

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

Adel EL-GAZZAR¹, Monier Abd EL-GHANI^{2*}, Nahed EL-HUSSEINI², Adel KHATTAB²

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

²Department 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; Ka-

jita 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

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.thepantlist.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 leafy 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

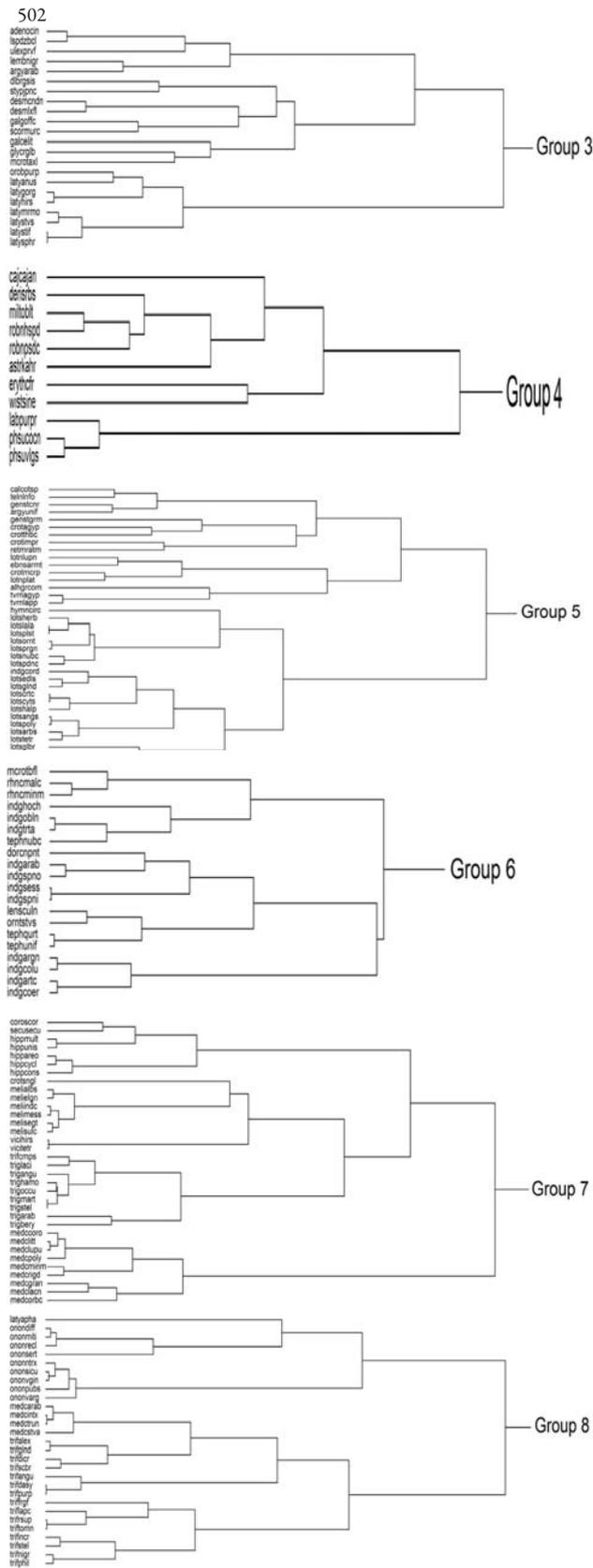


Fig. 2. The genera and species of groups 1-8 in Fig. 1. Names of taxa are abbreviated according to the list in the Appendix

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 *Papilionoideae* 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 (*Loteeae* to *Genisteeae*; 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
		Baphia (1/1)	A.C.1
2	Sophoreae	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
		Tephrosia (2/5)	A.C.1
		Tephrosia (3/5)	B.E.6
6	Tephrosieae	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
		Lepedeza (1/1)	A.C.3
		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
10	Phaseoleae	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	Psoraleae	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
		Ophrestia (1/1)	A.C.1
		Kennedia (1/1)	A.C.1
10	Phaseoleae	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	Psoraleae	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
		Astragalus (1/29)	A.C.1
16	Galegeae	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
		Hedysarum (1/2)	A.C.1
		Hedysarum (1/2)	A.C.2
18	Hedysareae	Onobrychis (1/2)	A.C.1
		Onobrychis (1/2)	A.C.2
		Ebenus (1/1)	B.E.5
		Taverniera (2/2)	B.E.5
		Tetragonolobus (1/1)	A.C.1
		Anthyllis (2/2)	A.C.2
19	Loteae	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
		Vicia (7/10)	A.C.1
		Vicia (1/10)	A.C.2
		Vicia (2/10)	B.F.7
21	Vicieae	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
		Melilotus (6/6)	B.F.7
		Trigonella (8/8)	B.F.7
		Ononis (9/9)	B.F.8
23	Trifolieae	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

