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Classification of the Leguminosae-*Papilionoideae*: A Numerical Re-assessment

Adel EL-GAZZAR[1], Monier Abd EL-GHANI[2*], Nahed EL-HUSSEINI[2], Adel KHATTAB[2]

[1]*Department of Biological and Geological Sciences, Faculty of Education, Suez Canal University, N. Sinai, Egypt*

[2]*Department of Botany , Faculty of Science, Cairo University, Giza 12613, Egypt; elghani@yahoo.com (*corresponding author)*

Abstract

The subdivision of the Leguminosae-*Papilionoideae* into taxa of lower rank was subject for major discrepancies between traditional classifications while more recent phylogenetic studies provided no decisive answer to this problem. As a contribution towards resolving this situation, 81 morphological characters were recorded comparatively for 226 species and infra-specific taxa belonging to 75 genera representing 21 of the 32 tribes currently recognized in this subfamily. The data matrix was subjected to cluster analysis using the Sørensen distance measure and Ward's clustering method of the PC-ord version-5 package of programs for Windows. This combination was selected from among the 56 combinations available in this package because it produced the taxonomically most feasible arrangement of the genera and species. The 75 genera are divided into two main groups A and B, whose recognition requires little more than the re-alignment of a few genera to resemble tribes 1-18 (Sophoreae to Hedysareae) and tribes 19-32 (Loteae to Genisteae), respectively, in the currently accepted classification. Only six of the 21 tribes represented by two or more genera seem sufficiently robust as the genera representing each of them hold together in only one of the two major groups A and B. Of the 29 genera represented by more than one species each 17, 7 and 5 are taxonomically coherent, nearly coherent and incoherent, respectively. The currently accepted circumscription and inter-relationships among the disrupted tribes and genera are in need of much detailed investigation.

Keywords: cluster analysis, epidermal trichomes, *Faboideae*, leguminosae, morphology, *Papilionoideae*

Introduction

The *Papilionoideae* DC. (nom. altern. *Fabaceae* Lindl.-*Faboideae*) is by far the largest of the three subfamilies of Leguminosae Adanson. It comprises 476 genera and 13855 species (APG 2012), distributed mainly in the temperate and subtropical parts of the world. Many of the species are of immense economic value globally as legume crops, including the innumerable cultivars of beans, faba beans, vetches (*Vicia* spp., *Phaseolus* spp., *Vigna* spp.), soybean (*Glycine max*), peas (*Pisum sativum*), chickpea (*Cicer arietinum*), lucerne or alfalfa (*Medicago sativa*), lentils (*Lens esculentus*), clovers (*Trifolium* spp.) and lupins (*Lupinus* spp.). Despite the huge range of variation in morphological features of their vegetative parts, members of the Papilionoideae are easily distinguishable from the other two subfamilies of the Leguminosae (*Mimosoideae* and *Caesalpinioideae*) by numerous morphological attributes including the papilionoid structure of the corolla, asymmetrical seeds, ovate-elliptical cotyledons, campylotropous ovules and the embryo axis is curved or a short spiral (Isely 1955 and 1981; Watson and Dallwitz 1992; onwards, Kirkbride et al. 2003; APG 2012; El-Gazzar *et al.* 2012). This clear distinction of the *Papilionoideae* from the rest of the Leguminosae gained substantial support from phylogenetic studies (Käss and Wink 1996-1997; Doyle *et al.* 1997; Kajita *et al.* 2001; Doyle and Luckow 2003; Wojciechowski *et al.* 2004; Champagne *et al.* 2007).

The subdivision of the *Papilionoideae* into taxa of lower rank was for many decades highly controversial (El-Gazzar and El-Fiki 1977, El-Gazzar 1979 and 1981, Käss and Wink 1995, 1996 and 1997, Doyle *et al.* 1997, Doyle and Luckow 2003, Wojciechowski *et al.* 2004, Champagne *et al.* 2007). This is clearly evident from the huge differences in the numbers and circumscription of tribes and sub-tribes recognized in the four major classifications of the *Papilionoideae* by De Candolle (1825), Bentham and Hooker (1865), Taubert (1894), Polhill and Raven (1981), who divided this subfamily into 6, 11, 10 and 32 tribes, respectively. Differences between the four systems in the number of subtribes are even greater. The apparently excessive fragmentation of the *Papilionoideae* in the system by Polhill and Raven (1981) into 32 tribes with 21 sub-tribes and 10 "groups" seems to have been universally accepted without being put to practical test.

The only common feature of all classificatory systems of the *Papilionoideae* to date is the recognition of tribes and sub-tribes on the basis of a limited range of floral characters with greater emphasis on petal morphology and stamen arrangement. Such few characters were used often singly to distinguish between chunky assemblages of genera. This seems to explain the unsettled disposition of

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most genera in the tribes and subtribes recognized in different classifications. The different arrangements of genera within the *Papilionoideae* are so great that a study based on a wider range of the plants' characters seemed urgently needed.

The present study was embarked upon in an attempt to answer the question: to what extent would the currently accepted classification of the *Papilionoideae* by Polhill and Raven (1981) withstand the test of numerical analyses of a comprehensive set of characters recorded comparatively from a cosmopolitan sample of genera and species using a number of computer programs with varying degrees of mathematical sophistication and taxonomic efficiency?

Material and methods

The sample of taxa

The present study was based on a cosmopolitan sample of 226 species and infra-specific taxa representing 75 genera of the *Papilionoideae*. This sample is necessarily small relative to the enormous size of the subfamily. However, it is fairly representative of the subfamily because: (a) it covers 21 of the 32 tribes and most of the sub-tribes in the currently accepted classification, (b) the genera are proportionately represented so that larger genera are represented by relatively larger numbers of species except in some relatively large genera (e.g. *Aspalathus*, *Eriosema*, *Mucuna* and *Ormosia*), and (c) it is geographically balanced in that all of the chief centers of distribution are proportionately catered for.

