

PHYLOGENY AND CLASSIFICATION OF PAKISTANI LEGUMES

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Abstract

The latest subfamilial classification of the legumes is reviewed, and the genera of Pakistani legumes are arranged according to it. The tribal organization of the subfamilies is summarized and discussed for Pakistan. The Pakistani legume flora is compared with that of the central Brazilian savannas, and a correspondence between the Pakistani legume flora and the climate and vegetation of Pakistan is noted.

Introduction

A new subfamilial classification of legumes was presented in 1978 at the first International Legume Conference, Royal Botanic Gardens, Kew, England, by 28 of the leading taxonomists actively working on legume systematics. The foundations of this classification were laid down by Bentham (1865) and modified by Hutchinson (1964). If Bentham's subtribes are considered together with his individual tribes, they are strikingly similar in composition to the tribes accepted in the new classification. Hutchinson's modified system has a lesser degree of similarity.

The final decisions on the new classification both supported many existing dispositions and made some new fundamental realignments. The majority opinion favored the maintenance of the grouping as one family, but a few still support its division into two or three families (El-Gazzar & El-Fiki, 1977; El-Gazzar, 1981). Between subfamilies the most significant decision was the firm placement of tribe Swartzieae in a basal position within subfamily Papilionoideae. This position is supported by data from wood anatomy, nodulation productivity, and chemistry, as well as morphology. The most apparent change has been the drastic reordering of taxa. This was done to reflect the idea that the most primitive member of a taxon should appear first and the most advanced last in a linear sequence. As a consequence, the subfamilies are presented in the following order: Caesalpinioideae, Mimosoideae, and Papilionoideae.

Sources and Methods

The legume treatments in the *Flora of Pakistan* (Ali, 1973, 1973a, 1977) were surveyed to compile a list of Pakistani genera and species. The list was modified to reflect current taxonomic opinions (Polhill & Raven, 1981; Irwin & Barneby, 1982; Podlech,

1983; Geesink, 1984; R.C. Barneby, pers. comm.), and the total number of species reported for each genus was added (Gunn, 1983). The list was then compared to worldwide (Allen & Allen, 1981; Halliday, 1984) and Pakistani (Athar & Mahmood, 1978, 1980, 1985; Mahmood, 1983, 1984) reports of legume nodulation or non-nodulation. The results of these surveys are presented in Table 1.

One hundred and six legume genera are known from Pakistan, of which 68 have one or more native species, and 539 legume species are reported to occur in Pakistan, of which 426 are native.

Discussion

1. Subfamily *Caesalpinioideae*

There are three lines of evolution in *Caesalpinioideae* without any surviving links between them, see Fig. 1. The basal groups for the three lines are: 1) the *Gleditsia* group of tribe *Caesalpinieae*, 2) subtribe *Ceratoninae* of tribe *Cassieae*, and 3) subtribe *Cercidinae* of tribe *Cercideae*. *Gleditsia* and *Gymnocladus*, composing group *Gleditsia*, possess a number of primitive characters, including functionally unisexual flowers, scarcely differentiated tepals, bilobate stigma, and fruit dehiscing like a follicle. These genera are basal in the primary radiation that gave rise to the *Mimosoideae* and *Papilionoideae* (Polhill et al., 1981; Corby et al., 1983).

Ceratonia, the sole member of subtribe *Ceratoninae*, has unisexual flowers lacking petals and with an exposed disc producing nectar. This genus is placed at the base of the radiation whose culmination is the assemblage of *Cassia*, s.l. (Polhill et al., 1981).

Cercideae are sharply distinguished from the rest of the family by their calyx tube and well-developed corolla, bilobed leaves with palmate venation, and lens of the seed above the micropyle, a character combination found nowhere else in the legumes. Also, *Cercis* is the only genus in the family to retain the base chromosome number $n = 7$ (Goldblatt, 1981). This restricted radiation has culminated in the genus *Bauhinia* (Polhill et al., 1981).

Tribe *Caesalpinieae* is first in the linear sequence (Table 2) because *Gleditsia* and *Gymnocladus*, considered the most primitive genera in the family, are both members of the tribe. In Pakistan, only two species of *Caesalpinia* are native out of 100 species in the genus (Table 1).

