate sculpturing.

Lotus rigidus (Benth.) Greene in Pittonia 2:142 (1890)

Grains spheroidal to square in equatorial view P:E 1.000, 25.6 µm (24.2-26.8 µm), tetracolporate; PAI 0.478, pores lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Lotus strigosus (Nutt. ex T. & G.) Greene in Pittonia 2:142 (1890)

Grains spheroidal P:E 1.000, 32.4 μm (29.3-36.9 μm), 6-colporate; PAI 0.345, pores lalongate to circular ora; ektexine and endexine 2.0 μm thick; verrucate processes 6-9 μm in diameter comprising the sculpturing.

Lotus strigosus (Nutt ex T. & G.) Greene in Pittonia 2:142 (1890) var. tomentellus Greene Isley in Mem. N.Y. Bot. Gard. 25:246 (1981)

Grains prolate P:E 1.149, 25.8 x 29.3 μm (24.2-26.8 x 28.1-30.6 μm), tetracolporate; PAI 0.502, pores lalongate ora; ektexine and endexine 1.0 μm thick; verrucate processes 4-5 μm in diameter comprising the sculpturing.

Lotus utahensis Ottley in Brittonia 5:108 (1944)

Grains spheroidal to square in equatorial view P:E 1.000, 29.1 μm (26.8-31.9 μm), tetracolporate and stephanocolporate; PAI 0.476, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus wrightii (Gray) Greene in Pittonia 2:143 (1890)

Grains spheroidal P:E 1.000, 28.0 μm (25.0–33.0 μm), stephanocolporate; PAI 0.670, pores lalongate ora; ektexine and endexine 1.0 μm thick; rugulate sculpturing. Note – verrucate sculpturing within the colpi.

SUBGENUS SYRMATIUM

Lotus argophyllus (Gray) Greene in Pittonia 2:149 (1890)

Grains spheroidal to square in equatorial view P:E 1.000, 26.8 μm (25.5–28.1 μm), tetracolporate; PAI 0.400, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus benthamii Greene in Pittonia 2:148 (1982)

Grains oblate, spheroidal to square in equatorial view P:E 0.970, 28.8 x 28.1 μm (26.8–30.6 x 26.8–30.6 μm), tetracolporate; PAI 0.435, pores circular ora; ektexine and endexine 1.5 μm thick; rugulate sculpturing.

Lotus dendroideus Greene in Pittonia 2:148 (1890)

Grains oblate, spheroidal to square in equatorial view P:E 0.989, 27.6 x 27.3 μm (25.5–29.3 x 25.5–28.1 μm), tetracolporate; PAI 0.499, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus dendroideus Greene var. traskiae (Eastwood ex Noddin) Isley in Mem. N.Y. Bot. Gard. 25:238 (1981)

Grains spheroidal to square in equatorial view P:E 1.000, 23.7 μm (21.7-25.5 μm), tetracolporate; PAI 0.444, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus hamatus Greene in Pittonia 2:150 (1890)

Grains spheroidal P:E 1.004, 22.9 x 23.0 μm (21.7-24.2 x 21.7-24.2 μm), tetracolporate; PAI 0.444, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus haydonii (Orcutt) Greene in Pittonia 2:149 (1890)

Grains spheroidal P:E 1.000, 23.3 μm (21.7-25.5 μm), tetracolporate; PAI 0.444, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus heermannii (Durand et Hilgard) Greene in Pittonia 2:150 (1890)

Grains spheroidal P:E 1.000, 22.8 μm (21.7-24.4 μm), tetracolporate; PAI 0.525, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus heermannii (Durand et Hilgard) Greene var. orbicularis (Gray) Isley in Brittonia 30:467 (1978)

Grains prolate P:E 1.107, 24.2 x 26.8 μm (23.0–25.5 x 24.2–28.1 μm), tetracolporate; PAI 0.387, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus junceus (Benth.) Greene in Pittonia 2:148 (1890) var. biolettii (Greene) Ottley in Univ. Calif. Publ. Bot. 10:231 (1923)

Grains prolate P.E. 1.122, 24.5 x 27.5 μm (23.0–25.5 x 25.5–29.3 μm), tetracolporate; PAI 0.422, pores lalongate ora; ektexine and endexine 1.5 μm thick; psilate sculpturing.

Lotus nevadensis (Wats.) Greene in Pittonia 2:149 (1890)

Grains spheroidal P:E 1.051, 25.5 x 26.8 μm (24.3-26.8 x 25.5.-28.1 μm), tetracolporate; PAI 0.478, pores circular ora; ektexine and endexine 1.5 μm thick; psilate-punctate sculpturing.

Lotus nevadensis (Wats.) Greene var. davidsonii (Green) Isley in Brittonia 30:467 (1978)

Grains spheroidal P:E 1.000, 21.2 μm (19.1–23.0 μm), tetracolporate; PAI 0.435, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus nevadensis (Wats.) Greene var. douglasii (Greene) Ottley in Brittonia 5:81 (1944)

Grains spheroidal to square in equatorial view P:E 1.000, 26.6 μm (20.4-30.6 μm), 30% tricolporate, 70% tetracolporate; PAI 0.476, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing. Note - 35% aberrant grains.

Lotus nudatus Greene in Pittonia 2:148 (1890)

Grains prolate P:E 1.226, 22.2 x 27.1 μm (20.4-24.2 x 25.5-28.1 μm), 5% tricolporate, 95% tetracolporate; PAI 0.591, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus nuttallianus Greene in Pittonia 2:150 (1890)

Grains spheroidal to square in equatorial view P:E 1.000, 24.1 μm (23.0-25.5 μm), tetracolporate; PAI 0.522, pores lalongate ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus procumbens (Greene) Greene in Pittonia 2:149 (1890)

Grains spheroidal to prolate P:E 1.107, 22.2 x 24.2 μm (19.0-26.8 x 21.7-26.8 μm), tetracolporate; PAI 0.457, pores lalongate to circular ora; ektexine and endexine; 1.0 μm thick, psilate sculpturing.

Lotus scoparius (Nutt.) Ottley in Univ. Calif. Publ. Bot. 10:227 (1923)

Grains spheroidal to square equatorial view P:E 1.000, 30.5 μm (27.5–35.0 μm), tetracolporate; PAI 0.556, pores lalongate ora; ektexine and endexine 1.5 μm thick; nanoprocessed to psilate sculpturing.

Lotus scoparius (Nutt.) Ottley var. brevialatus Ottley in Univ. Calif. Acad. Bot. 10:229 (1923)

Grains spheroidal to square P:E 1.000 equatorial view, 25.5 μm (24.2–26.8 μm), tetracolporate; PAI 0.485, pores circular ora; ektexine and endexine 1.0 μm thick; psilate sculpturing.

Lotus watsonii (Vasey et Coult.) Greene in Pittonia 2:149 (1890)

Grains spheroidal, to square in equatorial view P:E 1.000, 26.2 μm (24.2–28.1 μm), tetracolporate, 5% stephanocolporate; PAI 0.452, pores lalongate; ektexine and endexine 1.5 μm thick; psilate sculpturing.

TETRAGONOLOBUS

Tetragonolobus biflorus (Desr.) Ser. in DC. Prod. 2:215 (1825)

Grains prolate P:E 1.491, 16.1 x 24.0 μm (15.3–16.6 x 23.0–25.5 μm), tricolporate; PAI 0.422, pore circular ora; ektexine and endexine 1.0 μm thick; rugulate sculpturing.

Tetragonolobus maritimus (L.) Roth in Tent. Fl. Germ. 1:323 (1788)

Grains prolate P:E 1.406, 16.2 x 23.6 µm (13.0-20.4 x 21.7-25.5 µm), tricolporate; PAI 0.420, pores circular ora to lalongate ora; ektexine and endexine 1.0 µm thick; psilate sculpturing.

Tetragonolobus purpureus Moench in Meth. 164 (1794)

Grains prolate P:E 1.370, 20.8 x 28.5 µm (20.4-21.7 x 26.8-29.3 µm), tricolporate; PAI 0.147, pores lalongate ora; ektexine and endexine 1.0 µm thick; rugulate sculpturing.

Tetragonolobus purpureus Moench var. palaestinus

Grains prolate P:E 1.186, 21.5 x 25.5 µm (20.1-23.0 x 21.0-27.3 µm), tricolporate; PAI 0.690, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

VERMIFRUX

Vermifrux abyssinica (A. Rich.) J.B. Gillett in Kew Bull. 20:245 (1966)

Grains oblate to spheroidal P:E 1.000, 23.3 x 23.0 µm (21.7-24.2 x 20.4-24.2 µm), tricolporate; PAI 0.557, pores lalongate ora; ektexine and endexine 0.5 µm thick; psilate sculpturing.

CORONILLEAE

Coronilla emerus L., in Sp. Pl. 742 (1753)

Grains spheroidal to oblate P:E 0.974, 26.5 x 25.8 um (24.2-28.1 x 23.0-28.1 um), tricolporate; PAI 0.427, pores lalongate ora; ektexine and endexine 1.5 um thick; psilate sculpturing.

Coronilla minima L., in Cent. Pl. 2: 28 (1756)

Grains prolate P:E 1.217, 16.6 x 20.2 um (15.3-17.9 x 17.9-23.0 um), tricolporate; PAI 0.497, pores lalongate ora; ektexine and endexine 1.0 um thick; psilate sculpturing.

Coronilla scorpioides (L.) Koch., in Fl. Germ. ed. 1: 188 (1837)

Grains prolate P:E 1.156, 13.5 x 15.6 um (12.8-14.0 x 14.0-16.6 um), tricolporate; PAI 0.543, pores lalongate ora; ektexine and endexine 1.0 um thick; psilate sculpturing.

Coronilla varia L., in Sp. Pl. 743 (1753)

Grains prolate, oblate to spheroidal P:E 0.981, 25.8 x 25.3 um (23.0-28.0 x 23.0-26.8 um), tricolporate; PAI 0.302, pores lalongate ora; ektexine and endexine 1.0 um thick; psilate sculpturing.

HAMMATOLOBIUM

Hammatolobium lotoides Frenzl in Ill. Pl. Syr. 1 (1843)

Grains prolate P:E 1.231, 33.4 x 41.1 µm (31.9-34.4 x 38.3-42.1 µm), tricolporate, PAI 0.539, pores lalongate ora, ektexine and endexine 1.5 µm thick, psilate sculpturing.

HIPPOCREPIS

Hippocrepis comosa L. in Sp. Pl. 744 (1753)

Grains prolate P:E 1.152, 20.4 x 23.5 µm (19.1-21.7 x 21.7-25.5 µm), tricolporate, PAI 0.410, pores lalongate ora, ektexine and endexine 1.0 µm thick, psilate sculpturing.

ORNITHOPUS

Ornithopus compressus L., in Sp. Pl. 744 (1753)

Grains prolate P:E 1.188, 20.8 x 24.7 µm (19.1-21.7 x 21.7-26.8 µm), tricolporate, PAI 0.590, pore lalongate ora, ektexine and endexine 1.0 µm thick, psilate sculpturing.

Ornithopus perpusillus L. in Sp. Pl. 743 (1753)

Grains prolate P:E 1.199, 18.1 x 21.7 µm (17.9-19.1 x 20.4-23.0 µm), tricolporate, PAI 0.403, pore lalongate ora, ektexine and endexine 1.0 µm thick, psilate sculpturing.

SCORPIURUS

Scorpiurus muricatus L. var. subvillosus (L.) Fiori ex Fiori et Pasl.

Grains prolate P:E 1.290, 16.1 x 20.7 µm (15.3-16.6 x 19.1-21.7 µm), tricolporate, PAI 0.412, pores lalongate ora, ektexine and endexine 1.0 µm thick, psilate sculpturing.

B. Pollen Taxonomy and Taxonomic Notes on Loteae

Anthyllis L. spp. are distinguished from other Loteae by having inflated calyxes normally enclosing the legume (Polhill 1981, Isley 1982). Its 20-25 spp. are distributed around the Mediterranean, extending into Europe, the Atlantic Islands and North Africa (Polhill 1981, Callen 1968). Pollen grains are not highly ornamented. They are among the largest in size of the Loteae ranging from 25 to 47 µm; having a large polar area index ranging from 0.650 to 0.822; in shape they are spheroidal to prolate. SEM studies show a circular indentation with a raised centre on the polar ends.

Cytisopsis Jaub. & Spach spp. are distinguished from other Loteae by having a long tubular calyx and having sessile leaves; its two species are distributed one in the eastern Mediterranean and the other in North Africa. Pollen grains are rectangular prolate in shape due to the polar ends being abrupt; at the upper end of the colpi the sculpturing is verrucate; these observations being confirmed by SEM.

Dorycnium Miller is considered by Polhill (1981) to be a synonym of Lotus L. Ball (1968) and Isley (1982) separated Dorycnium from Lotus and other genera in the Loteae. The genus Dorycnium is characterized by them as having flowers in a capitate umbell on short pedicels and leaves which form a short rachis and are subsessile. It is

comprised of circa 12 spp. in the Mediterranean region and Canary Islands (Hutchinson, 1964). Dorycnium pollen grains closely resemble the grains of Old World Loteae. They possess, however, constricted polar ends after acetolysis (see Figures 1, 2 and 3).

Hymenocarpus Savi is monotypic, and is characterized by having a spirally twisted and flattened legume (Ball, 1968), somewhat resembling a Medicago-Trigonella legume (personal observation). Its species H. circinnatus (L.) Savi is in the Mediterranean region and Western Asia (Polhill, 1981). It also occurs as an adventive in Southern Europe (Ball, 1968). Pollen grains of this taxon are spheroidal with slightly compressed polar ends; their pores and sculpturing patterns are not distinctive.

Tetragonolobus Scop. Polhill (1981), included Tetragonolobus in the genus Lotus. This is in contrast to both Ball (1968) and Isley (1981). The genus is distinguished by plants having 3-foliate leaves, and flowers solitary or in a pair. Its legumes are square in transverse section with keeled or winged angles (Ball, 1968).
Pollen grains of Tetragonolobus are medium in size as compared to Lotus sensu lato. They have rugulate or psilate sculpturing under light microscopy and the PAI varies from 0.147 to 0.690 (see Figures 4, 5, 6 and 7).

Vermifrux Gillett (Gillett, 1966) is assigned by Polhill (1981) to the genus Lotus. Its pollen grains are oblate to spheroidal. Otherwise they are similar in morphology to taxa of other Old World Lotus.

Lotus pollen grains in Sections Lotus, Loteae, Krokeria, Erythrolotus and Pedrosia are stenopalynous. None of the 29 taxa examined can be adequately identified by pollen grain morphology, utilizing either light, interference contrast or SEM. See Figures 8 to 35 (interference microscopy) and Figures 70 to 78 (SEM). They are all tricolporate, prolate, and none have a particularly distinctive sculpturing pattern. They range in size from circa 9 x 13 µm to 20 x 25 µm. The smaller grains being mainly in the angustissimus-corniculatus groups, while larger grains are found in the namulensis group. Sculpturing is observed as either psilate or rugulate utilizing available types of light and SEM microscopy and most are rugulate using SEM. PAI are generally smaller in value in the namulensis-corniculatus groups than in the other Old World groups. Section Krokeria as represented by L. edulis has the smallest PAI at 0.226, while both L. collinus and L. creticus in the creticus group have the largest values at 0.695 and 0.703. SEM studies revealed that several taxa in section Pedrosia showed identical external morphology (see Figures 74 to 78).

New World Lotus are represented by the subgenera Hosackia, Acmispon and Syrmatium. These subgenera are eurypalynous. They have tricolporate, tetracolporate and stephanocolporate grains. Subgenus Hosackia is exclusively tricolporate, while pollen grains of subgenera Acmispon and Syrmatium are usually tetracolporate and often stephanocolporate, but rarely tricolporate. Each of the subgenera show diverse ornamentation of the exine under SEM (see Figures 79 to 101).

Subgenus Hosackia - Pollen grains were normally prolate to oblate in shape and tricolporate. The pores varied in shape depending on the species from lalongate to circular ora. Their sculpturing pattern under the light microscope varied from psilate to rugulate; SEM studies revealed a sculpturing, similar to that exhibited in Trifolium section Lupinaster Syringe (Gillett et al. 1973) in having foveate reticulate sculpturing. Some taxa such as L. crassifolius and L. oblongifolius had smooth polar ends; the colpi being somewhat serrated with intracolpi granular particles (see Figures 79 and 80). They appeared in the numerical taxonomic studies (NTS) to be allied with the Old World Lotus spp. This was no doubt due to the fact that the NTS was based upon light microscope observations under which the aforementioned

morphological characters were not visible. Therefore the analysis was biased or weighted towards linking size class, and pore number, rather than characteristics which were observed under SEM. Consequently, I feel that Hosackia, due to its divergence from Old World Lotus, should properly be linked with North American taxa.

Subgenus Simpeteria - Pollen grains are normally of various shapes from prolate to oblate, and rectangular to square in outline. They are tetracolporate to stephanocolporate and show psilate, rugulate and verrucate processes in the various taxa [see Figures 60 to 67 (interference microscopy) and Figures 90 to 95 (SEM)]. Some pollen samples of taxa, such as L. bryantii, L. cedrosensis, and L. plebeius, had various percentages of tetra-and stephanocolporate pollen. They had verrucate particles within the colpi and the sculpturing patterns were normally visible under techniques of light microscopy. Under SEM the various sculpturing patterns in the taxa showed great divergence even at the level of variety. Lotus strigosus var. strigosus had the most morphologically striking pollen grains of any taxa examined in this study (see Figures 94 and 95). They are stephanocolporate and have circular pores, highly ornamented colpus and the intercolpium areas are comprised of large raised irregular verrucate processes. In

contrast, pollen grains of its variety , var. tomentellus , were rugulate, tetracolporate and otherwise were not allied to L. strigosus var. strigosus, the typical variety. Lotus strigosus has the largest pollen grains of New World Lotus. The pollen grains of L. grandiflorus were stephanocolporate. This form of aperture seemed restricted to it and to L. strigosus sensu stricto. Therefore, the palynomorph was represented in widely divergent taxa. L. strigosus is a prostrate annual, mat-forming and diminutive. It occurs in the Arizona Desert. L. grandiflorus however, is a rhizomatous perennial, erect to decumbent in habit and it ranges throughout the California-Baja California coastal areas. Lotus humistratus also had divergent pollen grains. Its sculpturing pattern is striate-reticulate which palynologically separated it from all other Lotus spp. examined in this study [see Figures 52, 53 (interference microscopy) and Figures 88, 89 (SEM)]. Pollen morphological studies separated L. humistratus from its close relative L. wrangelianus by having tri-and tetracolporate apertures, rugulate sculpturing pattern and being smaller in size. Isley (1981) stated that "the two species commonly grow together in California with no signs of mingling." Therefore, pollen grain studies lend support to Isley's observations.

Subgenus Syrmatium - Under light microscopy there was a tendency for the pollen grains in Syrmatium to have a spheroidal shape. Some pollen grains per sample were obspheroidal, but several taxa had prolate grains. The common aperture form is tetracolporate, but several taxa had low percentages of tricolporate grains in individual samples; e.g. 3 and 30% in L. nevadensis and L. nudatus pespectively, and 5% stephanocolporate grains, such as were found in a collection of L. watsonii. A common feature of the pollen grains in Subgenus Syrmatium was that taxa had relatively consistent PAI values, usually about 0.470. The smallest PAI (0.387) was found in L. heermannii var. orbicularis and the largest PAI (0.591) was discovered in L. nudatus. Under the SEM, pollen grain sculpturing was mainly rugulate. Some were coarse rugulate, such as in L. scoparius and others were finely rugulate, as in L. argophyllus [see Figures 55 to 60 (interference microscopy) and Figures 96 to 101 (SEM)]. The colpi appeared to be somewhat short, forming a fairly large polar area. They were irregular along the margins and had granular processes which comprised a colpi membrane. The sculpturing pattern was distributed evenly over the entire grain surface.

C. Summary of major pollen taxonomic trends discovered in this study

The Loteae had not been surveyed for palynological taxonomy. The entire subfamily, or family Papilionoideae, was surveyed by Ferguson and Skvarla (1981), but due to the enormousness of their study, they were only able to examine and report on one species, Hymenocarpus circinnatus (L.) Savi. They suggested correctly, that much palynological work was required in particular tribes and genera. In the present study, I examined pollen grains of 2 species of Anthyllis, 2 of Cytisopsis, 8 taxa of Dorycnium, and 2 species of Hymenocarpus. In the genus Lotus, all of the higher taxonomic categories were examined. Several taxa were examined in each group, including the following; aegeus, corniculatus, namulensis, creticus, edulis, australis, gebelia, ornithopodioides, weilleri, pedrosia, hosackia, simpeteria, syrmatium, tetragonolobus and vermifrux.

In all, 77 Lotus taxa were studied and 14 other taxa, considered to be related to Lotus, were also examined. Since samples of several taxa in the Coronilleae tribe were available for study, these were examined for purposes of comparing Loteae-Coronilleae pollen sensu lato. An excellent palynomorphological study on the tribe Coronilleae by Ohashi (1971) supplied useful data for comparing the two tribes. Although some species had striking morphological

characteristics, no clear separation of phylogenetic groupings was possible based on the overall pollen-grain characters.

Pollen grains of Loteae generally show two types.

Type 1) Old World Loteae which are:

a) prolate to rarely oblate in equatorial view,
b) usually averaging less than 20 μm in length,
c) polar area index (PAI) is usually less than 0.500,
d) the exine diameter is never more than 1.5 μm thick,
e) the wall (exine) is usually difficult to differentiate into ektexine-endexine (1000 x using Nomarski interference constrast microscopy)
f) the sculpturing pattern is normally psilate,
g) all grains are tricolporate,
h) grains golden brown after acetolysis,
i) non-vestibulate pores

Type 2) New World Loteae which are:

a) prolate to spheroidal, square, retangular in either equatorial or polar view,
b) usually averaging more than 20 μm in length,
c) PAI is normally more than 0.500,
d) the exine diameter is normally 1.5 μm or more thick,
e) the exine is usually easy to differentiate into ektexine-endexine,

f) sculpturing pattern is either psilate, rugulate or verrucate,

g) most grains are either tetracolporate or stephanocolporate,

h) grains normally dark brown after acetolysis (probably due to optical density, although grains collected from herbarium specimens prior to acetolysis treatment appeared to be highly pigmented),

i) vestibulate pores.

Therefore, on the basis of pollen morphology it is possible to construct the following table:

TABLE 2 POLLEN TRENDS IN LOTEAE

OLD WORLD LOTEAE	NEW WORLD LOTEAE
Size: normally averaging less than 20 μm	Size: normally averaging more than 20 μm
Shape: prolate to rarely oblate	Shape: prolate to rectangular-square
Apertures: tricolporate (only)	Apertures: tricolporate (rarely), normally tetracolporate to stephanocolporate
Sculpturing: usually psilate	Sculpturing: usually rugulate, verrucate or striate
Wall laminations: usually indistinct; wall pigments: golden yellow	Wall laminations: usually distinct; wall pigments: brown to dark brown
Exception: Genus Anthyllis	Exception: Subgenus Hosackia

FIGS. 1-7 - DORYCNIUM and TETRAGONOLOBUS

Fig. 1. *Dorycnium germanicum*, polar view, equatorial optical section.

2. *D. germanicum*, equatorial view, colpus and porus.

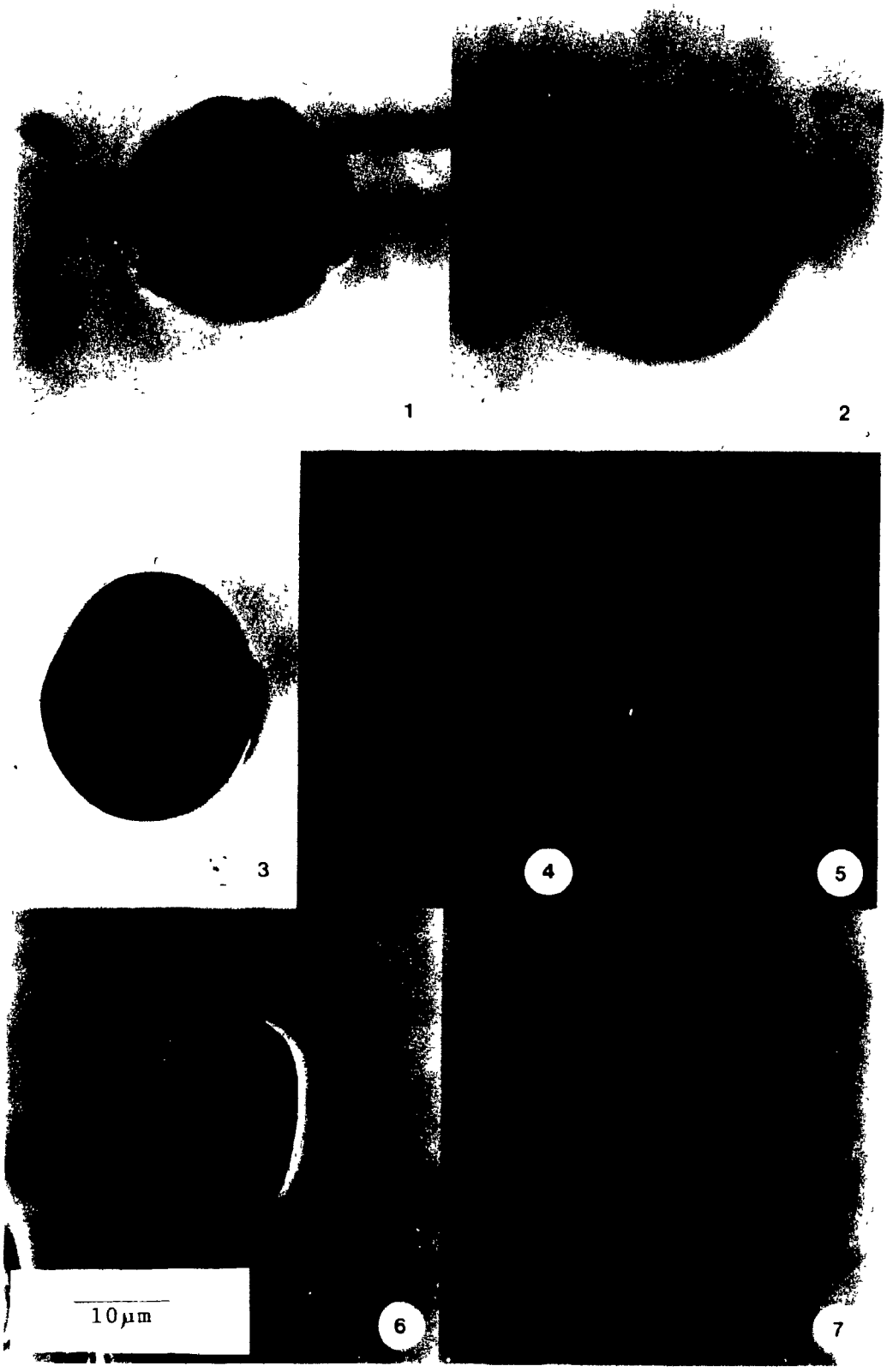
3. *D. germanicum*, equatorial view, optical section.

4. *Tetragonolobus* sp., equatorial view.

5. *T.* sp., equatorial view, surface sculpturing.

6. *T. maritimus*, equatorial view, optical section.

7. *T. biflorus*, equatorial view, colpus and porus.


1
2
3
4
5
10μm
6
7

FIGS. 8-13

Fig. 8. Lotus macrotrichus, equatorial view, colpus and porus.

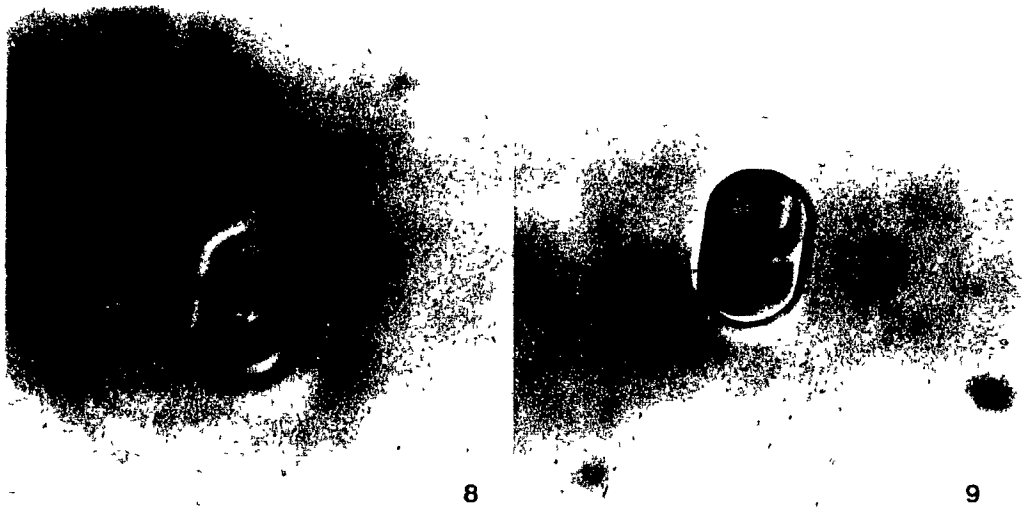
9. Lotus macrotrichus, equatorial view, optical section.

10. Lotus parviflorus, equatorial view, colpus and porus.

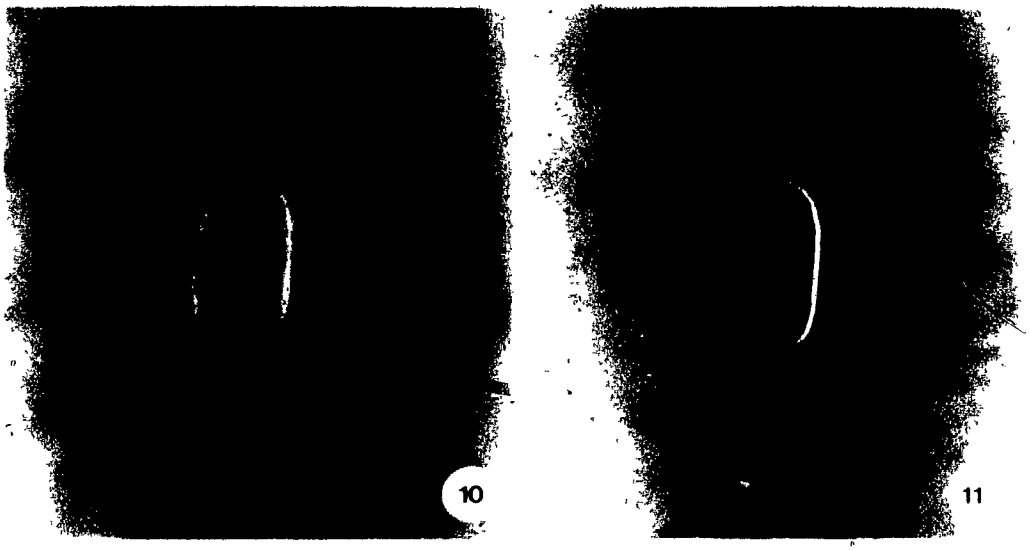
11. Lotus parviflorus, equatorial view, optical section.

12. Lotus subbiflorus, equatorial view, colpus and porus.

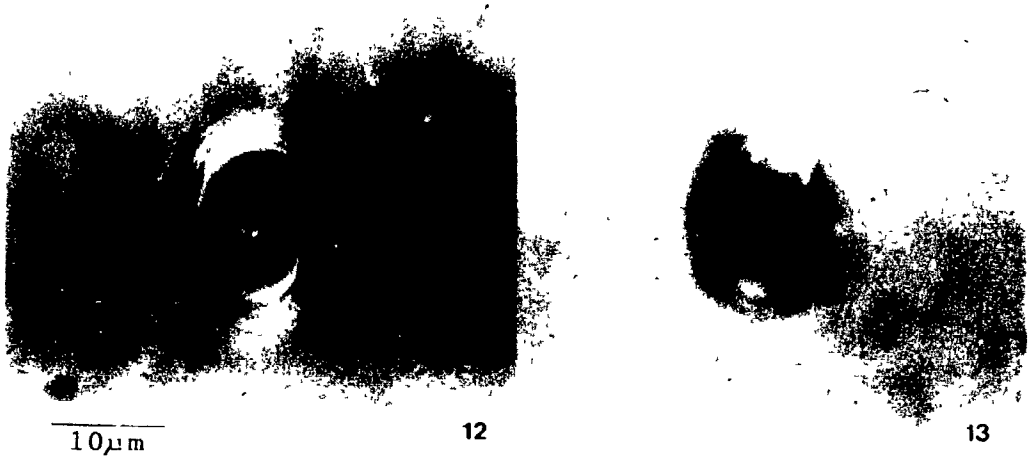
13. Lotus subbiflorus, equatorial view, surface sculpturing.



8 9



10 11



10μm

12 13

FIGS. 14-22

Fig. 14. Lotus corniculatus, equatorial view, colpus and porus.