		Crotalaria (4/5)	B.E.5
29	Crotalariaeae	Crotalaria (1/5)	B.F.7
		Lotononis (2/2)	B.E.5
31	Thermopsidaeae	Anagyris (1/1)	A.C.1
		Lupinus (3/3)	A.C.1
		Argyrobium (1/2)	A.C.3
		Argyrobium (1/2)	B.E.5
		Adenocarpus (1/1)	A.C.3
32	Genisteae	Lembotropsis (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 indicated a bio-geographic distinction within the combined tribe between the New World 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, *Argyrobium* 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 *Argyrobium* 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 intra-specific 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*; *Orobis* 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*, *Argyrobium*, *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.

References

- Allan GJ, Porter JM (2000). Tribal delimitation and phylogenetic relationships of *Loteae* and *Coronilleae* (*Faboideae*: *Fabaceae*) with special reference to *Lotus*: evidence from nu-

- clear ribosomal ITS sequences. *American J Bot* 87(12):1871-1881.
- Ali SI (2013). Papilionaceae Giseke, Flora of Pakistan. [www.tropicos.org/name/50304858?projectid=32].
- APG (2012). Angiosperm Phylogeny Group. Fabales. [www.mobot.org/mobot/research/APweb/orders/fabalesweb.htm].
- Andrews FW (1952). The Flowering Plants of the Anglo-Egyptian Sudan, 2. T. Buncle & Co. Ltd., Abroath, Scotland. p. 163-248.
- Bentham G, Hooker JD (1865). Leguminosae. *Genera Plantarum* 1(2):434-600. Lovell Reeve & Co, London.
- Boulos L (1999). Flora of Egypt. Azollaceae-Oxalidaceae. Al-Hadara Publishing, Cairo, 1:249-372.
- Boulos L (2009). Flora of Egypt Checklist. Revised annotated edition. Al-Hadara Publishing, Cairo, p. 88-118.
- Champagne CEM, Goliber TE, Wojciechowski MF, Mei RW, Townsley BT, Wang K, Paz MM, Geeta R, Sinha NR (2007). Compound leaf development and evolution in the legumes. *The Plant Cell* 19:3369-3378.
- Davis PH (1969). Leguminosae, Flora of Turkey and the East Aegean Islands, 3. Edinburgh University Press, Edinburgh. p 1-597.
- De Candolle AP (1825). Ordo LXIII Leguminosae. *Prodromus Systematis Naturalis Regni Vegetabilis* 2:93-524.
- Doyle JJ, Luckow MA (2003). The rest of the iceberg. Legume diversity and evolution in a phylogenetic context. *Plant Physiol* 131:900-910.
- Doyle JJ, Doyle GL, Ballenger JA, Dickson EE, Kajita T, Ohashi H (1997). A phylogeny of the chloroplast gene rbcL in the Leguminosae: taxonomic correlations and insights into the evolution of nodulation. *Am J Bot* 84(4):541-555.
- El-Gazzar A (1979). Ravenelia and its segregates (Uredinales) as indicators of taxonomic affinity in Leguminosae. *Symbolae Botanicae Upsaliense* 22(4):182-193.
- El-Gazzar A (1981). Systematic implications of susceptibility to Uromyces rusts in Leguminosae. In R.M. Polhill and P.H. Raven (eds.) "Advances in Legume Systematics". Part 2. Royal Botanic Gardens, Kew, UK. Academic Press, London and New York.
- El-Gazzar A, El-Fiki MA (1977). The main subdivisions of Leguminosae. *Botaniska Notiser* 129:71-375.
- El-Gazzar A, Abdel Ghani MM, El-Husseini NM, Khattab AA (2012). Computer-generated keys to the flora of Egypt. 5. The Leguminosae-Papilionoideae. *Assiut University J Bot* 41(2):129-181.
- Flora Iberica (2013). [www.floraiberica.es/floraiberica/texto/pdfs/07_LEGUMINOSAE.pdf].
- Flora of China (2013). [www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=10355#key-1-8].
- Holmgren PK, Holmgren NH, Barnett LC (1990). Index Herbariorum. Part 1. The Herbaria of the World. *Regnum Vegetabile* 120, p. 693.
- Isely D (1955). Observations on seeds of the Leguminosae: Mimosoideae and Caesalpinioideae. *Proceedings of the Iowa Academy of Science* 62:142-149.
- Isely D (1981). Leguminosae of the United States. *Memoirs of the New York Bot Gard* 25:128-213.
- Jer-Ming Hu, Sanderson MJ, Wojciechowski MF (2013). Introduction. [http://loco.biosci.arizona.edu/astragalus/introduction.htm].
- Käss E, Wink M (1995). Molecular phylogeny of the *Papilionoideae* (Family Leguminosae): RbcL gene sequences versus chemical taxonomy. *Acta Bot* 108:149-162.
- Käss E, Wink M (1996). Molecular evolution of the Leguminosae: phylogeny of the three subfamilies based on rbcL sequences. *Biochemical Systematics and Ecology* 24(5):365-378.
- Käss E, Wink M (1997). Phylogenetic relationships in the Papilionoideae (family Leguminosae) based on nucleotide sequences of cpDNA (rbcL) and ncDNA (ITS 1 and 2). *Mol Phylogenet Evol* 8(1):65-88.
- Kajita T, Ohashi H, Tateishi Y, Bailey CD, Doyle JJ (2001). rbcL and legume phylogeny, with particular reference to *Phaseoleae*, *Millettieae* and *Allies*. *System Bot* 26(3):515-536.
- Kirkbride JH Jr., Gunn CR, Weitzman AL (2003). Fruits and seeds of genera in the subfamily Faboideae (*Fabaceae*). Technical Bulletin number 1890, Agricultural Research Service, United States Department of Agriculture. p. 1-84. [also available at: www.ars.usda.gov/is/np/FruitsSeeds/FS1-00Front.pdf].
- McCune B (1997). PC-ORD version 5, for Windows. Specifications. [http://home.centurytel.net/~mjm/winspecs.htm].
- Polhill RM, Raven PH (1981). *Advances in Legume Systematics*. Part 1. Royal Botanic Gardens, Kew.
- Taubert P (1891-1894). Leguminosae. In: *Die Natürlichen Pflanzenfamilien*. Engler A and Prantl K (eds.), III(3):70-288.
- Watson L, Dallwitz MJ (1992 onwards). The Families of Flowering Plants, illustrations, identification, and information retrieval. Version 19th December 2012 [http://delta-intkey.com/angio/www/legumino.htm].
- Wojciechowski MF, Lavin M, Sanderson MJ (2004). A phylogeny of legumes (Leguminosae) based on analysis of the plastid MATK gene resolves many well-supported subclades within the family. *Am J Bot* 91(11):1846-1862.
- Zohary M (1987). *Flora Palaestina*. Part two. Platanaceae to Umbelliferae. The Israel Academy of Sciences and Humanities, Jerusalem, pp. 34-224.