The next tribe is *Cassieae*. This radiation has led to *Cassia*, s.l. In Pakistan, it is represented only by native members of subtribe *Cassiinae*, the most advanced element in the tribe. *Cassia*, s.s., with 30 species, has but a single native species; *Senna*, a genus

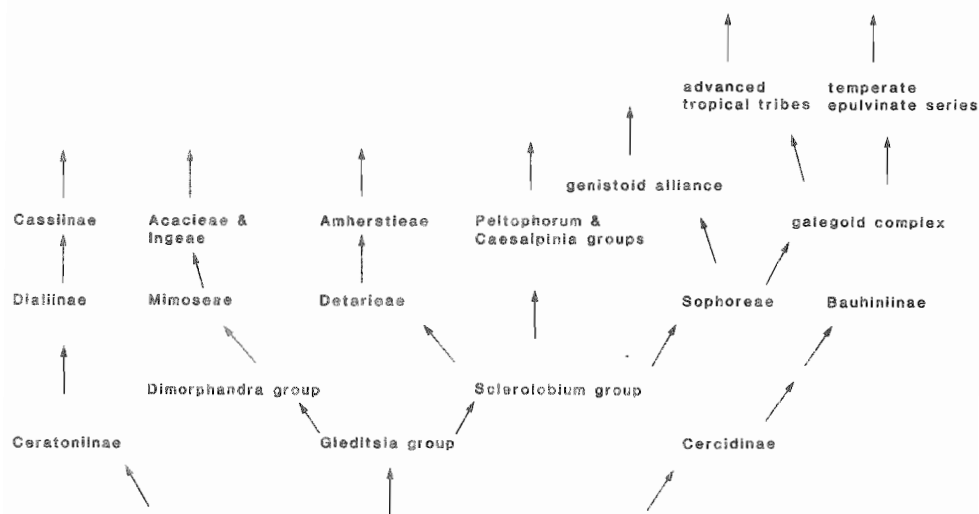


Fig. 1. The main evolutionary radiations in the legumes, adapted from Polhill et al. (1981).

of 240 species, has only six native species; and *Chamaecrista*, in excess of 250 species, has but four native species. This complex has been treated as a single genus, *Cassia*, s.l., but Irwin and Barneby's recent generic reorganization (1982), based on floral morphology, is supported by the presence or absence of nodules. *Cassia*, s.s. and *Senna* are non-nodulators, and *Chamaecrista* is a nodulator.

The last tribe in linear order with native species in Pakistan is Cercideae. This distinctive group is represented by five native species of *Bauhinia*. *Bauhinia*, with 250 species, is reported to have 26 non-nodulating species and only one nodulator.

Caesalpinioideae has slightly more than 1,900 species, approximately 11% of the known legume species. Only 18 of these are native to Pakistan, that is 4% of the Pakistani legume flora. The origins of this subfamily were probably in tropical and subtropical forests (Polhill et al., 1981). They have persisted in these habitats and have penetrated only feebly into more temperate ones. The low penetration of the subfamily into the Pakistani legume flora points to the narrowness of their habitat preferences and the scarcity of wet tropical and subtropical flora in Pakistan.

2. Subfamily Mimosoidae

Mimosoideae with approximately one-third as many genera and 50% more species than Caesalpinioideae is subdivided in a simpler manner, see Fig. 1. There are three principal groups, tribes Mimoseae, Acaciae, and Ingeae (Elias, 1981; Table 3). Mimoseae

Table 1. Pakistani genera of Leguminosae with their total number of species and the number in Pakistan, with the numbers of reported positive or negative nodulators world-wide and in Pakistan, and with their habit in Pakistan.