15. L. corniculatus, equatorial view, optical section.

16. L. corniculatus, equatorial view, surface sculpturing.

17. L. uliginosus, equatorial view, colpus and porus.

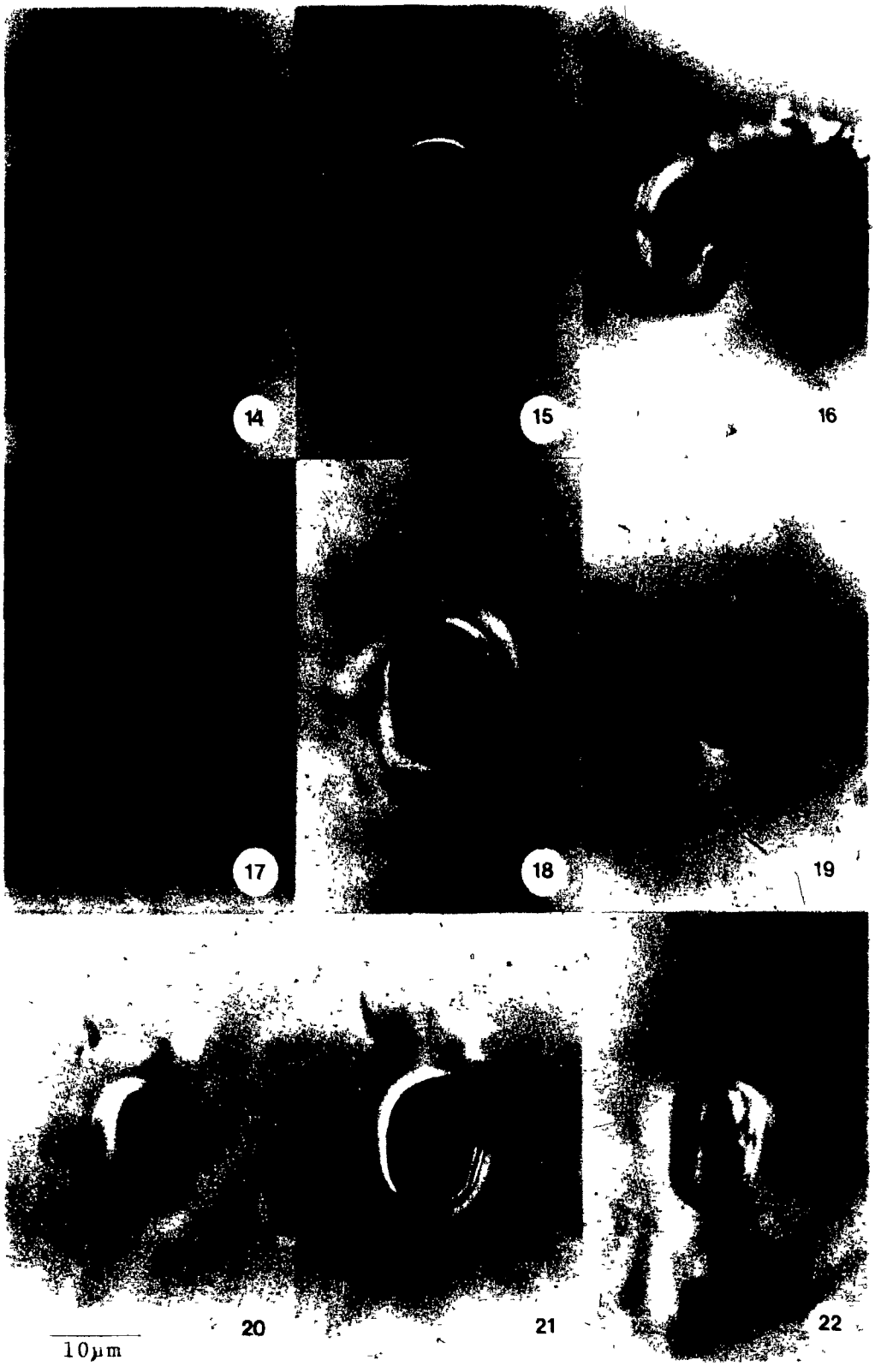
18. L. creticus, equatorial view, colpus and porus.

19. L. creticus, equatorial view, surface sculpturing.

20. L. cytisiodes, equatorial view, colpus and porus.

21. L. cytisiodes, equatorial view, optical section.

22. L. cytisiodes, equatorial view, surface sculpturing.


14
15
16
17
18
19
20
21
22
10μm

FIGS. 23-30

Fig. 23. *Lotus edulis*, equatorial view, colpus and porus.

24. *L. edulis*, equatorial view, optical section.

25. *L. edulis*, equatorial view, surface sculpturing.

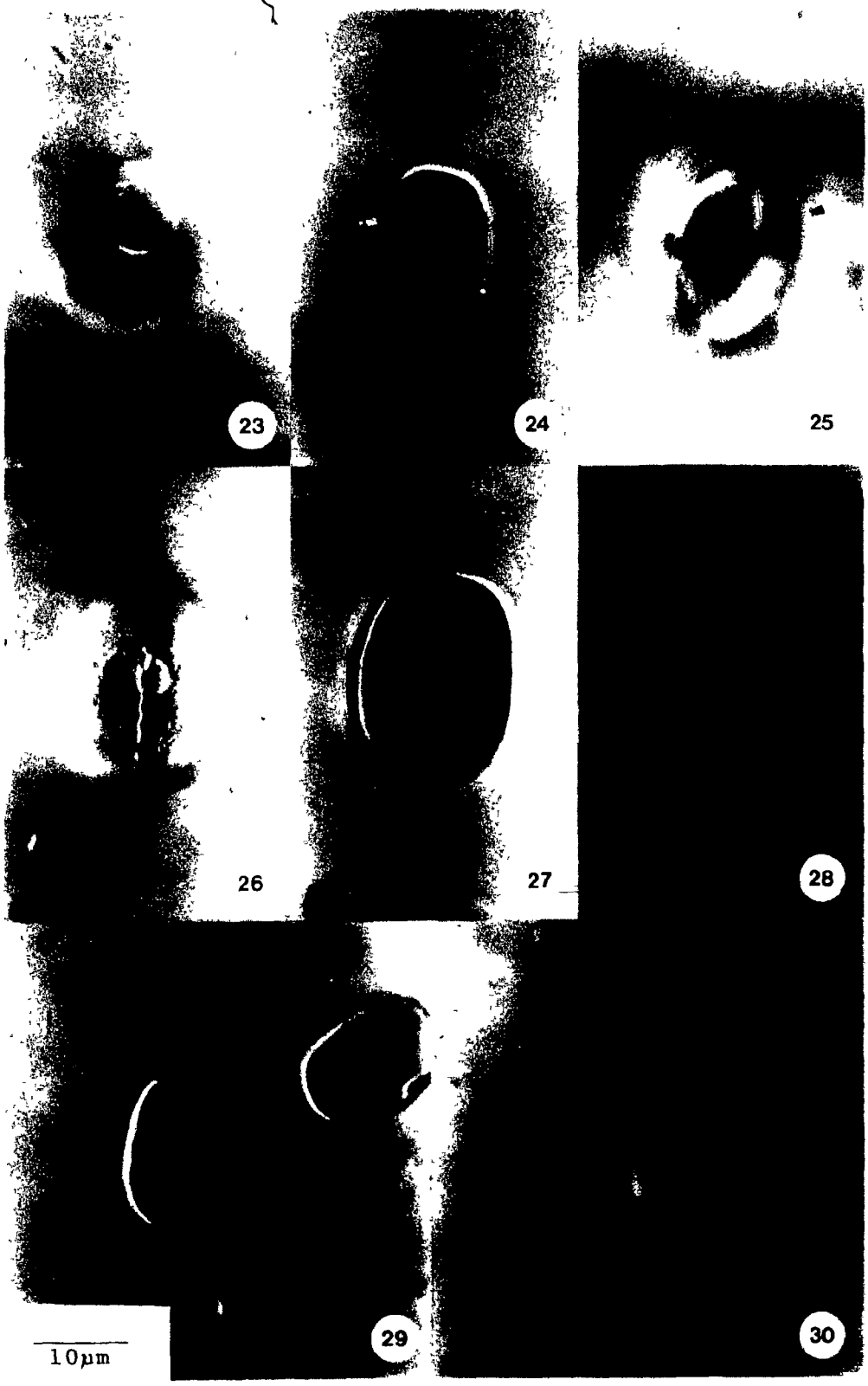
26. *L. gebelia*, equatorial view, colpus and porus.

27. *L. gebelia*, equatorial view, optical section.

28. *L. ornithopodioides*, equatorial view, colpus and porus.

29. *L. ornithopodioides*, equatorial view, optical section.

30. *L. ornithopodioides*, equatorial view, surface sculpturing.


23
24
25
26
27
28
29
30
10µm

FIGS. 31-35 - PEDROSIA

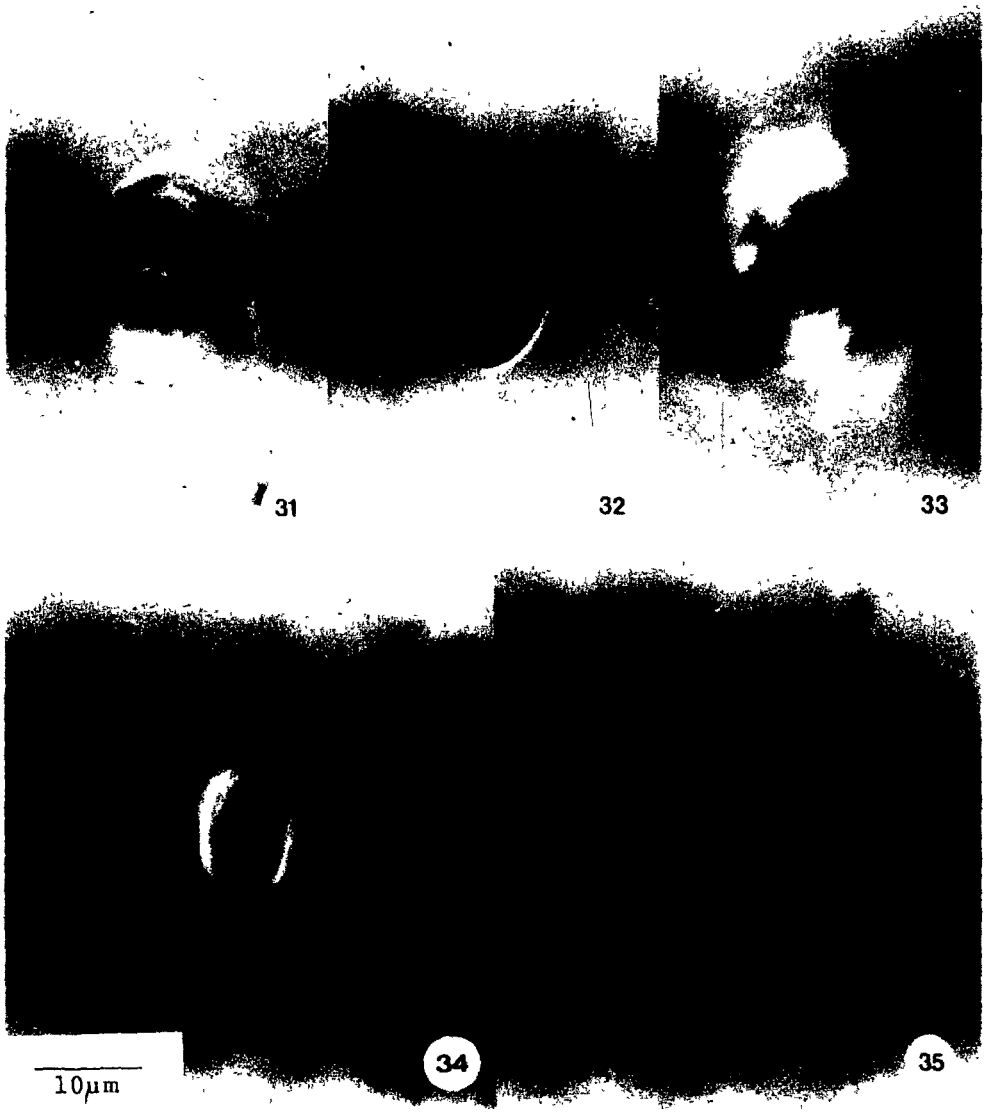
Fig. 31. Lotus glaucus, equatorial view, colpus and porus.

32. L. glaucus, equatorial view, optical section.

33. L. glaucus, equatorial view, surface sculpturing.

34. L. jacobaeus, equatorial view, colpus and porus.

35. L. jacobaeus, equatorial view, optical section.


31
32
33
34
35
10μm

FIGS. 36-41 - HOSACKIA

Fig. 36. Lotus aboriginus, polar view, optical equatorial section.

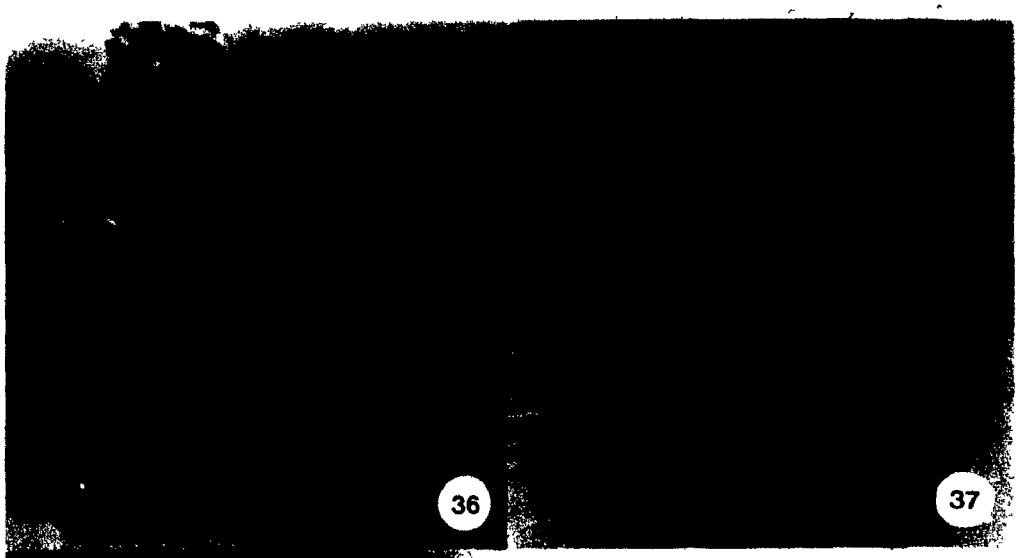
37. L. aboriginus, equatorial view, optical section.

38. L. aboriginus, equatorial view, colpus and porus.

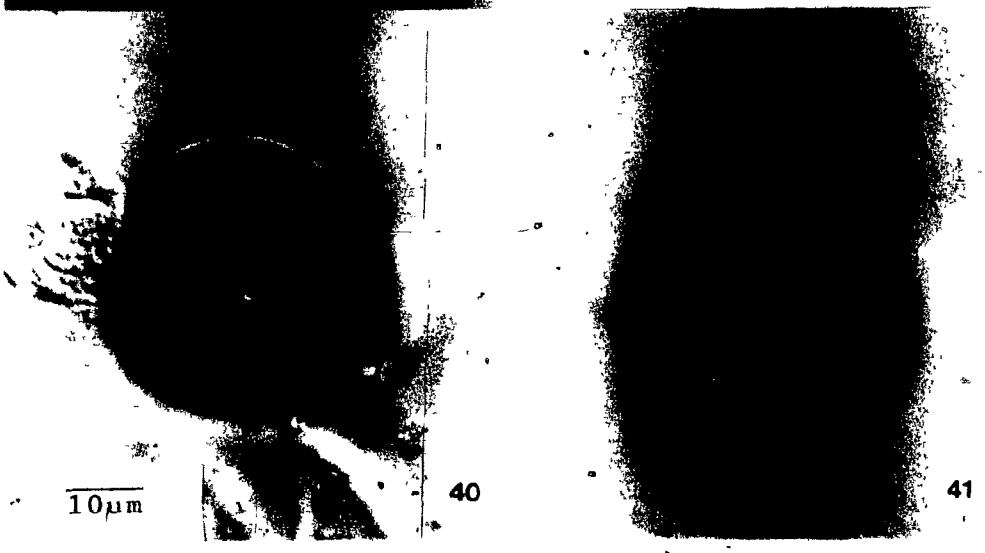
39. L. crassifolius, equatorial view, surface sculpturing.

40. L. formosissimus, equatorial view, colpus and porus.

41. L. formosissimus, equatorial view, surface sculpturing.


36
37


38
39


10μm
40
41

FIGS. 42-47 - HOSACKIA

Fig. 42. Lotus oblongifolius polar view, optical equatorial section.

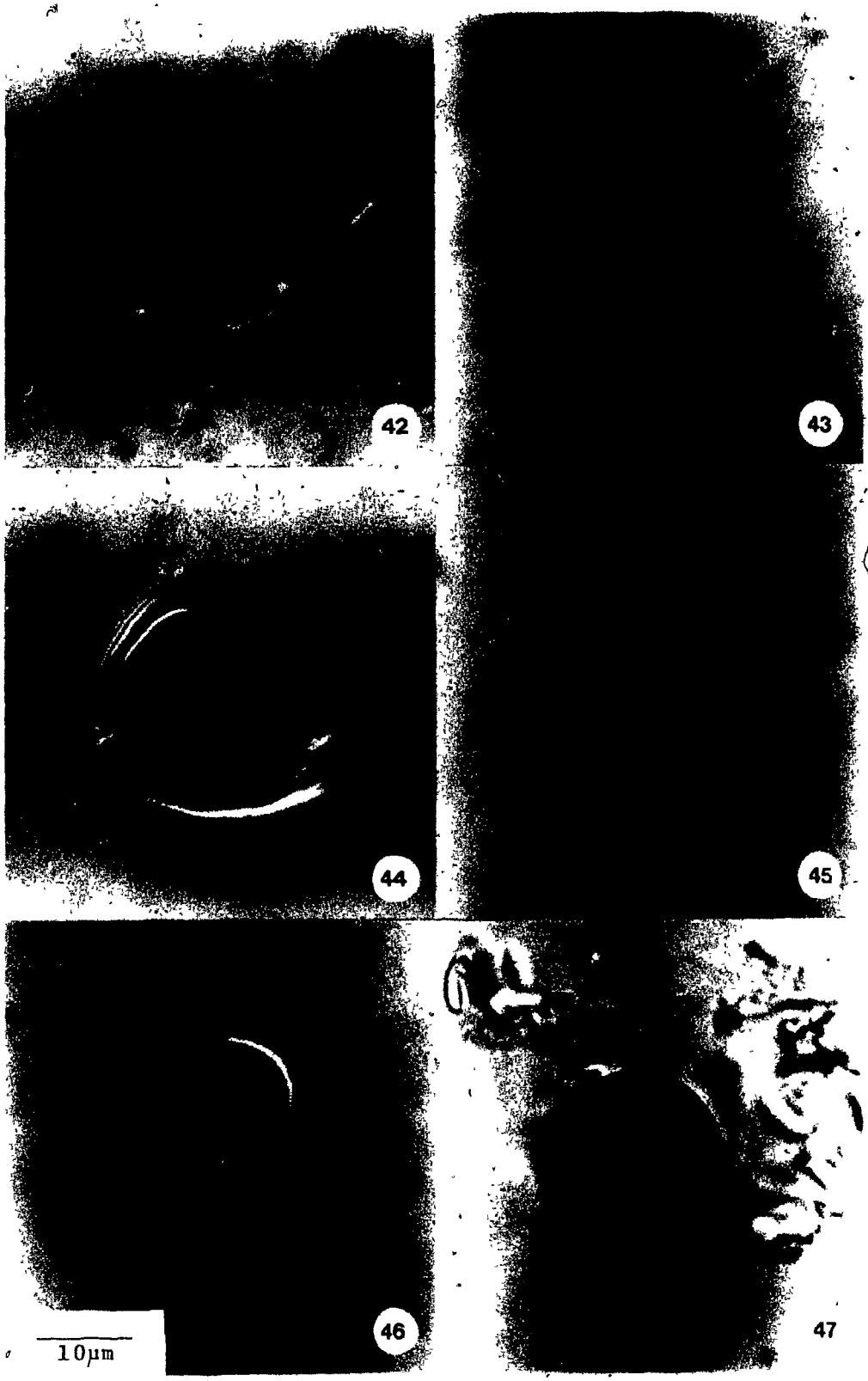
43. L. oblongifolius, equatorial view, colpus and porus.

44. L. pinnatus, polar view, optical equatorial section.

45. L. pinnatus, equatorial view, optical section.

46. L. pinnatus, equatorial view, colpus and porus.

47. L. crassifolius, equatorial view, optical section.


42
43
44
45
46
47
10μm

FIGS. 48-54 - ACMISPON

Fig. 48. Lotus micranthus, polar view, optical equatorial section.

49. L. micranthus, equatorial view, surface sculpturing.

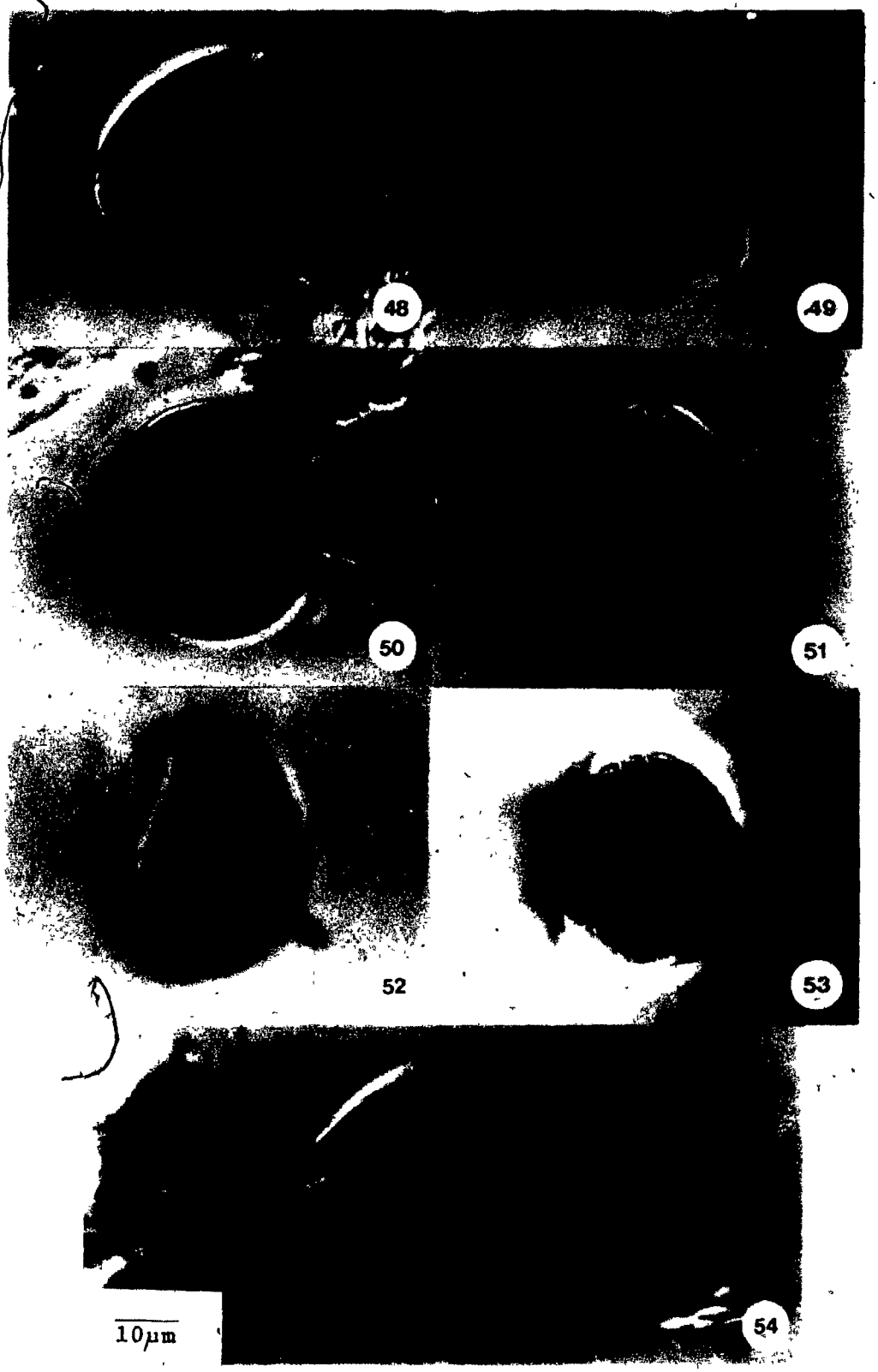
50. L. micranthus, equatorial view, optical equatorial section.

51. L. salsuginosus, polar view, optical equatorial section.

52. L. humistratus, equatorial view, intercolpium sculpturing.

53. L. humistratus, equatorial view, surface sculpturing.

54. L. purshianus, polar view, optical equatorial section.


48
49
50
51
52
53
54
10μm

FIGS. 55-60 - SYRMATIUM

Fig. 55. Lotus scoparius, polar view, optical equatorial section.

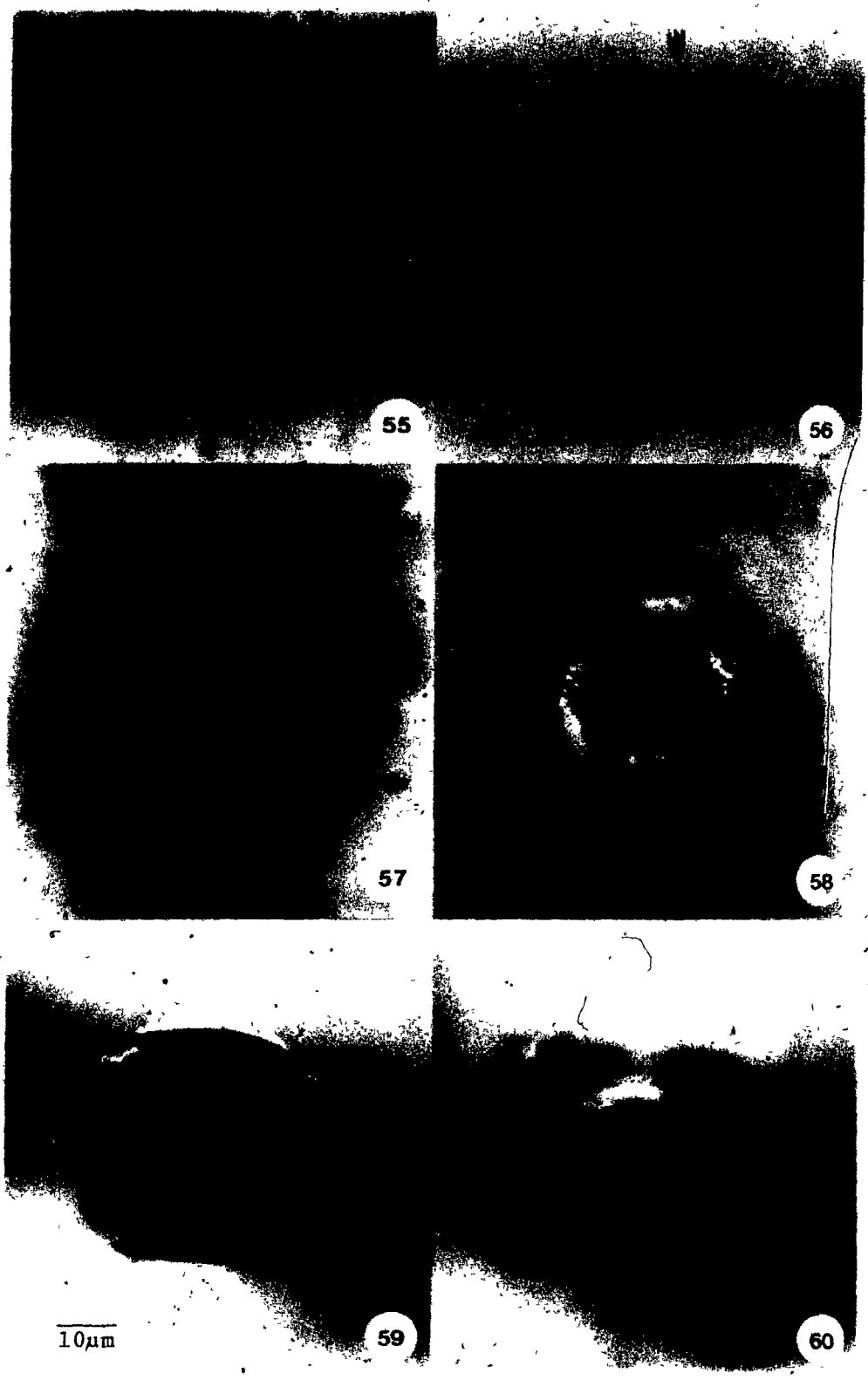
56. L. scoparius, equatorial view, surface sculpturing.

57. L. junceus, equatorial view, optical section.

58. L. junceus, equatorial view, surface sculpturing.

59. L. douglasii, polar view, optical equatorial section.

60. L. douglasii, polar view, surface sculpturing.


55
56
57
58
59
60
10µm

FIGS. 61-67 - SIMPETERIA

Fig. 61. Lotus wrightii, polar view, equatorial optical section.

62. L. wrightii, equatorial view, colpus and porus.

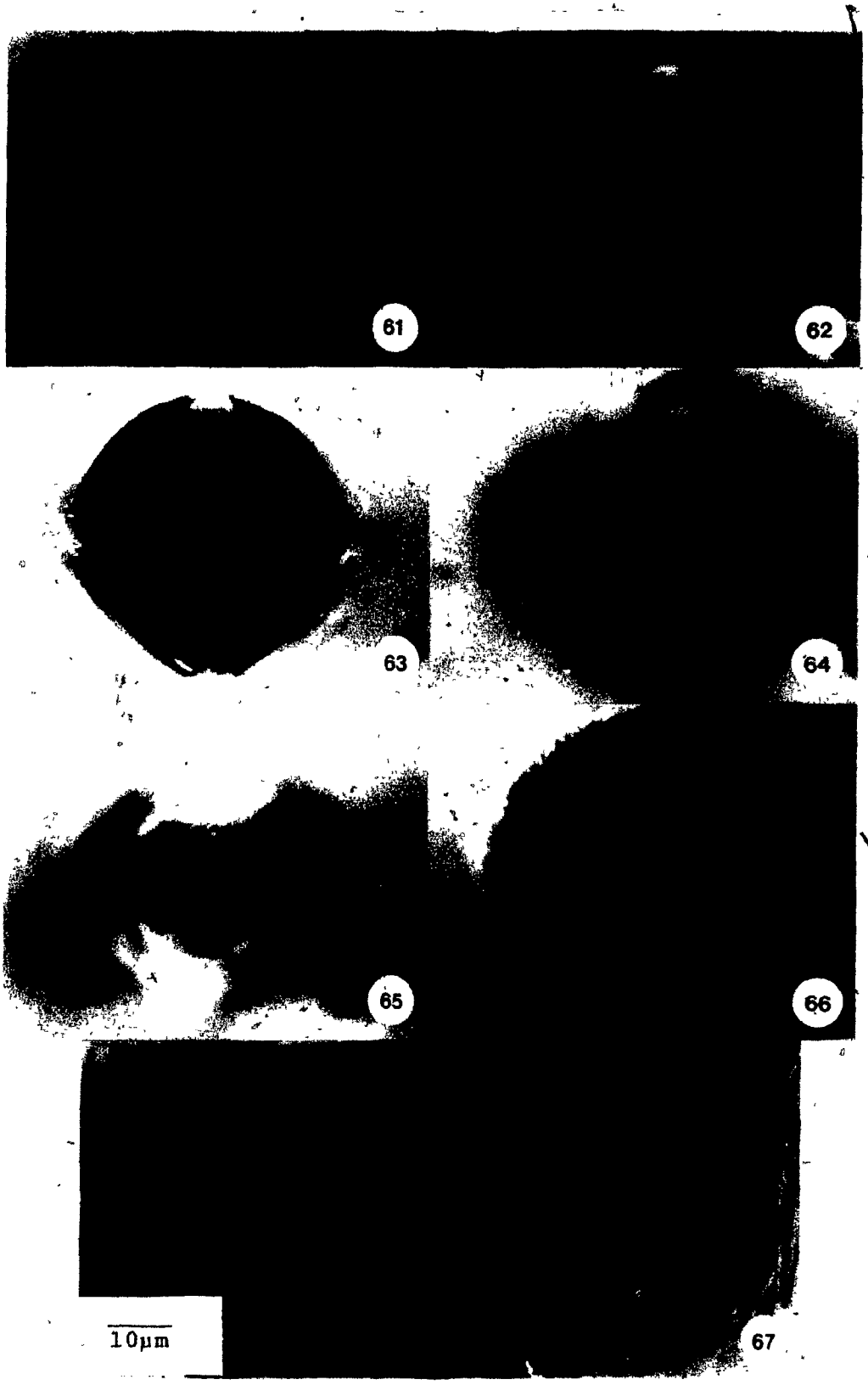
63. L. grandiflorus, polar view, equatorial optical section.