The number of fresh and herbarium specimens of individual species ranged between one and 35 with most of the species being represented by five-ten specimens each. The specimens are collected from some of the local botanic gardens (Orman Botanic Gardens in Giza, Alexandria University and Aswan) and the four major local herbaria (ALEX, CAID, CAI, CAIM; acronyms are according to Holmgren *et al.* (1990). Identification of the specimens was double checked using appropriate floras (Andrews 1952; Heywood and Ball 1968; Davis 1969; Zohary 1987; Boulos 1999 and 2009) and the online floras of China (Flora of China 2013), the Iberian Peninsula (Flora Iberica 2013) and Pakistan (Ali 2013). Identities were confirmed by matching with images of type and non-type material on various websites (e.g. www.aluka.org; www.tropicos.org, http://coldb.mnhn.fr; http://sweetgum.nybg.org). Nomenclature of all taxa was updated according to the two major online sources (www.tropicos.org; www.theplantlist.org).

Data analysis

A list of 81 characters recorded comparatively for 226 species belonging to 75 genera is given in Tab. 1. The data matrix was subjected to cluster analysis using the package of classificatory programs PC-ord version 5 for windows (McCune, 1997). It consists of seven distance measures and eight clustering (sorting or linkage) methods thus offering 56 possible hierarchical arrangements of the species. Pre-requisites of the program necessitated the abbreviation of names of taxa into only eight digits. Full valid names of taxa with their author citations and abbreviations are presented in Appendix 1.

Tab. 1. List of the 81 characters and their character-states recorded comparatively for 226 species of the Leguminosae-*Papilionoideae* and used to build a system of classification of the subfamily

1.	Plant: erect 1/ climbing 2/ prostrate 3
2.	Plant: herb 1/ shrub 2/ tree 3
3.	Lateral branches: spiny tipped 1/ not spiny tipped 2
4.	Spines on stem internodes: present 1/ absent 2
5.	Leaf midrib: turned into spine 1/ not turned into spine 2
6.	Stem: hairy 1/ glabrous 2
7.	Stem: rough 1/ smooth 2
8.	Stem: winged 1/ not winged 2
9.	Leaf-blade: simple 1/trifoliolate 2/ palmate 3/ pinnate 4
10.	Leaves or leaflets: ovate 1/ oblong 2/ linear 3/ lanceolate 4
11.	Leaf or leaflet apex: notched 1/ not notched 2
12.	Leaf or leaflet base of lamina: notched 1/ not notched 2
13.	Leaf or leaflet margin: entire 1/ not entire 2
14.	Leaves or leaflets: deciduous 1/ evergreen 2
15.	Leaves or leaflets: flat 1/ at least some modified into tendrils 2
16.	Upper surface of leaf or leaflet: hairy 1/ glabrous 2
17.	Lower surface of leaf or leaflet: hairy 1/ glabrous 2
18.	Lead width in cm
19.	Leaf length in cm
20.	Leaflet width in cm
21.	Leaflet length in cm
22.	Stipules: present 1/ absent 2
23.	Stipule margin: entire 1/ not entire 2
24.	Stipules: leafy 1/ not leaft 2
25.	Stipules: free 1/ adnate 2
26.	Stipule length in cm
27.	Stipule width in cm
28.	Inflorescence: raceme 1/ capitate 2/ umbel 3
29.	Petals: white 1/ not white
30.	Inflorescence length in cm
31.	Flower length in cm
32.	Calyx length in cm
33.	Calyx: number of veins
34.	Calyx: persistent 1/ deciduous 2
35.	Calyx teeth: four 1/ five 2
36.	Calyx teeth: equal 1/ unequal 2
37.	Eglandular hairs on calyx: present 1/ absent 2
38.	Glandular hairs on calyx: present 1/ absent 2
39.	Margin of calyx teeth: feathery 1/ not feathery 2
40.	Apex of standard: retuse 1/ obtuse-acute 2
41.	Color of vein in standard: same as blade 1/ different 2
42.	Standard: clawed 1/ not clawed 2
43.	Standard: length in cm

44.	Standard: width in cm
45.	Standard: hairy 1/ glabrous 2
46.	Apex of wings: retuse 1/ obtuse-acute 2
47.	Wing margin: entire 1/ not entire 2
48.	Color of veins in wing: same as blade 1/ different 2
49.	Wings: clawed 1/ not clawed 2
50.	Wing: length in cm
51.	Wing: maximum width in cm
52.	Wing sculpture or shrinks: present 1/ absent 2
53.	Apex of keel: retuse 1/ obtuse 2/ acute 3
54.	Color of veins in keel: same as blade 1/ different 2
55.	Keel: clawed 1/ not clawed 2
56.	Keel: length in cm
57.	Keel: maximum width in cm
58.	Staminal arrangement: type one 1/ type two 2
59.	Stamen length in cm (incl. tube): 1.7 or more 1/ 1.2 or less 2
60.	Stamens: monadelphous 1/ diadelphous 2
61.	Anthers: globose 1/ elongate 2
62.	Pod: length in cm
63.	Pod: width in cm
64.	Pod: curved 1/ straight 2/ helical 3
65.	Pod: hairy 1/ glabrous 2
66.	Spines on pod: present 1/ absent 2
67.	Pod apex: rounded 1/ acute 2/ acuminate 3
68.	Pod beak: straight 1/ curved 2
69.	Pod: terete 1/ flattened 2
70.	Opposite margins of pod joint: similar 1/ dissimilar 2
71.	Opposite margins of pod joint: straight 1/ rounded 2
72.	Seed: length in cm
73.	Seed color: red 1/ yellow 2/ black 3
74.	Seed surface: smooth 1/ corrugated 2
75.	Glandular hairs on upper leaf surface: present 1/ absent 2
76.	Glandular hairs on lower leaf surface: present 1/ absent 2
77.	Gland dots on leaves: present 1/ absent 2
78.	Calcium oxalate crystals in leaves: present 1/ absent 2
79.	Cell walls of lower epidermis: wavy 1/ not wavy 2
80.	Cell walls of upper epidermis: wavy 1/ not wavy 2
81.	Stomata in upper epidermis: present 1/ absent 2

