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Intergeneric relationships between *Psophocarpus* Necker ex DC. (Phaseoleae, Leguminosae) and its allies

NIGEL MAXTED

ABSTRACT

MAXTED, N. (1991). Intergeneric relationships between *Psophocarpus* Necker ex DC. (Phaseoleae, Leguminosae) and its allies. *Candollea* 46: 367-382. In English, English and French abstracts.

Morphological data were gathered from herbarium specimens representing 27 genera of the *Phaseoleae*, including *Psophocarpus*. OTUs were scored for four vegetative and 69 inflorescence characters. The initial data matrix was analysed using cluster analysis and the genera found to be most closely related to *Psophocarpus* were *Otoptera*, *Vigna*, *Sphenostylis*, *Nesphostylis*, *Dysolobium* and *Dolichos*. These genera, with *Phaseolus* as an outlier group, were then scored for three vegetative, 41 inflorescence, six legume and two seed characters. The resultant data matrix was analysed using cluster analysis and an ordination method. The results indicated *Otoptera* to be the closest phenetic ally of *Psophocarpus* and this is reflected in the classification produced. The classification is discussed in relation to previous placements of *Psophocarpus* in the *Phaseoleae*.

RÉSUMÉ

MAXTED, N. (1991). Relations intergénériques entre *Psophocarpus* Necker ex DC. (Phaseoleae, Leguminosae) et les genres voisins. *Candollea* 46: 367-382. En anglais, résumés anglais et français.

Les données morphologiques ont été rassemblées à partir de spécimens d'herbier et ont porté sur 27 genres de *Phaseolae*, y compris *Psophocarpus*. Des critères (OTU) ont été enregistrés sur quatre caractères végétatifs et 69 caractères de l'inflorescence. La matrice initiale des données a été soumise à l'analyse factorielle et les genres qui se sont révélés les plus proches de *Psophocarpus* sont: *Otoptera*, *Vigna*, *Sphenostylis*, *Nesphostylis*, *Dysolobium* et *Dolichos*. Ensuite, ces genres, de même que le groupe plus éloigné de *Phaseolus*, ont été jugés sur la base de deux caractères de graines, de la gousse, 41 de l'inflorescence et trois caractères végétatifs. La matrice ainsi formée a été soumise à l'analyse factorielle. Les résultats indiquent qu'*Otoptera* est le plus proche voisin phénotypique de *Psophocarpus*, ce qui se reflète dans la classification produite. Cette classification est discutée à la lumière des positions taxonomiques précédemment attribuées à *Psophocarpus* dans les *Phaseoleae*.

Psophocarpus Necker ex DC. consists of ten tropical legume species, nine of which are endemic to West, Central and East Africa (MAXTED, 1990). The genus contains the commercially important winged bean (*P. tetragonolobus* (L.) DC.), which is unknown in the wild and whose cultivation was until recently restricted to Asia.

The genus is variable with species showing climbing, prostrate and erect habits; uni- and trifoliolate leaves; flowers borne singly, in fascicles or on false racemes; ovaries with 3-21 ovules; and two distinct style apex shapes, one connate and the other distinctly laterally extended. However, the genus is clearly unified by the following characters: stipules prolonged below the point of insertion; upper pair of calyx teeth forming an entire or bifid lip; standard broad, auriculate and appendaged; keel beaked at right angles to the axis of the flower; style thickened above the ovary; presence of hairs below the stigma; pods oblong, 4-winged along the angles and septate between the seeds.

Nine species of *Psophocarpus* were accepted and revised by VERDCOURT & HALLIDAY (1978), and a tenth species was recently distinguished by VERDCOURT (pers. comm.). The authors

of this revision did not suggest alliances between *Psophocarpus* and other genera, although they did place it in the legume tribe *Phaseoleae* DC. The *Phaseoleae* (sensu LACKEY, 1981) is the largest tribe in the *Papilionoideae*, with about 84 genera and is economically the most important worldwide. LACKEY (1981) divided the tribe into eight subtribes. After searching the literature and discussing the problem of the breadth of the group to be investigated with *Phaseoleae* specialists (B. VERDCOURT, R. M. POLHILL, R. MARÉCHAL & J. C. BAUDET), it was decided to focus the investigation on two *Phaseoleae* subtribes, the *Phaseolinae* Benth. and *Clitoriinae* Benth. These two subtribes contain 27 genera and approximately 485 species (LACKEY, 1981). The initial phase of the study was to survey the 27 genera to select a subset of genera most closely allied to *Psophocarpus* followed by a more detailed study of the subset genera.

With the increasing importance of *P. tetragonolobus* in helping to alleviate the third world protein deficit, greater importance is being given to attempting wide crosses with other *Phaseoleae* species, such as *Vigna* Savi spp., *Dolichos* L. spp. and even *Glycine max* (L.) Merr. For plant breeders to utilize the potential genepool efficiently, the classification and the position of *Psophocarpus* in relation to its allies must be better understood. The objective of this research was to clarify the generic relationships between *Psophocarpus* and its allies.

Taxonomic history

The genus *Psophocarpus* was proposed by Necker in 1790, but was validly published by DE CANDOLLE (1825a). De Candolle included one species, *P. tetragonolobus* (L.) DC., based on the Linnaean species *Dolichos tetragonolobus*. He placed *Psophocarpus* in the tribe *Phaseoleae* between *Dioclea* Kunth and *Canavalia* DC., with the nearest genera of the *Phaseolinae* (sensu LACKEY, 1981) being *Lablab* Adans., *Vigna*, *Dolichos* and *Phaseolus* L. Later authors have considered *Otoptera* DC. as a possible close ally of *Psophocarpus*. DE CANDOLLE (1825b) discussed the generic position of *Otoptera* in detail. He referred to the possible inclusion of *Otoptera* in the *Phaseoleae*, but ultimately concluded it had more in common with *Clitoria* L. and thus included it in his tribe *Loteae*.

BENTHAM (1840) used the *Phaseoleae* and *Loteae* (sensu DE CANDOLLE, 1825a) to form what with minor changes is regarded as the modern *Phaseoleae*. His view of the placement of *Psophocarpus* is similar to that adopted by DE CANDOLLE. BENTHAM (1865) placed *Psophocarpus* between *Dolichos* and the *Vigna-Phaseolus* complex of genera in his *Phaseoleae* subtribe *Euphaseoleae*. He included the then newly described genus *Sphenostylis* E. Meyer in his classification and allied it to *Psophocarpus*, but did not link *Psophocarpus* with *Dysolobium* (Benth.) Prain, a genus subsequently considered closely allied to *Psophocarpus*.

TAUBERT (1894) placed *Psophocarpus* on the periphery of the *Phaseolinae*, with *Dolichos* as a close ally, then *Vigna* and *Phaseolus* even more remote. He considered *Dysolobium* a subgenus of *Phaseolus* and did not mention *Otoptera*. HARMS (1914) rearranges Taubert's *Phaseolinae* genera placing *Psophocarpus* centrally with *Otoptera* and *Vigna*, then *Dolichos* on one side, and *Sphenostylis*, *Dysolobium* and *Phaseolus* on the other. Essentially he moved *Psophocarpus* away from *Dolichos* and placed it in the spectrum of genera between *Phaseolus* and *Vigna*. Harms included *Vignopsis* De Wild. (syn. *Psophocarpus*) near *Vigna*, but at a distance from *Psophocarpus* itself. WILCZEK (1954) subsequently sank *Vignopsis* in *Psophocarpus*, giving *Vignopsis* sub-generic status.