64. L. grandiflorus, polar view, surface sculpturing.

65. L. grandiflorus, polar view, surface sculpturing.

66. L. strigosus, polar view, equatorial section.

67. L. strigosus, equatorial view, surface sculpturing.


61
62
63
64
65
66
67
10µm

FIGS. 68-73 - SEM - ANTHYLLIS AND LOTUS

Fig. 68. *Anthyllis vulneraria* X 2800, note circular area on polar end.

69. *Hymenocarpus* X 2600, note rectangular shape.

70. *L. corniculatus* X 2000, note granular sculpturing, colpi and pori.

71. *L. corniculatus* X 5100.

72. *L. arabicus* X 5000, note sculpturing similar to *L. corniculatus*.

73. *L. edulis* X 5000, note sculpturing similar to *L. corniculatus*.


68
69
70
71
72
73

FIGS. 74-78 - SEM - PEDROSIA

Fig. 74. *Lotus borzii* X 6000.

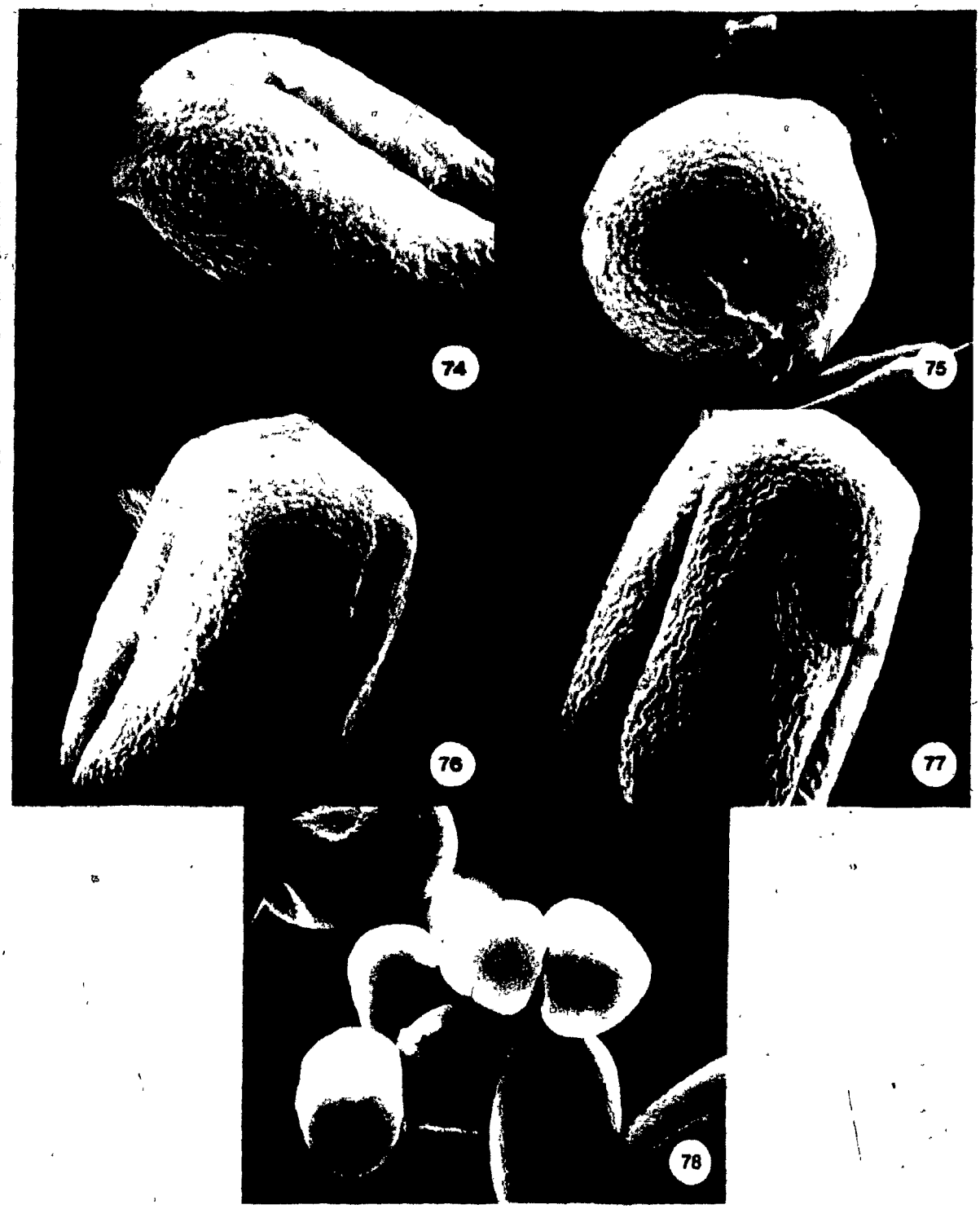
75. *L. campylocladus* X 6000.

76. *L. glaucus* X 6000.

77. *L. sessilifolius* X 6000.

78. *L. sessilifolius* X 2400.

Note similar sculpturing pattern of these taxa.


74
75
76
77
78

FIGS. 79-83 - SEM - HOSACKIA

Fig. 79. L. oblongifolius X 2400.

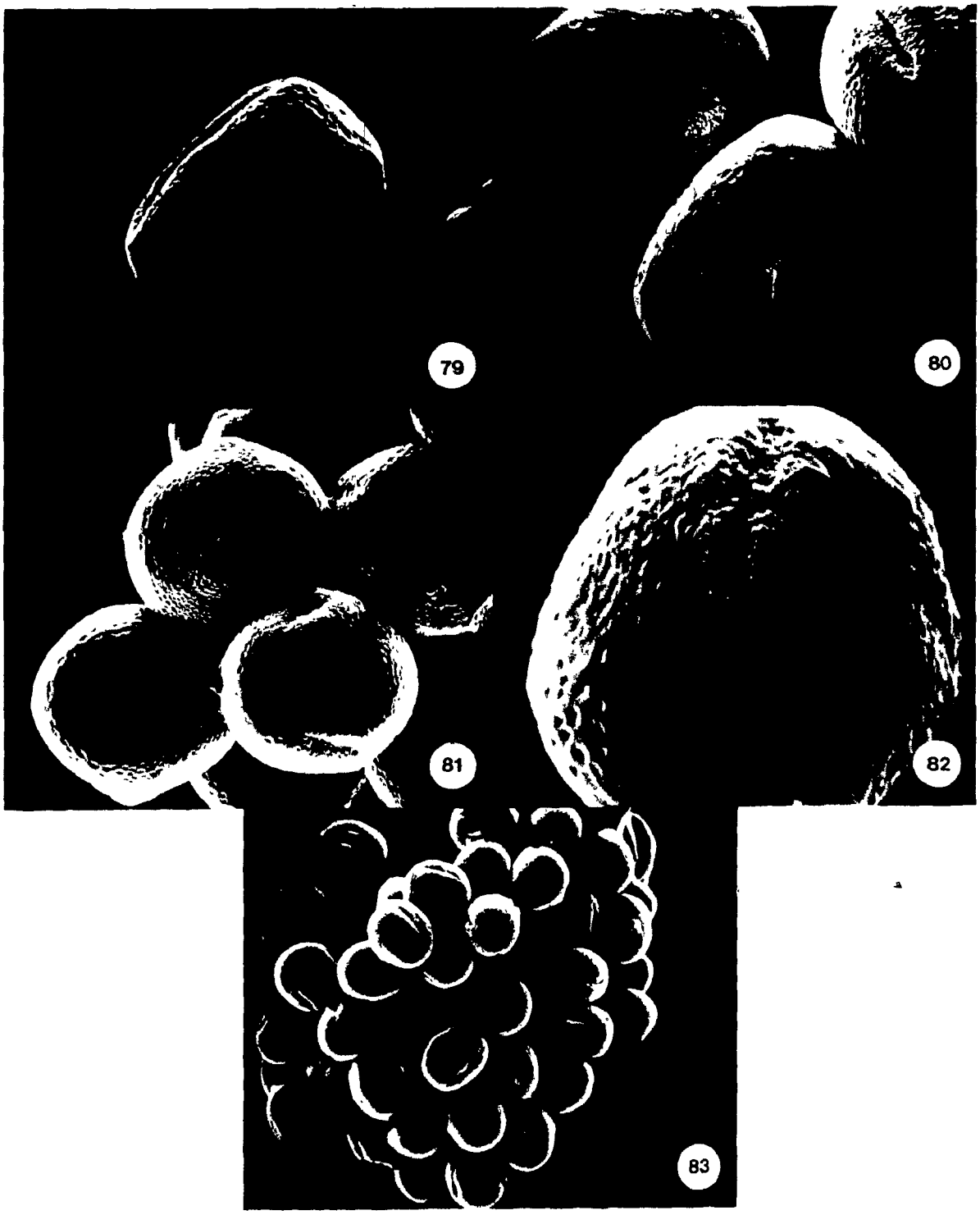
80. L. oblongifolius X 2400.

81. L. pinnatus X 2100.

82. L. stipularis X 6000.

83. L. yollabolliensis X 675.

Note smooth polar ends on pollen of L. oblongifolius, granular colpi margins and foveate-reticulate sculpturing. Common to HOSACKIA taxa examined in this study.


79
80
81
82
83

FIGS. 84-89 - SEM - ACMISPON

Fig. 84. Lotus purshianus X 1150.

85. L. purshianus X 2500.

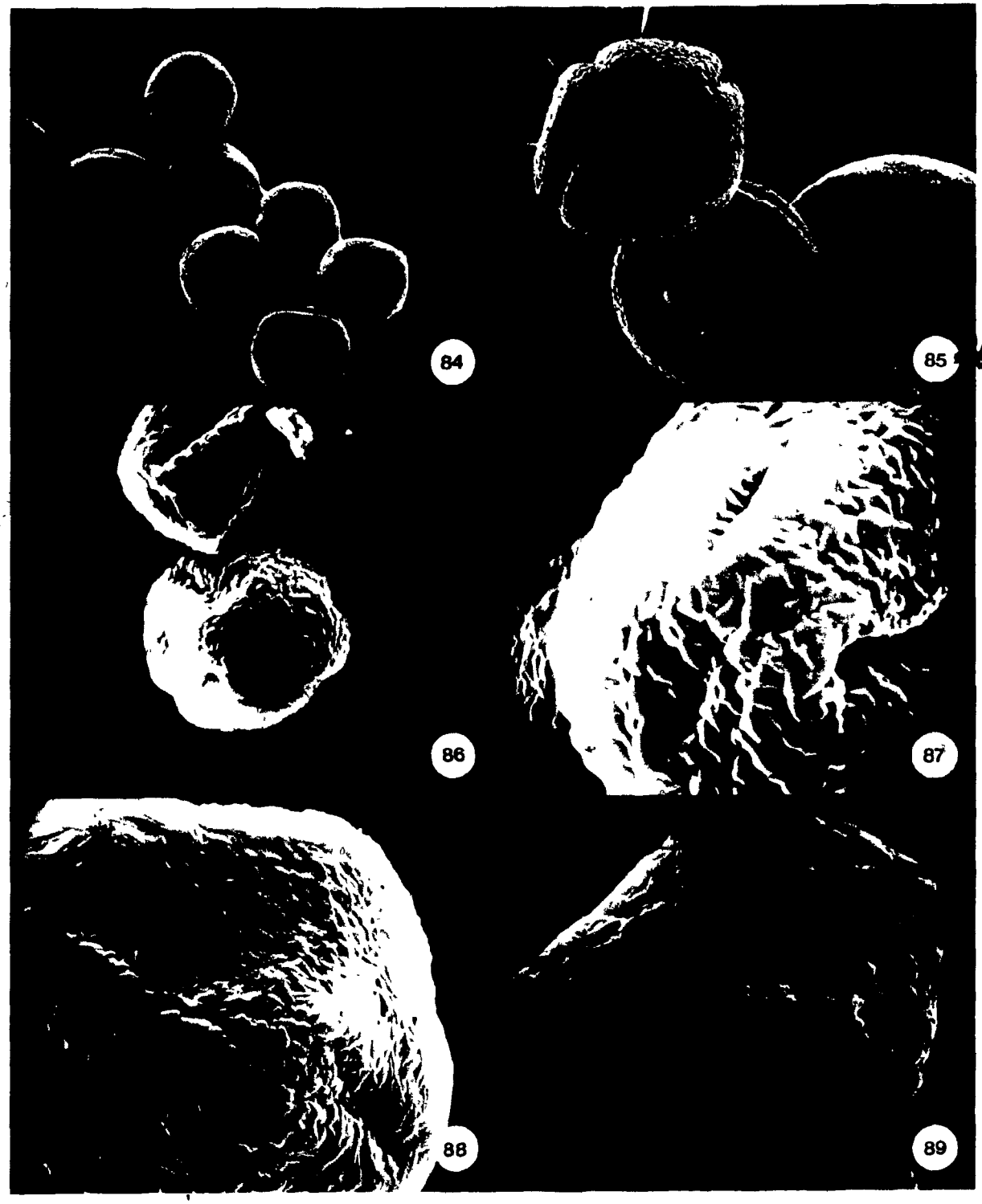
86. L. salsuginosus X 2700.

87. L. salsuginosus X 6700.

88. L. humistratus X 5900.

89. L. humistratus X 5900.

Note tricolporate grains, rugulate sculpturing type on Figs. 84-87 and striate sculpturing on Lotus humistratus.


84
85
86
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89

FIGS. 90-95 - SEM - SIMPETERIA

Fig. 90. *Lotus grandiflorus* X 2600.

91. *L. oroboides* (*neomexicana*) X 2500.

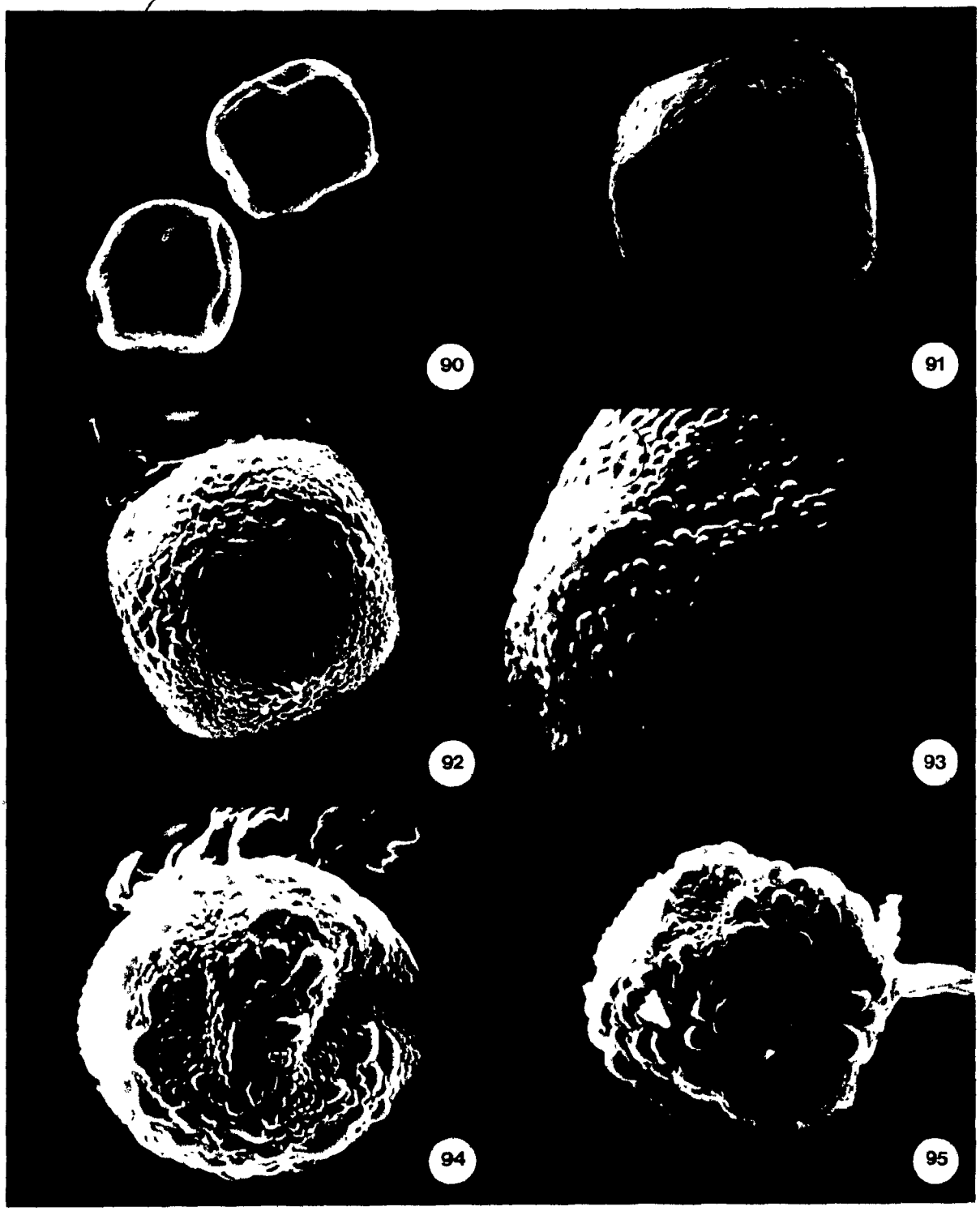
92. *L. strigosus* var. *tomentellus* X 2800.

93. *L. strigosus* var. *tomentellus* X 7000.

94. *L. strigosus* var. *strigosus* X 2700.

95. *L. strigosus* var. *strigosus* X 2700.

Note that the pollen grains in SIMPETERIA are extremely heteromorphic. They have various colpi arrangements and the sculpturing pattern varies from psilate to verrucate.


90
91
92
93
94
95

FIGS. 96-101 - SEM - SYRMATIUM

Fig. 96. Lotus argophyllus X 2650.

97. L. argophyllus X 6600.

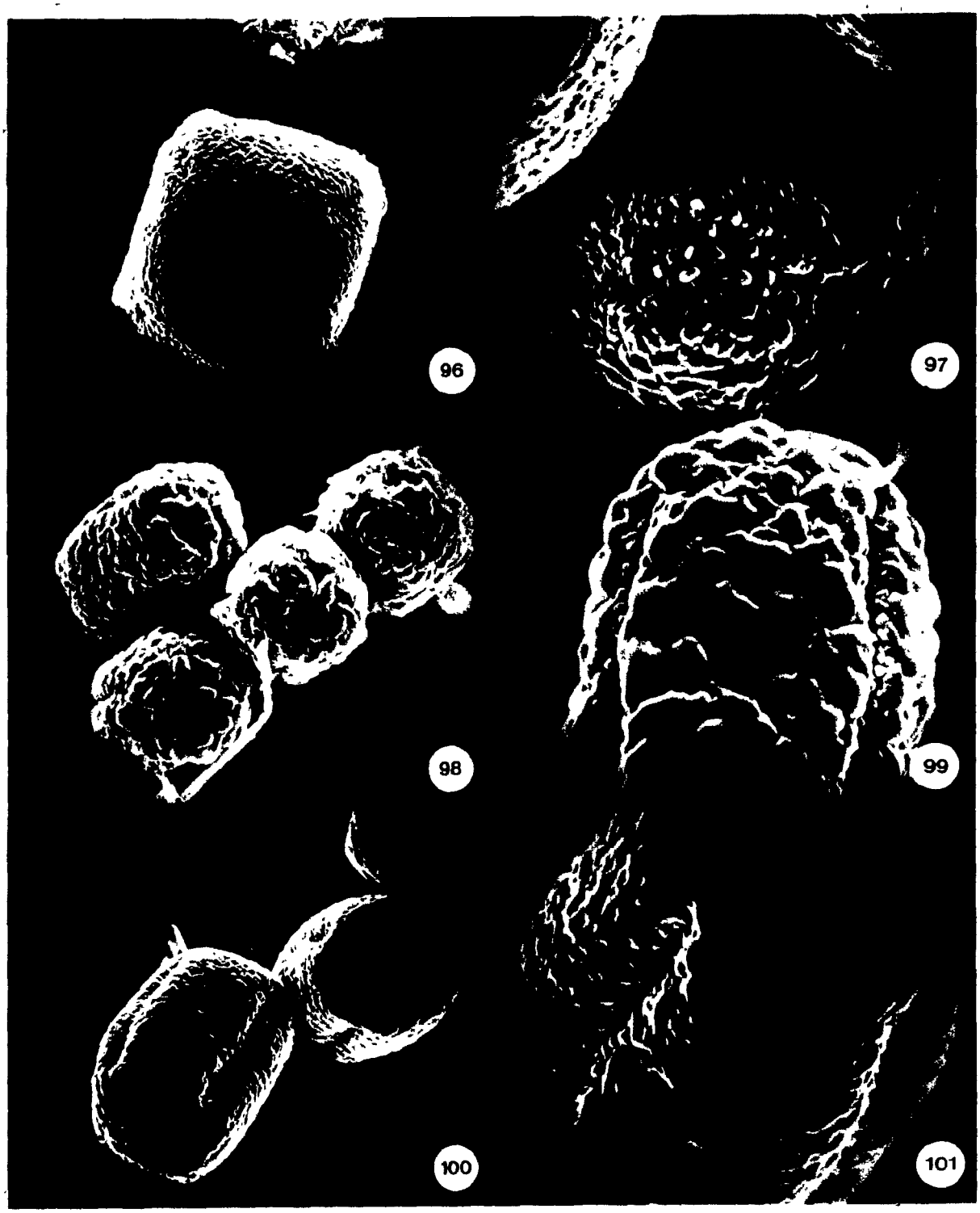
98. L. glabra X 2000.

99. L. glabra X 5000.

100. L. junceus X 2000.

101. L. junceus X 5000.

Note that the pollen grains in SYRMATIUM are heteromorphic. Sculpturing pattern ranges from finely to coarsely rugulate. L. junceus has punctate polar ends.


96
97
98
99
100
101

FIGS. 102-106 - SEM - CORONILLEAE

Fig. 102. *Ornithopus pinnatus* X 2800.

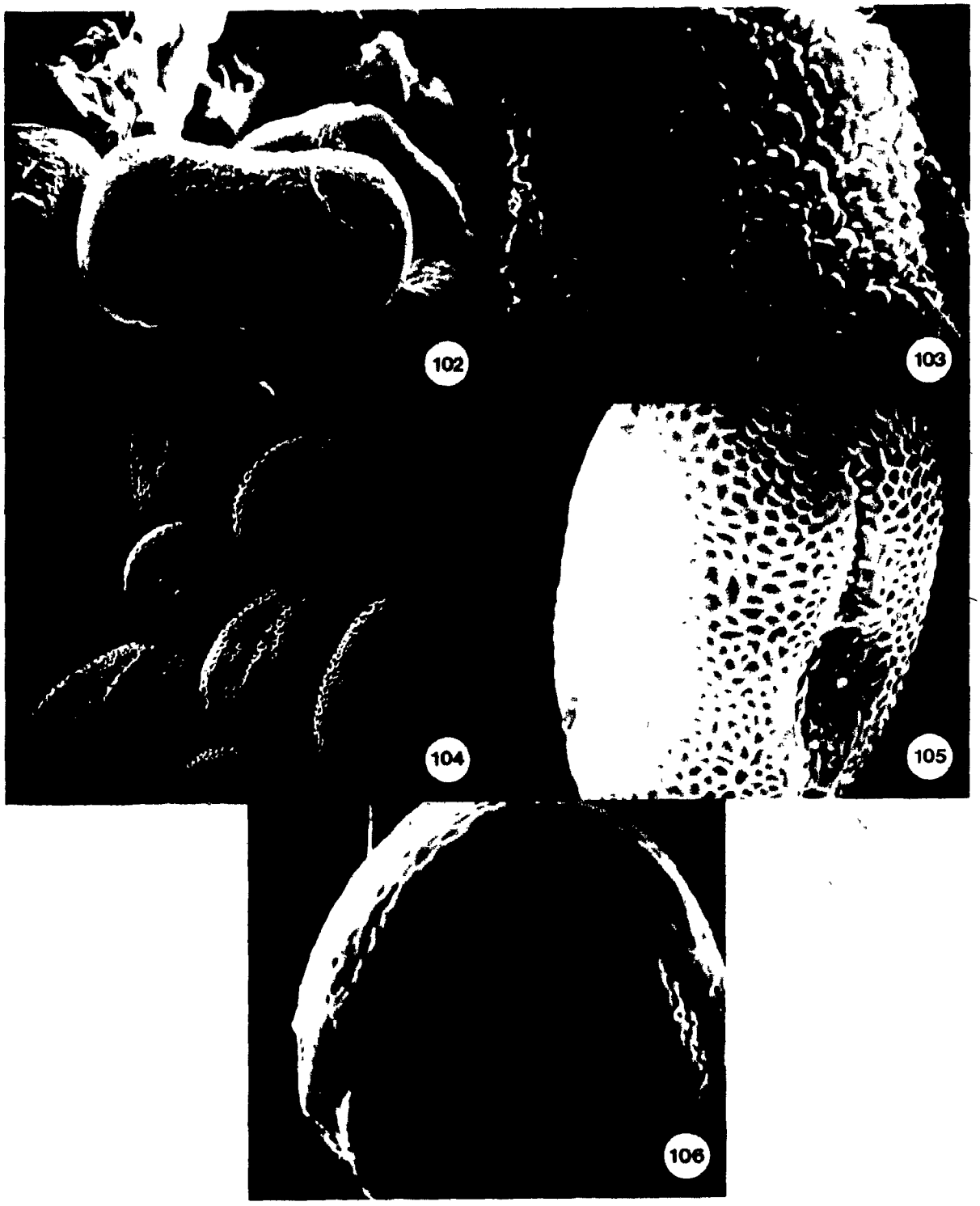
103. *O. pinnatus* X 6800.

104. *Scoparius muricatus* var. *subvillosus* X 2800.

105. *Scoparius muricatus* var. *subvillosus* X 7000.

106. *Hippocrepis ciliata* X 7000.

Note that the pollen grains of these few taxa examined in the CORONILLEAE are extremely different morphologically from Loteae. For instance, *Ornithopus* has verrucate clusters of sculpturing with nanoprocesses. Note that *Scoparius* is reticulate.. *Hippocrepis* does not have a very distinctive morphology.


102
103
104
105
106

FIGS. 107-111 - SECTIONED SPECIMENS

Fig. 107. X 11,200, *Lotus australis*

108. X 11,200, *L. edulis*

109. X 11,200, *L. humistratus*

110. X 12,500, *L. strigosus*

111. X 5,700, *L. corniculatus*

Note that the exine and endexine layers in these species are not clearly defined. It is interesting to observe the template or reverse negative effect inside the pollen grain indicative of their final sculpturing patterns.


107
108
109
110
111

D. Numerical taxonomy of pollen data

Dissimilarities, (distances) utilizing the incremental sum of squares, based upon Gower distances, the commonly used Manhattan metric (Sneath and Sokal, 1973) are presented in a computer generated dendrogram (Figure 113). Interestingly, the majority of OTU'S representing New World Lotus formed families on the left side of the dendrogram, while Old World Loteae formed families on the right. Principal co-ordinate analyses, Figure 112, yielded clusters of New World taxa on the left minus axis and plus axis, while Old World groups clustered right minus and right plus on the axes of first and second principal co-ordinates. Many taxa did not cluster; but certain trends were easily observed. To further examine the relationships between taxa in terms of their pollen morphology an analysis was conducted in terms of their higher taxonomic categories as classified under the following groups: Hosackia (HOSL), Simpeteria (SIML), Syrmatium (SYRL), Erythrolotus (ERYL), Acmispon (ACML), Lotus (LOTU), Lotea (LOTE), Tetragonolobus (TETL), Dorycnium (DORL), Pedrosia (PEDL), Krokeria (KROL), Anthyllis (ANTL), Cytisopsis (CDOL), Vermifrux (LABY).

For these groups the means of all the pollen characters were calculated over the total number of OTU's for the category. These means were then analysed by employing the same methods as indicated for the original data matrix.

The major taxonomic groupings are those referred to on page 7 and in the Discussion, pages 174 to 179. If one surveys the numerical taxonomic literature on phenetic NT it will show that ordination cluster analysis is the most frequently used NT technique (Duncan and Baum, 1981). These authors indicated that the sums of squares technique will normally separate variation at its midpoint and when OTU's are scattered, the technique will cluster groups. Duncan and Baum (1981), also indicated that the Lefkovitch (1976) method (used in this study) also consolidated OTU's into clusters.

Figure 112 shows the plot of OTU's on the first and second axes of the principle co-ordination. Figure 113 is the computer generated dendrogram of the OTU's based upon the incremental sum of squares method.

Figure 114 represents the principle co-ordinate analysis of the mean values for the classically recognized groups. Upon this axes is superimposed the minimum spanning tree (MST) which represents the nearest neighbour (single linkage) connective. Figure 115 is a dendrogram based upon the same data matrix.

Figures 116 and 117 are presented to indicate phenetically related groups. They showed the joining of the various groups when linked by dissimilarity distances of 0.600 and 0.650. OTU codings are presented in alphabetical

order of their taxa in Appendix IV and coding synonomy is given in Appendix V.

It may be noted that several taxonomic groups cluster at various positions (circled areas in Figure 12) on the axes, e.g. LORN, LCYT, LHIS, LEDU, LTEN, LCOR, LCOl, representing Lotus ornithopodioides, L. cytisoides, L. hispidus, L. edulis, L. tenuis, L. corniculatus, are taxa from the following Old World groups: corniculatus, angustissimus, ornithopodioides, and creticus according to Brand (1898). Therefore on the basis of pollen grain characteristics of these taxa, no confirmation of the Old World taxonomic groups was possible. Lotus uliginosus, a taxon which is placed in the corniculatus group, also did not cluster with its relatives. It is sufficient to observe that the major apparent trend shown on the axes is a separation into Old World and New World, as indicated by the black line in Figure 112, with some clustering of OTU's into natural groups.

On the basis of 11 pollen grain characteristics, it is interesting to note that the cluster of OTU's which formed on the lower left hand side of the axes is comprised mainly of taxa placed in the subgenus Syrmatium (Ottley, 1923). These taxa are LDAV, LWAT, LHAY, LWRI, ... etc., viz: Lotus davidsonii, L. watsonii, L. haydonii, L. wrightii; therefore, confirming her taxonomic treatment.

Co-phenetic analyses were considered for this study but the technique was not investigated. The reason for this decision is because co-phenetic analyses are normally used to compare the dissimilarities (distances) generated by various techniques and these calcualtions of geometric distances are then analyzed to evaluate the reliability of the different methods. Therefore, the results of co-phenetic analyses are not representative of a real data set, but are generated by the techniques. On the basis of only 11 pollen grain characters representing 153 OTU's the methods would divulge no real palyno-taxonomic data and would be unlikely to provide information (Dr. John McNeill, personal communication) upon which to evaluate whole-plant taxonomic treatments.

The NT of the Loteae pollen grain data supports the taxonomic decision of Brand (1898) to separate the North American Lotus taxa from the genus Lotus. The analyses, as represented in Figures 114, 115, 116 and 117, showed phenetic relationships between Acmispon, Simpeteria and Syrmatium. Hosackia is linked with Old World taxa (Figures 115 and 117), particularly Tetragonolobus, but Tetragonolobus does not connect to Old World Lotus or Loteae

as circumscribed by Polhill (1981), who considered Lotus and Tetragonolobus to be synonymous.

The data matrix upon which the NT studies are based is presented in Appendices II and III.