Genus	Number of Species		Nodulation Reports							Habit*
	World	Pakistan	World		Pakistan					
			Nat.	Intro.	Pos.	Neg.	Pos.	Neg.	Pos.	
<i>Abrus</i> Adans.	17	1	0	5	—	1	—	—	—	V
<i>Acacia</i> Mill.	1,200	10	16	200	11	4	—	14	—	STV
<i>Adenanthera</i> L.	8	0	1	1	2	—	—	—	1	T
<i>Aeschynomene</i> L.	150	2	0	44	—	2	—	—	—	S
<i>Albizia</i> Durazz.	150	4	3	32	—	4	—	2	—	T
<i>Alhagi</i> Adans.	3	1	0	1	—	1	—	—	—	S
<i>Alysicarpus</i> Desv.	25	8	0	13	—	7	—	—	—	H
<i>Amorpha</i> L.	15	0	1	7	—	—	—	1	—	S
<i>Arachis</i> L.	22	0	1	10	—	—	—	1	—	H
<i>Argyrobium</i> Eckl. & Zeyh.	70	3	0	25	—	2	—	—	—	H
<i>Astracantha</i> Podl.	250	1	0	1	—	—	—	—	—	HS
<i>Astragalus</i> L.	1,750	133	0	95	8	5	—	—	—	HS
<i>Bauhinia</i> L.	250	5	3	1	26	—	3	—	2	STV
<i>Butea</i> Roxb. ex Willd.	4	1	0	—	1	—	1	—	—	T
<i>Caesalpinia</i> L.	100	2	5	—	15	—	2	—	2	STV
<i>Cajanus</i> DC.	37	3	1	5	—	2	—	1	—	HSV
<i>Calliandra</i> Benth.	200	0	3	12	3	—	—	1	—	S
<i>Campylotropis</i> Bunge	65	3	0	—	—	—	—	—	—	S
<i>Canavalia</i> DC.	50	0	1	8	—	—	—	1	—	V
<i>Caragana</i> Fabr.	80	11	0	12	—	2	—	—	—	S
<i>Cassia</i> L., s.s.	30	1	3	1	5	—	1	—	2	T
<i>Castanospermum</i> A. Cunn.	1	0	1	—	1	—	—	—	1	T
<i>Ceratonia</i> L.	2	0	1	—	2	—	—	—	1	T
<i>Cercis</i> L.	6	0	1	—	—	2	—	—	1	ST
<i>Chamaecrista</i> (L.) Moench	250	4	0	38	1	3	—	—	—	HS
<i>Chesneya</i> Lindl. ex Endl.	20	5	0	—	—	—	—	—	—	H
<i>Cicer</i> L.	40	3	1	2	—	1	—	—	—	H
<i>Clitoria</i> L.	70	0	1	8	—	—	—	1	—	V
<i>Colutea</i> L.	28	3	0	3	—	—	—	—	—	S
<i>Coronilla</i> L.	20	0	1	12	—	—	—	1	—	H
<i>Crotalaria</i> L.	600	10	2	145	—	4	—	2	—	HS
<i>Cullen</i> Medik.	35	1	0	7	—	1	—	—	—	H
<i>Cyamopsis</i> DC.	3	1	0	1	—	1	—	—	—	H
<i>Dalbergia</i> L. f.	100	1	2	18	—	1	—	1	—	T
<i>Delonix</i> Rafin.	10	0	2	—	2	—	—	—	2	T
<i>Derris</i> Lour.	60	0	1	5	—	—	—	1	—	S
<i>Desmanthus</i> Willd.	25	0	1	5	—	—	—	1	—	S
<i>Desmodium</i> Desv.	300	10	1	78	—	7	—	—	—	HST
<i>Dichrostachys</i> (DC.) Wight & Arn.	12	0	1	3	—	—	—	1	—	S