Each of the resulting dendrograms has a certain % of chaining which is an expression of its clustering intensity. Low values of % chaining indicate a high clustering intensity of the dendrogram, and vice versa: the higher the clustering intensity, the more discrete (and taxonomically reliable) the groups in the dendrogram are. Comparison between the resulting dendrograms was carried out manually to select those which were closest to each other and to the currently accepted classification by Polhill and Raven (1981).

Results

The 56 dendrograms were shortlisted into four with the least percentages of chaining. They were based on the following combinations of distance measures and clustering methods:

Distance measure	clustering method	% chaining
Sørensen	Ward`s	0.70
Relative Sørensen	Ward`s	0.63
Euclidean	Ward`s	1.37
Relative Euclidean	Ward`s	1.00

A 'stopping level' was selected to produce basic groups in each of the four dendrograms and the species composition of the eight basic groups in the first dendrogram singled it out and favored its selection for further discussion. The lower reaches of each of groups 1-8 in Fig. 1 are shown in Fig. 2.

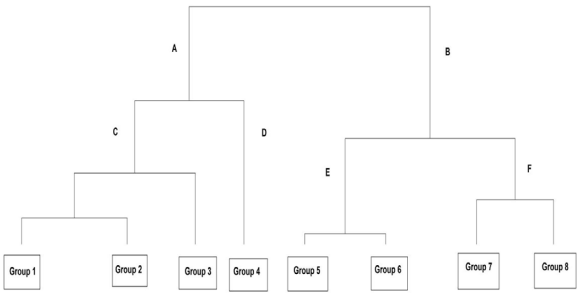
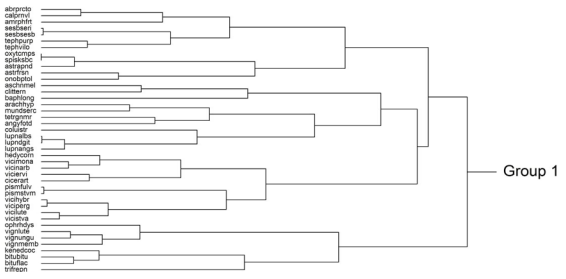
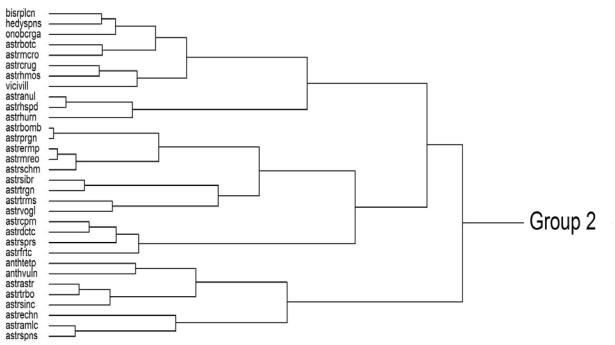


Fig. 1. Dendrogram based on the 81 characters listed in Tab. 1, recorded comparatively for 226 species of the Leguminosae-Papilionoideae, and analyzed by the Sørensen distance measure and Ward`s clustering method. The % chaining is 0.7