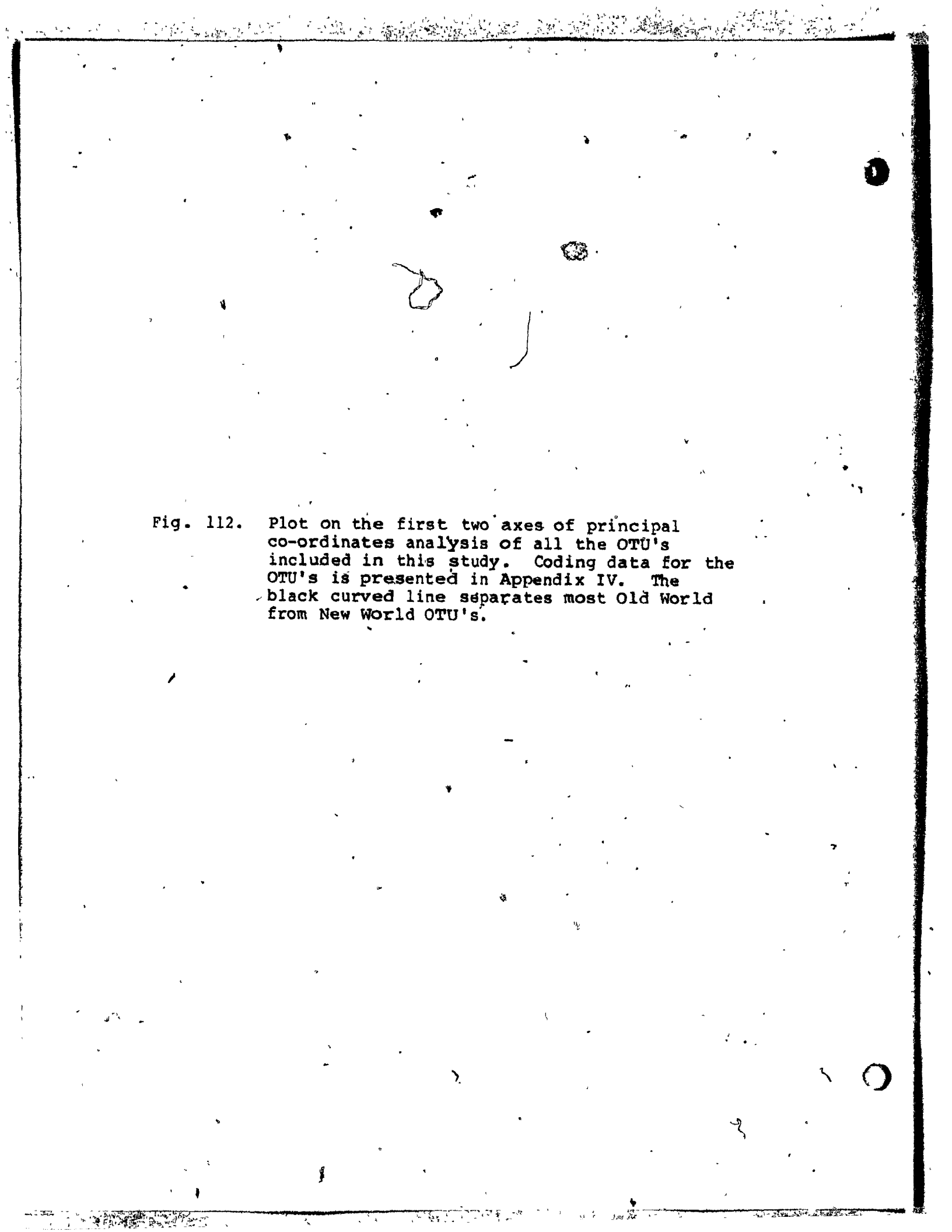


Fig. 112. Plot on the first two axes of principal co-ordinates analysis of all the OTU's included in this study. Coding data for the OTU's is presented in Appendix IV. The black curved line separates most Old World from New World OTU's.

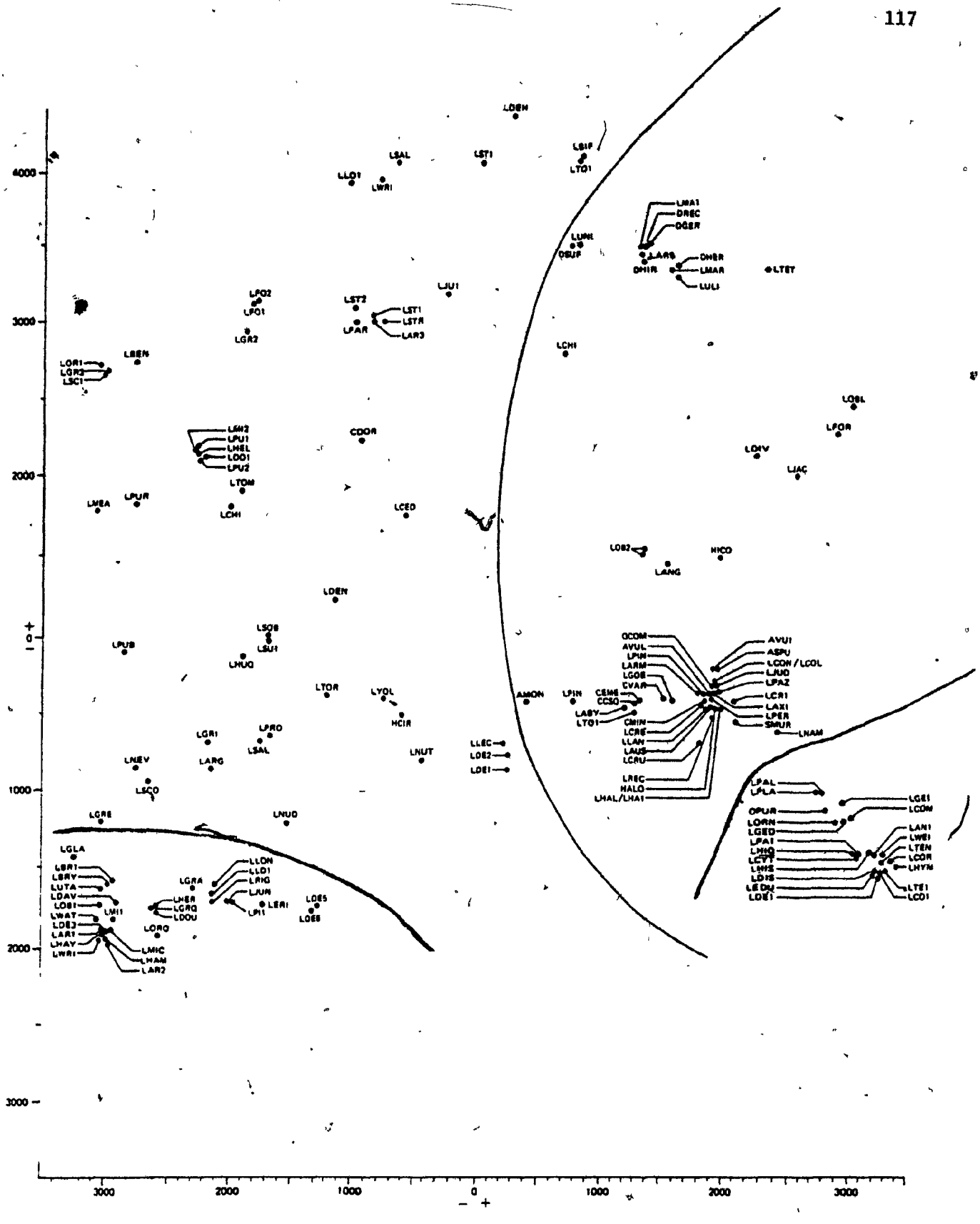
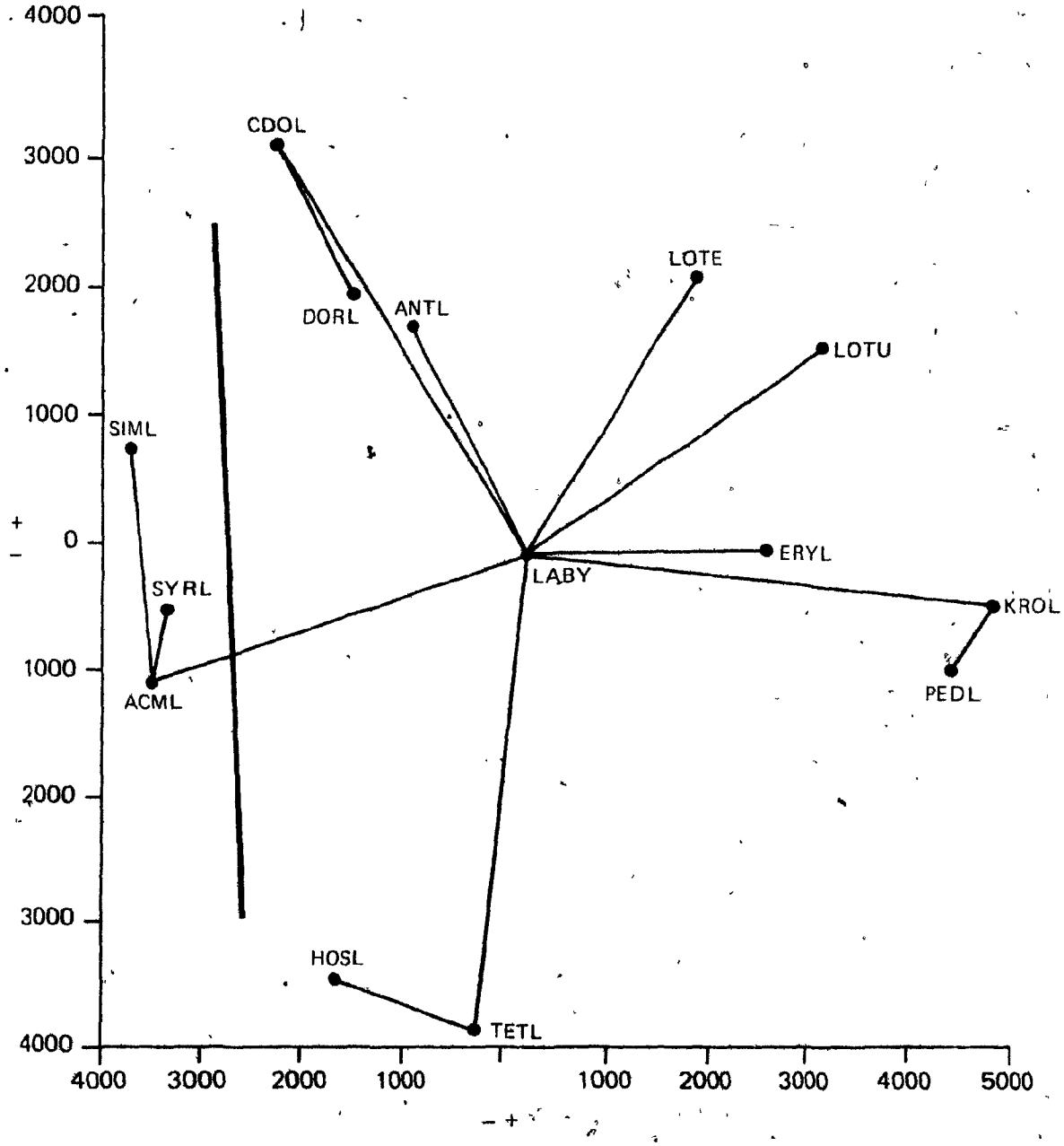

LOBH
LSAL
LST1
LSIF
LTO1
LLO1
LWRI
LMA1
DREC
OGER
LUPH
DSUF
LAR5
DHER
DHIR
LMAR
LTET
LULI
LUU1
LPO2
LPO1
LST2
LST1
LSTR
LPAR
LAR3
LGR2
LCHI
LOR1
LGR2
LSC1
LBEN
LOBL
LFOR
LOHV
LUAC
LSM2
LPU1
LHEL
LDO1
LPU2
CDOR
LTOM
LMEA
LPUR
LCHI
LCED
LOB2
HICO
LANG
LDEN
LSQB
LSUI
LPUB
LHUQ
LTOR
LYOL
HCIR
AMON
LPIN
CEME
CCSO
LABV
LTO1
OCOM
AVUL
LPIN
LARM
LGOB
CVAR
CMIN
LCRE
LLAN
LAUS
LCRU
LREC
HALO
LHAL/LHA1
AVU1
ASPU
LCON / LCOL
LJUD
LPAZ
LCR1
LAXI
LPER
SMUR
LNAM
LGR1
LPRO
LSAL
LARG
LNEV
LSCO
LNUT
LLEC
LDE2
LDE1
LPAL
LPLA
OPUR
LORN
LGED
LPAI
LHIQ
LCYT
LMHE
LDIS
LEON
LDE1
LGE1
LCOM
LAN1
LWE1
LTEN
LCOR
LHYM
LTE1
LCO1
LGRE
LNUO
LGLA
LBR1
LBRV
LUTA
LDAV
LOBI
LWAT
LDE3
LAR1
LHAY
LWR1
LMI1
LMIC
LHAN
LAR2
LGRA
LHER
LGRQ
LDOU
LORQ
LLON
LLD1
LRIG
LJUN
LPI1
LERI
LOES
LOEB
4000
3000
2000
1000
0
3000
2000
1000
0
1000
2000
3000

Fig. 113. Dendrogram based upon the incremental sum of squares technique showing dissimilarity distances for all taxa included in this study OTU codings are presented in Appendix IV.


50
40
30
20
10
0
DISSIMILARITY SCALE

Fig. 114. Principal co-ordinate analysis of the mean values for pollen of the various major groups included in this study. The diagram includes the minimum spanning tree.

Note the thick dark line indicates separation of *Lotus* into two major taxonomic groupings. For reference to abbreviations see Appendix III.


4000
3000
2000
1000
0
1000
2000
3000
4000
+
−
CDOL
DORL
ANTL
LOTE
LOTU
SIML
SYRL
ACML
ERYL
LABY
KROL
PEDL
HOSL
TETL
4000
3000
2000
1000
1000
2000
3000
4000
5000
− +

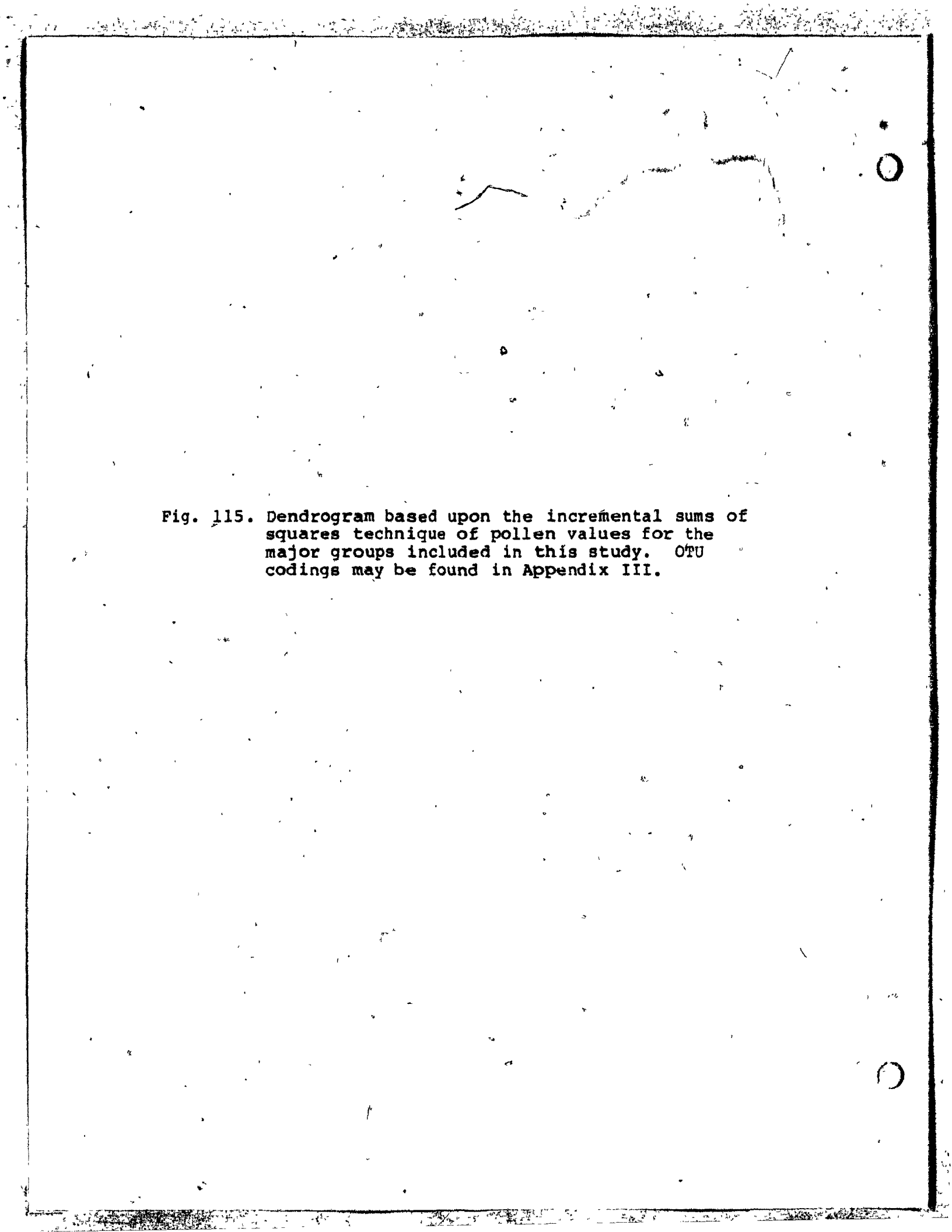


Fig. 115. Dendrogram based upon the incremental sums of squares technique of pollen values for the major groups included in this study. OTU codings may be found in Appendix III.

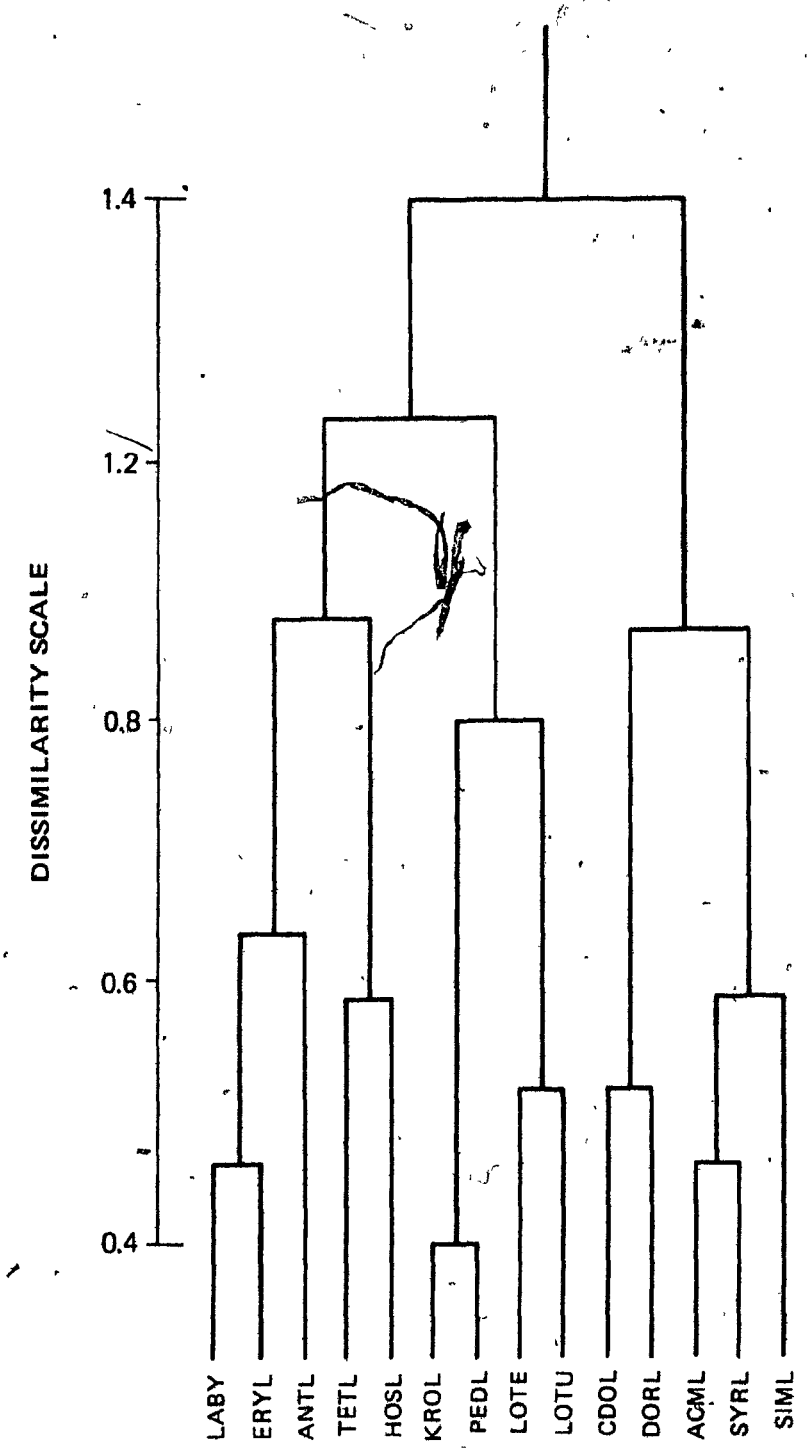
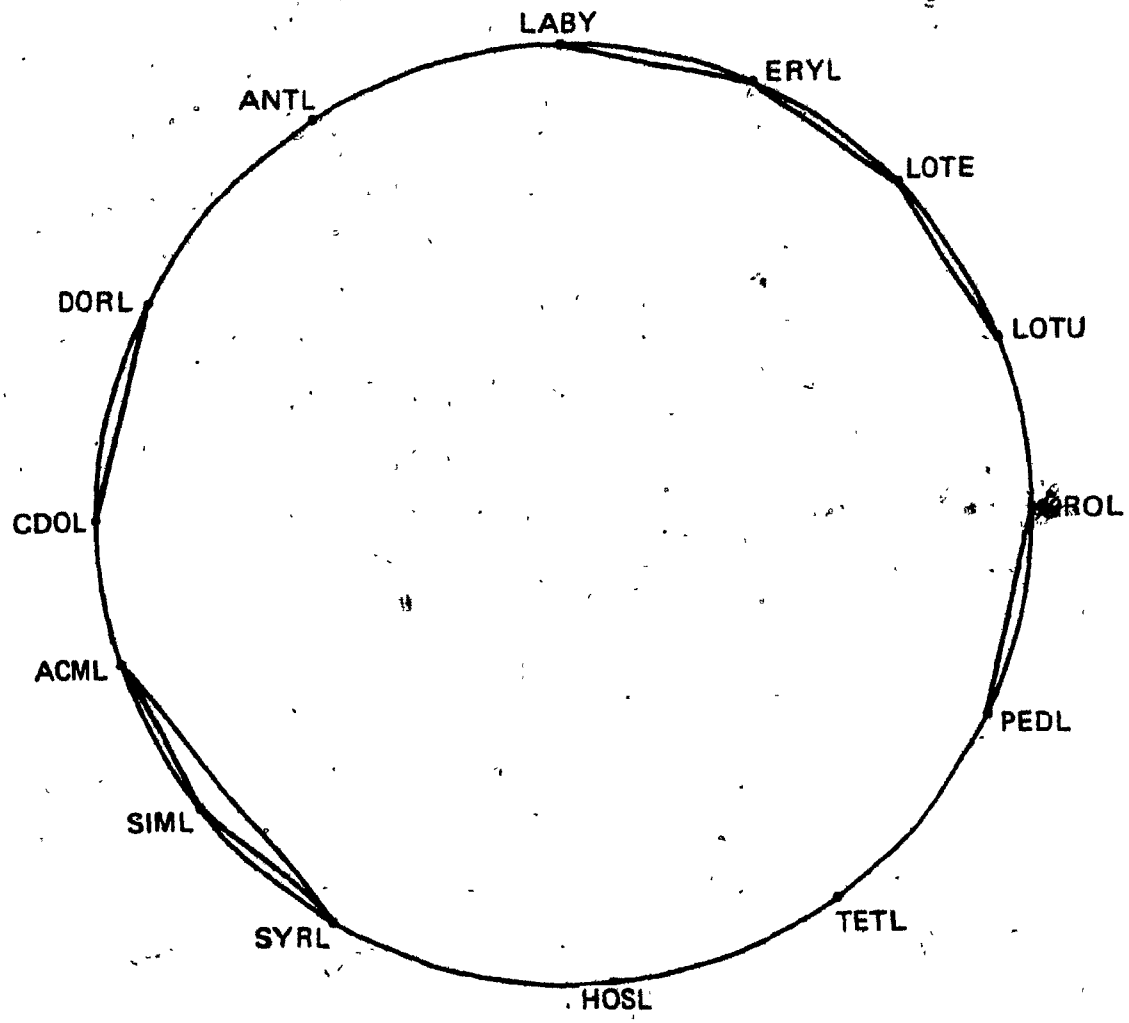

DISSIMILARITY SCALE
1.4
1.2
0.8
0.6
0.4
LABY
ERYL
ANTL
TETL
HOSL
KROL
PEDL
LOTE
LOTU
CDOL
DORL
ACML
SYRL
SIML

Fig. 116. Circular graph showing phenetic relationships revealed by numerical taxonomical analysis, lines joining the various groups indicated that they linked at a dissimilarity level of no greater than 0.600


LABY
ERYL
LOTE
LOTU
ROL
PEDL
TETL
HOSL
SYRL
SIML
ACML
CDOL
DORL
ANTL

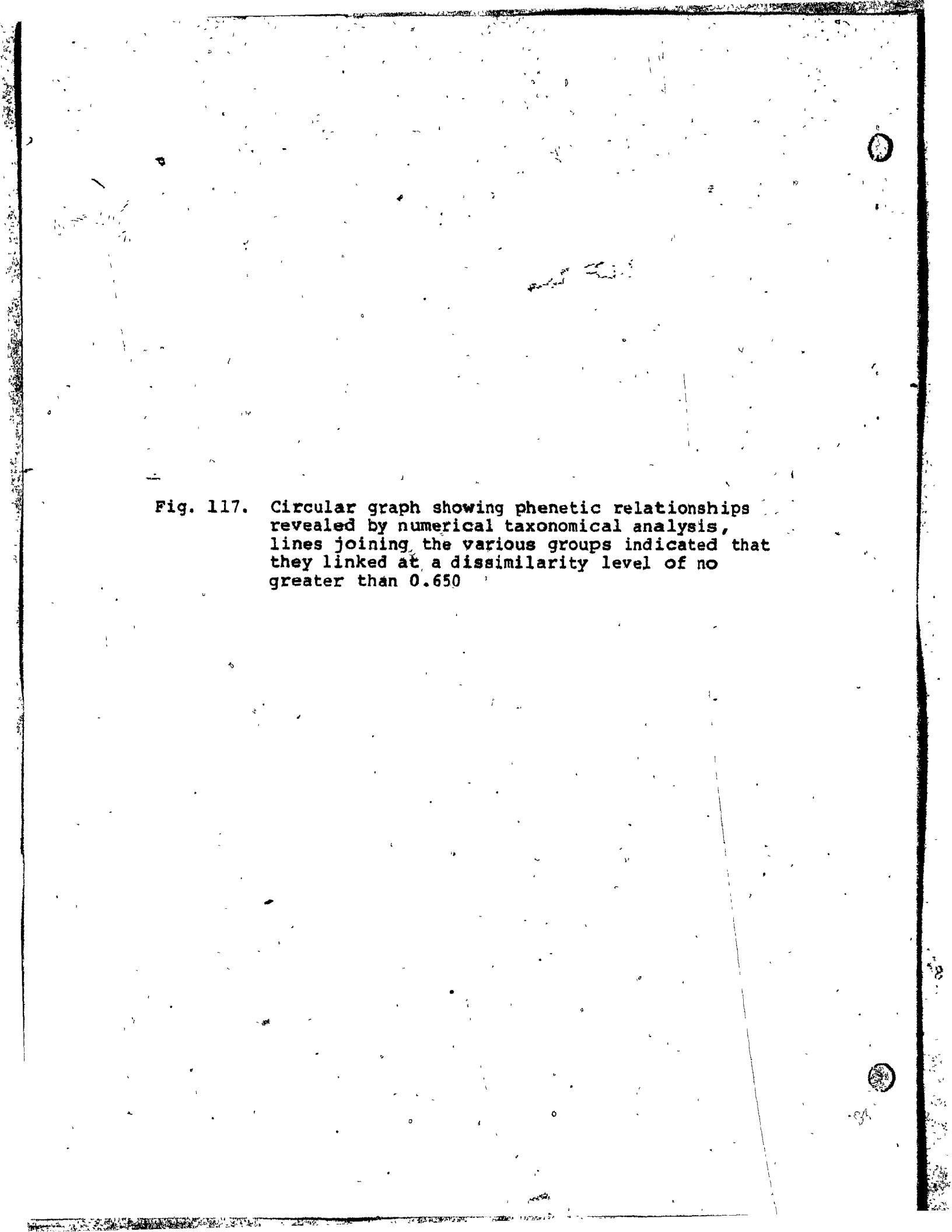
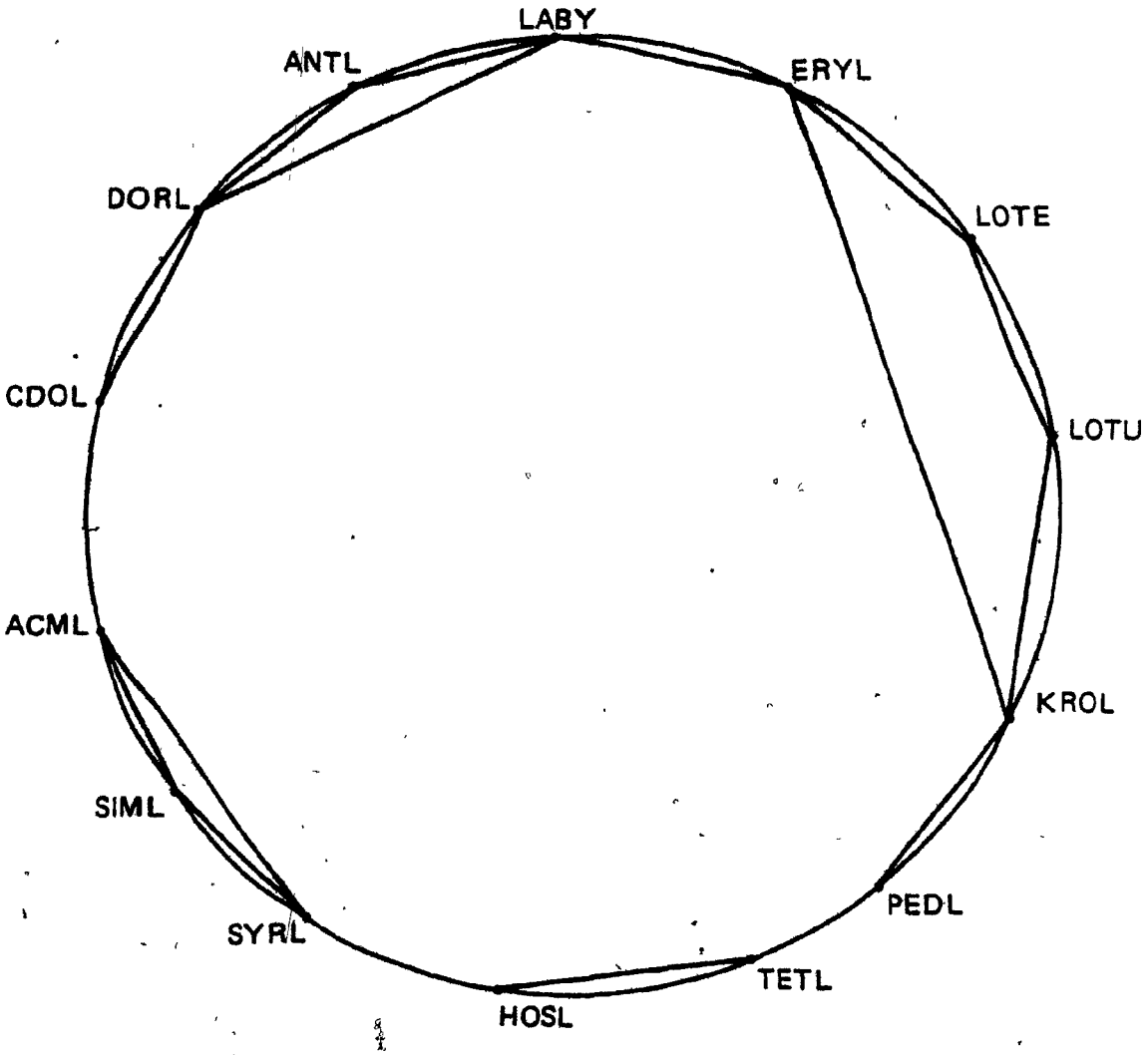


Fig. 117. Circular graph showing phenetic relationships revealed by numerical taxonomical analysis, lines joining the various groups indicated that they linked at a dissimilarity level of no greater than 0.650


LABY
ANTL
ERYL
DORL
LOTE
CDOL
LOTU
ACML
KROL
SIML
PEDL
SYRL
TETL
HOSL

VIII. DISCUSSION

A. Loteae classifications

All Lotus and Loteae taxonomic treatments, including Brand's 1898 monograph, have been controversial due to attempts by researchers to include or exclude the North American and African taxa. It can be observed in Table 1 that not only are tribal differences taxonomically inconsistent, but many genera are not clearly circumscribed by various authors. In spite of these differences at higher taxonomical ranks, much of the taxonomy at the species level is remarkably constant and relatively uncontroversial when taxonomic treatments of Greene (1890), Ottley (1923, 1944), Isley (1981) and Wiggins (1980) are studied. The main reason for problems at the higher taxonomic levels is the lack of an adequate modern phyletic treatment, which probably would indicate greater taxonomic convergence and dissimilarity. In the main, all older and recent treatments were not intended to be phyletic in scope, and tended to group many dissimilar taxa into somewhat artificial subgenera and sections. Therefore, they aided in the identification of taxa, but contributed scant information as to their biosystematical relationships.