LACKEY (1977) undertook a synopsis of the *Phaseoleae*, dividing the tribe into seven subtribes similar to those suggested by BENTHAM (1840). He placed *Psophocarpus* in the subtribe *Phaseolinae*, allied with *Dysolobium*, but he questioned the natural placement of both genera within the *Phaseolinae*. Lackey commented that he included these genera in the *Phaseolinae* because this is where they have traditionally been placed and because of the fact that these genera fit even less well in the other *Phaseoleae* subtribes. He argued strongly that the two genera are closely allied and listed several shared floral, fruit and seed characteristics. Subsequently, MARÉCHAL & al. (1978) have questioned the strength of this evidence in supporting Lackey's hypothesis, but they acknowledge that *Psophocarpus* and *Dysolobium* do have a closer relationship than had been previously noted.

In the same year a second classification of the *Phaseoleae* was published by BAUDET (1977). This involved a more radical rearrangement of the genera into three subtribes and eight supergenera, an idea originally proposed by BAUDET & MARÉCHAL (1976). Baudet effectively splits the *Phaseolinae* genera into two supergenera: the *Phaseolastrae* Baudet & Maréchal, based on the *Phaseolus*—*Vigna* complex and allied genera; and the *Dolichastrae* Baudet & Maréchal, based on *Dolichos* and its allies. He included *Psophocarpus* in the *Dolichastrae* and suggests *Dolichos*, *Decorsea* and *Otoptera* as close relatives.

Subsequently, LACKEY (1981) revised his classification of the *Phaseoleae*. His placement of *Psophocarpus* is still peripheral along with *Dysolobium*, although the order of major genera is reversed so that *Dolichos* is closest to *Psophocarpus*, then more remotely *Vigna* and *Phaseolus*. In the revised classification he excluded *Clitoria* and its allies from the *Phaseolinae*, reinstating Bentham's subtribe *Clitoriinae*. The *Phaseolinae* classifications of BAUDET (1977) and LACKEY (1981) are shown in Table 1.

Materials and methods

Due to the large number of taxa involved in this study and the difficulty in obtaining viable seed for the majority, the investigation was necessarily herbarium based. Specimens were loaned from a number of major international herbaria: K, BM, P, BR, G, TUS and SRGH.

The study was divided into two phases, an initial survey of all 27 genera of the *Phaseolinae* Benth. and *Clitoriinae* Benth., followed by a more vigorous investigation of those genera shown in the initial survey to be the most closely allied to *Psophocarpus*. For the initial survey a few specimens were carefully selected to represent species that were characteristic of each the 27 genera, but for the larger genera (*Vigna*, *Dolichos* and *Phaseolus*), a greater number of specimens were selected to reflect the greater internal variability in these genera. These three large genera were included in the more intensive survey of the genera closely allied to *Psophocarpus*, and in this second phase care was taken to select specimens of species which would fully represent the detailed subgeneric variation pattern.

The 151 specimens (OTUs) included in the initial survey were scored for four vegetative and 69 inflorescence characters. For the survey of the subset of genera shown to be most closely allied to *Psophocarpus* over 600 specimens were scored for 315 characters. Following the scoring of several specimens for each taxon, taxon (OTU) data was analysed. To produce the taxon data for each taxon the mode was calculated for each continuous character and the most common character state was used for the multistate characters. The mode was calculated by dividing the range into ten equal bands, scoring the number of records that fell in each band and then using the mean figure for the most common band. This method of calculating the taxon scores does imply a certain characteristic for the multistate data; that only one score is common, that character scores are not evenly distributed between two or more states. This assumption is valid for the majority characters and so was considered a satisfactory assumption for the analysis as a whole. The 88 taxa included in this study were scored for three vegetative, 41 inflorescence, six legume and two seed characters. The characters used were selected from the literature (VERDCOURT, 1970a, b and c, and 1971; MARÉCHAL & al., 1978; LACKEY, 1977; and BAUDET, 1977) and from personal observations of the material. These characters and character states are listed in Appendix 1. The number of character states used was determined in such a way as to reflect the greatest separation of OTUs.

The two computer programs used for the phenetic analysis were LINKAGE and CLUSTAN 1C. LINKAGE is a FORTRAN program written by WIRTH & al. (1966) which undertakes single linkage (nearest neighbour) cluster analysis using graph theory. The program uses the simple matching coefficient to calculate the similarity matrix. For the initial survey of the 27 genera there were many OTUs with missing data. LINKAGE is able to compensate for this and calculates similarity only for those character scores that are available. CLUSTAN 1C is a suite of FORTRAN programs written by WISHART (1975) for cluster and multivariate analysis. In the survey of the subset of genera closely allied to *Psophocarpus*, CLUSTAN was used to undertake group average cluster analysis, Ward's method of cluster analysis and principal components analysis (PCA).

BAUDET (1977) Subtribe <i>Phaseolinae</i> Supergenera		LACKEY (1981) Subtribe <i>Phaseolinae</i>
<i>Phaseolastrae</i>	<i>Dolichstrae</i>	
<i>Genera</i> <i>Vigna</i> <i>Voandzeia</i> <i>Physostigma</i> <i>Vatovaea</i> <i>Dipogon</i> <i>Lablab</i> <i>Spathionema</i> <i>Dysolobium</i> <i>Peckelia</i> <i>Oxyrhynchus</i> <i>Condyllostylis</i> <i>Dolichopsis</i> <i>Macroptilium</i> <i>Ramirezella</i> <i>Alepidocalyx</i> <i>Minklersia</i> <i>Phaseolus</i> <i>Strophostyles</i>	<i>Genera</i> <i>Dolichos</i> <i>Decorsea</i> <i>Psophocarpus</i> <i>Otoptera</i> <i>Alistilus</i> <i>Sphenostylis</i> <i>Nesphostylis</i> <i>Austrodolichos</i>	<i>Genera</i> <i>Dysolobium</i> <i>Psophocarpus</i> <i>Physostigma</i> <i>Vatovaea</i> <i>Decorsea</i> <i>Spathionema</i> <i>Otoptera</i> <i>Sphenostylis</i> <i>Nesphostylis</i> <i>Austrodolichos</i> <i>Neorautanenia</i> <i>Lablab</i> <i>Alistilus</i> <i>Dipogon</i> <i>Dolichos</i> <i>Macrotyloma</i> <i>Vigna</i> <i>Ramirezella</i> <i>Oxyrhynchus</i> <i>Dolichopsis</i> <i>Strophostyles</i> <i>Macroptilium</i> <i>Phaseolus</i>

Table 1. — *Phaseolinae* classifications of BAUDET (1977) and LACKEY (1981).

Results

The results of the initial 27 genera analysis using LINKAGE are produced in the form of a series of linkage diagrams, 136 for the data set analysed. The diagrams are arranged in order of decreasing similarity from a level of 0.88 to a level of 0.59, when all the OTUs are joined in one cluster. Figure 1 shows the diagram with a similarity level of 0.64 in which the *Psophocarpus* OTUs begin to form links with the closely allied genera. If the similarity level is reduced further the *Psophocarpus* OTUs form multiple links with many other genera. So at this level of similarity *Psophocarpus* can be seen to have links with the subset of genera, which are most closely allied to it.

The interpretation of the linkage diagrams requires some discussion. At a given threshold level of similarity each pair of OTU's will cluster and this is demonstrated in the diagram by a line connecting the OTU's. This connecting line may be of three kinds, indicating three possible kinds of relationships between OTU's; a single line indicating a relationship established at a higher level of similarity, a double line indicating a new relationship established at that particular similarity level and a broken line which indicates a new internal (within cluster) link at that similarity level. To simplify interpretation of the diagrams highly intra-connected clusters are encircled. The criterion for inclusion into a circle is that each OTU should have at least three links with other members of the same cluster. A key to the symbols representing OTUs in each figure is provided in Table 2.