<i>Dumasia</i> DC.	8	1	0	2	-	1	-	-	-	V
<i>Ebenus</i> L.	20	1	0	-	-	-	-	-	-	S
<i>Erythrina</i> L.	108	2	1	27	-	-	-	2	-	ST
<i>Flemingia</i> Roxb. ex Ait. f.	30	5	0	5	-	3	-	-	-	S
<i>Galega</i> L.	6	1	0	5	-	1	-	-	-	H
<i>Gleditsia</i> L.	14	0	2	-	5	-	-	-	2	T
<i>Glycine</i> Willd.	9	0	1	6	-	-	-	1	-	H
<i>Glycyrrhiza</i> L.	20	3	0	4	-	1	-	-	-	HS
<i>Gueldenstaedtia</i> Fisch.	10	1	0	-	-	-	-	-	-	H
<i>Haematoxylum</i> L.	3	0	1	-	1	-	-	-	1	ST
<i>Hardwickia</i> Roxb.	1	0	1	1	-	-	-	-	-	T
<i>Hedysarum</i> L.	100	8	0	11	-	1	-	-	-	H
<i>Hippocrepis</i> L.	21	1	0	4	-	-	-	-	-	H
<i>Indigofera</i> L.	700	24	0	194	3	10	-	-	-	HS
<i>Indoptadenia</i> Brenan	1	0	1	-	-	-	-	-	-	T
<i>Lablab</i> Adans.	1	1	0	1	-	1	-	-	-	HV
<i>Laburnum</i> Fabr.	2	0	1	4	-	-	-	1	-	T
<i>Lathyrus</i> L.	150	9	1	47	-	8	-	1	-	HV
<i>Lens</i> Mill.	5	0	1	2	-	-	-	1	-	H
<i>Lespedeza</i> Mich.	40	5	0	30	-	1	-	-	-	S
<i>Leucaena</i> Benth.	40	0	1	10	-	-	-	1	-	ST
<i>Lotononis</i> (DC.) Eckl. & Zeyh.	100	1	0	31	-	1	-	-	-	H
<i>Lotus</i> L.	100	4	0	58	-	1	-	-	-	H
<i>Lupinus</i> L.	200	0	3	56	-	-	-	3	-	HS
<i>Macroptilium</i> (Benth.) Urban	20	0	1	2	-	-	-	1	-	H
<i>Macrotyloma</i> (Wight & Arn.) Verdc.	24	1	0	11	-	1	-	-	-	HV
<i>Medicago</i> L.	50	8	0	40	-	7	-	-	-	H
<i>Melilotus</i> Mill.	20	3	1	16	-	3	-	1	-	H
<i>Millettia</i> Wight & Arn.	100	0	3	6	-	-	-	1	-	TV
<i>Mimosa</i> L.	400	2	1	22	3	1	-	1	-	S
<i>Mucuna</i> Adans.	100	2	0	17	-	2	-	-	-	V
<i>Onobrychis</i> Mill.	130	9	0	10	-	1	-	-	-	H
<i>Ononis</i> L.	75	2	0	18	-	1	-	-	-	HS
<i>Oxytropis</i> DC.	300	21	0	22	-	2	-	-	-	H
<i>Paracalyx</i> Ali	6	0	1	-	-	-	-	-	-	V
<i>Parkinsonia</i> L.	15	0	1	-	2	-	-	-	1	ST
<i>Peltophorum</i> (Vogel) Benth.	7	0	1	-	2	-	-	-	1	T
<i>Phaseolus</i> L.	50	0	3	21	-	-	-	3	-	V
<i>Pisum</i> L.	2	0	1	2	-	-	-	1	-	H
<i>Pithecellobium</i> Mart.	20	0	1	13	1	-	-	1	-	T
<i>Prosopis</i> L.	44	2	2	6	3	1	-	2	-	ST
<i>Psophocarpus</i> DC.	20	0	1	5	-	-	-	1	-	V
<i>Psoralea</i> L.	20	2	0	25	-	-	-	-	-	HS
<i>Pueraria</i> DC.	20	1	1	2	-	-	-	1	-	V
<i>Rhynchosia</i> Lour.	200	7	0	58	-	3	-	-	-	HSV
<i>Robinia</i> L.	10	0	1	6	-	-	-	1	-	T
<i>Saraca</i> L.	8	0	1	1	4	-	-	-	1	T
<i>Schotia</i> Jacq.	4	0	1	-	3	-	-	-	1	T

Table 1. (Cont'd.)

Genus	Number of Species		Nodulation Reports							Habit*
	World	Pakistan	World		Pakistan					
			Nat.	Intro.	Pos.	Neg.	Native	Introduced		
				Pos.	Neg.	Pos.	Neg.	Pos.	Neg.	
<i>Senna</i> Mill.	240	6	9	4	31	--	6	1	7	HST
<i>Sesbania</i> Scop.	50	3	1	34	--	3	--	1	--	HST
<i>Shutteria</i> Wight & Arn.	5	1	0	1	--	--	--	--	--	V
<i>Smithia</i> Ait.	30	1	0	12	--	3	--	--	--	H
<i>Sophora</i> L.	45	3	3	16	1	1	--	2	--	ST
<i>Spartium</i> L.	1	0	1	1	--	--	--	1	--	S
<i>Stracheya</i> Benth.	1	1	0	--	--	--	--	--	--	H
<i>Tamarindus</i> L.	1	0	1	--	1	--	--	--	1	T
<i>Taverniera</i> DC.	10	4	0	2	--	2	--	--	--	HS
<i>Tephrosia</i> Pers.	400	9	1	95	--	4	--	1	--	HS
<i>Teramnus</i> P. Br.	8	1	0	7	--	--	--	--	--	V
<i>Thermopsis</i> R. Br.	23	2	0	5	--	--	--	--	--	H
<i>Trifolium</i> L.	250	4	4	142	--	4	--	4	--	H
<i>Trigonella</i> L.	80	16	0	20	--	8	--	--	--	H
<i>Uria</i> Desv.	20	1	0	2	--	--	--	--	--	S
<i>Vicia</i> L.	140	12	2	65	--	9	--	2	--	HV
<i>Vigna</i> Savi	150	7	1	46	--	6	--	1	--	HV
<i>Wisteria</i> Nutt.	6	0	1	8	--	--	--	1	--	V
<i>Zornia</i> J.F. Gmel.	80	1	0	12	--	1	--	--	--	H