Palynological NT studies at the species level have indicated (Figures 112 and 113) that many divergent OTU's

cluster, yet at the same time clusters of many taxonomically related taxa were grouped by the analysis.

In Polhills (1981) treatment, the Loteae-Coronilleae tribes were avoided in terms of a taxonomic treatment. He keyed out the genera of both tribes in a common treatment because of the considerable taxonomic difficulty encountered in morphologically deliminating the tribes and genera, which he discussed thoroughly. Ohashi (1971) observed pollen grains of 54 taxa comprising or representing seven subtribes of Tribe Coronilleae. His diagnosis revealed that the tribe is considerably more eurypalynous than Loteae, as indicated in the present study. Some taxa in the subtribes Hedysarinae and Desmodiinae have pollen resembling those of Old World Loteae in being tricolporate, prolate and somewhat psilate in sculpturing type. Pollen of most Coronilleae taxa were diagnosed and figured as possessing unusual pore configurations, strongly reticulated exine sculpturing and as having columellate walls with well developed tecta. Loteae taxa were more stenopalynous (morphologically constant) in Old World taxa and eurypalynous (morphologically divergent) as regards North American taxa.

This present study indicates several aspects about Loteae and Lotus taxonomy-palynology: 1) palynology is a useful tool to determine certain taxonomic affinities;

2) palynological morphology (based upon the characters chosen for this study) cannot (NT) cluster some purportedly related taxa because they are probably not related and have converged with regard to pollen grain characteristics; 3) taxonomic affinities are not yet adequately understood by researchers.

Palynological taxonomy as presented in this study clearly identified subgenera Syrmatium-Acmispon and Simpeteria as a phyletic group. It clearly separated subgenus Hosackia and genus Tetragonolobus from Old World Loteae. SEM studies of pollen revealed convergent exine patterns in Hosackia and New World subgenera. SEM studies showed several Lotus taxa of Section Pedrosia to have identical sculpturing patterns.

B. Cytology

There are numerous reports in the botanical literature where chromosome ploidy level influenced pollen grain size. The higher ploidy levels such as hexaploidy, octoploidy or decaploidy resulted in plants having larger pollen grains. In Lotus, for example, polyploids based upon $x = 6$ gave rise to $2n = 10, 12, 24, 28$ and 36. Grant (1965), Moore (1973), and Goldblatt (1981) reported that Old World Loteae were different from North American taxa which were diploid $2n = 14$. In this study, with the exception of the genus Anthyllis, the pollen grains of diploid North American

members of Loteae are usually greater in size than Old World polyploids.

C. Phytogeographical considerations regarding Loteae

Numerous theories have been postulated regarding disjunct plant distributions. Advances in geomagnetic technology have redefined the term continental drift in terms of ocean floor spreading and plate tectonics. Baumbach et al. (1980) stated "the history of our earth has followed a nonrepetitive path through time". For instance, Smith et al. (1973) indicated a similar Tertiary geomorphology between California, west-coastal North America, parts of Arizona-New Mexico, the central Mexican plateau, and Eurasian-African-Mediterranean regions. Coincidentally these are the major areas of Loteae and Lotus sensu lato speciation.

Holloway (1973) understood that subsequent separation of land mass could mean that floras could polarize into temperature regions. In geological studies related to the Canary Islands (where many species of Section Pedrosia occur) for instance, some islands were perceived as oceanic volcanoes, while others formed as uplifts or separations from the Continental Shelf (Bramwell, 1972). For whatever reasons, it is evident from morphological studies of plants and pollen, that in several areas of the world Loteae, and particularly within the genus Lotus, that polyphyletic groups

have arisen. It is obvious from examination of the taxonomic literature that the major centres of Loteae radiation appeared to have a Mediterranean type of climate. For example, Section Pedrosia occurs endemic in West Africa, Canary Islands and Cape Verde Islands. Monod (1980) listed 54 species referrable to Section Pedrosia occurring endemic to those areas. Pedrosia may be separated from all other Lotus taxa by having evolved a bipartate or dentate style (Callen, 1959). Sections or subgenera, such as Acmispon, Syrmatium and Simpeteria are endemic to Western North America and other groups are endemic to Eurasia or the Middle East. The genus Lotus sensu lato, according to the taxonomy of Polhill (1981), is essentially cosmopolitan temperate in distribution.

Groups creticus, angustissimus and peregrinus are Mediterranean, while taxa assigned to the corniculatus group may have arisen in European Southern Mediterranean, Asia Minor, Turkey and Iraq, based upon their present day distribution as indicated by Heyn (1970 a, b), Ball (1968) and Townsend (1974), who have prepared taxonomic accounts for taxa occurring in those areas.

The palynological-geological record for Loteae is scant. In a recent review article Muller (1981) indicated that tricolporate pollen was first observed in the Lower

(early) Cretaceous (circa 120, yr. B.P., Tschudy and Scott, 1969). According to Muller's (1981) table, the Fabaceae (Papilionoideae) appeared as a group much later in geological time than either the Caesalpinaceae (69-65m yr. B.P.) or Mimosaceae (50m yr. B.P.). Therefore, based upon fossil pollen records, the Loteae must have evolved in the Late-Quaternary. Muller (1981) reported Pliocene Fabaceae (5m yr. B.P.) pollen from Germany. Pliocene records of Indigofera and Astragalus pollen, genera presumably not related to Loteae taxa were reported from the Sahara.

It is therefore sufficient to observe that until pollen analysis can be linked with proper identification of modern pollen grains in the Leguminosae little can be learned about that family's geological past. In support of this statement Hughes (1977) indicated that many taxa became extinct between the paleogene and Late Cretaceous. He considered that the only organs usable for fossil records were in the following order of importance: pollen, leaves, wood and fruits, none of which have been positively identified to Loteae taxa.

D. Loteae pollination

According to Knuth (1908) and Leppik (1966), the papilionoid flower is highly specialized and adapted to bee pollination. Bird flowers are also evident (ornithophily) in being red, larger in size and having the petals not tightly

interlocked (Kalin Arroyo, 1981). Grant and Grant (1968) reported that hummingbirds visited Lotus flowers. Ferguson and Skvarla (1982) showed a photomicrograph of a pollen grain of Millettia theuszii (Buttn.) De Wild. (Papilionoideae) from Gabon which closely resembled that of Lotus strigosus in sculpturing pattern. They clearly stated that more comprehensive surveys of groups must be attempted so that pollen grain evolutionary trends may be distinguished from secondary adaptive modifications.

Ferguson and Skavarla (1982) also indicated that rugulate and verrucate pollen sculpturing types resulted in an increase in pollenkit, which can adhere to the pollen wall, hence making the grain more sticky or adherent to pollinators. In preparing microscope slides of pollen for this study, I noted that some plants had sticky secretions on their stigmas, even after being stored as dried herbarium specimens for several decades. Small and Brooks (in prep.) examined many papilionoid stigmas and observed similar secretions on the stigmas of fresh flowers prepared for SEM studies. Therefore, stigma secretions may aid in the reciprocal transfer of pollen to flowers by pollinators.

I am in agreement with Ferguson and Skvarla (1982) in observing that where sculpturing types are similar in widely distinctive taxonomic entities, this may be attributed to

convergent evolution. These similarities may however, in a restricted sense, show taxonomic significance when observed at taxonomic levels such as subgenus, genus, species and variety. An example in Lotus is Lotus strigosus amd Lotus humistratus, both considered to be closely related, yet having widely divergent pollen types; the former verrucate-rugulate, the latter striate-rugulate.

Lotus and allies are reported by Proctor and Yeo (1973) to use the conical end of the fused keel petals to act as a vent through which pollen is expelled by a pushing action of the stamens. This technique deposits pollen on the body of visiting pollinators. Clearly, stigma secretions would aid pollination through providing sticky pollen grains. This method of pollination requires further study to determine if it is adopted throughout the Loteae.

Fig. 118. *Anthyllis montana*, herbarium specimen showing capitate infloresence, woody habit (sub-shrub) and pinnatifid leaves.

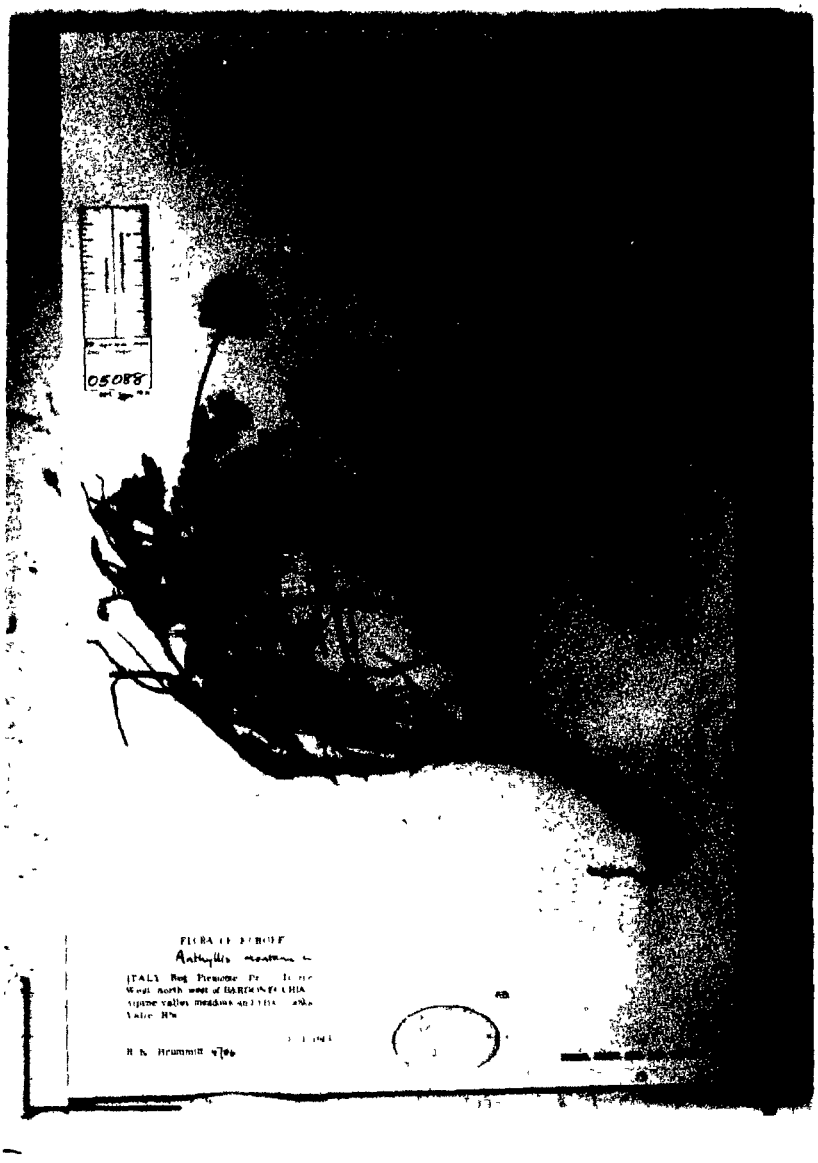

05088

Fig. 119. Cytisopsis dorycniifolia, herbarium specimen showing tubular corolla, reflexed flowers and sub-shrub habit.

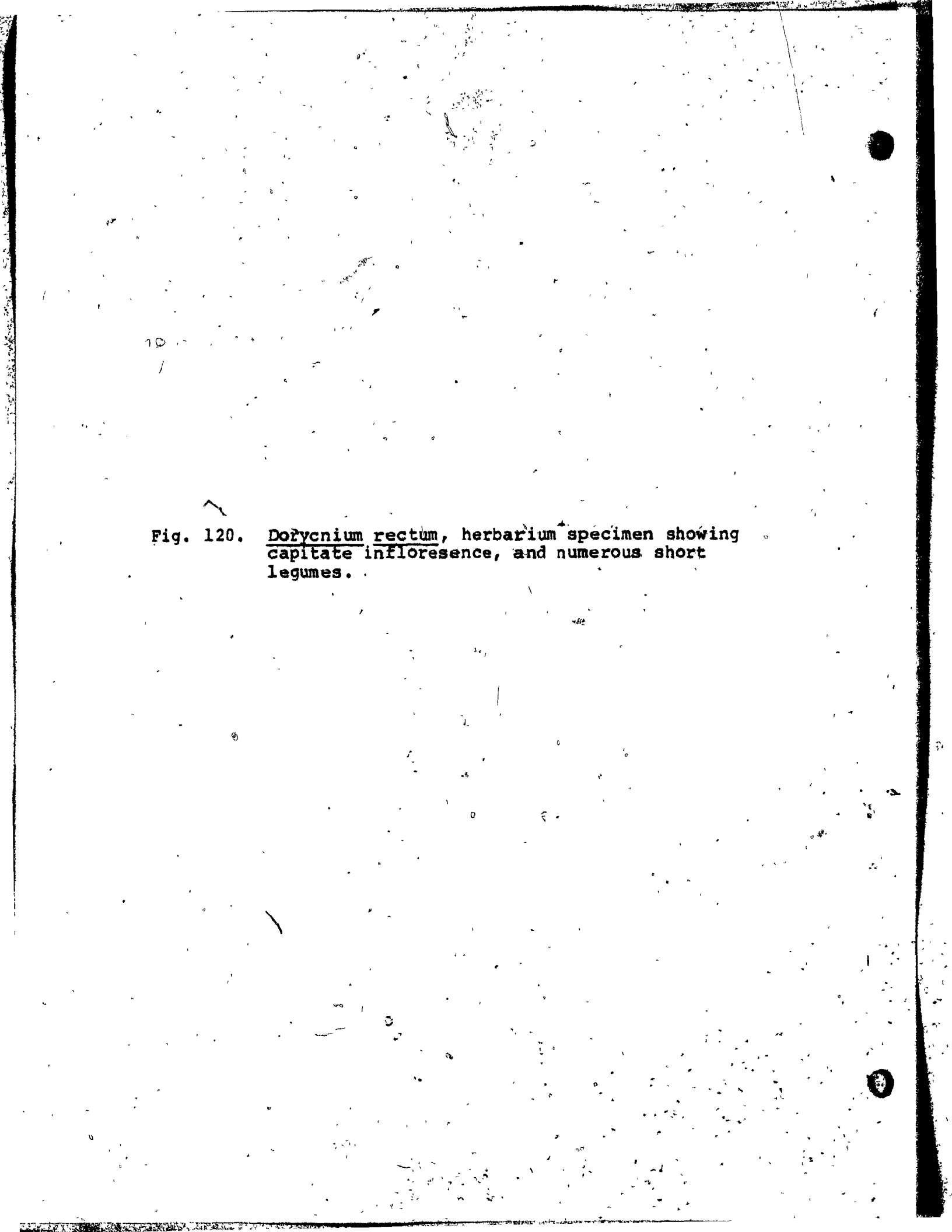


Fig. 120. Dorycnium rectum, herbarium specimen showing capitate infloresence, and numerous short legumes.

Fig. 121. Hymenocarpus circinnatus, herbarium specimen showing entire basal leaves, and radiate, coiled legumes.

Fig. 122. Lotus macrotrichus, herbarium specimen showing habit.

Fig. 123. Lotus angustissimus, herbarium specimen showing leaflet and legume characteristics; note slightly upcurved ends of legumes.

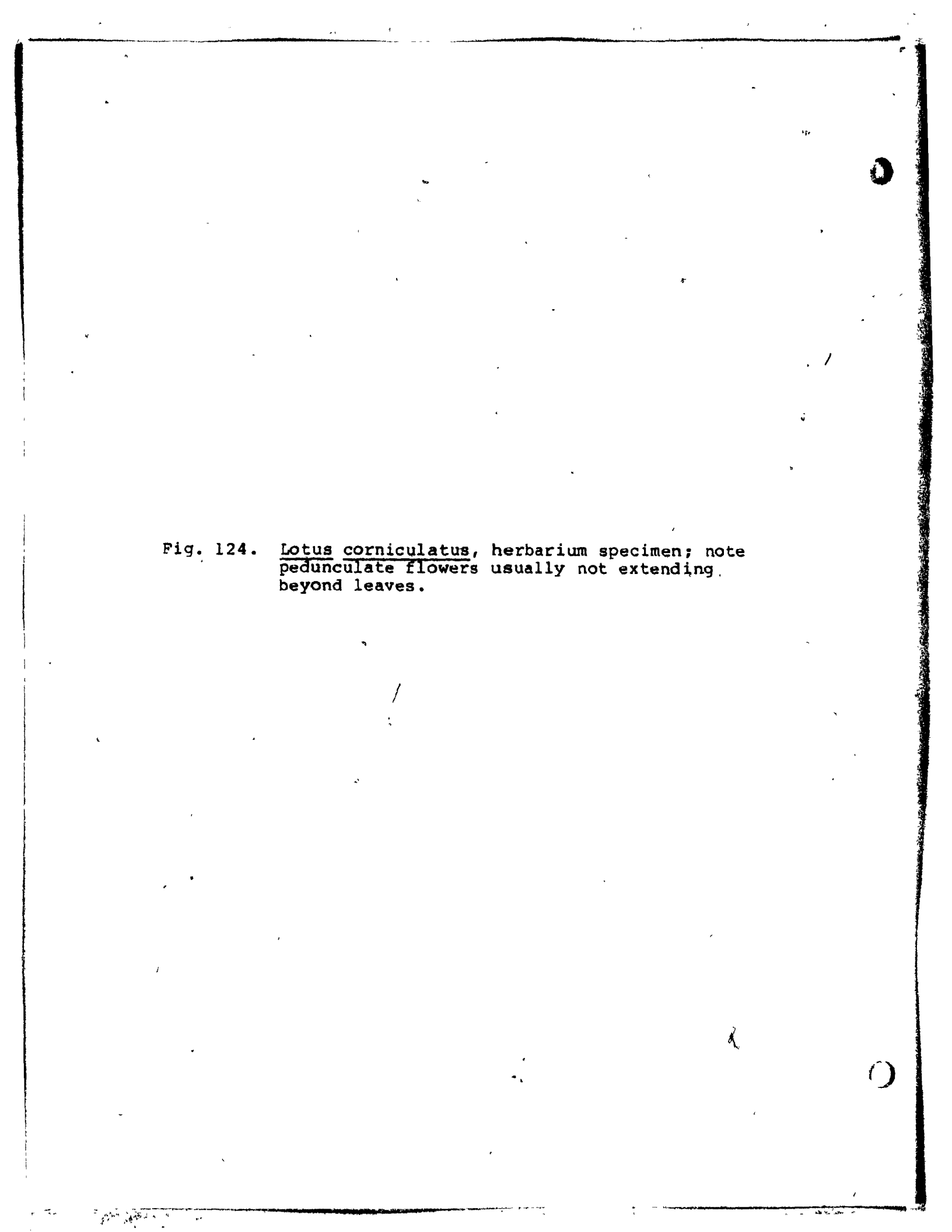
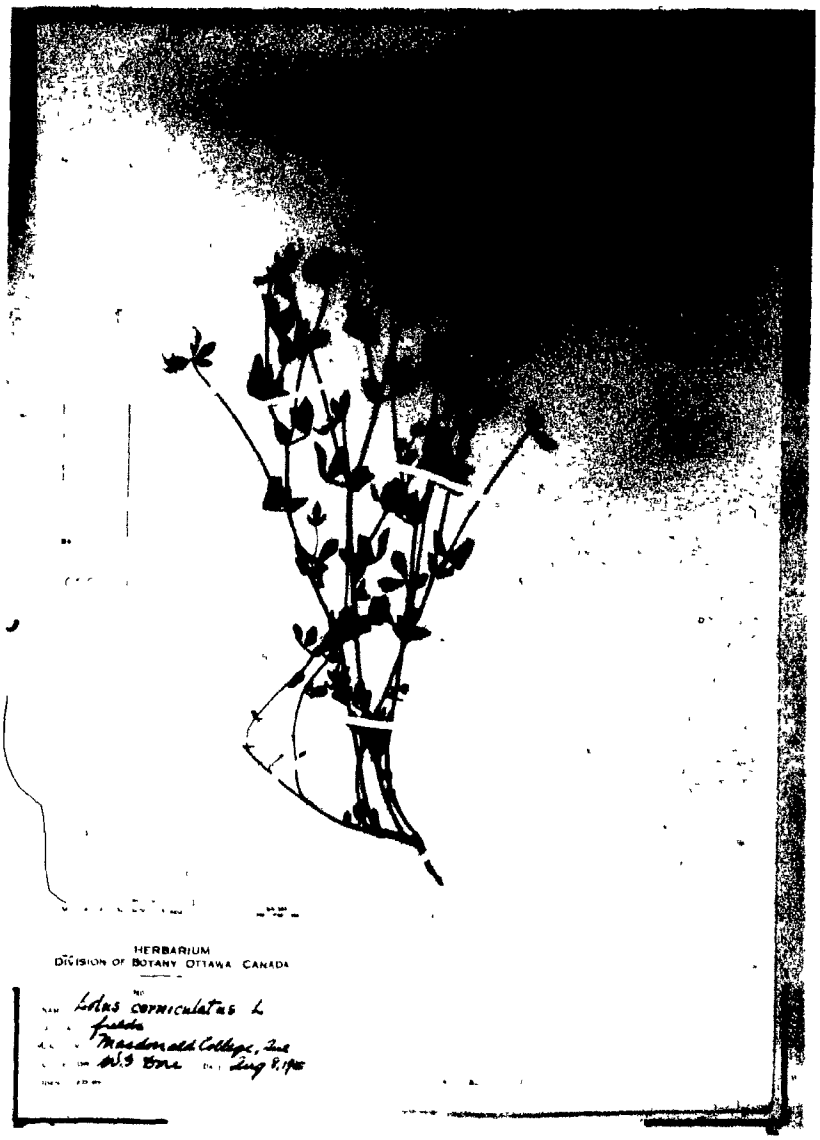


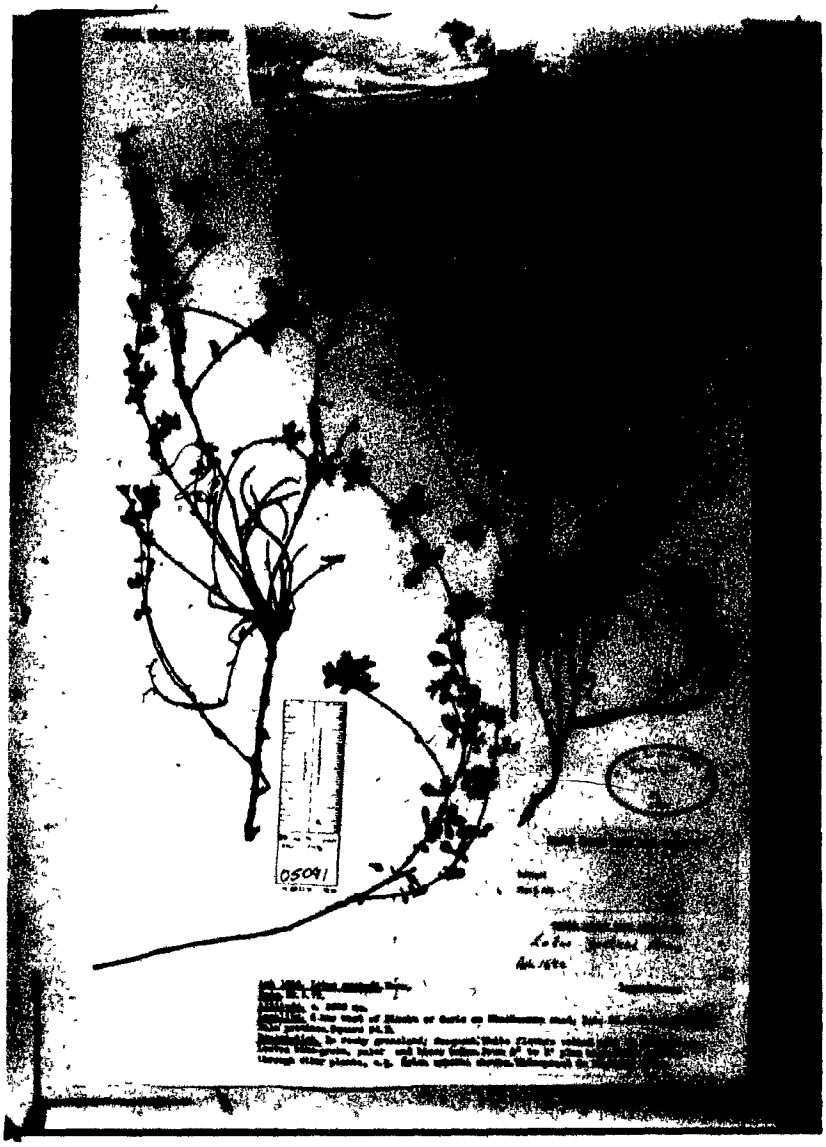
Fig. 124. Lotus corniculatus, herbarium specimen; note pedunculate flowers usually not extending beyond leaves.



HERBARIUM
DIVISION OF BOTANY OTTAWA CANADA

No.
Name Lotus corniculatus L.
" fistula
Locality Macdonald College, Que.
Collector W.J. Boivin Date Aug 8, 1940

Fig. 125. Lotus goetzii, herbarium specimen; note sprawling perennating habit.


05091

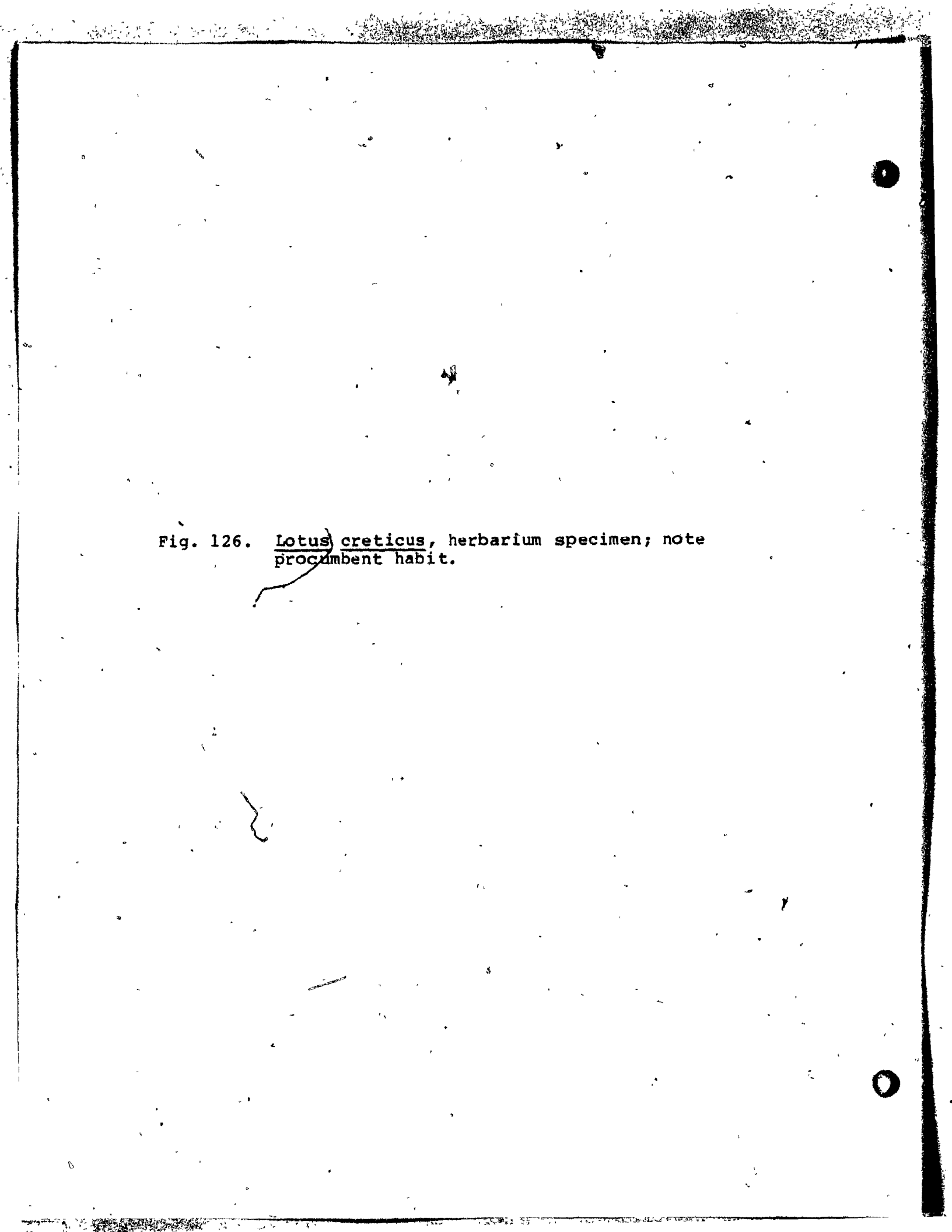


Fig. 126. Lotus creticus, herbarium specimen; note procumbent habit.

Fig. 127. *Lotus edulis*, herbarium specimen; note large, broad, semi-cythe-shaped legumes.

Fig. 128. Lotus australis, herbarium specimen; note similarity to Fig. 124 L. corniculatus.

Fig. 129. Lotus onithopodioides, herbarium specimen; note cythe-shaped legumes which are evidently torulose.

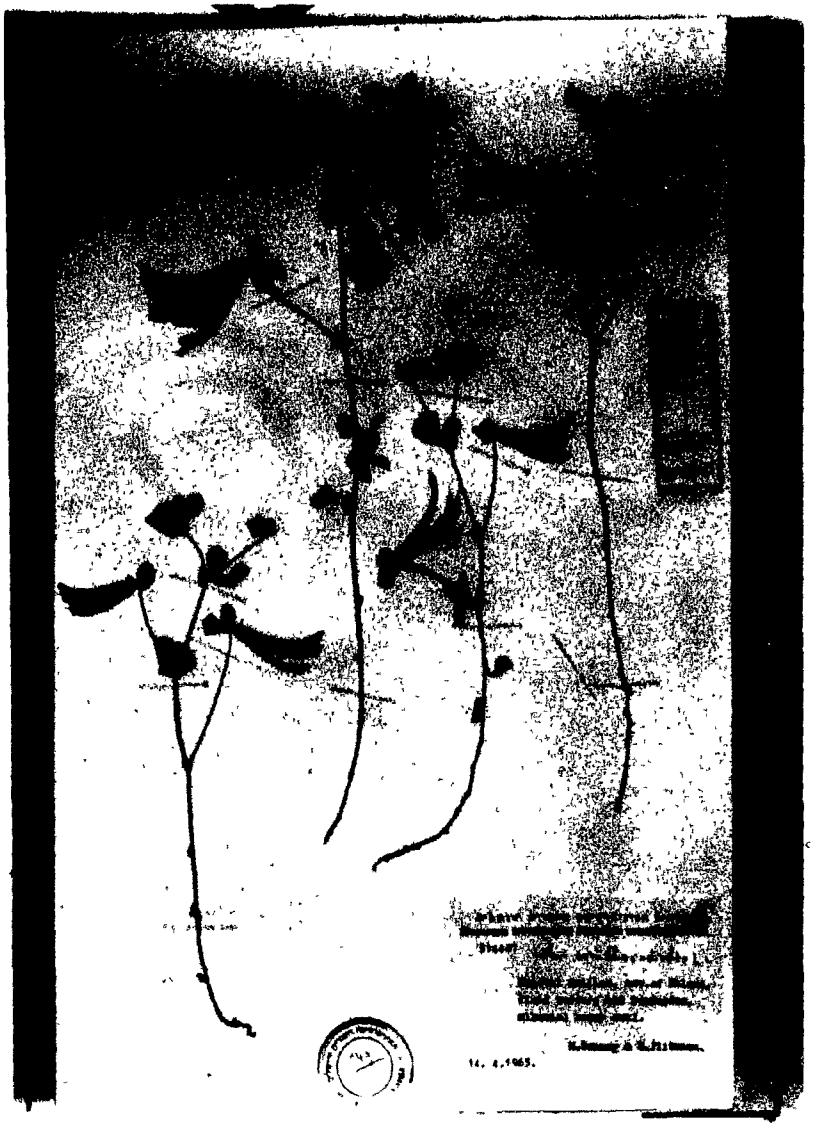
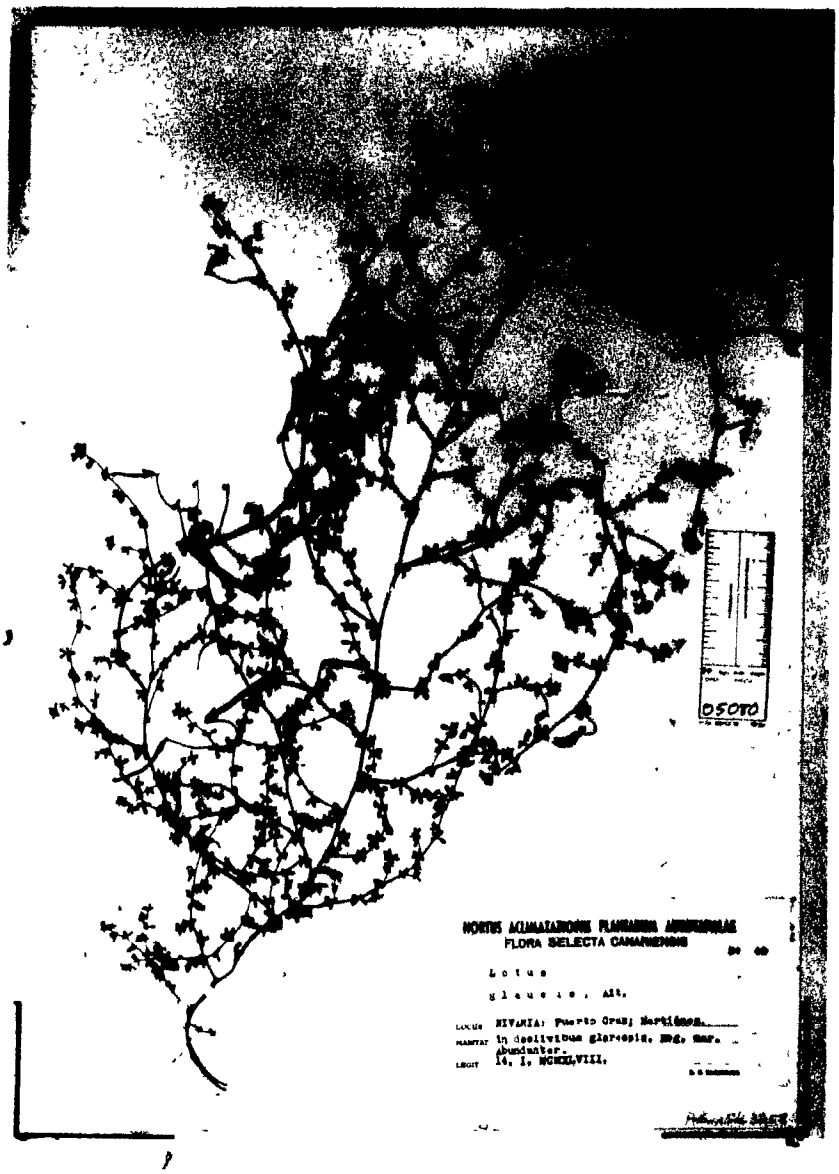


Fig. 130. *Lotus weilleri*, herbarium specimen; note asymmetrical habit, zig-zag stems and torulose legumes.