The linkage diagram shown in Figure 1 shows two main clusters of OTUs, one representing the genera of *Clitoriinae* and the other the genera of *Phaseolinae*. All the *Psophocarpus* OTUs are grouped together in one encircled cluster, this cluster also contains one non-*Psophocarpus* OTU, a specimen of *Neorautanenia ficifolius* (Benth.) C. A. Smith. Other genera forming direct links with *Psophocarpus* are *Otoptera*, *Vigna*, *Sphenostylis*, *Dysolobium* and *Dolichos*. These six genera plus *Nesphostylis* Verdc., *Phaseolus* and *Psophocarpus* were used for the detailed investigation.

Table 2. — Key to the symbols used to represent genera in figures.

Subtribe <i>Clitoriinae</i>			
Genus		Symbol	
<i>Centrosema</i>		+	
<i>Periandra</i>		×	
<i>Clitoria</i>		^	
<i>Clitoriopsis</i>		v	
Subtribe <i>Phaseolinae</i> — Supergenera			
<i>Phaseolastrae</i>		<i>Dolichastrae</i>	
Genera	Symbol	Genera	Symbol
<i>Vigna</i>	■	<i>Dolichos</i>	□
<i>Macrotyloma</i>	▀	<i>Decorsea</i>	◊
<i>Physostigma</i>	◐	<i>Psophocarpus</i>	○
<i>Vatovaea</i>	◑	<i>Otoptera</i>	☆
<i>Dipogon</i>	▼	<i>Alistilus</i>	▷
<i>Lablab</i>	▶	<i>Sphenostylis</i>	△
<i>Spathionema</i>	✂	<i>Nesphostylis</i>	▽
<i>Dysolobium</i>	▲	<i>Austrodolichos</i>	◁
<i>Oxyrhynchus</i>	◓	<i>Neorautanenia</i>	◊
<i>Dolichopsis</i>	◔		
<i>Macroptilium</i>	◄		
<i>Ramirezella</i>	★		
<i>Phaseolus</i>	●		
<i>Strophostyles</i>	◆		

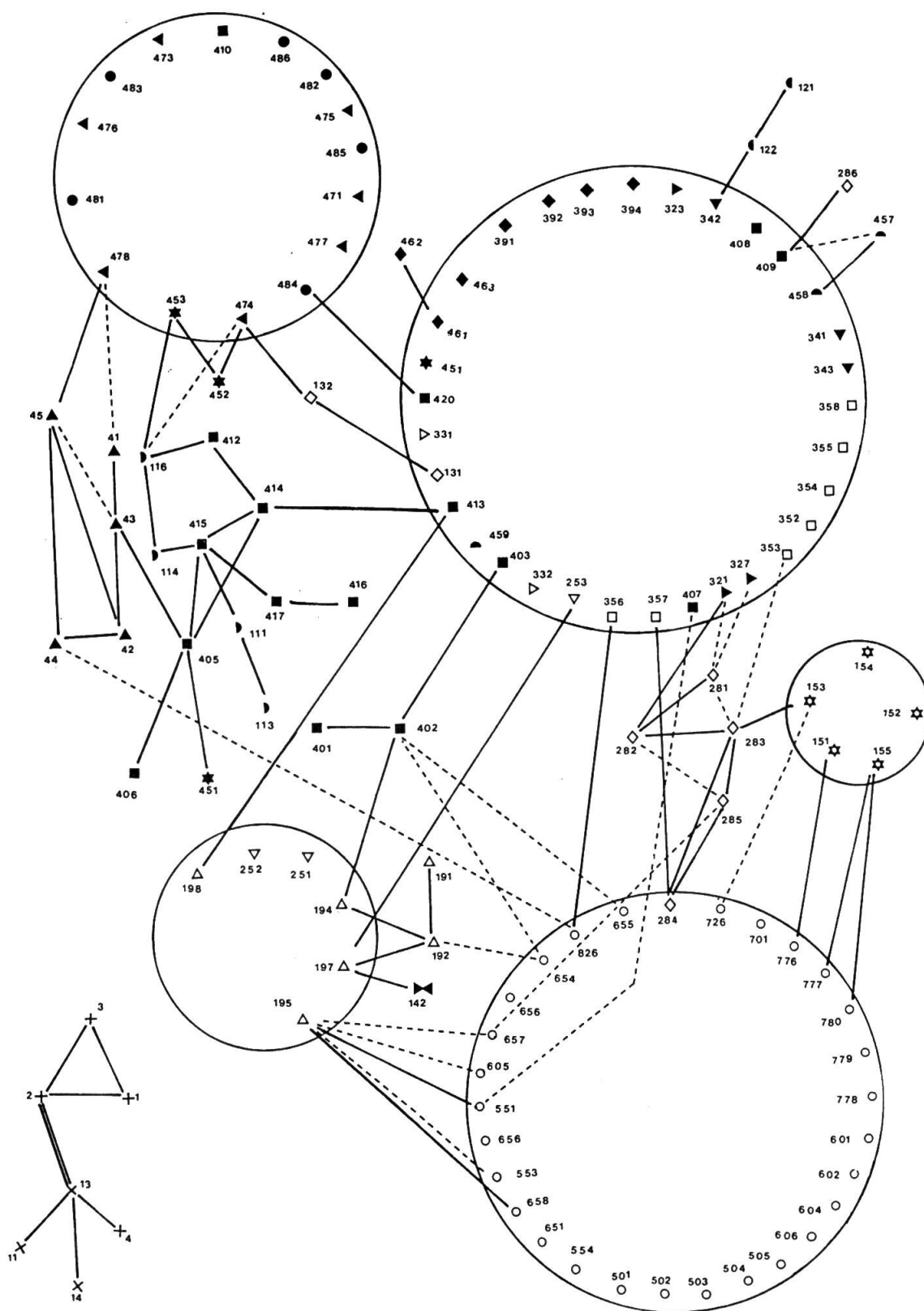


Fig. 1. — Single linkage cluster analysis of the 27 genera of the *Phaseolinae* and *Clitoriinae*. Linkage level 129 at a similarity level of 0.6389. Seven OTUs not yet linked.

Nesphostylis was added because the diagram shows it so intimately linked to *Sphenostylis*, from which it had only recently been split (VERDCOURT, 1970a) and *Phaseolus* was added to act as an outlier group to give scale to the results.

The data-set for the nine genera was first analysed using group average cluster analysis via the program CLUSTAN. The resulting dendrogram is shown in Figure 2, where the *Psophocarpus* OTUs can be seen to form a distinct generic cluster. The first genus to cluster with *Psophocarpus* is *Ooptera*, followed by *Dysolobium*. These three genera form a distinct grouping, while the remaining genera form the larger cluster of the dendrogram. Within the larger cluster, two smaller clusters of OTUs are found, one containing *Dolichos* and its allies *Neorautanenia*, *Sphenostylis* and *Nesphostylis* and the second containing *Phaseolus* and *Vigna*.

The result of the analysis using Ward's method of cluster analysis is shown in Figure 3. The dendrogram shows the OTUs dividing into two main clusters, one containing the *Phaseolus*—*Vigna* OTUs with *Dysolobium* as a distinct unit. The second major cluster is further split into two, one cluster containing *Psophocarpus* and *Ooptera*, while the other is made up of *Dolichos*, *Sphenostylis*, *Nesphostylis* and *Neorautanenia*.

The results of the principal components analysis shown in Figure 4 give groupings of OTUs similar to those obtained using the cluster analysis methods, *Psophocarpus* is placed near *Ooptera* and these two genera are slightly remote from the other genera. Within the main cluster *Neorautanenia*, *Sphenostylis* and *Dysolobium* OTUs are spatially closest to *Psophocarpus*. As in the previous analysis *Dolichos* on one hand and *Phaseolus* and *Vigna* on the other form two distinct clusters within the main cluster of OTUs.