*H = herb; S = shrub; T = tree; V = vine or climber.

is the most primitive of the three and shares various phenetic characters with more advanced members of Caesalpinoideae. It is separated from Acacieae and Ingeae by its staminal number of ten or less. The more advanced and closely related Acacieae and Ingeae are separated from each other only by the degree of connation exhibited by their filaments, free in Acacieae and united in Ingeae. There are two other tropical tribes, Parkieae with two genera, and Mimozygantheae with one, whose composition and placement are controversial; none of their members are found in Pakistan.

Mimoseae is represented in Pakistan by *Prosopis* with two native species and *Mimosa* also with two. Acacieae consists of the genus *Acacia* with 10 native species, and Ingeae is represented by *Albizia* with 4 native species.

Mimosoideae has slightly less than 3,000 species, approximately 17.5% of the known legume species. Only 18 of these species are native to Pakistan, that is 4% of the Pakistani legume flora. Again this subfamily, also predominately tropical, has not assumed a position in the Pakistani legumes commensurate with its overall size in relation to the legumes. This is surprising considering the size and broad diversity found in such genera as *Acacia* with 1,200 species and *Mimosa* with 400-450.

Table 2. Pakistani genera of subfamily Caesalpinioideae (Leguminosae) in systematic order and numbered according to Polhill & Raven (1981).

1. tribe	CAESALPINIEAE	3. tribe	CERCIDEAE
	1a. <i>Gleditsia</i> group		subtribe Cercidinae
1.2	<i>Gleditsia</i> Linnaeus*	3.1	<i>Cercis</i> Linnaeus*
	1d. <i>Peltophorum</i> group		subtribe Bauhiniinae
1.14	<i>Peltophorum</i> (Vogel) Bentham*	3.4	<i>Bauhinia</i> Linnaeus
1.18	<i>Delonix</i> Rafinesque*		
	1e. <i>Caesalpinia</i> group	4. tribe	DETARIEAE
1.25	<i>Caesalpinia</i> Linnaeus		4a. <i>Cynometra</i> group
1.34	<i>Haematoxylum</i> Linnaeus*	4.8	<i>Schotia</i> Jacquin*
1.35	<i>Parkinsonia</i> Linnaeus*		4b. <i>Hymenostegia</i> group
2. tribe	CASSIEAE	4.16	<i>Saraca</i> Linnaeus*
	2a. subtribe Ceratoniinae		4d. <i>Crudia</i> group
2.1	<i>Ceratonia</i> Linnaeus*	4.33	<i>Hardwickia</i> Roxburgh*
	2d. subtribe Cassiinae	5. tribe	AMHERSTIEAE
2.16	<i>Cassia</i> Linnaeus, s.s.		5c. <i>Amherstia</i> group
2.17	<i>Senna</i> Miller	5.18	<i>Tamarindus</i> Linnaeus*
2.18	<i>Chamaecrista</i> (Linnaeus) Moench		

*introduced.

3. Subfamily Papilionoideae

The Papilionoideae has twice as many genera and two and a half times as many species as the Caesalpinioideae and Mimosoideae together. They have been undergoing a geologically more recent and rapid generic evolution than the other two subfamilies. Consequently, the subfamily has a more complex and ramified existing radiation. Recently there has been an informal grouping of tribes into five main clusters: the tribes Sophoreae and Swartzieae, the galeoid complex, the genistoid alliance, the advanced tropical tribes, and the temperate epulvinate series, see Fig. 1 (Polhill et al., 1981; Polhill, 1981; Corby et al., 1983).