85077
CULTIVATED PLANTS

Fig. 131. Lotus glaucus, herbarium specimen; note large flowers, reduced leaf size, and long narrow legumes.


HORTUS ACLIMATATIONIS PLANTARUM ARBORESCENTIUM
FLORA SELECTA CANARIENSIS
Lotus
glaucus, Ait.
LOCUS INSULA: Puerto Orus; Martinora
HABITAT in declivibus glareosis, mrg. mar. abundanter.
LEGIT M. J. MONOD, VIII.
D5010

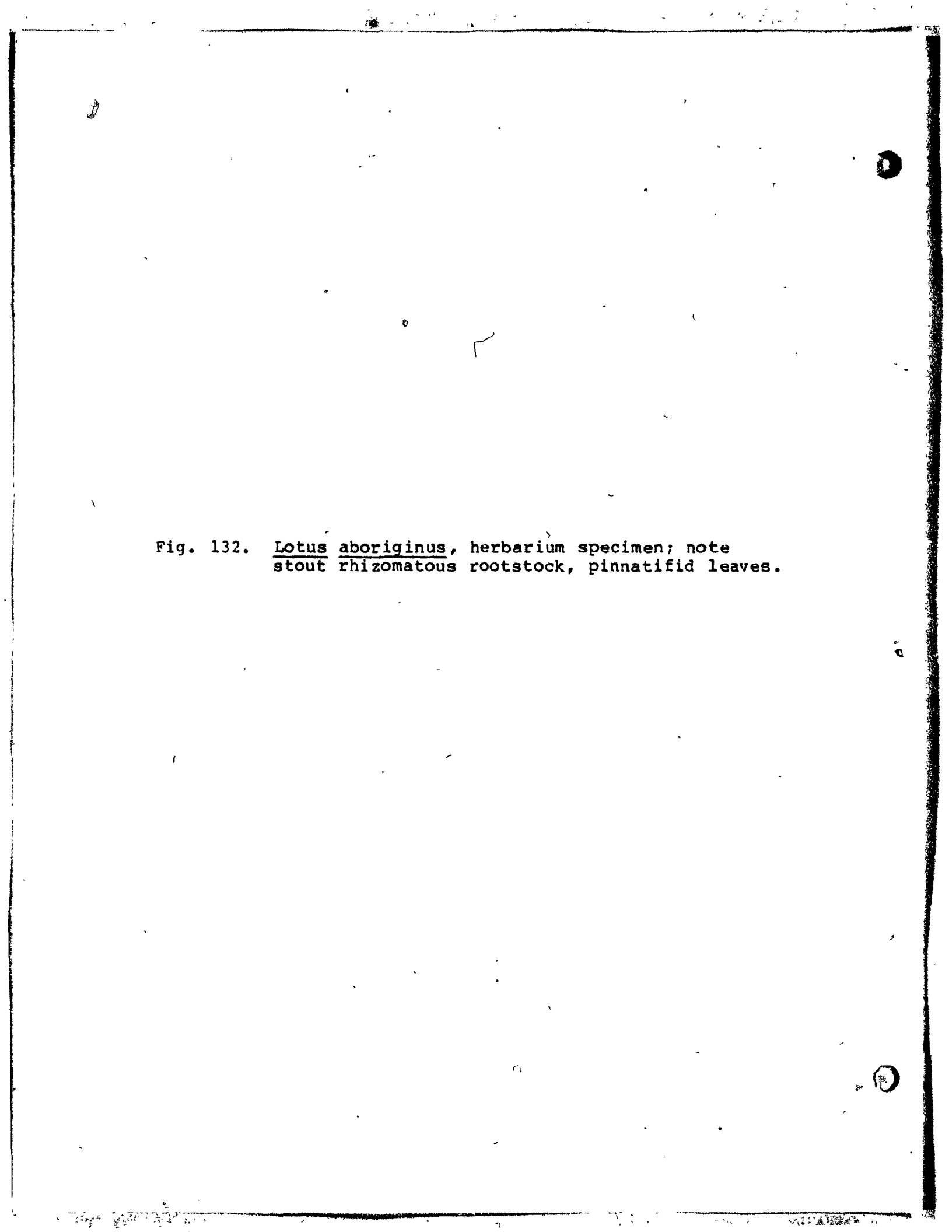


Fig. 132. *Lotus aboriginus*, herbarium specimen; note stout rhizomatous rootstock, pinnatifid leaves.


05086

Fig. 133. Lotus humistratus, herbarium specimen; note decumbent habit of upper plant, and habitat data on label.

Fig. 134. Lotus grandiflorus, herbarium specimen; note similarity to Fig. 132 L. aboriginus.

Fig. 135. Lotus hamatus, herbarium specimen; note annual condition.

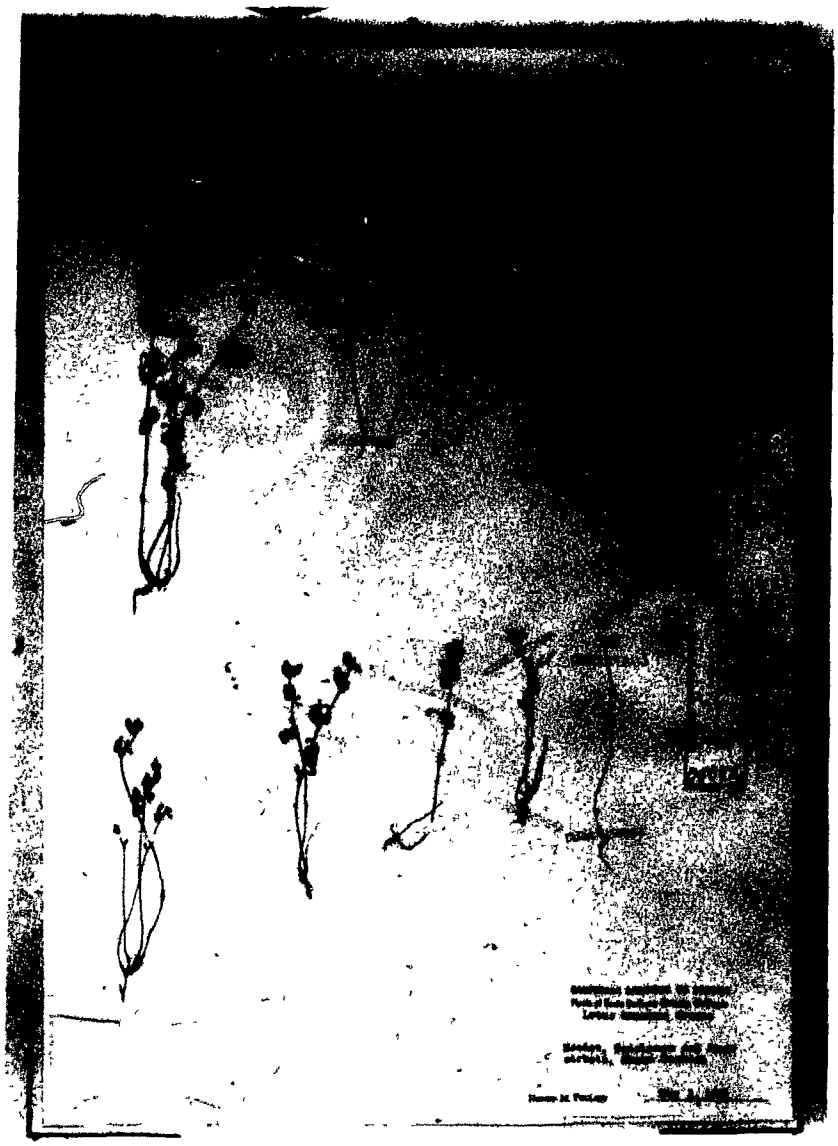


Fig. 136. Tetragonolobus maritimus, herbarium specimen; note single flowers and legumes, and winged legumes on the lower left hand plant.

E. Taxonomic hierarchy of Loteae and Lotus

For purposes of understanding the various morphological expressions exhibited by different taxa, included in the Loteae and Lotus, Figures 118 to 136 are presented. The following taxonomic treatments show how numerous students of Loteae and Lotus have divided, or subdivided, taxa. Major characteristics of Old World Lotus groups, according to Brand (1898), who excluded the North American taxa, are:

Subgenus Pedrosia - toothed style

Sect. 1. Heinekenia

2. Eupedrosia

Subgenus Edentolotus - non-toothed style

Sect. 1. Xantholotus - yellow flowers

Ser. I two lipped calyx - unequal teeth

(a) ornithopodioides group - latterly compressed pods

(b) peregrinus group - non-latterally compressed pods

(c) creticus group - indistinctly 2-lipped calyx, flowering pedicles longer than (a) and (b)

Ser. II. bell-shaped calyx teeth, teeth of equal length

(d) corniculatus group

(e) angustissimus group

(f) aegeus group

Sect. 2. Erythrolotus - red flowers

Ser. I. mottled or spotted seeds

(a) arabicus group

Ser. II. plain seeds

(b) herbranicus group

(c) gebelia group

(d) australis group

Sect. Ononidium (subtropical and tropical orient) L. garcinii, L. stockii and L. mollis

Sect. Quadrifolium L. tetraphyllus Balearic Islands.

Characteristics of American Lotus groups according to Greene (1890) are:

Acmispon, annuals having gland-like traces of stipules, leaves pinnately 3-foliolate (often 1, rarely 5 leaflets), flowers of a typical Lotus, pods straight, readily dehiscent.

Anisolotus, annuals having gland-like stipules, leaflets 4 to 10 unequally distributed on the opposite

margins of a dilated rachis, pods readily dehiscent, flowers solitary on short pedicles, not bracteate, claws of petals approximate and with a pointed keel, flowers one or several, the elongated peduncle, mostly bracteate, claw of banner (standard petal) commonly remote from the others, keel petals mostly obtuse.

Hosackia, perennials with true stipules, leaflets distributed equally on opposite sides of a linear rachis, flowers in bracteate umbels, pods long, straight subterete, tardily dehiscent.

Syrmatium, shrubs or suffrutescent plants having dot-like stipules; foliage of few and unequilaterally distributed leaflets, flowers umbellate or solitary, the mature calyx deciduous, with indehiscent, usually small, arcuate, slender pointed, few-seeded pods.

Characteristics of American Lotus groups according to Ottley (1923) are:

Subgenus I Hosackia, perennials having odd pinnate stipules, flowers more than 1 cm long, several to many in long-pedunculate umbels, legumes dehiscent, straight, abruptly

short beaked, several to many seeded, fruit not reflexed.
Subgenus II Acmispon, annuals or perennials, leaves pinnate or in a few species subpalmate, short (except L. grandiflorus), stipules gland-like, flowers 4 mm to 2.5 cm long, solitary or umbellate mostly peduncled, legumes dehiscent, straight or nearly so, abruptly short-beaked, two to many seeded, not reflexed.
Subgenus III Syrmatium, mostly perennials, (often flowering the first season), leaves short-pinnate with gland-like stipules, flowers 1 to 12 mm, umbellate (umbells sometimes reduced to a single flower), legumes small, less than 2 cm in length, arcuate to nearly straight, mostly attenuate forming a long incurved beak, one to several seeded, fruits reflexed, indehiscent, deciduous at base of pedicle.

Subsequently Ottley (1944) keyed out the North American taxa utilizing the following morphological characters:

Stipules foliaceous, membranous or scarious; legumes straight, dehiscent ..... Subgenus Hosackia Bentham

Stipules a small hard, blackish or reddish-brown gland. Legumes straight or slightly curved at apex, abruptly beaked by a hard persistent style base (stylopodium), dehiscent ..... Subgenus Acmispon Rafinesque

Stigma surrounded at base by a ring of short projecting hairs ..... Sect. Simpteria

Stigma not surrounded at base by hairs ..... Sect. Microlotus Bentham

Legumes reflexed, curved, alternate into the style, indehiscent ..... Subgenus Syrmatium Vogel

Hutchinson's (1964) treatment of the genera in Loteae was based upon the following characteristics:

Dehiscent fruit

Cytisopsis, spreading shrublets, leaves sessile 7(-5) foliolate; stipules absent, calyx long tubular, peduncles axillary.

Dorycnium, flowers are capitate, subumbellate, axillary to subterminal.

Lotus, keel petals beaked, calyx lobes longer than the tube, lower leaves stipule-like.

Hosackia, calyx teeth shorter than the tube, lower leaflets not stipule-like, flowers in axillary umbels or solitary.

Non-dehiscent fruit

Anthyllis, calyx inflated-tubular enclosing the fruit, stamens monadelphous.

Hymenocarpus, calyx deeply 5-lobed, fruit excerted from calyx compressed, lower leaves not resembling stipules.

Major generic characteristics as presented by Isley (1981) are:

Anthyllis, calyx inflated, normally enclosing the legume.

Dorcynium, calyx not inflated, keel petal black or dark red, flowers in a capitate umbel with short pedicles (somewhat like many Trifolium spp.), leaves in a short rachis or subsessile.

Tetragonolobus, flowers umbellate to solitary, normally with evident pedicles, leaves with a well-developed rachis, legumes 2- or 4-winged, stipules evident and adenate to the petiole.

Lotus, flowers as Tetragonolobus, legume not winged, stipules evident or reduced to glands, normally not adenate to petiole.

Key characteritics as presented by Polhill (1981) are:

Lotus, style hardened from base, flowers often in pedunculate umbels, sometimes one or two in heads, petioles distinct if leaves compound, fruits not jointed, standard claw normally with thickened infolded margins.

Hymenocarpus, style not as above, pods excerted, calyx persistent, pods flattened and curved.

Cytisopsis, flowers tubular, somewhat reflexed (as if for bird pollination), 1-3 per head, subtended by well developed simple bracts.

Major characteristics of "groups" of Lotus according to Isley (1981) are:

Pedrosia, suffrutescent shrubs, leaves sessile palmately 5-foliolate, stigma bifrucated.

Lotus, leaves of the Edentolotus type, stipules reduced, legumes dehiscent.

Hosackia, leaves pinnate, 5-15 leaflets, stipules evident, legumes dehiscent.

Syrmatium, leaflets 3-5, stipules reduced, legume indehiscent turgid, deflexed, slightly or moderately (-strongly) excerted from calyx, the much exserted confluent beak as long as the body, usually strongly curved.

Microlotus, annual, leaflets 3-5 usually pinnate, stipules reduced, wing petals (+) keel or keel longer, stigma not pencillate, legume dehiscent.

Simpeteria, leaflets 3-5 irregularly pinnate or sub-palmate, stipules reduced, wing petals (+-) keel, asymmetrically positioned, stigma evidently or obscurely pencillate, legume dehiscent.

F. Hybridization and introgression in Lotus

There are no substantiated reports of hybrids occurring in nature in Old World Lotus. Ottley (1923, 1944), and Isley (1981), believe that many Lotus taxa which occur in North America hybridize. They mention that L. aboriginus is supposed to hybridize with L. nevadensis and with L. scoparius. L. argyraeus is supposed to be related to the L. oroboides complex which is a "catch-all" taxon for hybrids. They also report that L. greenii may have formed hybrids with L. oroboides. Many other hybrids have been mentioned by Ottley (1923) based upon examination of plants which had aberrant pollen. In the course of this study, only a few specimens were examined which had abnormal pollen grains. Therefore, I suspect that the technique used by Ottley gave erroneous results. Further, biosystematic studies are urgently needed to substantiate the amount of hybridization and/or introgression in Lotus taxa.

IX. SUMMARY

Loteae, and the genus Lotus seemed to pose interesting taxonomical problems. Some taxonomists considered Lotus to include taxa which other taxonomists considered to be distinct genera. Pollen morphological studies were undertaken to confirm or refute the investigations of former taxonomists. No previous authors in Loteae-Lotus had utilized palynological-taxonomy as a tool to help understand taxonomic relationships in the groups.

The morphological study of Loteae-Lotus pollen grains showed through numerous taxonomical analyses the following: a) Loteae is palynologically extremely variable; b) Old World Lotus taxa are not variable with respect to pollen morphology; c) several North American groups, whether they are considered as subgenera or sections in Lotus, are palynologically diverse; d) pollen analyses gave no indication of hybridization or introgression between most of the taxa. Three taxa of subgenus Sympeteria had aberrant pollen grains.

An attempt was made in this study to bring the taxonomical concepts of many Loteae-Lotus researchers together for palynological evaluation. It is shown in this work that many more taxonomical, cytological and biosystematical studies are required before questions related to Loteae-Lotus phylogeny and evolution can be answered.

The nature of exine adaptation has not been solved for many of the taxa. Why, for instance, does the New World Lotus have such divergent pollen types? Pollen researchers have, for example, considered phylogenetically "so to speak" that colpory and complex aperture arrangements constitute a more advanced character state. This question remains to be assessed in the Loteae. The Coronilleae tribe, according to this premise, would be therefore more advanced or divergent than Tribe Loteae.

Lotus as a genus, appears to be based upon nebulus morphological criteria (See pages 174 to 179) and pollen morphological studies have confirmed this opinion. Until the entire Loteae is investigated and its boundaries with other tribes adequately delimited by usable criteria such as: phytogeographical, morphological, chromosomal and biosystematical analysis, no recommendation should be made based upon this study to dismantle previous taxonomic treatments. Such a practice would result in biological inaccuracy and nomenclatural chaos.

Little is known about the breeding or pollination biology of Lotus or Loteae with the exception of economically important taxa such as Lotus corniculatus (birdsfoot trefoil) and their allies.

Many taxa are drought resistant and are important as range land plants or as ecological components of plant communities. They provide browse for animals and fix nitrogen, thus improving soil nutrient levels. It is therefore very important that taxonomic relationships in the Loteae are correctly understood.

As a result of palynological studies it can be stated that Loteae and Lotus relationships remain controversial, thus allowing for further study, as previously indicated, by students and researchers. It is probable, however, that the

Old World Loteae relationships are understood more fully by biologists, ecologists and taxonomists than relationships in New World Loteae. This statement is supported by the results of the palynological study in this thesis.

This study also indicates that the plant morphological basis upon which the present-day taxonomy of Loteae and Lotus is maintained may be taxonomically and biologically faulty. The palynological study carried out in this thesis supports the position taken by Brand (1898) in not including New World "Lotus" in his concept of the genus.

APPENDIX I

NOMENCLATURAL NOTES AND SPECIMENS EXAMINED

TRIBE LOTEAE

ANTHYLLIS Riv. ex L. in Sp. Pl.: 719 (1753)

1. A. montana L. in Sp. Pl.: 719 (1753)

* HUJ 20 Anthyllis montana L.
N.W. of Montepellier, France
A. Danin 72-9-1

2. A. vulneraria L. in Sp. Pl.: 719 (1753)

KEW 19 Anthyllis vulneraria
Swanage Dist., Dorset, U.K.
W.B. Turrill No. 35/58

HUJ 18 Anthyllis velneraris L.
N.W. of Montpellier, France
A. Danin 72-9-4
Lapsu, sp. epith. = vulneraria

a. ssp. maura Beck in Ann. Nat. Hofmus. Wien 11: 63 (1896)

SEM Anthyllis vulneraria L. ssp. maura Beck
Algeria
B. De Retz No. 31606 (DAO)

b. ssp. spruneri (Boiss.) Bornm. in Bot. Jahrb. 59: 483 (1925) [Heyn erroneously equated ssp. praepropera (Beck non Kerner) Bornm. with ssp. spurneri and thereby incorrectly assigned priority to the former taxon.]

HUJ 19 Anthyllis spruneri (Boiss.) Beck
Crete
N. Feinbrun No. 539

*

CYTISOPSIS Jaub. et Spach in Illustr. 1: 154 (1842)

1. C. dorycniifolia Jaub. et Spach in Illustr. 1: 155 (1842)

KEW 17 Cytisopsis dorycniifolia
Amanus, Syria
G. Samuelsson 24.2.1933

2. C. pseudocytisus (Boiss.) Fertig in Israel Journ. Bot. 19: 294 (1970) = Cornicina pseudocytisus Boiss. in Diagn. Ser. 7(2): 5 (1849)

SEM Cytisopsis pseudocytisus (Boiss.) Fertig
Mt. Carmel, Israel
M. Zohary & A. Grizi 26.2 1947 (DAO)

DORYCNIUM P. Miller in Gard. Dict. Abr. ed. 4 (1754)

A. SECTION BONJEANIA (Reichenb.) Boiss. in Fl. Or. 2: 164 (1872)

1. D. hirsutum (L.) Ser. in DC. Prod. 2: 208 (1825)

3233 Dorycnium hirsutum
France
M. Vinet 4862 (DAO)

2. D. rectum (L.) Ser. in DC. Prod. 2: 208 (1825) = Lotus rectus L. in Sp. Pl. ed. 2: 1092 (1762)

3234 Dorcycnium rectum
San Miguel Del Fay, Spain
St. Lager 2518 (DAO)

HUJ 15 Dorycnium rectum (L.) Ser.
Hula Plain, Jordan R., Palestine
U. Plitman 23.5.1963

B. SECTION Dorycnium (Sect. Eudorycnium Boiss.)

1. D. axilliflorum Huber-Morath in Feddes Rep. 46: 138, t. 270 (1939)

HUJ 16 Dorycnium axilliflorum Hub-Mor.
Burdur (Anatolia) Turkey
A. Huber-Morath No. 8511

2. D. amani Zohary in Pal. J. Bot., Jer. Ser. 2: 165, f. 16-18 (1941)

HUJ 17 Dorycnium armain Zohary
S. of Akyozi, N.W. Turkey
U. Plitman No. 54246
lapsu, sp. epith. = amani

3. D. pentaphyllum Scop. in Fl. Carn. ed. 2, V.2: 87 (1772)

a. ssp. pentaphyllum

3235 Dorycnium pentaphyllum Scop. ssp. pentaphyllum
Portugal
A. Teles & B. Rausha 128 (DAO)

b. ssp. herbaceum (Vill.) Rouy ex Foucaud et Rouy, Fl. Fr. 5: 137 (1899)

3232 Dorycnium pentaphyllum Scop. ssp. herbaceum (Vill.) Rouy
E.& K. Ronniger 5442
July 1911 (DAO)

c. ssp. germanicum (Gremli) Gams in Hegi, Ill. Fl. Mitteleur. 4(3): 1380 (1923)

3231 Dorycnium pentaphyllum Scop. ssp. germanicum (Gremli) Gams
loc. unknown
K.H. Rechinger 17030 (DAO)

HYMENOCARPUS (L.) Savi in Fl. Pis. 2: 205 (1798), nom. conserv. = circinnus Medicus in Vorl. Churpf. Phys. 2: 384 (1787), nom. rejec.

*1. H. circinnatus (L.) Savi in Fl. Pis. 2: 205 (1798)

KEW 1 Hymenocarpus circinnatus
Attica, Greece
S.C. Archley No. 614 (DAO)

LOTUS L. in Sp. Pl.: 773 (1753)

LOTUS sensu Hutchinson pro parte in Gen. Fl. Pl. 1: 460 (1964) et sensu Isley pro parte in Mem. N.Y. Bot. Gard. 25(3): 128 (1981) = Lotus Tourn. ex L. [excl. Dorycnium P. Miller (1754) et Tetragonolobus Scop. (1772), in Sp. Pl.: 773 (1753)]; Acmispon Raf. in Atl. Journ.: 144 (1832); Andaca Raf. in Fl. Tellur. 3: 82 (1836); Anisolotus Bernh. in Sem. Hort. Erf. (1837); Drepanolobus Nutt. ex T. et G. in

Fl. N. Am. 1: 324 (1840); Flundula Raf. in Fl. Tellur. 2: 96 (1836); Heinekenia Webb ex Benth. et Hook. f. in Gen. 1: 491 (1865); Hosackia Dougl. ex Benth. in Bot. Reg. t. 1257 (1829); Hosakia Steudel in Nom. ed. 2(1): 776 (1840); Krokeria Moench in Meth.: 143 (1794); Lotea Medicus in Vorles. Churpf. Phys. Ges. 2: 384 (1787); Lotos St. Lager in Ann. Soc. Bot. Lyon 7: 87 (1880); Pedrosia Lowe in Hook. Kew Journ. 8: 293 (1856); Rafinesquia Raf. in Fl. Tellur. 2: 96 (1836) non Raf. in New Fl. Am. 3: 51 (1838) nec Nutt. (1841).

I SUBGENUS LOTUS [= Subg. Edentolotus Brand in Bot. Jahrb. 25: 204 (1898)]

A. SECTION LOTUS [= Sect. Xantholotus Brand pro parte, in Bot. Jahrb. 25: 204 (1898)]

Lotus aegeus group:

1. L. macrotrichus Boiss. in Ann. Sci. Nat. ser. 4(2): 250 (1854)

3251 Lotus divaricatus
Cult. C.E.F. Ottawa
Source U.S.D.A. (DAO)

auct. = Boiss. (1854) non Solander ex Buch (1816)

Lotus angustissimus group:

2. L. angustissimus L. in Sp. Pl.: 774 (1753).

HUJ 13 Lotus angustissimus L.
Crete
F. Guiol No. 209

HUJ 14 Lotus angustissimus L.
Upper Galilee, Palestine
M. Zohary et al. 30.5.1964

3237 Lotus angustissimus L.
Jersey Islands
F. Louis-Arsene 8 July 1951 (DAO)

3244 Lotus ciliatus Koch
Hungary
G. Lengyel 8.VI.1930 (DAO)
lapsu, auct. = Tenore [Viz. Koch in Syn. deut. u. schweiz. Fl. (1838)]

3. L. palustris Willd. in Sp. Pl. etc. 3: 1394 (1802).

3273 Lotus palustris Willd.
Jerusalem, Dr. Boyko
J.M. Armstrong (Cult.) Sept. 1961(DAO)

HUJ 5 Lotus palustris Willd.
Beith Shean Valley, Palestine
D. Zohary 16.4.1941

4. L. parviflorus Desf. in Fl. Atl. 2: 206 (1799).

3274 Lotus parviflorus Desf.
Portugal
B. Raviha 2689 (DAO)

5. L. subbiflorus Lag. in Varied. Ci. Lit. Art. (Madrid) 2(4): 213 (1805). [Heyn (1970) considers this a nom. ambig. and substitutes L. suaveolens Pers. in Synops. Pl. 2: 354 (1807)]

a. ssp. subbiflorus

3262 Lotus hispidus Desf.
Jersey Islands
F. Louis-Arsene 6-VII-51 (DAO)

3263 Lotus hispidus Desf.
Copenhagen, Denmark
L. Jenkins 3938 (Cult.) (DAO)

auct. = Desf. ex DC. 1815 non 1805

b. ssp. castellanus (Boiss. et Reuter) P.W. Ball in Fedd. Rep. 79: 41 (1968)

3243 Lotus subbiflorus Lag. ssp. castellanus (Boiss. & Reuter) P.W. Ball
Lisbon Univ., Portugal
J.M. Gillett Cultivated 36-106-91 (DAO)

SEM Lotus castellanus
W.F. Grant No. B783
2n = 10(MTMG).

auct. = Boiss. et Reuter in Diagn. Ser. 1 9: 34

Lotus corniculatus group:

*6. L. corniculatus L. in Sp. Pl.: 775 (1753)

2495 Lotus corniculatus L.
Bonaventure Co., P.Q.
G. Lemieux 5322 (DAO)

2496 Lotus corniculatus L.
Brandon, Manitoba
G.A. Stevenson 2313 (DAO)

2500 Lotus corniculatus L.
Rougemont, P.Q.
L. Cinq-Mars 66-270 (DAO)

3245 Lotus corniculatus L.
Bonaventure Co., P.Q.
G.M. Grandtner 1963 (DAO).

KEW 13 Lotus corniculatus L.
Sissu, Lahul
N.L. Bar 5.7.38

SEM Lotus corniculatus L.
Vaudreuil Co., P.Q.
L. Newstrom No. 319 (DAO)

SEM Lotus corniculatus L.
Macdonald College, Ste. Anne de Bellevue, P.Q.
W.G. Dore 8 Aug. 1935 (DAO)

7. L. pedunculatus Cav. in Icon. Descr. 2: 52 (1793).

2499 Lotus pedunculatus Cav.
Durieu, B.C.
D. Faris, Jr. 190 (DAO)

8. L. tenuis Waldst. et Kit. ex Willd. in Enum. Pl. Hort. Berol: 797 (1809)

HUJ 2 Lotus tenuis Waldst. et Kit.
Palmahim Beach, Philistean Plain, Palestine
M. Zohary and Y. Waisel 8.6.1958

2497 Lotus tenuis Waldst. et Kit.
Paul Creek, B.C.
J. Grant 64-54 (DAO)

3282 Lotus tenuis Waldst. et Kit.
S.E. of Hedley, B.C.
J. Grant 64-54 (DAO)

9. L. uliginosus Schk. Whr. in Bot. Handb. 2: 412 (1808)

2498 Lotus uliginosus Schk.
Halifax, N.S.
W.G. Dore 45.1097 (DAO)

2501 Lotus uliginosus Schk.
Monte Hruby Jesenik, Czechoslovakia
J. Podpera, July 28, 1947 (DAO)

3284 Lotus uliginosus Schk.
Prince Edward Co., Ontario
F.H. Montgomery & W. Shumovich
Aug. 19, 1954 (DAO)

Lotus namulensis group:

10. L. discolor E. H.F. Meyer in Comm. pl. Afr. austr. fasc. 1 92: (1836)

KEW 16 Lotus discolor E. Mey
Bafut-Ngemba Reserve, Nigeria
E. Ujor 29973

11. L. goetzei Harms in Bot. Jahrb. 30: 324 (1901)

KEW 9 Lotus goetzei Harms
W. of Dinchu, Ethiopia
J. Ash No. 1684

12. L. namulensis Brand in Bot. Jahrb. 25: 213 (1898)

KEW 10 Lotus namulensis Brand
Tarka Forest Reserve, (Rhodesia) Zimbavive
B. Goldsmith No. 97/68

B. SECTION LOTEAE (Medicus) DC in Fl. Fr. 4: 554 (1805) [= Sect. Xantholotus Brand pro parte, in Bot. Jahrb. 25: 205 (1898)]

Lotus creticus group:

13. L. collinus (Boiss.) Heldr. in Herb. Graec. Norm. no. 1320 (1896)

HUJ 11 Lotus collinus (Boiss.) Heldr.
Antiochia, Turkey
M. Zohary 8.5.1931

14. L. creticus L. non Sibth. ex Sibth. et Smith (1935) 1935, nec Viv. (1802), in Sp. Pl.: 775 (1753)

HUJ 23 Lotus commutatus Guss.
Sharon, Palestine
G. Orshan No. 15588

3247 Lotus creticus
Algeria
A. Dubois 2971 (DAO)

HUJ 21 Lotus creticus L.
Acre Plain, Palestine
S. Leinkram No. 15602

15. L. cytisoides L. in Sp. Pl.: 776 (1753)

3248 Lotus cytisoides L.
France
G. Gravelle 16 Apr. 1961 (DAO)

HUJ 12 Lotus judaicus Boiss.
Daliya, Palestine
D. Zohary No. 15634

C. SECTION KROKERIA Ser. ex DC. in Prod. 2: 209 (1825)

16. L. edulis L. in Sp. Pl.: 774 (1753)

3253 Lotus edulis L.
Algeria
Herbeux Fraia 20 Mar. 1959 (DAO)

3254 Lotus edulis L.
C.E.F. Ottawa, Cult.
L. Jenkins 3934 (DAO)

SEM Lotus edulis
Pointe des Sardines et St. Maxime, France
G. Gavelle 16 Avril 61 (DAO)

SEM Lotus edulis
Attica, Greece
M. Phitos No. 7868 (DAO)

D. SECTION ERYTHROLOTUS Brand in Bot. Jahrb. 25: 5 (1898)

Lotus australis group:

17. L. australis Andrews in Bot. Rep.: 624 (1811)

3240 Lotus australis Andr.
SEM Rennick, S. Australian Border
G.C. Shepherd Nov. 1950 (DAO)

KEW 14 Lotus australis Andr.
Timor Rock, N.S.W., Australia
B.G. Briggs & L.A.S. Johnson 6226

SEM Lotus australis Andr.
S. Australian Border
J.H. Willis 8-8-1951 (DAO)

18. L. coccineus Schlecht. non Vell. (1825), in Linnaea 21: 452 (1848)

KEW 15 Lotus cruentus Court
Lake Torrens, South Australia
J.Z. Weber 1329

Lotus gebelia group:

19. L. arabicus L. non Bourg ex Coss (1880), in Mant. I: 104 (1767)

SEM Lotus arabicus
Madrid, Spain (cult.)
J.M. Gillett No. 40-164-35 (DAO)

20. L. conimbricensis Brot. in Phyt. Lusit., fasc. 1, n. 28 (1800)

HUJ 10 Lotus conimbricensis Brot.
Sharon Plain, Palestine
R. Berliner 5.4.1976

21. L. gebelia Ventenat in Hort. Cels. t. 57 (1801)

3257 Lotus gebelia Vent.
Transcaucasia, Russia
E. Chalilov 26.IV.60. (DAO)

HUJ 22 Lotus gebelia Vent.
Sueda, Jebel Druz, Syria
A. Eigand and M. Zohary 15.5.1931

22. L. lanuginosus Ventenat in Jard. Malm.: 92 (1803)

HUJ 9 Lotus lanuginosus Vent.
Southern Negiv, Palestine
J. Larch 15653

23. L. varius Boiss. ex Brand in Bot. Jahrb. 25: 14 (1898)

HUJ 1 Lotus varius Boiss. ex Brand
N.E. of Malatya, E. Turkey
M. Zohary, 372122

Lotus ornithopodioides group:

24. L. halophilus Boiss. et Spruner ex Boiss., Diagn. Pl. Or. Nov. 1(2): 37 (1843)

a. var. halophilus

HUJ 7 Lotus halophilus Boiss. and Sprun var. halophilus
Sharon Plain, Palestine
I. Amdursky and A. Grizi 11.5.1953

b. var. macranthus (Boiss.) Heyn in Israel J. Bot. 15: 43 (1966)

HUJ 8 Lotus halophilus Boiss. & Sprun var. macranthus (Boiss.) Heyn
Tel-Aviv, Palestine
M. Zohary

25. L. ornithopodioides L. in Sp. Pl.: 775 (1753)

3272 Lotus ornithopodioides L.
France
G. Gravelle 21 Apr. 1961 (DAO)

HUJ 4 Lotus ornithopodioides L.
Hula Plain, Palestine
Lev-Ari, Mattatia and Dafni 29.3.1969

26. L. peregrinus L. non Burman f. (1768), in Sp. Pl.: 774 (1753)

a. var. carmeli (Boiss.) Post in Fedd. Rep. 83(9): 640 (1973)

HUJ 3 Lotus peregrinus L. var. carmeli (Boiss.) Post
Mt. Carmel, Palestine
M. Zohary 15.5.1954

Lotus weilleri group:

27. L. weilleri Maire in Bull. Soc. Hist. Nat. Afr. Nord 19: 40 (1928)

3286 Lotus weilleri Maire
(Cult.) Forage Plant Nursery
C.E.F. Ottawa
L. Jenkins 3955 (DAO)

II. SUBGENUS PEDROSIA (Lowe) Brand in Bot. Jahrb. 25: 198 (1898)

A. SECTION PEDROSIA [= Sect. EUPEDROSIA Brand in Bot. Jahrb. 25: 198 (1898)]

28. L. borzii Pitard in Pitard, Proust, II: 167 (1908)

3242 Lotus borsii
Czechoslovakia
M. Smejkal 14.V.1961 (DAO)
lapsu, sp. epith. = borzii

SEM Lotus borzii Pitard
Tenerife, Canary Is.
E. Asplund 27.3.1933 (DAO)

29. L. campylocladus Webb et Berth. in Phyt. Canar. 2: 83 (1836)

SEM Lotus campylocladus Webb & Berth.
Nuvaria, Canary Is.
E.R. Sventenius No. 47 (DAO)

30. L. glaucus Dryander ex Aiton non Sieber ex Reichenb. (1832) in Hort. Kew. ed. 1: (3) 92 (1789)

3258 Lotus glaucus Ait.
Nivaria: Puerto Cruz, Martinez
E.R. Sventenius 49 (DAO)

SEM Lotus glaucus Dryander
Tenerife, Canary Is.
E. Asplun 8.4.1933 (DAO)

31. L. jacobaeus L. in Sp. Pl.: 775 (1753)

3265 Lotus jacobaeus L.
Lisbon, Portugal
L. Jenkins 3943 (Cult.) (DAO)

32. L. sessifolius DC. in Cat. Hort. Monsp.: 122 (1813)

SEM Lotus sessilifolius DC.
Tenerife, Canary Is.
E. Asplund 20.3.1933 (DAO)

III. SUBGENUS HOSACKIA Dougl. ex Benth. in Bot. Reg. t. 1257 (1829)

33. L. aboriginus Jepson in Fl. Calif. 2: 315 (1936)

3288 Lotus arboriginum Jepson
Mason Co., Washington
W.C. McCalla 5436 (DAO)
lapsu, sp. epith. = arboriginus

34. L. angustifolius Mocinzo et Sesse ex G. Don, Gen. Syst. 2: 200 (1832) non Gouan (1764) nec Gueldenst. (1791)

UCB54 Lotus angustifolius G. Don
S.W. de San Miguel, Suchixtepec,
Oaxaca, Mexico
M. Sousa & A. Delgado 7561

35. L. chihuahuanus (Wats.) Greene in Pittonia 2: 146 (1890)

UCB31 Lotus chihuahuanus (Wats.) Greene
Los Cascarones, Chihuahua, Mexico
H.S. Gentry No. 2662

UCB51 Lotus chihuahuana Wats.
Sierra Madre, Chihuahua
C.G. Pringle 27 September 1888
lapsu: [Hosackia chihuahuana Wats. in Proc. Am. Acad. 23: 270 (1888)].

36. L. crassifolius (Benth.) Greene in Pittonia 2: 147 (1890)

3246 Lotus crassifolius (Benth.) Greene
Eldorado Co., Calif.
J. McCorskill 457 (DAO)

UCB47 Lotus crassifolius Greene
Potter Valley, Mendocino Co., Calif.
C.A. Purpus, April 1898

[Benth. = Hosackia crassifolia in Trans. Linn. Soc. 17: 365 (1837)]

SEM Lotus crassifolius (Benth.) Greene
Riverside Co., Calif.
J.M. Gillett & A.G. Moulds 18 June 1964 (DAO)

37. L. formosissimus Greene in Pittonia 2: 147 (1890)

3255 Lotus formisissimus Greene
B. Boivin Cult. 65 (DAO)

3256 Lotus formisissimus Greene
Mendocino Co., Calif.
E.K. Balls 16527 (DAO)

UCB33 Lotus formisissimus Greene
Requa, Del Norte. Co., Calif.
Davy and Blasdale No. 5903

SEM Lotus formisissimus
Del Norte Co., Calif.
C.B. Wolf, 10 Aug. 1937

38. L. incanus (Torr.) Greene non Dougl. ex Hook. (1831), in Pittonia 2: 147 (1890)

UCB50 Lotus incana (Torr.) Greene
Sterling City, Butte. Co., Calif.
H.M. Hall, May 27, 1913
lapsu, sp. epith.; Hosackia incana Torr. in Pac. R.R. Rept. 4(5): 79 (1857) = L. incanus (Torr.) Greene

39. L. oblongifolius (Benth.) Greene in Pittonia 2: 146 (1890)

3271 Lotus oblongifolius Greene
Humboldt Co., Calif.
J.P. Tracey 7629 (DAO)
lapsu, auct.; Hosackia oblongifolia Benth. in Pl. Hartw. 2: 305 (1849)

SEM Lotus oblongifolius (Benth.) Greene
San Gabriel Mts., Los Angles Co., Calif.
R.F. Thorne & M.Z. Thorne No. 37186

SEM Lotus oblongifolius Benth.
San Gabriel Mts. Calif.
A.J. Breitung No. 15129 (DAO)
[lapsu, Benth. = Hosackia oblongifolia in Pl. Hartw. 2: 305 (1849)]

a. var. cupreus (Greene) Ottley in Univ. Calif. Publ. Bot. 10: 206 (1923)

UCB16 Lotus oblongifolius Greene var. cupreus Ottley
Owens Lake, 3600', Inyo Co., Calif.
H.M. Hall and H.P. Chandler No. 7327

b. var. oblongifolius [Viz. Isley in Mem. N.Y. Bot. Gard. 25: 242 (1981)]

UCB15 Lotus oblongifolius Greene var. torreyi Ottley
Horse Mt., Humboldt Co., 4800', Calif.
Tracy 7629
[lapsu, auct. var. torreyi = (Gray) Ottley in Univ. Calif. Publ. Bot. 10: 205 (1923); Hosackia torreyi Gray in Proc. Amer. Acad. Arts Sci. 8: 625 (1873)]

UCB2 Lotus oblongifolius (Benth.) Greene
SEM var. nevadensis
N. Fork, Coffee Creek, Trinity Co., Calif.
Alexander and Kellog No. 211

3283 Lotus torreyi (Gray) Greene
Trinity Summit, Humboldt Co., Calif.
E.E. Tracy Aug. 1, 1919 (DAO)

UCB3 Lotus torreyi Greene
Swift Creek, Trinity Co., Calif.
H.M. Hall 8682
[lapsu auct. = (Gray) Greene in Pittonia 2: 146 (1890); Gray = Hosackia torreyi Gray in Proc. Amer. Acad. Arts Sci. 8: 625 (1873)

UCB12 Lotus torreyi (Gray) Greene
Donner Lake, Sierra Nevada Mts., Calif.
C.F. Sonne July 1888

SEM Lotus torreyi Greene
Trinity Co., Calif.
H.H. Hael No. 8682 (UCB)

40. L. pinnatus Hook. in Curtis Bot. Mag. 56: 2913 (1829)

3275 Lotus pinnatus Hook.
Corvallis, Oregon
W.H. Baker May 9, 1947 (DAO)

UCB11 Lotus pinnatus Hook.
Donner Lake, Sierra Nevada Mts., Calif.
C.F. Sonne July 1888

UCB60 Lotus pinnatus Hook.
Balke Look-Out, Trinity Co., Calif.
H. & M. Dearing 3721

SEM Lotus pinnatus
Redwood State Park, Calif.
Rossback No. 332 (UCB)

41. L. stipularis (Benth.) Greene in Pittonia 2: 147 (1890) = Hosackia stipularis Benth. in Trans. Linn. Soc. London 17: 365 (1837)

3279 Lotus stipularis Benth. Greene
Alpha Rd., Nevada Co., Calif.
L.S. Rose 71004 (DAO)

SEM Lotus stipularis (Benth.) Greene
Sequoia Park, Oakland, Calif.
P.F. Covel No. 557 (UCB)

SEM Lotus stipularis (Benth.) Greene var. stipularis
Mariposa Co., Calif.
V. Miller Mar. 12, 1941 (UCB)

42. L. yollabolliensis Munz in Aliso 3: 117 (1955)

UCB4 Lotus yollabolliensis Munz
SEM South Fork Mt., 8 mile ridge, 5500'
J.P. Tracy 15568 (UCB)

IV. SUBGENUS ACMISPON (Rafin) Ottley in Univ. Calif. Publ. Bot. 10: 197 (1923)

A. SECTION MICROLOTUS Benth. in Trans. Linn. Soc. 17: 367 (1837); [= Genus Anisolotus Bernh. in Hort. Efr. (1837)]

43. L. denticulatus (Drew) Greene in Pittonia 2: 139 (1890)

3249 Lotus denticulatus Greene
British Columbia
V.J. Krajina 65,062,452 (DAO)

3250 Lotus denticulatus Greene
Whatcom Co., Washington, U.S.A.
W.C. Muencher 10, 001 (DAO)

3289 Lotus denticulatus Greene
Cult. C.E.F. Ottawa
J.M. Armstrong 1893-4823 (DAO)

UCB40 Lotus denticulatus Greene
Edgewood, Calif.
K. Brandegee July 1887

UCB41 Lotus denticulatus Greene
Horse Mt., Humboldt Co., Calif.
J.P. Tracy 13219
lapsu, auct. = (Drew) Greene; Hosackia denticulata Drew in Bull. Torr. Bot. Club 16: 151 (1889)

44. L. humistratus Greene in Pittonia 2: 139 (1890)

3264 Lotus humistratus Greene
California
W.C. McCalla 6129 (DAO)

SEM Lotus humistratus Greene
Pima Co., Arizona
N.H. Holmgren No. 6685 (UCB)

SEM Lotus humistratus
Eldorado Co., California
Bacigalupi & Heckard No. 8540 (UCB)

45. L. micranthus Benth. in Trans. Linn. Soc. 17: 367 (1837)

3269 Lotus micranthus Benth.
Gatineau Park, P.Q.
J.M. Gillett 12418 (DAO)

UCB20 Lotus micranthus Benth.
1.5 mi. N.N.W. of Lake School
San Juan Baptista, Monterey Co., Calif.
B. Schreiber No. 2216

3229 Lotus parviflorus Benth.
California
A.J. Breitung 17985 (DAO)

46. L. purshianus (Benth.) Clements et Clements in Rocky Mt. Flowers: 183 (1914) = Hosackia purshiana Benth. in Lindley, Bot. Reg. 15: t.1257 (1829)

3276 Lotus purshianus Benth.
Ventura Co., Calif.
H.M. Pollard Oct. 12, 1966 (DAO)

SEM Lotus purshianus (Benth.) C. & C.
Santa Cruz Co.
J.H. Thomas No. 3430

SEM Lotus purshianus
San Benito Co., Calif.
R.E. Frenkel No: 451

SEM Lotus purshianus
Received from W.F. Grant
Artificial tetraploid (MTMG)

a. var. helleri (Britt.) Isley in Brittonia 30: 468 (1978)

3261 Lotus helleri Britton
Davie Co., North Carolina
Sept. 1, 1897 No. 5619b (DAO)

b. var. purshianus

3236 Lotus americanus Bish.
Ottawa, cultivated
J.M. Armstrong 1893-4819 (DAO)
[lapsu, auct. = (Nutt.) Bischoff; Trigonella americana Nutt. in Gen. Am. 2: 120 (1818); L. americanus (Nutt.) Bisch. non Vell. (1825), in Del. Sem. Hort. Heidelb: 132 (1840)]

UCB55 Lotus americanus (Nutt.) Bisch.
5 mi. S. of Santo Palo, Pinto Co., Texas
R. McVaugh No. 10752

3285 Lotus unifoliatus Hook.
Santa Rosa Mts., Calif.
E. Jaeger 7-25-49 (DAO)

47. L. salsuginosus Greene in Pittonia 2: 140 (1890)

3277 Lotus salsuginosus Greene
Los Angeles Co., Calif.
L.S. Rose Apr. 24, 1949 (DAO)

a. var. brevivexillus Ottley in Univ. Calif. Publ. Bot. 10: 217 (1923)

UCB7 Lotus salsuginosus Greene var. brevivexillus Ottley
Cedros I. Mexico, Near Red Rock.
A.L. Haines and G. Hale 21 Mar. 1939

SEM Lotus salsuginosus var. brevivexillus Ottley
Pozo Alemean, Baja California, Mexico
F. Shreve No. 7001 (UCB)

48. L. wranglianus Fisch. et Meyer in Index Sec. Sem. Hort. Petrop. 2: 41 (1836)

3281 Lotus subpinnatus
Constance, Santa Barbara Co., Calif.
H.M. Pollard, May 3, 1958 (DAO)

UCB57 Lotus subpinnatus F. & M. var. wrangelianus Jepson
Berkley, Calif.
J.P. Tracy No. 1416 (UCB)

B. SECTION SIMPETERIA Ottley in Brittonia 5(2): 81 (1944)

49. L. argyraeus (Greene) in Pittonia 2: 144 (1890) = Hosackia argyraeus Greene in Bull. Calif. Acad. 1(4): 184 (1885)

3230 Lotus argyraeus Greene
Mojave Desert, Calif.
P.O. Schallert May 6, 1939 (DAO)

UCB58 Lotus argyraeus (Greene)
Sierra Juarez, Baja California, Nord., Mexico
W. Hohenthal No. 27

a. var. multicaules (Ottley) Isley in Mem. N.Y. Bot. Gard. 25: 237 (1981) = L. wrightii var. multicaulis Ottley in Univ. Calif. Publ. 10: 211 (1923)

UCB27 Lotus argyraeus Greene var. multicaulis Ottley
Near Barnwell, San Bernardino Co., Calif.
F.F. Ferris & R. Bacigalupi No. 8105

50. L. bryantii (Brandegee) Ottley in Brittonia 5(2): 98 (1944) = Hosackia bryantii Brandegee in Proc. Calif. Acad. 2(2): 144 (1890)

UCB25 Lotus bryantii (Brandg.) Ottley
20.6 km. south of (60m) rd. to San Quentin
Baja California, Mexico
P.H. Raven, M. Mathias and J. Turner 12415

UCB26 Lotus bryantii (Brandg.) Ottley
Malarrimo, Baja Calif., Mexico
R. Morgan & J.L. Reveal 19834

51. L. cedrosensis Greene in Pittonia 2: 144 (1890)

UCB59 Lotus cedrosensis Greene
Cedros I., Mexico
R. Moran 10759

52. L. grandiflorus (Benth.) Greene in Pittonia 2: 145 (1890) = Hosackia grandiflora Benth. in Trans. Linn. Soc. (Lond.) 17: 366 (1837)

3259 Lotus grandiflorus (Benth.) Greene
San Diego Co., Calif.
W.C. McCalla Apr. 29, 1940 (DAO)

UCB19 Lotus grandiflorus (Benth.) Greene var. mutabilis (Gray) Ottley
1 mi. above mouth of Strawberry Creek, 4000' San Jacinto Canyon, Calif.
Munz & I.M. Johnston No. 5403

UCB34 Lotus grandiflorus (Benth.) Greene
Hornitos, Mariposa Co., Calif.
L.V. Compton No. 120

a. var. grandiflorus [viz. Isley in Mem. N.Y. Bot. Garden 25: 240 (1981)]

SEM Lotus leucophaeus
San Bernadino Co., Calif.
A.J. Breitung No. 14848 (UCB)
auct. = Greene in Pittonia 2: 145 (1890)

53. L. greenei (Woot. et Standl.) Ottley ex Kearney et Peebles in Journ. Wash. Acad. Sci. 29: 483 (1939)

UCB32 Lotus greenei Ottley
Santa Rita Range Reserve, Arizona
R.C. Foster and J.F. Arnold 140
[lapsu auct.: Anisolotus greenei Woot. et Standl. in Contrib. U.S. Nat. Herb. 16: 135 (1913)]

54. L. mearnsii (Britton) Greene non de Wild. (1925) in Pittonia 2: 144 (1890)

UCB21 Lotus mearnsii Britton
Ash Fork 6100-6200', Coconino Co., Arizona
M.C. Ferguson and A.M. Ottley No. 5075
[lapsu, Britton = Hosackia mearnsii in Trans. N.Y. Acad. Sci. 8: 65 (1889)]

55. L. oroboides (Humboldt et al.) Ottley ex Kearney et Peebles in Journ. Wash. Acad. Sci. 29: 483 (1939)

UCB14 Lotus oroboides (H.B.K.) Ottley
Durango, Mexico
E. Palmer 383

UCB62 Lotus oroboides (H.B.K.)
Otinapa, Durango, Mexico
D. Palmer No. 383

a. var. oroboides [viz. Isley, Mem. N.Y. Bot. Gard. 25: 242 (1981)]

UCB63 Lotus puberulus (Benth.) Greene
Toyahvale, Reeves Co., Texas
W.R. & J.P. Moore No. 11

b. var. nanus (Gray) Isley in Brittonia 30: 468 (1978)

SEM Lotus neomexicanus Greene
Pima Co., Arizona
N.H. & P.K. Holmgren No. 6797

c. var. nummaralis (Jones) Isley in Mem. N.Y. Bot. Gard. 25: 242 (1981)

3268 Lotus longibracteatus Rydb.
Garfield Co., Utah
N.H. Holmgren 2103 (DAO)

UCB22 Lotus longibracteatus Rydb.
Toquerville, Washington Co., Utah
B. Maguire 20518

UCB23 Lotus longibracteatus Rydb.
Garfield Co., Utah, Hellsbackbone
N.H. Holmgren, J.L. Reveal, C. LaFrance
2103 (DAO)

56. L. plebeius (Brabdegee) Barnaby in prep. (1981) = Hosackia plebeius Brandegee in Proc. Calif. Acad. 2(2): 144 (1889)

UCB13 Lotus plebeius (Brandegee) Barnaby
Lower California, La Chupanosa
G.S. Brandegee Oct. 16, 1893

57. L. rigidus (Benth.) Greene in Pittonia 2: 142 (1890) = Hosackia rigida Benth. in Pl. Hntw.: 305 (1848)

3239 Lotus argensis Coville
Tucson, Arizona
A. & R. Nelson 1439 (DAO)

UCB8 Lotus rigidus (Benth.) Greene
2 mi. E. of Congress, Ariz., Yavapai Co.
P. Munz, D. Gregory and W. Klein 22973

58. L. strigosus (Nutt. ex T. et G.) Greene in Pittonia 2: 141 (1890)

3280 Lotus strigosus (Nutt.) Greene
San Diego Co., Calif.
E.B. Higgins Apr. 13, 1951 (DAO)

UCB6 Lotus strigosus Nutt. in T. & G.
Madera Co., Calif., San Joaquin Experiment Range
H.H. Biswel 136

UCB56 Lotus strigosus Greene
1.25 mi. N.W. of Pleyte Well
Monterey Co., Calif.
C.A. Graham No. 241

SEM Lotus strigosus (Nutt. in T. & G.) Greene
Madera Co., Calif.
H.H. Biswell No. 136

a. var. tomentellus (Greene) Isley in Mem. N.Y. Bot. Garden 25: 246 (1981)

UCB1 Lotus tomentellus Greene
29 Palms, San Bernardino Co., Calif.
A.M. Alexander & L. Kellog 866

SEM Lotus tomentellus Greene
Cocupah, Laguna Maguata, Lower Calif.
Epling et al. Feb. 19, 1933

SEM Lotus tomentellus Greene
Clarke Co., Nevada
N.H. & P.K. Holmgren No. 7923

59. L. utahensis Ottley in Brittonia 5(2): 108 (1944)

UCB61 Lotus utahensis Ottley
Zion National Park, Utah
W.S. Boyle Z166

60. L. wrightii (Gray) Greene in Pittonia 2: 143 (1890) = Hosackia wrightii Gray in Pl. Wright 2: 42 (1853)

3287 Lotus wrightii (Gray) Greene
N.E. of Parker, Douglas Co., Colorada
J. Wingate & A. Daraghy No. 42

V. SUBGENUS SYRMATIUM (Vogel) Ottley in Univ. Calif. Publ. Bot. 10: 198 (1923) [= Genus Syrmatium Vogel in Linneae 10: 590 (1836)]

61. L. argophyllus (Gray) Greene in Pittonia 2: 149 (1890) = Hosackia argophylla Gray in Mem. Amer. Acad. Apts. Sci. Ser. 2(Pl. Thurb.) 5: 316 (1854)

3238 Lotus argophyllus (Gray) Greene
San Diego Co., Calif.
W.C. McCalla 5895 (DAO)

SEM Lotus argophyllus
South Yuba River
W.R. Dudley, 14 June 1893

SEM Lotus argophyllus
San Diego Co., Calif.
W.C. McCalla No. 5895

a. var. argophyllus

UCB28 Lotus argophyllus (A. Gray) Greene
var. argophyllus
Big Sur, Monterey Co., Calif.
J.B. Davy No. 7429

62. L. benthamii Greene in Pittonia 2: 148 (1890)

UCB30 Lotus benthamii Greene
Monterey, Calif.
Davy 7223

63. L. dendroideus (Greene) Greene in Pittonia 2: 148 (1890) = Syrmatium dendroideum Greene in Bull. Calif. Acad. Sci. 2: 146 (1887)

UCB49 Lotus dendroideus (Greene) Greene
Santa Catalina I., Calif.
C.W. Wolf 3438

a. var. traskiae (Eastwood ex Noddin) Isley in Mem. N.Y. Bot. Gard. 25: 238 (1981)

UCB39 Lotus dendroideus Greene var. traskiae
(Eastwood ex Noddin) Isley in Ed.
San Clemente Is.
I.L. Wiggins 11956

64. L. hamatus Greene in Pittonia 2: 150 (1890)

UCB36 Lotus hamatus Greene
Sierra San Borja, Rancho la Heurta
Baja Calif., Mexico
Reid Moran No. 12771

65. L. haydonii (Orcutt) Greene in Pittonia 2: 149 (1890) = Hosackia haydonii Orcutt in W. Amer. Sci. 6: 63 (1889)

UCB35 Lotus haydonii (Orcutt) Greene
15 mi. E. of Jacumba, San Diego Co.
C.L. Hitchcock No. 5968

66. L. heermannii (Durand et Hilgard) Greene in Pittonia 2: 150 (1980) = Hosackia heermannii Durand et Hilgard in Journ. Acad. Nat. Sci. Phil. Ser. 2(3): 39 (1855)

UCB37 Lotus heermannii (Durand et Hilard) Greene
Coronado, San Diego Co., Calif.
L.S. Rose

a. var. orbicularis (Gray) Isley in Brittonia 30: 467 (1978)

UCB45 Lotus eriophorus Greene
San Francisco, Calif.
G.T. Robbins 314

UCB38 Lotus eriophorus Greene var. hermannii Ottley
Palm Springs, Calif.
L.D. Coupland, May 1904

SEM Lotus tomentosus (Hook. & Arn.) Greene
San Diego Co., California
J. Breitung No. 15047

67. L. junceus (Benth.) Greene in Pittonia 2: 148 (1890)

a. var. biolettii (Greene) Ottley in Univ. Calif. Publ. Bot. 10: 231 (1923)

3241 Lotus biolettii (Greene) Ottley
Sonoma Co., Calif.
R.F. Hoover 9286

3266 Lotus junceus Greene var. biolettii (Greene) Ottley
Marin Co., Calif.
L.S. Rose (DAO)

UCB24 Lotus junceus (Benth.) Greene var. biolettii (Greene) Ottley
4 mi. S.E. Ft. Bragg, Mendocino Co., Calif.
E. Crum No. 1905

UCB29 Lotus biolettii Greene
Point Arena, Mendo. Co., Calif.
Davy & W.C. Blasdale No. 6021

SEM — Lotus biolettii Greene
Sonoma Co., Calif.
R.F. Hoover No. 9286 (DAO)

68. L. nevadensis (Wats.) Greene in Pittonia 2: 149 (1890)

3270 — Lotus nevadensis Greene
Copper Creek, Fresno Co., Calif.
L.S. Rose 60044 (DAO)
[lapsu, Watson = Hosackia decumbens var. ? nevadensis in Bot. Calif. 1: 138 (1876)]

UCB44 — Lotus nevadensis (Wats.) Greene
Santa Rosa Mts., 6600', Calif.
P.A. Munz 5851

a. var. davidsonii (Greene) Isley in Brittonia 30: 467 (1978)

UCB48 — Lotus davidsonii Greene
Mt. Pinos, Ventura Co., Calif
H.M. Hall 6537

b. var. douglasii (Greene) Ottley in Brittonia 5: 81 (1944)

3252 — Lotus douglasii Greene
Spokane, Washington
W.C. McCalla, June 12, 1936 (DAO)

UCB10 — Lotus douglasii Greene var. nevadensis Ottley
Millspaugh, Argus Mts., Inyo Co., Calif., 6000'
Munz 26521

UCB43 — Lotus douglasii Greene var. douglasii
Near Greka, Siskiyou Co., Calif.
G.D. Butler No. 1441

UCB42 — Lotus douglasii Greene var. congestus Ottley
Klamath R., Orleans Bar. to ? Bar
Humboldt Co., Calif.
H.P. Chandler 1487

69. L. nudatus Greene in Pittonia 2: 148 (1890)

UCB18 Lotus nudatus Greene
Cedros I., Mexico
A.L. Haines and G. Hale 17 Mar. 1939

70. L. nuttallianus Greene in Pittonia 2: 150 (1890)

UCB17 Lotus nuttallianus Greene
Silver Strand, San Diego Co., Calif.
E.B. Higgins, Apr. 26, 1954

71. L. procumbens (Greene) in Pittonia 2: 149 (1890) = Hosackia procumbens Greene in Bull. Calif. Acad. Sci. 1: 82 (1886)

3267 Lotus leucophyllus Greene
San Bernardino Co., Calif.
I.W. Clokey 6715 (DAO)

UCB9 Lotus procumbens (Green) Greene
S. fork Seymour Creek, Mt. Pinos, Ventura Co., Calif.
F.W. Peirson June 11, 1923

72. L. scoparius (Nutt.) ex T. et G.) Ottley in Univ. Calif. Publ. Bot. 10: 227 (1923) = Hosackia scoparia Nutt. ex T. et G. in Fl. N. Amer. 1: 325 (1838) = Drepanolobus scoparius Nutt. Mss.