Discussion

The phenetic classification of the relationship between *Psophocarpus* and its close allies in the *Phaseolinae* is presented in Figure 5. It is worth stressing the degree of agreement between the results of the different methods of analysis, this strengthens the value of the proposed classification and indicates that it is more likely to be based on natural generic relationships.

The general conclusion indicated by each method of phenetic analysis is that *Psophocarpus* is most closely related to *Ooptera* and these two genera are relatively isolated from the other genera. A third genus, *Dysolobium*, is shown to be more remotely related to *Psophocarpus*. The intimate relationship of *Psophocarpus* with *Ooptera* clearly supports the views of BAUDET (1977) who allied the genera in his classification of the *Phaseoleae*.

The classification of the *Phaseolinae* proposed by LACKEY (1981) does not suggest a close relationship between *Ooptera* and *Psophocarpus*, but he does suggest that *Dysolobium* is closely allied to *Psophocarpus*. LACKEY (1977) discusses this relationship in detail and provides several synapomorphic characters which support his thesis. He did not note, however, that some of the character states shared by *Dysolobium* and *Psophocarpus* are also shared by *Ooptera*, e.g. keel petals joined weakly and intermittently at the apex, fruits septate with spongy tissue and the prominence of the lower calyx tooth. The present study highlighted a group of characters which link *Psophocarpus* with *Ooptera*: stipules lanceolate, produced below their point of attachment, base of bract and bracteole produced below point of attachment, absence of tooth on ventral edge of wing, style thickened at base and the presence of two callosities at the base of the vexillum limb.

The results broadly support the splitting of the sub-tribe *Phaseolinae* into two groupings. Each method of analysis shows the *Phaseolinae* genera studied falling into two broad clusters, one centred around *Dolichos* and the other around the *Phaseolus*—*Vigna* complex. These two clusters are consistent with the supergenera, *Dolichastrae* and *Phaseolastrae* proposed by BAUDET & MARÉCHAL (1976).

Having established that the results in general support the use of two supergenera within the *Phaseolinae*, it is difficult to place *Psophocarpus* in either the *Dolichastrae* or the *Phaseolastrae*. It could be argued that *Psophocarpus* is sufficiently distinct to warrant the establishment of a third mono-generic supergenus. *Psophocarpus* exhibits characteristics of both existing supergenera and as such it seems to form a natural link between these two distinct supergeneric groupings.