The Sophoreae group is a diverse basal element connecting the bulk of the Papilionoideae through the Swartzieae to the Caesalpinioideae. Swartzieae floral morphology is equal to that of Caesalpinioideae, but its wood anatomy, nodulation types, and chemistry are similar to those of Papilionoideae (Cowan, 1981; Polhill, 1981, 1981a; Polhill et al., 1981). The Swartzieae and Sophoreae groups comprise the papilionoid genera with free stamens. In Sophoreae, corolla and androecial structures vary from that typical of Caesalpinioideae to that typical of Papilionoideae with all intermediate stages present. No

Table 3. Pakistani genera of subfamily Mimosoideae (Leguminosae) in systematic order and numbered according to Polhill and Raven (1981).

3.	tribe	MOMOSEAE		
		3d. <i>Newtonia</i> group	3.34	<i>Dichrostachys</i> (de Candolle) Wight & Arnott*
3.5		<i>Indoptadenia</i> Brenan*		
		3e. <i>Adenantha</i> group	3.36	<i>Desmanthus</i> Willdenow*
3.8		<i>Adenantha</i> Linnaeus*		
		3h. <i>Prosopis</i> group	4.	tribe ACACIEAE
3.15		<i>Prosopis</i> Linnaeus	4.2	<i>Acacia</i> Miller
		3i. <i>Piptadenia</i> group		
3.27		<i>Mimosa</i> Linnaeus	5.	tribe INGEAE
		3k. <i>Leucaena</i> group	5.4	<i>Albizia</i> Durazzini
3.32		<i>Leucaena</i> Bentham*	5.7	<i>Calliandra</i> Bentham*
		3l. <i>Dichrostachys</i> group	5.8	<i>Pithecellobium</i> Martius*

*Introduced.

members of Swartzieae occur naturally in Pakistan, and only *Sophora* of Sophoreae is found there with three native species (Tables 1 and 4).

The huge galeoid complex is the central radiation through the subfamily. It is distinguished from the Sophoreae-Swartizeae by staminal fusion, presence of canavanine, and general stabilization of the base chromosome number at $X = 11$ or 10 in tropical woody members (Polhill et al., 1981; Corby et al., 1983). This group is scarcely represented in Pakistan only by *Dalbergia* and *Abrus*, each having one native species (Tables 1 and 4).

The genistoid alliance is a lateral group that has evolved in areas of Mediterranean climate throughout the world with two principal lines, one in the northern hemisphere and the other in the southern hemisphere (Polhill et al., 1981; Polhill, 1981; Corby et al., 1983). Many of the advanced characters found in other groups occur here, but the trends in these characters do not resemble those in the other groups. In Pakistan *Crotalaria*, with 10 native species, and *Lotononis* with one, of Crotalariaeae, *Thermopsis* with two of Thermopsidaeae, and *Argyrolobium* with three of Genisteeae, are found (Tables 1 and 4). Only *Crotalaria*, a very advanced genus within the group, has expanded in Pakistan, indicating that the area is probably not well suited to the group climatically.

The advanced tropical tribes forming the remainder of the pulvinate members of the subfamily are best arranged with the Millettieae, formerly known as Tephrosieae, as a core element and a series of advanced, principally tropical tribes, clustered about it. The entire group demonstrates strong tendencies towards increased floral specialization and variation and reduced variation in root nodules, leaves, inflorescences, fruits, seeds, and

Table 4. Pakistani genera of subfamily Papilionoideae (Leguminosae) in systematic order and numbered according to Polhill and Raven (1981).