3278 Lotus scoparius (Nutt.) Ottley
San Luis Obispo Co., Calif.
R.F. Hoover 8663 (DAO)

SEM Lotus scoparius
Baja California, Mexico
Moran & Reveal No. 19910 (UCB)

a. var. brevialatus Ottley in Univ. Calif. Publ. Bot. 10: 229 (1923)

UCB5 Lotus scoparius (Nutt) Ottley var. brevialatus Ottley
Baja Calif. Sur. 3 mi. w. of San José de Castra
R. Moran and J.L. Reveal 19910

b. var. scoparius

3228 Lotus glaber (Torr.) Greene
Lassen Co., Calif.
Heller 15199 (DAO)
[lapsu; Torrey = Hosackia glabra (Vog.) Torr. in Bot. Wilkes Exp. 274 (1874)]

SEM Lotus glabrus
Whitewater, California
G.R. Vasey 1881

[auct. = (Vog.) Greene; Vogel = Syrmatium glabrum in Linneae 10: 591 (1836) lapsu, sp. epith. = glaber]

73. L. watsonii (Vasey et Rose) Greene in Pittonia 2: 149 (1890) = Hosackia watsonii Vasey et Rose in Proc. U.S. Mus. 11: 528 (1889)

UCB52 Lotus watsonii (Vasey and Rose) Greene
San Quentin Bay, Baja California, Mexico
E. Palmer No. 690

TETRAGONOLOBUS Scop. in Fl. Carn. ed. 2 V.2: 87 (1772)

1. T. biflorus (Desr.) Ser. in DC. Prod. 2: 215 (1825) = Lotus biflorus Desr. non Huet. ex Nym., in Lam. dict. 3(2): 604 (1792)

3291 Tetragonolobus biflorus (Desr.) Ser.
Algerie
B. Ritz 31462 (DAO)

2. T. maritimus (L.) Roth in Tent. Fl. Germ. 1: 323 (1788)

3292 Tetragonolobus maritimus (L.) Roth
Germany
W. Lippert 25.8.1964 (DAO)

3293 Tetragonolobus maritimus (L.) Roth
Austria
26 Maio 1874 (DAO)

3294 Tetragonolobus maritimus (L.) Roth
Cult. C.E.F. Ottawa
J.M. Armstrong 1893-4513 (DAO)

3. T. purpureus Moench in Meth.: 164 (1794) = Lotus tetragonolobus L. in Sp. Pl.: 773 (1753) and 1089 (1762) et L. siliquosus L. in Sp. Pl.: 1089 (1762)

a. var. purpureus

3290 Tetragonolobus purpureus Moench
Cult. St. Thomas, Ontario
L.E. James 2244 (DAO)

b. var. palaestinus (Boiss.) Post in Fl. Syr.: 251 (1896)

HUJ 6 Tetragonolobus plalestinus Boiss.
Jerusalem, Palestine
C. Parmet, 16545
[lapsu, sp. epith. = palaestinus]

VERMIFRUX J.B. Gillett in Kew Bull. 20: 245 (1966) = Helminocarpon A. Richard in Tent. Fl. Abyss. 1: 200 (1847) non Fée (1837)

*1. V. abyssinica (A. Richard) J.B. Gillett in Kew. Bull. 20: 245 (1966)

KEW 18 Vermifrux abyssinica (A. Rich.) Gillett
Mt. Fure, Southern Addis Ababa, Ethiopia
J. Ash 23.6. 74

TRIBE CORONILLEAE

CORONILLA Tourn. ex L. in Sp. Pl.: 742 (1753)

1. C. emerus L. non Sibeth. ex Sibeth. et Smith (1832) in Sp. Pl.: 742 (1753)

KEW 8 Coronilla emerus L.
Cult. from Barcelona, Spain

2. C. minima L. non Jacq. (1775), in Cent. Pl. 2: 28 (1756)

KEW 5 Coronilla minima L.
Milla-Breziers, France
B. Verdcourt 4280

3. C. scorpioides (L.) Koch in Syn. Fl. Germ: 188 (1835)

KEW 7 Coronilla scorpioides (L.) Koch
Sogut to Bozborun, Turkey
Davis 41158

*4. C. varia L. in Sp. Pl.: 743 (1753)

KEW 6 Coronilla varia L.
N.E. of Varegoz, Turkey
P.H. Davis 45709

HAMMATOLOBIUM Fenzl in Ill. Pl. Syr. 1: 7; t. 7 (1843)
= Hamatolobium Fenzl in Pug. Pl. Nov. Syr.: 3 (1842)

*1. H. lotoides Fenzl in Ill. Pl. Sur. 1: t. 1 (1843)

KEW12 Hammatolobium lotoides Tenge
Mt. Amanus, Syria
M. Haradjian No. 754
lapsu, auct. = Fenzl.

HIPPOCREPIS L. in Sp. Pl.: 744 (1753)

1. H. ciliata Willd. non Del Campo ex Willk. et Lange (1868) in Ges. Naturf. Fr. Berl. Mag. 2: 173 (1808)

SEM Hippocrepis ciliata
San Giacomo, Bordeghera
C. Bicknell 15.v.1895 (KEW)

2. H. comosa L. non Lucé (1823), nec Willk. ex Scheele (1848), in Sp. Pl.: 744 (1753)

KEW2 Hippocrepis comosa L.
6 km. S. of Bourges, France
B. Verdouy No. 4261

ORNITHOPUS L. in Sp. Pl.: 743 (1753)

1. O. compressus L. non Sieber ex Stend. (1840), in Sp. Pl.: 744 (1753)

KEW4 Ornithopus compressus L.
Platnes, Cyprus
W.E. Kennedy No. 1300

*2. O. perpusillus L. in Sp. Pl.: 743 (1753)

KEW3 Ornithopus perpusillus L.
Sussex, Storrington, near Mill, U.K.
B.L. Burtt, J.R. Sealy & L.R. Craig 1611

3. O. pinnatus (P. Mill.) Druce in J. Bot. (London) 45: 420 (1907)

SEM Ornithopus pinnatus (Mill.) Druce
For-de-l'Eau, Algeria
A. Dubois et L. Faurel No. 3425 (DAO)

SCORPIURUS L. in Sp. Pl.: 744

1. S. muricatus L. in Sp. Pl.: 745 (1753)

KEW11 Scorpiurus muricatus L.
Kurdistan, Iran
J.C. Archibald No. 1853

a. var. subvillosus (L.) Fiori ex Fiori et Paol. in Fl. Anal. Ital. 2: 89 (1900)

SEM Scorpiurus subvillosus L.
Jola Sustrand aux Stoje Musil
K. Untchj 17.6.1903 (K)

([1]) The classification of Lotus and its allies used here follows the treatment of Polhill (1981) at the tribal and generic level, and that of Taubert (1894) at the sectional level. In the absence of a world monograph of Lotus, the following regional treatments were used as the basis for specific circumscription and synonymy: Isley (1981), Nearctic; Ottley (1944), Mexican; Ball (1968), European; Monod (1980), North African; Gillett (1958), Subsaharan; and Heyn (1966, 1970 a,b) and Heyn and Heernstadt (1967), Middle Eastern. Acronyms used are based on Holmgren et al. 1981, and the numbers (e.g. HUJ2, KEW2, 3282 ... etc.) refer to pollen slides deposited in the Canada Department of Agriculture Permanent Pollen Collection (DAO). "SEM" refers to material used for scanning electron microscopy studies. "*" indicates the typus of a genus.

APPENDIX II

POLLEN CHARACTER VALUES (1)

OTU'S	1	2	3	4	5	6	7	8	9	10	11
LTOM	25.5	29.3	2	2	2	1	2	1	2	1	1
LOBL	18.4	23.7	2	1	1	2	1	1	1	2	1
LTOR	22.4	27.5	2	3	2	1	1	1	1	1	1
LYOL	24.2	27.9	2	2	2	1	1	1	1	1	1
LSCO	25.5	25.5	2	2	2	1	1	3	2	1	1
LSTR	31.1	31.1	1	3	2	2	2	2	3	2	2
LSAL	19.1	23.0	2	2	2	1	1	1	2	1	1
LRIG	25.6	25.6	2	2	2	2	1	2	2	1	1
LPRO	19.4	23.2	2	2	2	1	1	1	2	1	1
LDOU	24.0	24.0	2	2	2	2	1	3	2	1	1
LPIN	20.7	24.5	2	2	2	2	1	1	1	2	1
LTOI	21.7	23.0	2	2	2	1	1	1	1	2	1
LOBI	26.2	26.4	2	3	2	2	1	3	3	1	1
LORO	28.6	28.6	2	2	2	2	1	3	2	1	1
LOB2	19.8	24.2	2	2	2	1	1	1	1	2	1
LOB3	23.5	27.3	2	2	2	1	1	1	1	2	1
LNUT	24.1	24.1	2	2	2	2	1	3	2	2	1
LNUD	22.1	27.1	2	2	2	2	1	1	2	1	1
LGRA	28.7	30.6	3	2	2	2	1	3	2	1	1
LMIC	21.3	21.3	2	3	2	2	1	3	2	1	1
LPUB	28.8	28.8	2	3	2	1	1	3	2	1	2
LORL	29.0	29.0	2	3	2	2	4	3	2	1	2
LUTA	29.1	29.1	2	3	2	2	1	3	3	1	1
LPIN	29.3	29.3	2	3	2	2	1	2	1	2	1
LCED	29.1	29.1	2	2	2	2	2	3	2	2	1
LARG	26.0	27.1	1	2	2	2	1	3	2	1	1
LSUB	19.9	23.2	2	2	2	2	5	1	2	1	1
LSTI	33.7	33.7	1	4	2	2	2	2	3	2	2
LPUR	20.7	20.7	2	2	2	2	1	3	2	1	1
LANG	22.5	24.5	1	2	2	1	1	1	1	2	1
LWRI	28.1	28.1	2	3	2	2	1	3	2	1	1
LWAT	26.2	26.2	2	3	2	2	1	3	3	1	1
LCHI	22.5	24.2	1	3	2	1	3	1	1	2	1
LDEN	27.6	27.3	2	3	2	2	1	3	2	2	2
LDAV	21.2	21.2	2	4	2	2	1	3	2	1	1
LGRE	26.6	26.6	2	3	2	2	1	3	2	1	2
LERI	24.2	26.8	1	3	2	2	1	1	2	1	1
LNEV	25.5	26.8	2	3	2	1	1	2	2	1	1
LDEI	18.6	30.4	2	3	2	2	1	1	2	2	1
LDE2	22.5	22.5	2	2	2	1	1	1	2	1	1
LDE3	23.7	23.7	2	3	2	2	1	3	2	1	1
LHER	22.8	22.8	2	3	2	2	1	2	2	1	1
LHAM	22.9	23.0	2	3	2	2	1	3	2	1	1
LHAY	23.3	23.3	2	3	2	2	1	3	2	1	1
LGRI	31.9	35.5	2	3	2	1	1	1	2	1	1

OTU'S	1	2	3	4	5	6	7	8	9	10	11
LCHI	23.2	23.4	2	3	2	1	3	3	1	1	1
LBEN	29.0	28.1	2	3	2	1	4	2	2	1	1
LARI	26.8	26.8	2	3	2	2	1	3	2	1	1
LAR2	26.3	26.5	2	3	2	2	1	3	2	1	1
LBRY	29.1	25.2	2	3	2	2	1	4	3	1	1
LBRI	30.2	28.7	2	3	2	2	1	4	3	1	1
LJUN	24.5	27.5	2	3	2	2	1	1	2	1	1
LLON	24.4	24.8	2	2	2	2	1	2	2	1	1
LLOI	28.6	28.3	2	2	2	2	1	2	2	1	1
LMEA	25.1	25.1	2	3	2	2	4	3	3	1	1
LMII	22.4	21.5	2	3	2	2	1	4	2	1	1
LFOR	23.7	25.0	2	4	2	2	3	2	1	2	1
LGR2	26.4	32.8	1	4	2	2	4	1	2	1	2
HCIR	26.8	26.8	2	2	2	2	1	2	3	2	2
HICO	20.4	23.5	2	2	2	2	1	1	1	2	1
OPUR	18.1	21.7	2	2	1	2	1	1	1	2	1
OCOM	20.8	24.7	2	2	2	2	1	1	1	2	1
CMIN	16.6	20.2	2	2	2	2	1	1	1	2	1
CVAR	25.8	25.3	1	2	2	2	1	2	1	2	1
CCSO	13.5	15.6	2	2	2	2	1	2	1	2	1
CEME	26.5	25.8	2	2	2	2	1	2	1	2	1
LNAM	19.8	22.7	1	1	2	2	1	1	1	2	1
SMUR	16.1	20.4	2	1	2	2	1	1	1	2	1
HALO	33.4	41.1	2	2	2	2	1	1	1	2	1
LCOR	13.1	15.6	1	1	1	2	1	1	1	2	1
LAUS	16.3	19.9	2	2	2	2	1	1	1	2	1
LCRU	18.3	19.5	1	1	2	2	1	2	1	2	1
LDIS	20.4	25.2	1	1	1	2	1	1	1	2	1
CDOR	34.2	37.3	2	2	2	2	2	1	1	1	2
LABY	23.3	23.0	2	2	2	2	1	2	1	2	1
AVUL	36.2	42.6	2	2	2	2	1	1	1	2	1
LTEN	13.8	16.3	1	1	1	2	1	1	1	2	1
LPER	16.9	22.9	2	2	2	2	1	1	1	2	1
LORN	12.6	18.1	2	2	1	2	1	1	1	2	1
LPAL	11.0	14.5	3	2	1	2	1	1	1	2	1
LPLA	21.5	25.5	3	2	1	2	1	1	1	2	1
LHAL	13.1	18.2	2	2	2	2	1	1	1	2	1
LHAI	13.0	17.9	2	2	2	2	1	1	1	2	1
LLAN	15.6	19.4	2	2	2	2	1	1	1	2	1
LCON	15.1	18.5	3	2	2	2	1	1	1	2	1
LCOL	12.0	18.0	3	2	2	2	1	1	1	2	1
LJUD	14.8	21.4	2	2	2	2	1	1	1	2	1
LHYM	10.2	14.6	1	1	1	2	1	1	1	2	1
LANI	10.2	12.8	1	1	1	2	1	1	1	2	1
LREC	20.2	23.5	2	2	2	2	1	1	1	2	1

OTU'S	1	2	3	4	5	6	7	8	9	10	11
LAXI	26.0	30.3	2	2	2	2	1	1	1	2	1
LARM	22.1	24.2	2	2	2	2	1	1	1	2	1
AVUI	33.5	37.3	3	2	2	2	1	1	1	2	1
ASPU	29.3	34.2	3	2	2	2	1	1	1	2	1
AMON	28.5	28.5	3	2	2	2	1	3	3	2	1
LCRE	15.6	20.9	2	2	2	2	1	1	1	2	1
LGEB	16.0	21.1	3	1	1	2	1	1	1	2	1
LCOM	12.8	16.6	3	1	1	2	1	1	1	2	1
LPAR	37.1	37.1	3	4	2	2	2	2	3	2	2
LAR3	35.9	35.9	2	2	2	2	4	3	3	2	1
LMAR	14.8	23.6	1	2	2	2	4	1	1	2	1
LSIL	18.4	23.2	2	2	2	1	4	1	1	2	1
LMA1	14.9	23.1	2	2	2	2	4	1	1	2	1
LBIF	16.1	24.0	2	2	2	1	4	1	1	2	1
LTET	20.8	28.5	1	2	2	2	4	1	1	2	1
LDE2	22.7	26.3	3	2	2	1	4	1	1	2	2
LWEI	9.8	15.0	1	1	1	2	1	1	1	2	1
LWRI	28.8	28.8	3	2	2	2	4	2	3	2	2
LARB	16.4	22.2	3	2	2	2	4	1	1	2	1
LUNI	19.8	20.0	2	2	2	2	4	2	1	2	1
LULI	12.8	20.5	1	2	2	2	4	1	1	2	1
LTO1	17.2	24.8	2	2	2	1	4	1	1	2	1
LTE1	9.2	14.5	1	1	1	2	1	1	1	2	1
LSU1	17.0	22.2	2	2	2	2	5	1	2	1	1
LST2	33.3	33.3	2	4	2	2	2	2	3	2	2
LST1	20.1	22.0	2	3	2	1	4	2	1	2	1
LSC1	30.5	30.5	2	3	2	2	4	3	2	1	2
LSAL	24.9	26.0	2	2	2	2	4	2	2	2	2
LPA1	9.0	14.0	2	1	1	2	1	1	1	2	1
LPAZ	12.6	17.4	2	2	2	2	1	1	1	2	1
LPI1	18.4	18.7	2	2	2	2	1	2	2	1	1
LPUI	24.3	24.8	2	2	2	2	4	2	2	1	1
LMI2	23.9	24.4	2	2	2	2	4	2	2	1	1
LLO1	32.3	32.9	2	3	2	2	4	2	2	2	2
LLEC	23.8	24.2	2	2	2	2	1	2	2	2	1
LJUI	26.3	26.9	2	2	2	2	4	1	1	2	1
LJAC	8.4	15.8	1	1	1	2	4	1	1	2	1
LHIS	12.2	18.6	1	1	1	2	1	1	1	2	1
LHEL	20.6	20.6	2	2	2	2	4	2	2	1	1
LGR3	31.9	31.3	2	3	2	2	4	3	2	1	2
LGLA	16.3	19.7	1	1	1	2	1	1	1	2	1
LGEI	17.2	23.2	2	2	2	2	4	1	1	2	1
LFO1	23.5	24.7	2	3	2	1	4	2	1	1	1
LFO2	23.7	24.6	2	3	2	1	4	2	1	1	1

OTU'S	1	2	3	4	5	6	7	8	9	10	11
LEDU	12.5	19.0	1	1	1	2	1	1	1	2	1
LED1	13.0	19.0	1	1	1	2	1	1	1	2	1
LDO1	27.2	27.2	2	2	2	2	4	2	2	1	1
LDIV	10.5	14.6	1	2	1	2	4	1	1	2	1
LDE2	22.5	23.5	1	1	2	2	1	2	2	1	1
LDE3	22.7	23.9	1	1	2	2	1	2	2	1	1
LCYT	10.0	14.9	2	1	1	2	1	1	1	2	1
LCR1	12.8	18.6	2	1	1	2	4	1	1	2	1
LCO1	12.6	19.1	1	1	1	2	1	1	1	2	1
LPU2	23.3	23.0	2	2	2	2	4	2	2	1	1
DSUF	23.1	24.1	2	2	2	2	4	2	1	2	1
DREC	17.7	23.8	2	2	2	2	4	1	1	2	1
DHER	21.3	25.7	2	2	2	2	4	1	1	2	1
DHIR	26.0	32.2	2	2	2	2	4	1	1	2	1
DGER	22.0	25.0	2	2	2	2	4	1	1	2	1
LGRQ	28.1	29.1	2	3	2	2	1	2	2	1	1
LHIQ	12.4	16.5	2	1	1	2	1	1	1	2	1
LHUQ	24.0	26.8	1	3	2	2	5	1	2	1	1

([1]) List of Characters and How They Were Assessed

1 = Mean width: based on 20 grains per sample.
2 = Mean length: based on 20 grains per sample.
3 = Polar area index: 1 = 0.250 - 0.400; 2 = 0.401 - 0.650; 3 = 0.651 - 0.850.
4 = Exine diameter: 1 = 0.5 um; 2 = 1.0 um; 3 = 1.5 um; 4 = 2.0 um.
5 = Distinctness of ektexine - endexine: 1 = indistinct; 2 = distinct.
6 = Pore shape: 1 = lalongate ora; 2 = circular ora.
7 = Sculpturing type: 1 = psilate; 2 = verrucate. 3 = reticulate; 4 = rugulate; 5 = striate.
8 = Shape: 1 = prolate; 2 = spheroidal; 3 = rectangular to square in outline; 4 = oblate.
9 = Aperture number: 1 = 3; 2 = 4; 3 = 5 or more.
10 = Pore morphology: 1 = vestibulate; 2 = non-vestibulate.
11 = Furrow morphology: 1 = non-ornamented; 2 = ornamented.

APPENDIX III

TABLE OF MEAN VALUES OF MAJOR LOTEAE GROUPS (CONSOLIDATED FROM ORIGINAL OTU'S)

OTU'S	L	W	PAI	EXINE DIAMETER	ENDEXINE EXTEXINE VISIBILITY	PORE SPADE SHAPED CIRCLE SHAPED	SCULPTURING 1	SCULPTURING 2	SCULPTURING 3	SCULPTURING 4	SCULPTURING 5	PORE NO.	PORE VESTIBULATE NON-VESTIBULATE
HOSL.	217	245	194	244	194	167	0555	0000	0167	0278	0000	1000	167
SIML.	287	291	197	269	193	193	0276	0655	0000	0069	0000	2350	124
SYRL.	237	237	195	265	200	185	0800	0000	0000	0200	0000	2050	115
ERYL.	149	178	209	182	164	200	1000	0000	0000	0000	0000	1000	200
AOML.	227	239	200	239	200	185	0230	0000	0000	0308	0385	1940	128
LOTU	142	186	127	133	127	200	0870	0000	0000	0130	0000	1000	100
LOTE	130	184	233	168	168	200	1000	0000	0000	0000	0000	1000	100
TETL.	160	228	183	200	183	167	0000	0000	0000	1000	0000	1000	200
DORL.	223	261	188	188	200	200	0375	0625	0000	0000	0000	1000	100
PEDL.	124	178	100	100	100	200	0500	0000	0000	0500	0000	1000	200
KROL.	128	190	100	100	100	200	1000	0000	0000	0000	0000	1000	200
ANTL.	319	357	275	200	200	200	1000	0000	0000	0000	0000	1500	200
CODL.	342	373	200	200	200	200	0000	1000	0000	0000	0000	1000	100
LABY	233	230	200	200	200	200	1000	0000	0000	0000	0000	1000	200

HOSL = HOSACKIA, SIML = SIMPETERIA, SYRL = SYRMATIUM, ERYL = ERYTHROLOTUS, AOML = AOMISPON, LOTU = LOTUS, LOTE = LOTEAE,
TETL = TETRAGONOLOBUS, DORL = DORYCNIUM, PEDL = PEDROSIA, KROL = KROKERIA, ANTL = ANTHYLLIS, CODL = CYTISOPSIS, LABY = VERMIFUGE.
Sculpturing - 1 = Psilate, 2 = verrucate, 3 = reticulate, 4 = rugulate, 5 = striate

APPENDIX IV

TAXA, THEIR SYNONYMS AND OTU CODING (1)

1. Anthyllis montana L. AMON
2. Anthyllis spruneri (Boiss.) Beck = A. vulneraria L. var spruneri ASPU
3. Anthyllis vulneraria L. ssp. maura Beck AVUL
4. Anthyllis vulneraria L. ssp. spruneri (Boiss.) Bornm. AVUI
5. Coronilla emerus L. CEME
6. Coronilla minima L. non Jacq. CMIN
7. Coronilla scorpioides (L.) Koch CSCO
8. Coronilla varia L. CVAR
9. Cytisopsis dorycnifolia Jaub. et Spach CDOR
10. Cytisopsis pseudocytisus (Boiss.) Fertig
11. Dorycnium amani Zohary LARM
12. Dorycnium axilliflorum- Huber-Morath. LAXI
13. Dorycnium germanicum Vill. = D. pentaphyllum ssp. germanicum DGER
14. Dorycnium herbaceum Vill. = D. pentaphyllum ssp. herbaceum DHER
15. Dorycnium hirsutum (L.) Ser. DHIR
16. Dorycnium pentaphyllum Scop. spp.herbaceum (Vill.) Gams
17. Dorycnium pentaphyllum Scop. spp. herbaceum (Vill.) Rouy
18. Dorycnium pentaphyllum Scop. var. pentaphyllum
19. Dorycnium rectum (L.) Ser. DREC, LREC
20. Hammatolobium lotoides Fenzl HALO
21. Hippocrepis ciliata Willd.

22. Hippocrepis comosa L. non Lucé, nec Willk. ex Scheele HICO

23. Hymenocarpus circinnatus (L.) Savi HYCI, LHYM

24. Lotus aboriginus Jepson LARB

25. Lotus agrophyllus (Gray) Greene LARZ

26. Lotus agrophyllus (Gray) Greene var. agrophyllus LARI

27. Lotus americanus (Nutt.) Bisch. non Vell. = Lotus purshianus (Benth.) Clements et Clements var. purshianus LPUR

28. Lotus angustifolius Mocino et Sesse ex G. Don LANG

29. Lotus angustissimus L. LANI

30. L. arabicus L. non Bourg ex Coss

31. Lotus argensis Coville = L. rigidus

32. Lotus argyraeus (Greene) Greene LARG, LARB

33. Lotus australis Andrews LAUS

34. Lotus benthamii Greene LBEN

35. Lotus biolettii Greene = L. junceus var. biolettii

36. Lotus borzii Pitard

37. Lotus bryantii (Brandegee) Ottley LBRI, LBRY

38. L. campylocladus Webb et Berth.

39. Lotus castellanus Boiss. et Reuter = L. subbiflorus Lag. ssp. castellanus

40. Lotus cedrosensis Greene LCED

41. Lotus chihuahuanus (Wats.) Greene LCHl, LCHI

42. Lotus ciliatus Koch = L. angustissimus L.

43. L. coccineus Schlecht. non Vell.

44. Lotus collinus (Boiss.) Heldr.

45. Lotus commutatus Guss. = L. creticus L. LCOM

46. Lotus conimbricensis Brot. LCON

47. Lotus corniculatus L. LCO1, LCOR

48. Lotus crassifolius (Benth.) Greene

49. Lotus creticus L. non Viv., nec Sibth. ex Sibth. et Smith LCR1, LCRE

50. Lotus cruentus Court = L. coccineus Schlecht. LCRU

51. Lotus cupreus Greene = L. oblongifolius var. cupreus

52. Lotus cytisoides L. LCYT

53. Lotus davidsonii Greene = L. nevadensis var. davidsonii LDAV

54. Lotus dendroideus (Greene) Greene LDEN

55. Lotus dendroideus (Greene) Greene var. traskiae (Eastwood ex Noddin) Isley LDE3, LDE2.

56. Lotus denticulatus (Drew) Greene LDE1, LDE3, LDE4

57. Lotus discolor E.H.F. Meyer LDIS

58. Lotus divaricatus Boiss. non Solander ex Buch = L. macrotrichus Boiss. LDIV

59. Lotus douglasii Greene = L. nevadensis var. douglasii LDO1

60. Lotus douglasii Greene var. congestus Ottley = L. nevadensis var. douglasii

61. Lotus douglasii Greene var. douglasii = L. nevadensis var. douglasii

62. Lotus douglasii Greene var. nevadensis Ottley = L. nevadensis var. douglasii LDOV

63. Lotus edulis L. LDE1, LEDU

64. Lotus eriophorus Greene = L. heermannii var. orbicularis LER1

65. Lotus formosissimus Greene LFOR, LFO2, LFO1

66. Lotus gebelia Venenat LGE1, LGEB

67. Lotus glaucus Dryander ex Aiton non Sieber ex Reichenb. LGLA

68. Lotus goetzei Harms LGOE

69. Lotus grandiflorus (Benth.) Greene LGR3

70. Lotus grandiflorus (Benth.) Greene var. grandiflorus

71. Lotus grandiflorus (Benth.) Greene var. mutabilis (Gray) Ottley = L. grandiflorus var. grandiflorus LGRA, LGRQ

72. Lotus greenei (Wooton et Standl.) Ottley ex Kearney et Peebles LGR2, LGRE

73. Lotus halophilus Boiss. et Spruner ex Boiss. var. halophilus LHAl

74. Lotus halophilus Boiss. et Spruner ex Boiss. var. macranthus (Boiss.) Heyn

75. Lotus hamatus Greene LHAM

76. Lotus haydonii (Orcutt) Greene LHAY

77. Lotus heermannii (Durand et Hilgard) Greene LHER

78. Lotus heermannii (Durand et Hilgard) Greene var. orbicularis (Gray) Isley

79. Lotus helleri Britt. = Lotus purshianus var. helleri LHEL

80. Lotus hispidus Desf. = Lotus subbiflorus Lag. spp. subbiflorus LHIS, LHIQ

81. Lotus humistratus Greene LHUQ

82. Lotus incanus (Torr.) Greene non Dougl. ex Hook.

83. Lotus jacobaeus L. LJAC

84. Lotus judaicus Boiss. = L. cytisoides L. LJUD

85. Lotus junceus (Benth.) Greene

86. Lotus junceus (Benth.) Greene var. biolettii (Greene) Ottley LJUl, LJUN

87. L. lanuginosus Ventenat LLAN

88. Lotus leucophaeus Greene = L. grandiflorus var. grandiflorus LLEC

89. Lotus leucophyllus Greene = L. procumbens

90. Lotus longibracheatus Rydb. = L. oroboides var. nummaralis LLOI, LLON

91. Lotus macranthus Boiss.

92. Lotus macrotrichus Boiss.

93. Lotus micranthus Benth. LMI2, LMIC, LMI1

94. Lotus mearnsii (Britton) Greene LMEA

95. Lotus namulensis Brand LNAM

96. Lotus neomexicanus Greene = L. oroboides var. nanus

97. L. nevadensis (Wats.) Greene LNEV, LNE1

98. L. nevadensis (Wats.) Greene var. davidsonii (Greene) Isley

99. Lotus nevadensis (Wats.) Greene var. douglasii (Greene) Ottley

100. Lotus nudatus Greene LNUD

101. Lotus nuttallianus Greene LNUT

102. Lotus oblongifolius (Benth.) Greene var. cupreus (Greene) Ottley LOB3

103. Lotus oblongifolius (Benth.) Greene var. nevadensis (Gray) Munh = Lotus oblongifolius (Benth.) Greene var. oblongifolius LOBL

104. Lotus oblongifolius (Benth.) Greene var. oblongifolius LOB1

105. Lotus oblongifolius (Benth.) Greene var. torreyi (Gray) Ottley = Lotus oblongifolius (Benth.) Greene var. oblongifolius LOB2

106. Lotus ornithopodioides L. LORN

107. Lotus oroboides (Humboldt et al.) Ottley ex Kearney et Peebles LOR1, LORO

108. Lotus oroboides (Humboldt et al.) Ottley ex Kearney et Peebles var. nanus (Gray) Isley

109. Lotus oroboides (Humboldt et al.) Ottley ex Kearney et Peebles var. nummaralis (Jones) Isley

110. Lotus oroboides (Humboldt et al.) Ottley ex Kearney et Peebles var. oroboides

111. Lotus palustris Willd. LAP1, LPAL

112. L. parviflorus Desf. LPAR, LPAZ

113. Lotus pedunculatus Cav.

114. Lotus peregrinus L. non Burm. f. LPER

115. Lotus pinnatus Hook LPIN, LPI1,

116. Lotus plebeius (Brandegee) Barnaby

117. Lotus procumbens (Greene) Greene LPRO

118. Lotus puberulus (Benth.) Greene = L. oroboides var. oroboides LPUB

119. Lotus purshianus (Benth.) Clements et Clements LPU2, LPU1

120. Lotus purshianus (Benth.) Clements et Clements var. helleri (Britt.) Isley

121. Lotus purshianus (Benth.) Clements et Clements var. purshianus LPU2

122. Lotus rigidus (Benth.) Greene LRIG

123. Lotus salsuginosus Greene var. brevivexillus Ottley LSAL

124. Lotus scoparius (Nutt. ex T. et G.) Ottley LSC1

125. Lotus scoparius (Nutt. ex T. et G.) Ottley var. brevialatus Ottley LSCO

126. Lotus scoparius (Nutt. ex T. et G.) Ottley var. scoparius

127. Lotus sessifolius DC.

128. Lotus stipularis (Benth.) Greene LSTI

129. Lotus strigosus (Nutt. ex T. et G.) Greene LST1, LST2, LSTR

130. Lotus strigosus (Nutt. ex T.& et G.) Greene var. tomentellus (Greene) Isley LTOM

131. Lotus subbiflorous Lag.

132. Lotus subbiflorous Lag. spp. castellanus (Boiss. et Reuter) P.W. Ball

133. Lotus subbiflorus Lag. spp. subbiflorus

134. Lotus subpinnatus Lagasca = L. wranglianus Fisch. et Meyer LSUB, LSU1

135. Lotus subpinnatus Lagasca var. wranglianus (Fisch. et Meyer) Jepson = L. wranglianus

136. Lotus tenuis Waldst. et Kit. ex Willd. LTE1, LTEN

137. Lotus torreyi (Gray) Greene = Lotus oblongifolius var. oblongifolius LTO1, LTOR

138. Lotus uliginosus Schkuhr LULI

139. Lotus unifoliatus Hook. = Lotus purshianus var. purshianus LUNI

140. Lotus utahensis Ottley LUTA

141. Lotus varius Boiss.

142. Lotus watsonii (Vasey et Rose) Greene LWAT

143. Lotus weilleri Maire LWE1

144. Lotus wranglianus Fisch. et Meyer

145. Lotus wrightii (Gray) Greene LWRI, LWR1

146. Lotus yollaboliensis Munz LYOL

147. Ornithopus compressus L. non Sieber ex Stend. OCOM

148. Ornithopus perpusillus L. OPUR

149. Ornithopus pinnatus (P. Miller) Druce

150. Scoparius muricatus L. SMUR

151. Scoparius muricatus L. var. subvillosus (L.) Fiori ex Fiori et Paol.

152. Tetragonolobus biflorus (Desr.) Ser. LBIF

153. Tetragonolobus maritimus (L.) Roth LMA1, LMAR

154. Tetragonolobus purpureus Moench.

155. Tetragonolobus purpureus Moench. var. palaestinus (Boiss.) Post LPLA

156. Vermifrux abyssinica (A. Rich.) J.G. Gillett LABY

(1) Names not coded were examined under their varieties or synonyms (see Appendix V for coding synonyms). Taxa examined for SEM are included in this listing. They do not form part of the numerical analysis.

APPENDIX V

CODING SYNONYMS

ASPU = Anthyllis vulneraria var. spruneri

DGER = Dorycnium pentaphyllum ssp. germanicum

LPU2 = Lotus purshianus

LJUN = Lotus junceus var. biolettii

LCOM = Lotus creticus

LCRU = Lotus coccineus

LOB3 = Lotus oblongifolius var. cupreus

LDAV = Lotus nevadensis var. davidsonii

LDIV = Lotus macrotrichus

LDO1 = Lotus nevadensis var. douglasii

LDOU = Lotus nevadensis var. douglasii

LERI = Lotus heermannii

LGRA, LGRQ = Lotus grandiflorus var. grandiflorus

LHEL = Lotus purshianus var. helleri

LHIS, LHIQ = Lotus subbiflorus spp. subbiflorus

LJUD = Lotus cytisiodes

LLDN, LLO1 = Lotus oroboides var. nummularis

LOBL, LOB1 = Lotus oblongifolius var. oblongifolius

LPUB = Lotus oroboides

LSU1, LSUB = Lotus wranglianus

LTOR, LTO1 = Lotus oblongifolius var. oblongifolius

LUNI = Lotus purshianus var. purshianus

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