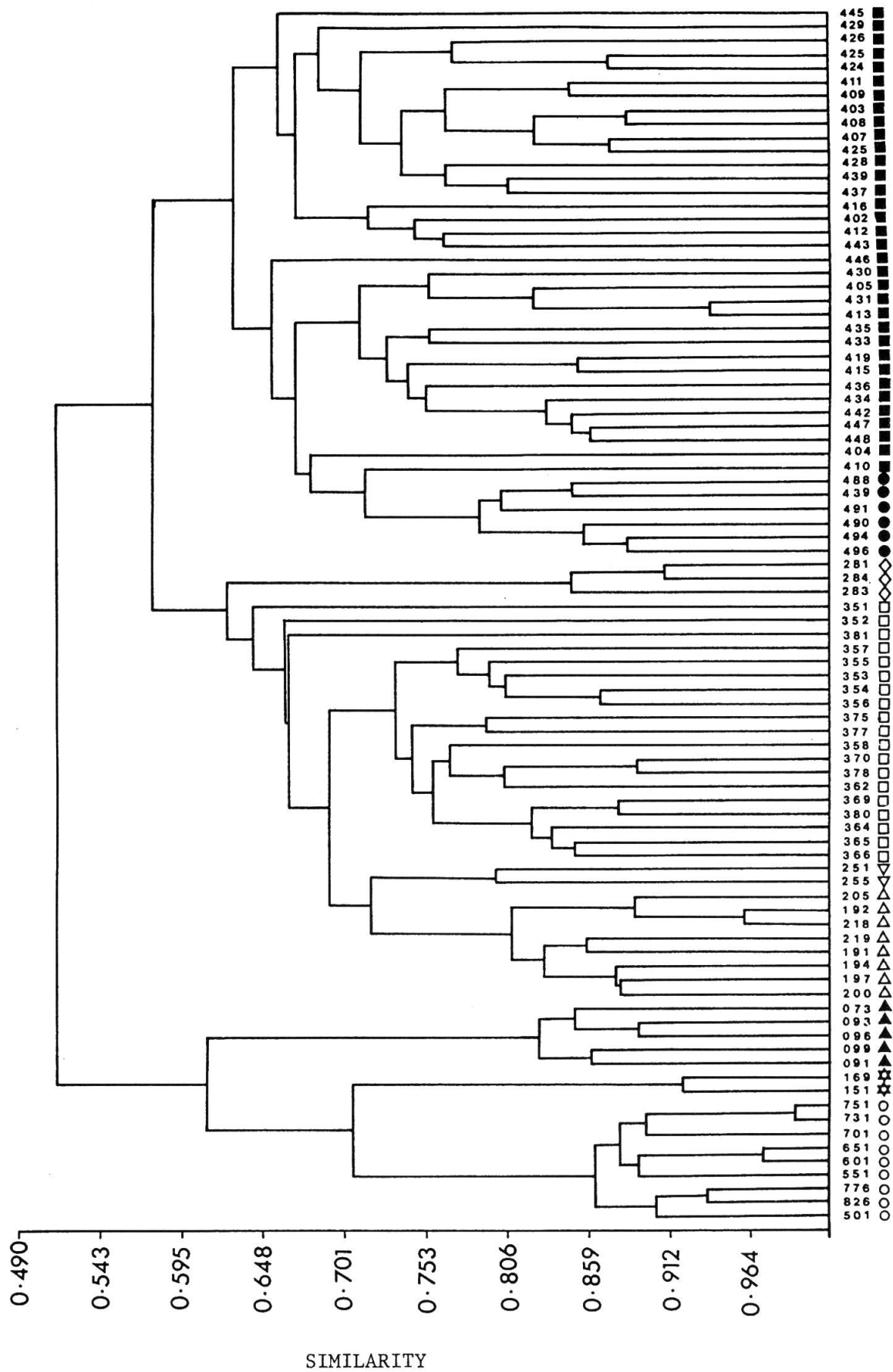
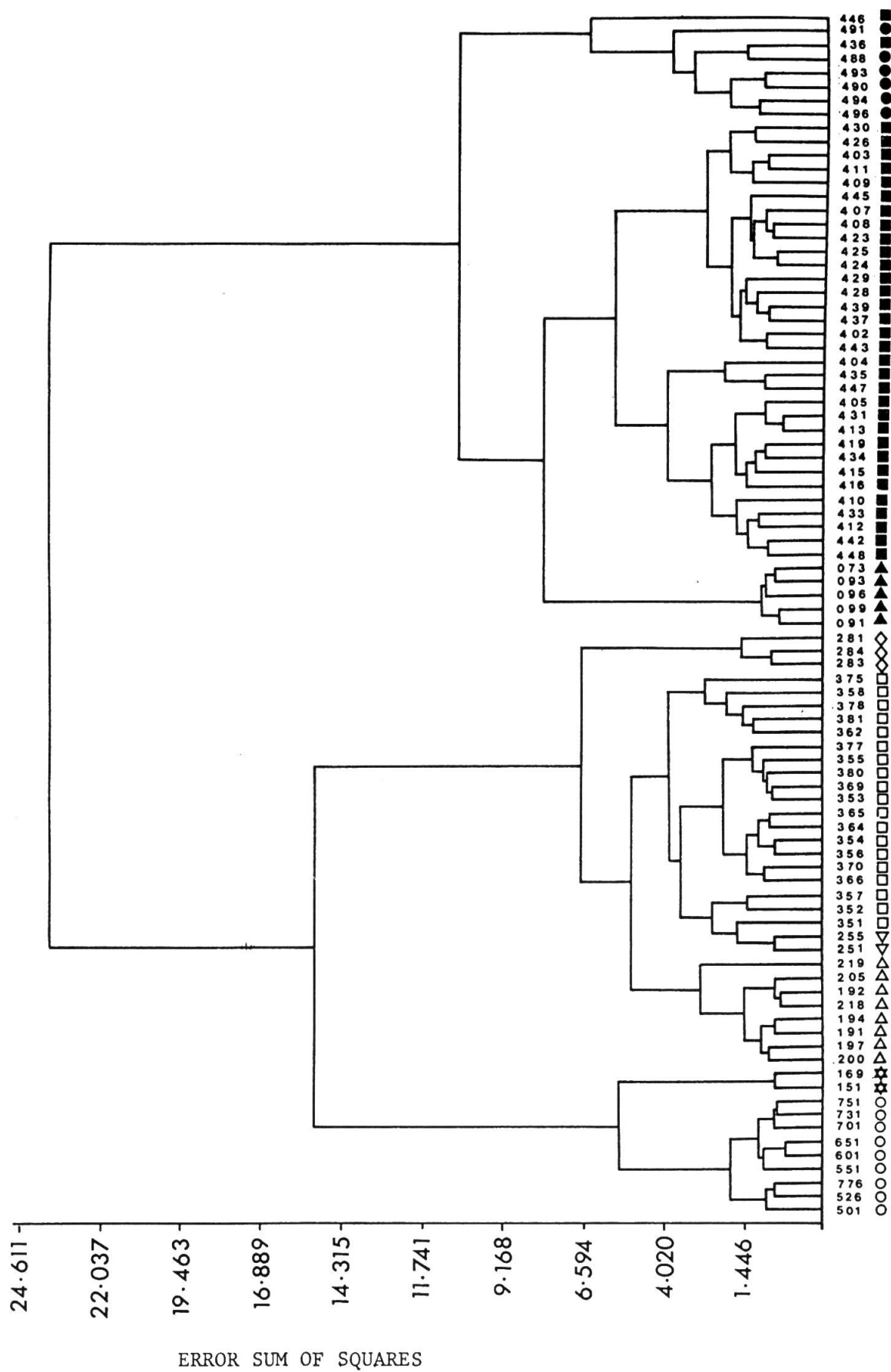
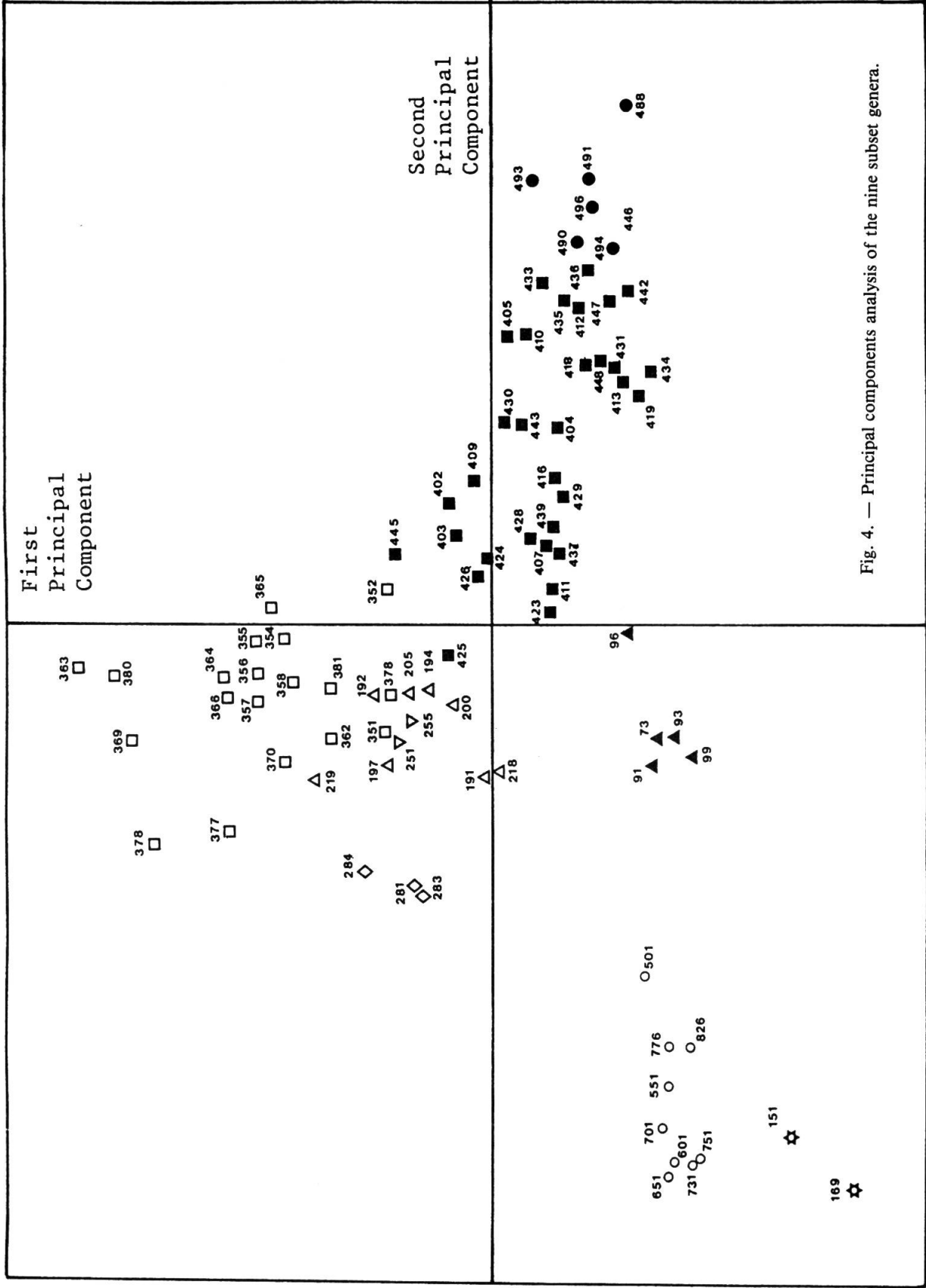


Fig. 2. — Group average cluster analysis of the nine subset genera.