2.	tribe SOPHOREAE	10.3	<i>Mucuna</i> Adanson
	2c. <i>Angylocalyx</i> group	10.4	<i>Butea</i> Roxburgh ex Willdenow
2.16	<i>Castanospermum</i> A. Cunningham*	10b.	subtribe Diocleinae
	2h. <i>Sophora</i> group	10.13	<i>Canavalia</i> de Candolle*
2.47	<i>Sophora</i> Linnaeus	10c.	subtribe Glycininae
		10.26	<i>Pueraria</i> de Candolle
		10.29	<i>Glycine</i> Willdenow*
4.	tribe DALBERGIEAE	10.30	<i>Teramnus</i> P. Browne
4.6	<i>Dalbergia</i> Linnaeus filius	10.35	<i>Shutteria</i> Wight & Arnott
		10.36	<i>Dumasia</i> de Candolle
5.	tribe ABREAE	10f.	subtribe Clitoriinae
5.1	<i>Abrus</i> Adanson	10.47	<i>Clitoria</i> Linnaeus*
		10g.	subtribe Phaseolinae
6.	tribe MILLETTIEAE	10.50	<i>Psophocarpus</i> de Candolle*
	<i>Derris</i> Loureiro*	10.60	<i>Lablab</i> Adanson
	<i>Millettia</i> Wight & Arnott*	10.64	<i>Macrotyloma</i> (Wight & Arnott) Verdcourt
	<i>Tephrosia</i> Persoon	10.65	<i>Vigna</i> Savi
	<i>Wisteria</i> Nuttall*	10.70	<i>Macroptilium</i> (Bentham) Urban*
7.	tribe ROBINIEAE	10.71	<i>Phaseolus</i> Linnaeus*
7.4	<i>Robinia</i> Linnaeus*	10h.	subtribe Cajaninae
7.20	<i>Sesbania</i> Scopoli	10.72	<i>Cajanus</i> de Candolle
		10.78	<i>Flemingia</i> Roxburgh ex W.T. Aiton
8.	tribe INDIGOFEREAE	10.81	<i>Rhynchosia</i> Loureiro
8.2	<i>Indigofera</i> Linnaeus	10.83	<i>Paracalyx</i> Ali*
8.4	<i>Cyamopsis</i> de Candolle		
		11.	tribe PSORALEEAE
9.	tribe DESMÓDIEAE	11.1	<i>Psoralea</i> Linnaeus
	subtribe Desmodiinae	11.4	<i>Cullen</i> Medikus
9.9	<i>Desmodium</i> Desvaux		
9.16	<i>Uraria</i> Desvaux	12.	tribe AMORPHEAE
9.19	<i>Alysicarpus</i> Desvaux	12.4	<i>Amorpha</i> Linnaeus*
	subtribe Lespedezinae		
9.24	<i>Campylotropis</i> Bunge	14.	tribe AESCHYNOMENEAE
9.25	<i>Lespedeza</i> Michaux	14b.	subtribe Aeschynomeninae
		14.8	<i>Aeschynomene</i> Linnaeus
10.	tribe PHASEOLEAE	14.11	<i>Smithia</i> W. Aiton
	10a. subtribe Erythrinae	14d.	subtribe Poirètiinae
10.1	<i>Erythrina</i> Linnaeus	14.20	<i>Zornia</i> J.F. Gmelin

	14e. subtribe Stylosanthinae	21. tribe VICIEAE
14.25	<i>Arachis</i> Linnaeus*	21.1 <i>Vicia</i> Linnaeus
		21.2 <i>Lathyrus</i> Linnaeus
16. tribe	GALEGEAE	21.3 <i>Lens</i> Miller*
	16a. subtribe Coluteinae	21.4 <i>Pisum</i> Linnaeus*
16.5	<i>Colutea</i> Linnaeus	
	16b. subtribe Astragalinae	22. tribe CICEREAE
16.11	<i>Caragana</i> Fabricius	22.1 <i>Cicer</i> Linnaeus
16.13	<i>Chesneya</i> Lindley ex Endlicher	
16.14	<i>Astragalus</i> Linnaeus	23. tribe TRIFOLIEAE
16.15	<i>Oxytropis</i> de Candolle	23.1 <i>Ononis</i> Linnaeus
16.17	<i>Gueldenstaedtia</i> Fischer	23.2 <i>Melilotus</i> Miller
16.18	<i>Alhagi</i> Adanson	23.4 <i>Trigonella</i> Linnaeus
	16c. subtribe Galeginae	23.6 <i>Medicago</i> Linnaeus
16.19	<i>Galega</i> Linnaeus	23.7 <i>Trifolium</i> Linnaeus
	16d. subtribe Glycyrrhizinae	
16.20	<i>Glycyrrhiza</i> Linnaeus	29. tribe CROTALARIEAE
		29.6 <i>Crotalaria</i> Linnaeus
18. tribe	HEDYSAREAE	29.8 <i>Lotononis</i> (de Candolle) Ecklon & Zeyher
18.2	<i>Hedysarum</i> Linnaeus	
18.3	<i>Taverniera</i> de Candolle	
18.4	<i>Stracheya</i> Bentham	31. tribe THERMOPSIDEAE
18.6	<i>Onobrychis</i> Miller	31.4 <i>Thermopsis</i> R. Brown
18.7	<i>Ebenus</i> Linnaeus	
		32. tribe GENISTEAE
19. tribe	LOTEAE	32a. subtribe Lupininae
19.4	<i>Lotus</i> Linnaeus	32.1 <i>Lupinus</i> Linnaeus*
		32b. subtribe Genitstinae
20. tribe	CORONILLEAE	32.2 <i>Argyrolobium</i> Ecklon & Zeyher
20.1	<i>Coronilla</i> Linnaeus*	32.4 <i>Laburnum</i> Fabricius*
20.2	<i>Hippocrepis</i> Linnaeus	32.14 <i>Spartium</i> Linnaeus*