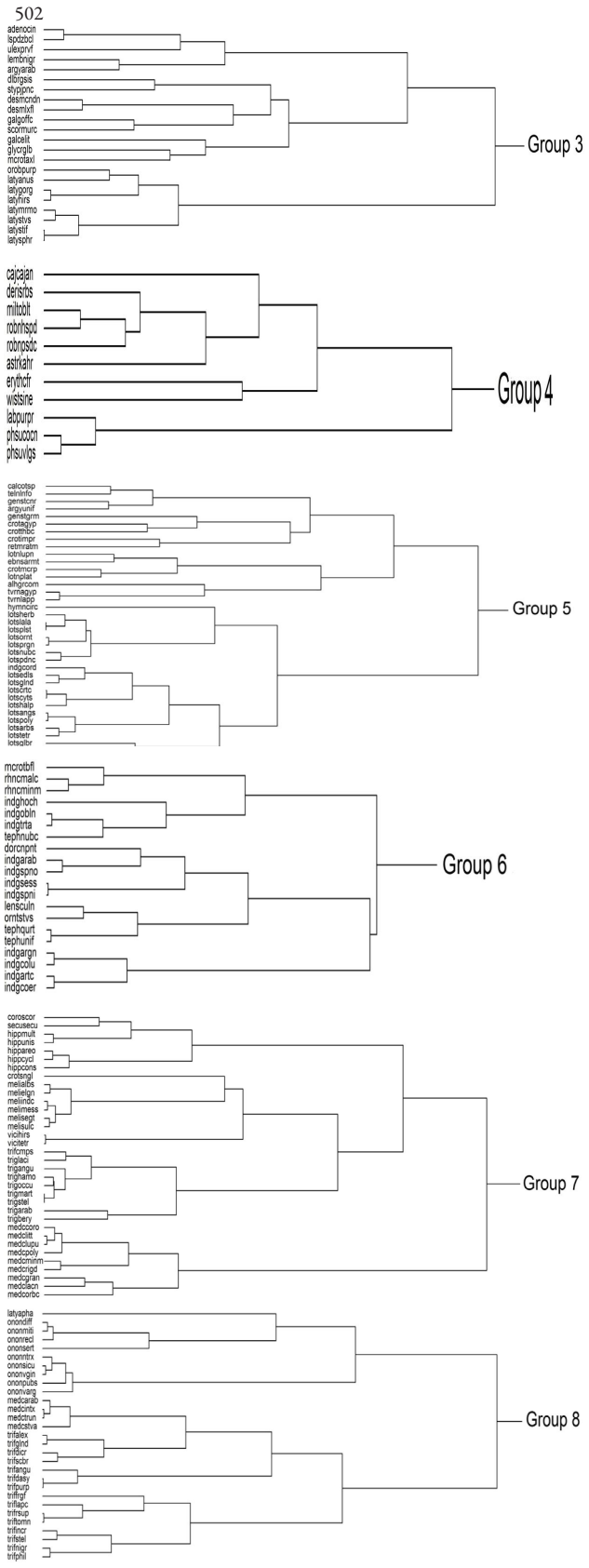


Fig. 2. The genera and species of groups 1-8 in Fig. 1. Names of taxa are abbreviated according to the list in the Appendix

Discussion

The present arrangement

The groups and sub-groups of genera and species displayed in Figs. 1 and 2 are by no means intended as a formal classification of the *Papilionoideae* and will not be given any scientific names. They are merely a preliminary framework expressing the phyletic relationships between the genera included in the present study in terms of the recorded characters. It is open for future improvement by the addition of taxa and/or characters. The choice of the hierarchical level leading to the recognition of the eight basic groups in the present study remains highly subjective. For instance, if this stopping level was lowered slightly than the eight-group level so that the relatively large group A.C.1 is divided into four smaller and taxonomically meaningful sub-groups, other seemingly intact groups as B.E.5 and B.E.6 would have been unnecessarily fragmented.

Comparison with the accepted classification

Although the traditional classifications of the P*apilionoideae* have the advantage of being comprehensive and cover the entire generic content of the subfamily known at the time of their establishment, the majority of groupings recognized in them are based on single characters of the flowers and pods. On the other hand, the present study is based on a much smaller sample of genera and species but with a much wider range of the variation in vegetative and floral morphology. In view of this basic difference, it is to be expected that the groupings in the present study would diverge to some extent from those in any of the traditional classifications. This is clearly evident from Tab. 2 where the agreements and disagreements between groups A and B and their eight sub-groups in Figs. 1 and 2 and Tab. 2 and the classification proposed by Polhill and Raven (1981) may be summed up in the following:

1. The sequence of tribes 1-32 in Polhill and Raven's (1981) classification seems taxonomically meaningful in terms of the two major groups A and B in Tab. 2. Thus, the great majority of genera belonging to tribes 2-18 (*Sophoreae* to *Hedysareae*) fall in group A, whereas most of the genera representing tribes 19-32 (*Loteae* to *Genisteae*; shaded in Tab. 2) appear in group B. It seems that the recognition of groups A and B requires only the re-allocation of some genera to coincide with the sequential arrangement of traditional tribes and that a major division within the *Papilionoideae* is worthy of further investigation.

2. Only six of the 32 tribes represented by two or more genera in the present study seem coherent as their genera hold together in either group A or group B. They are the *Sophoreae* (3 genera), *Robinieae* (2 genera), *Desmodieae* (2 genera) and *Aeschynomeneae* (2 genera) in group A, and the *Crotalarieae* (2 genera) and *Trifolieae* (5 genera) in group B. The nearly coherent tribes include the *Phaseoleae* (10 genera), *Tephrosieae* (5 genera), *Vicieae* (5 genera) and *Galegeae* (8 genera) in group A, and the *Coronilleae*

(5 genera) in group B. The placement of *Rhynchosia* in *Phaseoleae*, *Alhagi* in *Galegeae* and *Scorpurus* in *Coronilleae* seems questionable. Each of the *Genisteae* (9 genera) and *Loteae* (5 genera) is almost equally divided between the two major groups A and B.

Tab. 2. Comparison between the distribution of 75 genera of the Papilionoideae among groups 1-8 in the arrangements presented in Figs. 1 and 2, and the tribes recognized by Polhill and Raven (1981). Numbers of species are given in parentheses. Genera belonging to Group B are shaded. Genera treated by Polhill and Raven (1981) as sections of other genera are asterisked