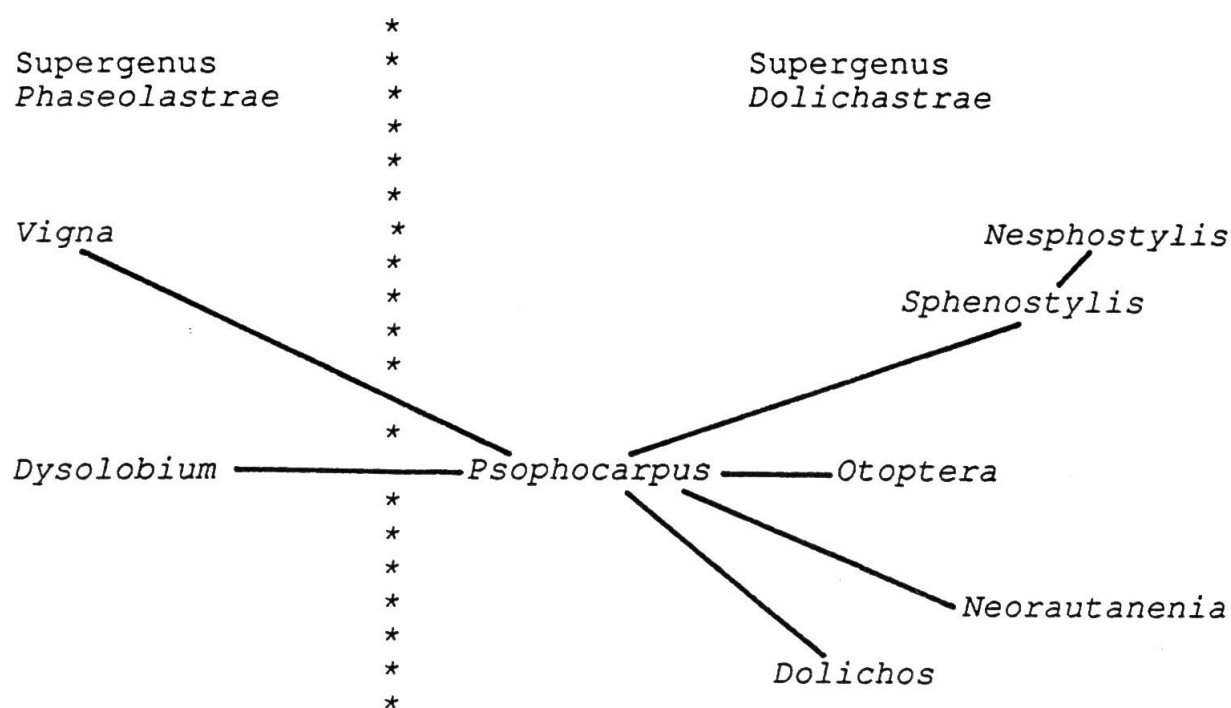
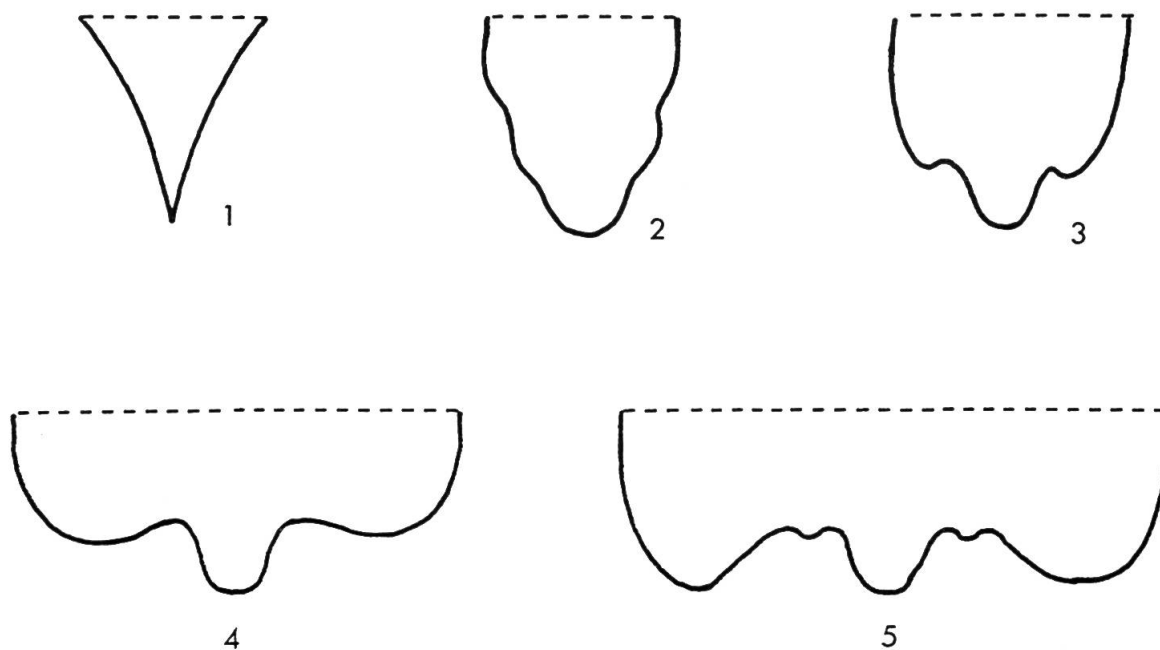


Fig. 5. — Phenetic classification of *Psophocarpus* and its close *Phaseolinae* allies. Lines joining and distances between generic names indicates the relative taxonomic affinities.

Fig. 6. — Corolla base shape, character 26.



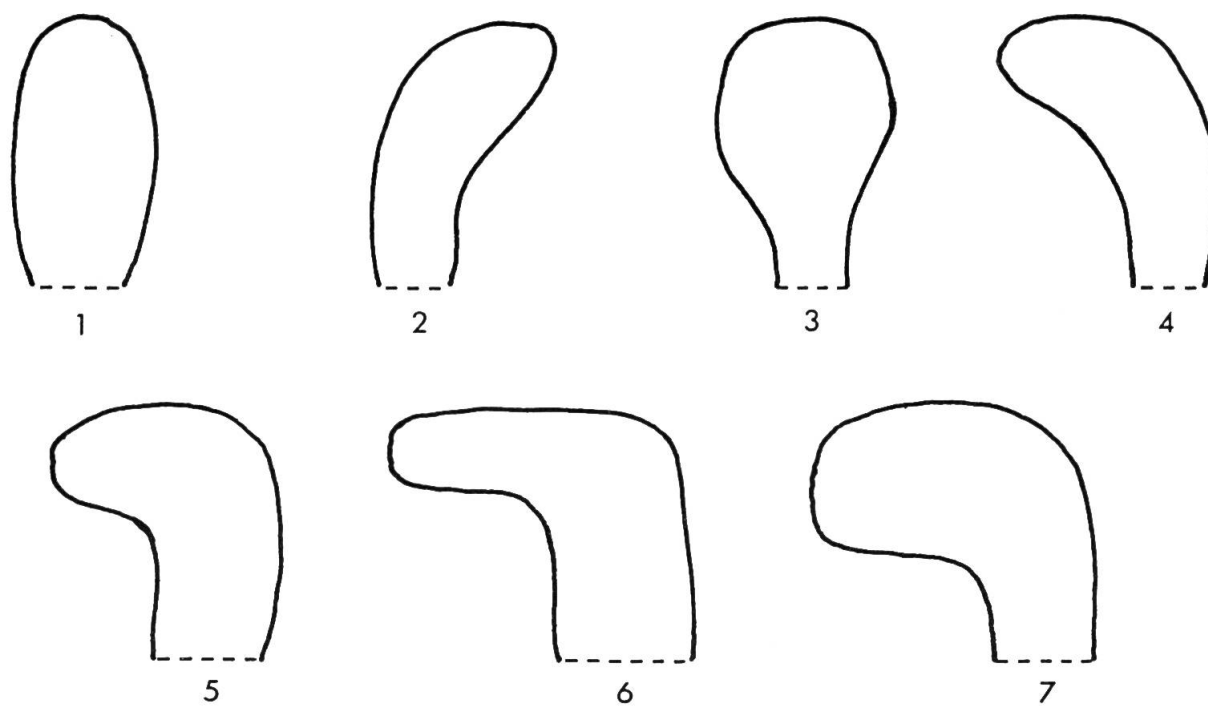
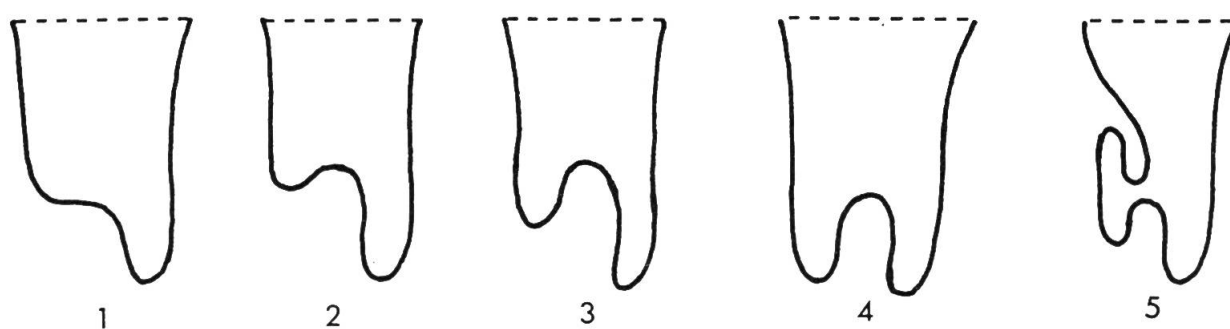


Fig. 7. — Wing shape, character 35.