*Introduced.

seedlings (Polhill et al. 1981; Corby et al, 1983). The Millettieae, represented only by *Tephrosia* with nine native species in Pakistan (Tables 1 and 4), present one of the more difficult problems of generic delimitation in the legumes. After intensive study (Geesink, 1981, 1984), it still can not be organized in a satisfactory phylogenetic manner. Of the advanced tribes surrounding it, six are native to Pakistan: Indigofereae, Desmodieae, Phaseoleae, Psoraleae, Robinieae, and Aeschynomeneae (Table 4). The first four are centered in the eastern hemisphere, with the understanding that Phaseoleae are pantropical, and the last two in the western himisphere. Robineae, represented in Pakistan by

Sesbania with three native species, and Aeschynomeneae, represented by *Aeschynomene*, *Smithia*, and *Zornia* with 2, 1, and 1 native species respectively (Table 1), are minor elements in the Pakistani legume flora (Table 1). The remaining four tribes are well represented in Pakistan by 23 of their more advanced genera with 89 species. The largest genera are *Indigofera* with 24 native species and *Desmodium* with 10 (Table 1).

The last and most important group is the temperate epulvinate series. It is sharply delimited by lack of a basal foliar pulvinus, closure of the vascular system, and leaves tending to be distichous and with phloem transfer cells (Polhill et al., 1981; Corby et al., 1983). These characteristics are linked to the herbaceous habit predominating in the group which is mainly temperate. The Galegeae, the most important legume tribe in Pakistan with 180 native species (Tables 1 and 4), link this group directly to the Millettieae; it is an Old World temperate offshoot of this tribe but well separated from it by the distinct characters given above. *Astragalus*, the largest native genus in Pakistan with 133 species (Table 1) and often mentioned as the largest genus of angiosperms in the world, resides here. It has undergone explosive evolution into all habitats, and comprises 31% of the native Pakistani legumes. Other significant genera, such as *Oxytropis* with 21 native species, are also members of Galegeae (Tables 1 and 4). About the Galegeae are a series of satellite tribes all but one of which are represented in Pakistan. Hedy-sareae and Loteae are closest to subtribe Astragalinae of the Galegeae. *Cicer* has been separated off from the Viciae as a monotypic tribe and has more in common with the Trifolieae. Trifolieae are agriculturally the most important of the group with the genera *Medicago*, *Trifolium*, and others, all important soil improvement and fodder plants.

The Papilionoideae show a continuation of the trend clearly demonstrated in the Caesalpinioideae and the Mimosoideae: the most primitive members are poorly represented in Pakistan or not at all, and the most advanced, more recent radiations are well represented. This trend has been carried to its climax with almost all of the advanced temperate tribes represented in Pakistan, and the explosive development of *Astragalus*.

Comparison with a Tropical Flora

Comparison of the Pakistani legume flora with that of a seasonally wet tropical area will support the hypotheses presented above; the savannas of central Brazil are such an area. They cover a zone more than twice as large as Pakistan, and the legumes are represented there by 72 genera with 527 native species (Kirkbride, 1984). The Mimosoideae are represented equally in both areas. Differences are found in Caesalpinioideae and Papilionoideae. Whereas Caesalpinioideae are poorly represented in Pakistan, in Brazilian savannas they are the dominant legume subfamily, with explosive radiation in *Chamaecrista* with 137 species. In Papilionoideae the more primitive elements are represented in the Brazilian savannas, and many of the more advanced groups are poorly represented or totally absent, such as the temperate epulvinate series. The situation is reversed in

Pakistan where the temperate epulvinate series dominate with 133 species of *Astragalus*, and the primitive groups are poorly represented.

Legume representation in Pakistan reflects climate and resulting vegetation types. The rainfall and temperature patterns approximately coincide, with the more tropical southern areas drier and the temperate northern areas wetter. Consequently there has been greater development of Papilionoideae and much poorer representation of the Caesalpinioideae, especially of its primitive members.

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