	Tribes(Polhill & Raven,1981)	Genera (no of species)	Groups in Figs 1 and 2
2	Sophoreae	Baphia (1/1)	A.C.1
		Calpurnia (1/1)	A.C.1
		Styphnolobium (1; ~ Sophora)*	A.C.3
4	Dalbergieae	Dalbergia (1/1)	A.C.3
5	Abreae	Abrus (1/1)	A.C.1
6	Tephrosieae	Tephrosia (2/5)	A.C.1
		Tephrosia (3/5)	B.E.6
		Mundulea (1/1)	A.C.1
		Milletia (1/1)	A.D.4
		Derris (1/1)	A.D.4
		Wisteria (1/1)	A.D.4
7	Robinieae (Sesbanieae)	Sesbania (2/2)	A.C.1
		Robinia (2/2)	A.D.4
8	Indigofereae	Indigofera (1/12)	B.E.5
		Indigofera (11/12)	B.E.6
9	Desmodieae	Desmodium (2/2)	A.C.3
		Lespedeza (1/1)	A.C.3
10	Phaseoleae	Ophrestia (1/1)	A.C.1
		Kennedia (1/1)	A.C.1
		Clitoria (1/1)	A.C.1
		Vigna (3/3)	A.C.1
		Galactea (1/1)	A.C.3
		Macrotyloma (1/2)	A.C.3
		Macrotyloma (1/2)	B.E.6
		Cajanus (1/1)	A.D.4
		Erythrina (1/1)	A.D.4
		Phaseolus (2/2)	A.D.4
		Rhynchosia (2/2)	B.E.6
11	Psoraleeae	Bituminaria (2/2)	A.C.1
12	Amorpheae	Amorpha (1/1)	A.C.1
14	Aeschynomeneae	Aeschynomene (1/1)	A.C.1
		Arachis (1/1)	A.C.1
10	Phaseoleae	Ophrestia (1/1)	A.C.1
		Kennedia (1/1)	A.C.1
		Clitoria (1/1)	A.C.1
		Vigna (3/3)	A.C.1
		Galactea (1/1)	A.C.3
		Macrotyloma (1/2)	A.C.3
		Macrotyloma (1/2)	B.E.6
		Cajanus (1/1)	A.D.4
		Erythrina (1/1)	A.D.4
		Phaseolus (2/2)	A.D.4
		Rhynchosia (2/2)	B.E.6
11	Psoraleeae	Bituminaria (2/2)	A.C.1
12	Amorpheae	Amorpha (1/1)	A.C.1
14	Aeschynomeneae	Aeschynomene (1/1)	A.C.1
		Arachis (1/1)	A.C.1
		Colutea (1/1)	A.C.1
		Oxytropis (1/1)	A.C.1
		Spiesia (1; ~ Oxytropis)*	A.C.1
16	Galegeae	Astragalus (1/29)	A.C.1
		Astragalus (26/29)	A.C.2
		Astragalus (2/29)	A.D.4
		Biserrula (1/1)	A.C.2
		Galega (1/1)	A.C.3
		Glycyrrhiza (1/1)	A.C.3
		Alhagi (1/1)	B.E.5
18	Hedysareae	Hedysarum (1/2)	A.C.1
		Hedysarum (1/2)	A.C.2
		Onobrychis (1/2)	A.C.1
		Onobrychis (1/2)	A.C.2
		Ebenus (1/1)	B.E.5
		Taverniera (2/2)	B.E.5
19	Loteae	Tetragonolobus (1/1)	A.C.1
		Anthyllis (2/2)	A.C.2
		Hymenocarpus (1/1)	B.E.5
		Lotus (18/18)	B.E.5
		Dorycnium (1; ~ Lotus)*	B.E.6
20	Coronilleae	Scorpurus (1/1)	A.C.3
		Ornithopus (1/1)	B.E.6
		Coronilla (1/1)	B.F.7
		Hippocrepis (5/5)	B.F.7
		Securigera (1/1)	B.F.7
21	Vicieae	Vicia (7/10)	A.C.1
		Vicia (1/10)	A.C.2
		Vicia (2/10)	B.F.7
		Pisum (2/2)	A.C.1
		Orobus (1; ~ Vicia)*	A.C.3
		Lathyrus (7/8)	A.C.3
		Lathyrus (1/8)	B.F.8
		Lens (1/1)	B.E.6
22	Cicereae	Cicer (1/1)	A.C.1
23	Trifolieae	Melilotus (6/6)	B.F.7
		Trigonella (8/8)	B.F.7
		Ononis (9/9)	B.F.8
		Trifolium (15/17)	B.F.8
		Trifolium (1/17)	B.F.7
		Trifolium (1/17)	A.C.1
		Medicago (9/13)	B.F.7
		Medicago (4/13)	B.F.8

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		Crotalaria (4/5)	B.E.5
29	Crotalarieae	Crotalaria (1/5)	B.F.7
		Lotononis (2/2)	B.E.5
31	Thermopsideae	Anagyris (1/1)	A.C.1
		Lupinus (3/3)	A.C.1
		Argyrolobium (1/2)	A.C.3
		Argyrolobium (1/2)	B.E.5
		Adenocarpus (1/1)	A.C.3
32	Genisteae	Lembotropis (1; ~ Cytisus)*	A.C.3
		Ulex (1/1)	A.C.3
		Calicotome (1/1)	B.E.5
		Genista (2/2)	B.E.5
		Teline (1; ~ Genista)*	B.E.5
		Retama (1/1)	B.E.5

Based on data of sequencing nuclear ribosomal DNA, Allan and Porter (2000) proposed submerging the *Coronilleae* into the *Loteae* and a indicated a bio-geographic distinction within the combined tribe between the New Word Lotus s.l clade and the Old World Lotus s.l. clade. Although the sample of species representing these two tribes in the present study belongs predominantly to the Old World, the dispersal of their species among the three basal groups of group A.C. and three of the basal groups of Group B (B.E.5, B.E.6 and B.F.7) in Tab. 2 does not corroborate the results of Allan and Porter (2000).

The generic concept in Papilionoideae

The distribution of species representing the 75 genera among the eight groups in Figs. 1 and 2 is set against the tribes and sub-tribes recognized in the latest and most comprehensive classification of the Papilionoideae by Polhill and Raven (1981) in Tab. 2. This arrangement facilitated putting the taxonomic robustness of these genera to a practical test. Accordingly, the 29 genera represented in the present study by more than one species each are distinguishable into the following three categories:

1. Highly coherent genera with all of their representatives appearing together in only one of groups 1-8 (17 genera): *Sesbania* (2 spp.), *Lupinus* (3 spp.), *Pisum* (2 spp.), *Vigna* (3 spp.), *Bituminaria* (2 spp.), *Anthyllis* (2 spp.), *Desmodium* (2 spp.), *Robinia* (2 spp.), *Phaseolus* (2 spp.), *Lotononis* (2 spp.), *Taverniera* (2 spp.), *Lotus* (18 spp.), *Hippocrepis* (5 spp.), *Melilotus* (6 spp.), *Ononis* (9 spp.), *Trigonella* (7 spp.), and *Genista* (2/2).