Fig. 8. — Wing base shape, character 36.



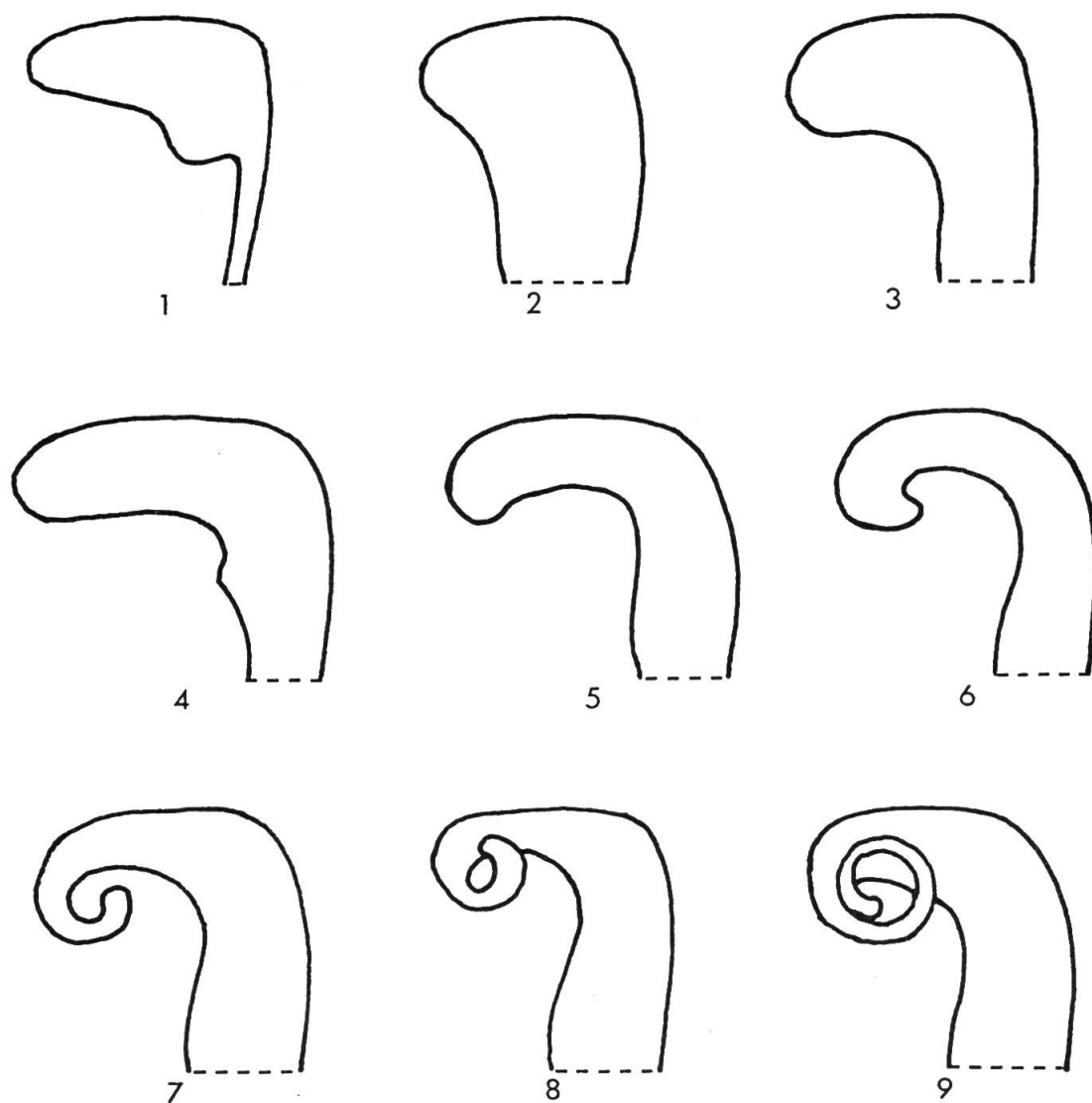
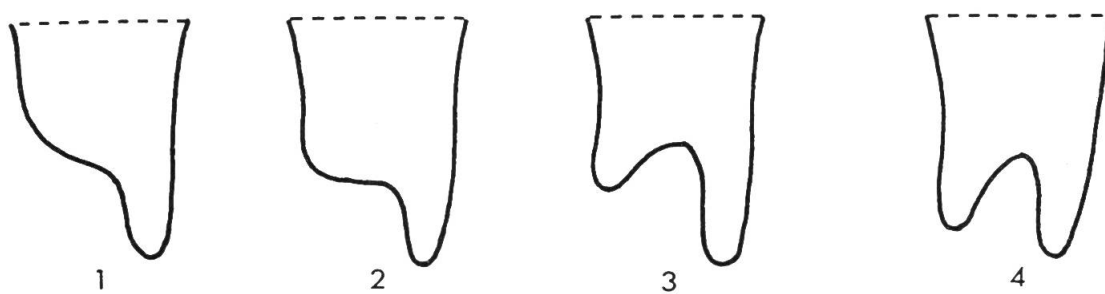


Fig. 9. — Keel shape, character 51.

Fig. 10. — Keel base shape, character 52.



The fact that *Psophocarpus* does not fit ideally into either of these supergenera may explain why previous authors have had such problems in describing its generic relationship with the three larger genera of the *Phaseolinae*, (*Dolichos*, *Vigna* and *Phaseolus*). The overall results, however, indicate that *Psophocarpus* has a closer link with the *Dolichastrae* genera, than with those in the *Phaseolastrae*.

Appendix 1. — Phenetic character set.

The character set is displayed in the order: character number; character name; character states if applicable; + indicates use in Initial (I) analysis or in Subset (S) analysis.

	I	S
1. Growth habit: erect, ascending, climbing, scrambling, procumbent	+	—
2. Stipule base shape: truncate, extended below point of attachment	+	+
3. Stipule lateral to terminal length ratio: lateral longer, approx. equal length	+	—
4. Pattern of leaflet venation: reticulate, parallel	—	+
5. Leaflet abaxial hair apex: hooked, straight	+	+
6. Type of inflorescence: panicle, pseudoraceme	—	+
7. Type of inflorescence node: nodose, not nodose	+	+
8. Number of nodes per inflorescence	+	—
9. Number of flowers per node	+	—
10. Flower orientation: resupinate, not resupinate	+	—
11. Shape of upper calyx tooth: obtuse, rounded, acute, emarginate, bifid	—	+
12. Shape of lateral calyx teeth: obtuse, rounded, acute, acuminate	+	—
13. Shape of lower calyx tooth: obtuse, rounded, acute, acuminate	+	—
14. Lower calyx tooth to length: mm	+	—
15. Lateral calyx teeth to length: mm	+	—
16. Ratio of calyx length to lateral teeth length	+	—
17. Ratio of calyx length to upper tooth length	+	—
18. Ratio of calyx length to calyx tube length	+	+
19. Calyx interior hair position: absent, teeth edge only, teeth only, teeth and top of tube, teeth and tube	+	—
20. Calyx interior hair tuft: present, absent	+	—
21. Corolla exterior papillate: present, absent	—	+
22. Corolla length: mm	+	—
23. Corolla claw width: mm	+	—
24. Ratio of corolla length to width	+	—
25. Corolla apex shape: emarginate, rounded, obtuse	+	+
26. Corolla base shape: see Figure 6	+	+
27. Corolla symmetry: bilateral, asymmetric	+	+
28. Corolla auricle shape: absent, two diverging diagonals, other shapes	+	+
29. Corolla pubescence: glabrous, pubescent	+	+
30. Wing length: mm	+	—
31. Wing width: mm	+	—
32. Wing claw length: mm	+	—
33. Wing spur length: mm	+	—
34. Wing width above claw: mm	+	—
35. Wing shape: see Figure 7	+	+
36. Wing base shape: see Figure 8	+	+
37. Wing pouch: present, absent	+	+
38. Wing spiralling: present, absent	+	+
39. Wing pubescence: glabrous, pubescent	+	+
40. Wing-keel adhesion: wing adheres to keel, wing free from keel	+	+
41. Wing extra tooth: tooth present on abaxial surface, tooth absent	+	+
42. Ratio of wing length to width	+	—
43. Ratio of wing length to claw length	+	—
44. Ratio of corolla to wing length	+	—
45. Keel length: mm	+	—
46. Keel width: mm	+	—
47. Keel claw length: mm	+	—
48. Ratio of keel length to width	+	—
49. Ratio of keel length to claw length	+	—
50. Ratio of corolla to keel length	+	—
51. Keel shape: see Figure 9	+	+
52. Keel base shape: see Figure 10	+	+
53. Keel pouches: absent, present on one side, present on both sides	+	+
54. Keel spiralling: absent, present	+	+
55. Keel corrugation: absent, present	+	+