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. (*amrphfrit*), *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 boeoticus* 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. (*astrfritc*), *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. (*clittrn*), *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. (*ebnsarnt*), *Erythrina caffra* Thunb. (*erythcfr*).

G: *Galactia elliottii* Nutt. (*galcelit*), *Galega officinalis* 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*), *Hymenocarpus 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. (*indgobl*), *Indigofera sessiliflora* DC. (*indgsses*), *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. (*lspdzblc*), *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. (*lotsrctc*), *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 polyphyllus* 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* Robde 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. (*meliseqt*), *Melilotus sulcatus* Desf. (*melisulc*), *Milletia oblata* Dunn (*miltobl*), *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 (*ononvagin*), *Ononis variegata* L. (*ononvarg*), *Ophrestia hedysaroides* (Willd.) Verdc. (*ophrhdy*), *Ornithopus sativus* Brot. (*ornstsv*), *Orobolus atropurpureus* Desf. (*orobpurp*), *Oxytropis campestris* (L.) DC. (*oxycmp*).

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

R: *Retama raetam* (Forssk.) Webb & Berthel. (*retmatm*), *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. (*sesbsb*), *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 (*telnlfn*), *Tephrosia nubica* (Boiss.) Baker in Oliv. subsp. *nubica* (*tephnubc*), *Tephrosia purpurea* (L.) Pers. (*tephpurp*), *Tephrosia quartiniiana* Cuf. ex Greuter & Burdet (*tephqurt*), *Tephrosia uniflora* Pers. subsp. *petrosa* (Blatt. & Hallb.) J. B. Gillett & Ali (*tephunif*), *Tephrosia villosa* (L.) Pers. subsp. *ebrenbergiana* (Schweinf.) Brummitt (*tephvilo*), *Tetragonolobus maritimus* (L.) A.W. Roth (*tetrgrnmr*), *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 oculata* 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 (*vichirs*), *Vicia hybrida* L. (*vichybr*), *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*).