2. Nearly coherent genera (7 genera): *Vicia* (7/10 spp. in group A.C.1), *Astragalus* (26/29 spp. in group A.C.2), *Lathyrus* (7/8 spp. in group A.C.3), *Crotalaria* (4/5 spp. in group B.E.5), *Indigofera* (11/12 spp. in group B.E.6), *Medicago* (9/13 spp. in group B.F.7), and *Trifolium* (15/17 spp. in group B.F.8).

3. Disrupted genera (5 genera): *Tephrosia* with two species in group A.C.1 and three species in group B.E.6, *Argyrolobium* with one species in each of groups A.C.3 and B.E.5, *Macrotyloma* with one species in each of groups A.C.3 and B.E.6, and *Onobrychis* and *Hedysarum* with 1 species each in each of groups A.C.1 and A.C.2.

Out of these 29 genera, 17 seem taxonomically robust, followed by seven almost equally coherent genera, whereas the two species representing each of *Onobrychis* and *Hedysarum* were disbanded in groups A.C.1 and A.C.2. *Representatives* of *Tephrosia*, *Macrotyloma* and *Argyrolobium* together with some species of *Vicia*, *Lathyrus* and *Trifolium* crossed the boundary between the two major groups A and B in Fig. 1 and Tab. 2. In the category of seven nearly coherent genera, the separation of some splinter species from the main aggregation of their relatives in the same genus emphasizes the need to re-evaluate the intraspecific relationships of such genera by more detailed studies based on larger numbers of their species. This is best exemplified by the isolation of *Astragalus* kahiricus in group A.D.4 and A. fresenii and A. penduliflora in group A.C.1 instead of group A.C.2 where all other 26 *Astragalus* species are placed together. Generally, this categorization of genera seems to indicate a relatively sound generic concept in the *Papilionoideae*, especially in the case of such megagenera as *Astragalus* which occupies a prominent position among the largest angiosperm genera (Jer-Ming Hu *et al.*, 2013).

It is worth noting that Tab. 2 includes six genera treated by Polhill and Raven (1981) as sections or sub-sections of larger genera but recognized as distinct genera comprising species with currently accepted names in "www.the plant list.org" and "www.tropicos.org". Four of these segregate genera (*Spiesia* as ~*Oxytropis*; *Dorycnium* as ~*Lotus*; *Orobus* as ~*Vicia*; *Teline* as ~*Genista*), appear inseparable from their larger relatives, thus supporting the treatment of Polhill and Raven (1981) and providing fresh evidence favoring re-uniting them with their close allies.

In view of the foregoing remarks it seems advisable to subject larger samples of genera and species of the Leguminosae-*Papilionoideae* to much detailed studies based on the comparative recording of the widest possible range of variation in the plants' characters and subjecting the output to a number of numerical analyses with variable combinations of similarity assessment algorithms and clustering procedures, in order to select the classification which best imposes a clear pattern on the distribution of the recorded characters among the plants. Special emphasis should be laid on such genera as *Tephrosia*, A*rgyrolobium, Macrotyloma*, *Hedysarum* and *Onobrychis* as well as such relatively large tribes as the *Genisteae* and *Loteae* whose representative species failed to emerge together in only one of groups 1-8 or were dispersed between the two major Groups A and B.

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Appendix. Alphabetical arrangement of full names of 226 species and infra-specific taxa representing 75 genera of the Leguminosae-Papilionoideae and their abbreviations (heavy-bold in parentheses) used in the construction of the dendrograms in Figs. 1 and 2.

A: Abrus precatorius L. (abrprcto), Adenocarpus cincinnatus (Ball.) Maire (adenocin), Aeschynomene elaphroxylon (Guill. & Perr.) Taub. (aschnmel), Alhagi graecorum Boiss. (alhgrcom), Amorpha fruticosa L. (amrphfrt), Anagyris foetida L. (angyfotd), Anthyllis tetraphylla L. (anthtetp), Anthyllis vulneraria L. subsp. maura (Beck) Maire (anthvuln), Arachis hypogea L. (arachhyp), Argyrolobium arabicum (Decne.) Jaub.& Spach (argyarab), Argyrolobium uniflorum (Decne.) Jaub.& Spach (argyunif), Astragalus amalecitanus Boiss. (astramlc), Astragalus annularis Forssk. (astranul), Astragalus asterias Steven (astrastr), Astragalus boeticus L. (astrbotc), Astragalus bombycinus Boiss. (astrbomb), Astragalus caprinus L. (astrcprn), Astragalus corrugatus Bertol. (astrcrug), Astragalus dactylocarpus Boiss. subsp. acinaciferus (Boiss.) E. Ott (astrdctc), Astragalus echinus DC. (astrechn), Astragalus eremophilus Boiss. (astrermp), Astragalus fresenii Decne. (astrfrsn), Astragalus fruticosus Forssk. (astrfrtc), Astragalus hamosus L. (astrhmos), Astragalus hauarensis Boiss. (astrhurn), Astragalus hispidulus DC. (astrhspd), Astragalus kahiricus DC. (astrkahr), Astragalus macrocarpus DC. subsp. macrocarpus (astrmcro), Astragalus mareoticus Delile (astrmreo), Astragalus penduliflora Lam. (astrapnd), Astragalus peregrinus Vahl subsp. peregrines (astrprgn), Astragalus schimperi Boiss. (astrschm), Astragalus sieberi DC. (astrsibr), Astragalus sinaicus Boiss. (astrsinc), Astragalus sparsus Decne. (astrsprs), Astragalus spinosus (Forssk.) Muschl. (astrspns), Astragalus tribuloides Delile (astrtrbo), Astragalus trigonus DC. (astrtrgn), Astragalus trimestris L. (astrtrms), Astragalus vogelii (Webb) Bornm. (astrvogl).

B: Baphia longipedicellata De Wild. subsp. keniensis (Brummitt) Soladoye (baphlong), Biserrula pelecinus L. subsp. pelecinus (bisrplcn), Bituminaria bituminosa (L.) C.H.Stirt. (bitubitu), Bituminaria flaccida (Nabelek.) Greuter (bituflac).

C: Calpurina villosa Harv. (calprnvl), Cajanus cajan (L.) Millsp. (cajcajan), Calicotome spinosa (L.) Link (calcotsp), Cicer arietinum L. (cicerart), Clitoria ternatea L. (clittern), Colutea istria Mill. (coluistr), Coronilla scorpioides (L.) Koch (corscorp), Crotalaria aegyptiaca Benth. (crotagyp), Crotalaria impressa Nees. ex Walp. (crotimpr), Crotalaria senegalensis (Pers.) DC. (crotsngl), Crotalaria thebaica (Delile) DC. (crotthbc), Crotalaria microphylla Vahl (crotmcrp).

D: Dalbergia sissoo Roxb. ex DC. (dlbrgsis), Derris robusta (DC.) Benth. (derisrbs), Desmodium canadense (L.) DC. (desmcndn), Desmodium laxiflorum DC. (desmlxfl), Dorycnium pentaphyllum Scop. subsp. germanicum (Grimli) Gams (dorcnpnt).

E: Ebenus armitagei Schweinf.& Taub. (ebnsarmt), Erythrina caffra Thunb. (erythcfr).

G: Galactia elliottii Nutt. (galcelit), Galega officialis L. (galgoffc), Genista canariensis DC. (genstcnr), Genista germanica L. (genstgrm), Glycyrrhiza glabra L. (glycrglb).

H: Hedysarum coronarium L. (hedycorn), Hedysarum spinosissimum L. subsp. spinosissimum (hedyspns), Hippocrepis areolata Desv. (hippareo), Hippocrepis constricta Kunze (hippcons), Hippocrepis cyclocarpa Murb. (hippcycl), Hippocrepis multisiliquosa L. (hippmult), Hippocrepis unisiliquosa L. (hippunis), Hymenocarpos circinnatus (L.) Savi (hymncirc).

I: Indigofera arabica Jaub.& Spach (indgarab), Indigofera argentea Burm. f. (indgargn), Indigofera articulata Gouan. (indgartc), Indigofera coerulea Roxb. var. coerulea (indgcoer), Indigofera colutea (Burm. f.) Merr. (indgcolu), Indigofera cordifolia Roth (indgcord), Indigofera hochstetteri Baker (indghoch), Indigofera oblongifolia Forssk. (indgobln), Indigofera sessiliflora DC. (indgsess), Indigofera spiniflora Boiss. (indgspni), Indigofera spinosa Forssk. (indgspno), Indigofera trita L. subsp. subulata (Vahl ex Poir.) Ali var. nubica (J. B. Gillett) Boulos & Schrire (indgtrta).

K: Kennedia coccinea (Curtis) Vent. (kenedcoc).

L: Lablab purpureus (L.) Sweet (labpurpr), Lathyrus annuus L. (latyanus), Lathyrus aphaca L. (latyapha), Lathyrus gorgonei Parl. (latygorg), Lathyrus hirsutus L. (latyhirs), Lathyrus marmoratus Boiss.& Blanche (latymrmo), Lathyrus sativus L. (latystvs), Lathyrus setifolius L. (latystif), Lathyrus sphaericus Retz. (latysphr), Lembotropis nigricans (L.) Griseb. (lembnigr), Lens culinaris Medik. subsp. culinaris (lensculn), Lespedeza bicolor Turcz. (lspdzbcl), Lotononis lupinifolia (Boiss. ex Jaub. & Spach) Benth. (lotnlupn), Lotononis platycarpa (Viv.) Pic. Serm. (lotnplat), Lotus angustissimus L. (lotsangs), Lotus arabicus L. (lotsarbs), Lotus creticus L. (lotscrtc), Lotus cytisoides L. (lotscyts), Lotus edulis L. (lotsedls), Lotus glaber Mill. (lotsglbr), Lotus glinoides Delile (lotsglnd), Lotus halophilus Boiss.& Spruner (lotshalp), Lotus hebranicus Hochst. ex Brand (lotsherb), Lotus lalambensis Schweinf. (lotslala), Lotus lanuginosus Vent. (lotslanu), Lotus nubicus Baker (lotsnubc), Lotus ornithopodioides L. (lotsornt), Lotus palustris Willd. (lotsplst), Lotus pedunculatus Cav. (lotspdnc), Lotus peregrinus L. (lotsprgn), Lotus polyphyllos E. D. Clake (lotspoly), Lotus tetragonolobus L. (lotstetr), Lupinus albus L. (lupnalbs), Lupinus angustifolius L. (lupnangs), Lupinus digitatus Forssk. (lupndgit).

M: Macrotyloma axillare (E. Mey.) Verdc. (mcrotaxl), Macrotyloma biflorum (Schum. & Thonn.) Hepper (mcrotbfl), Medicago arabica (L.) Huds. (medcarab), Medicago coronata (L.) Bartal. (medccoro), Medicago granadensis Willd. (medcgran), Medicago intertexta (L.) Mill. var. Ciliaris (L.) Heyn (medcintx), Medicago laciniata (L.) Mill. (medclacn), Medicago littoralis Rohde ex Loisel. (medclitt), Medicago lupulina L. (medclupu), Medicago minima (L.) L. (medcminm), Medicago orbicularis (L.) Bartal. (medcorbc), Medicago polymorpha L. (medcpoly), Medicago rigidula (L.) All. (medcrigd), Medicago sativa L. (medcstva), Medicago truncatula Gaertn. (medctrun), Melilotus albus Medik. (melialbs), Melilotus elegans Salzm. ex Ser. (melielgn), Melilotus indicus (L.) All. (meliindc), Melilotus messanensis (L.) All. (melimess), Melilotus segetalis (Brot.)

Ser. (melisegt), Melilotus sulcatus Desf. (melisulc), Millettia oblata Dunn (miltoblt), Mundulea sericea (Willd.) A. Chev. (mundserc).

O: Onobrychis crista-galli (L.) Lam. (onobcrga), Onobrychis ptolemaica (Delile) DC. (onobptol), Ononis diffusa Ten. (onondiff), Ononis mitissima L. (ononmiti), Ononis natrix L. (ononntrx), Ononis pubescens L. (ononpubs), Ononis reclinata L. (ononrecl), Ononis serrata Forssk. (ononsert), Ononis sicula Guss. (ononsicu), Ononis vaginalis Vahl (ononvgin), Ononis variegata L. (ononvarg), Ophrestia hedysaroides (Willd.) Verdc. (ophrhdys), Ornithopus sativus Brot. (orntstvs), Orobus atropurpureus Desf. (orobpurp), Oxytropis campestris (L.) DC. (oxytcmps).

P: Phaseolus coccineus L. (phsucocn), Phaseolus vulgaris L. (phsuvlgs), Pisum fulvum Sm. (pismfulv), Pisum sativum L. (pismstvm).

R: Retama raetam (Forssk.) Webb& Berthel. (retmratm), Rhynchosia malacophylla (Spreng.) Bojer (rhncmalc), Rhynchosia minima (L.) DC. (rhncminm), Robinia hispida L. (robnhspd), Robinia pseudoacacia L. (robnpsdc).

S: Scorpiurus muricatus L. (scormurc), Securigera securidaca (L.) Degen& Dorfl. (secusecu), Sesbania sericea (Willd.) Link (sesbseri), Sesbania sesban (L.) Merr. (sesbsesb), Spiesia kasbecki (Bunge ex Boiss.) Kuntze (spisksbc), Styphnolobium japonicum (L.) Schott (stypjpnc).

T: Taverniera aegyptiaca Boiss. (tvrnagyp), Taverniera lappacea (Forssk.) DC. (tvrnlapp), Teline linifolia (L.) Webb (telnlnfo), Tephrosia nubica (Boiss.) Baker in Oliv. subsp. nubica (tephnubc), Tephrosia purpurea (L,) Pers. (tephpurp), Tephrosia quartiniana Cuf. ex Greuter& Burdet (tephqurt), Tephrosia uniflora Pers. subsp. petrosa (Blatt.& Hallb.) J. B. Gillett & Ali (tephunif), Tephrosia villosa (L.) Pers. subsp. ehrenbergiana (Schweinf.) Brummitt (tephvilo), Tetragonolobus maritimus (L.) A.W. Roth (tetrgnmr), Trifolium alexandrinum L. (trifalex), Trifolium angustifolium L. (trifangu), Trifolium campestre Schreb. in Sturm (trifcmps), Trifolium dasyurum C. Presl (trifdasy), Trifolium dichroanthum Boiss. (trifdicr), Trifolium fragiferum L. (triffrgf), Trifolium glanduliferum Boiss. var. nervulosum (Boiss.&Heldr.) Zohary (trifglnd), Trifolium incarnatum L. (trifglnd), Trifolium lappaceum L. (triflapc), Trifolium nigrescens Viv. (trifnigr), Trifolium philistaeum Zohary (trifphil), Trifolium purpureum Loisel. (trifpurp), Trifolium repens L. (trifrepn), Trifolium resupinatum L. (trifrsup), Trifolium scabrum L. (trifscbr), Trifolium stellatum L. (trifstel), Trifolium tomentosum L. (triftomn), Trigonella anguina Delile (trigangu), Trigonella arabica Delile (trigarab), Trigonella berythea Boiss.& Blanche in Boiss. (trigbery), Trigonella hamosa L. (trighamo), Trigonella laciniata L. (triglaci), Trigonella maritima Poirr. in Lam. (trigmart), Trigonella occulata Ser. in DC. (trigoccu), Trigonella stellata Forssk. (trigstel).

U: Ulex parviflorus subsp. africanus (Webb) Greuter (ulexprvf).

V: Vicia ervilia (L.) Willd. (viciervi), Vicia hirsuta (L.) Gray (vicihirs), Vicia hybrida L. (vicihybr), Vicia lutea L. (vicilute), Vicia monantha Retz (vicimona), Vicia narbonensis L. (vicinarb), Vicia peregrina L. (viciperg), Vicia sativa L. (vicistva), Vicia tetrasperma (L.) Schreb. (vicitetr), Vicia villosa Roth (vicivill), Vigna luteola (Jacq.) Benth. in Mart. (vignlute), Vigna membranacea A. Rich. (vignmemb), Vigna unguiculata (L.) Walp. subsp. sesquipedalis (L.) Verdc. (vignungu).

W: Wisteria sinensis (Sims) DC. (wistsine).