56.	Keel pubescence: absent, present	+	+
57.	Keel fusion: abaxial surface only, abaxial and adaxial surface	+	+
58.	Keel fusion type: complete fusion, slight toothing, strong toothing	+	+
59.	Staminal filament dilation: absent, present	+	+
60.	Staminal tube apex shape: acuminate, acute, obtuse, truncate	+	—
61.	Staminal tube curvature: straight, curved	+	+
62.	Vexillary staminal attachment: free, loosely joined to tube, fused to tube	+	+
63.	Vexillary staminal base shape: straight, curved, swollen, base at right angle to the filament	+	+
64.	Staminal filament length pattern: truncate, stepped and acute, acute	+	—
65.	Staminal pubescence: glabrous, pubescent	+	—
66.	Ovary shape: linear, intermediate, oblong	+	+
67.	Ovary cross-sectional shape: rounded, channelled, ridged	+	+
68.	Ovary pubescence: glabrous, abaxial surface only, abaxial and adaxial surface, adaxial surface only, all over ovary	—	+
69.	Style apex cross-sectional shape: laterally flattened, rounded, ventrally flattened, triangular	+	—
70.	Style thickness: filiform, intermediate, large	—	+
71.	Style spiralling: absent, present	+	+
72.	Style pubescence: glabrous, pubescent	+	—
73.	Style post-stigma: absent, present	+	+
74.	Style apex hairs: glabrous, apex only, apex and lower surface, apex and behind apex	+	+
75.	Style thickening: absent, thickened at base, thickened in middle, thickened at apex	+	+
76.	Style to ovary curvature: right angled, intermediate, smooth curvature	+	—
77.	Degree of style curvature: not curved, 45, 90-180, 180-360, over 360 degrees	+	+
78.	Style apex spatulate: absent, present	+	—
79.	Stigma position: lateral, apical, terminal	+	+
80.	Style apex channelling: absent, present	—	+
81.	Style apex shape: simple, like <i>Otoptera</i> , spatulate, capitate, at right angles to style	—	+
82.	Stigma shape: round, elongated	—	+
83.	Legume shape: linear, oblong, rectangular	—	+
84.	Legume wing: absent, present	—	+
85.	Legume cross-sectional shape: round, laterally flattened, square	—	+
86.	Legume twisting after dehiscence: very loose, loose, intermediate, tight, very tight	—	+
87.	Legume partition type: absent, woolly, spongy, papery	—	+
88.	Persistence of calyx on legume: absent, seen on immature pod, seen on mature pod	—	+
89.	Ratio of seed circumference to hilum length	—	+
90.	Seed finish: shiny, matt, velvet	—	+

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REFERENCES

- BAUDET, J. C. (1977). *Essai de classification générique des Papilionaceae-Phaseoleae*. Thesis, Univ. Paris-VI.
- BAUDET, J. C. & R. MARÉCHAL (1976). Signification taxonomique de la présence de poils uncinulés chez certain genres de Phaseoleae et d'Hedysareae (Papilionaceae). *Bull. Jard. Bot. Natl. Belgique* 46: 419-426.
- BENTHAM, G. (1840). De Leguminosarum generibus commentationes. *Ann. Wiener Mus. Naturgesch.* 2: 61-142.
- BENTHAM, G. (1865). Leguminosae. In: BENTHAM, G. & J. D. HOOKER, *Genera Plantarum* 1: 434-600. London, Lovell Reeve and Co.
- DE CANDOLLE, A. P. (1825a). *Prodromus systematis naturalis regni vegetabilis*. Paris, Treuttel Et Wurtz.
- DE CANDOLLE, A. P. (1825b). *Mémoires sur la famille des Légumineuses*. Paris, A. Belin.
- HARMS, H., (1914). Phaseoleae. In: ENGLER, A. & K. PRANTL, *Die natürlichen Pflanzenfamilien, Nachtrag* 4: 148-151. Leipzig, Withelm Engelmann.
- LACKEY, J. A. (1977). A revised classification of the tribe Phaseoleae (Leguminosae, Papilionoideae), and its relation to canavanine distribution. *Bot. J. Linn. Soc.* 74: 163-178.
- LACKEY, J. A. (1981). Phaseoleae. In: POHILL, R. M. & P. H. RAVEN, *Advances in legume systematics*: 301-327. London, Crown Agents.
- MARÉCHAL, R., J. MASCHERPA & F. STAINIER (1978). Etude taxonomique d'un groupe complexe d'espèces des genres Phaseolus et Vigna (Papilionaceae) sur la base de données morphologiques et polliniques, traitées par l'analyse informatique. *Boissiera* 28: 1-273.
- MAXTED, N. (1990). A phenetic investigation of Psophocarpus Neck. ex DC. (Leguminosae-Phaseoleae). *Bot. J. Linn. Soc.* 102: 103-122.

- NECKER, N. J. (1790). Psophocarpus. *Elementa botanica* 3: 45.
- TAUBERT, P. (1894). Leguminosae. In: ENGLER, A. & K. PRANTL, *Die natürlichen Pflanzenfamilien* 3(3): 70-396. Leipzig, Wilhelm Englemann.
- VERDCOURT, B. (1970a). Studies in the Leguminosae—Papilionoideae for the Flora of Tropical East Africa. II. *Kew Bull.* 24: 253-307.
- VERDCOURT, B. (1970b). Studies in the Leguminosae—Papilionoideae for the Flora of Tropical East Africa. III. *Kew Bull.* 24: 379-447.
- VERDCOURT, B. (1970c). Studies in the Leguminosae—Papilionoideae for the Flora of Tropical East Africa. IV. *Kew Bull.* 24: 507-569.
- VERDCOURT, B. (1971). Phaseoleae. In: MILNE-REDHAED, E. & R. M. POLHILL, *Flora of Tropical East Africa, Leguminosae (part 4)—Papilionoideae* 2: 503-807. London and Tonbridge, Whitefriars Press.
- VERDCOURT, B. & P. HALLIDAY (1978). A revision of Psophocarpus (Leguminosae—Papilionoideae—Phaseoleae). *Kew Bull.* 33: 191-227.
- WILCZEK, E. (1954). Phaseoleae. In: *Flora Du Congo Belge et du Rwanda-Urundi* 6:260-409. Bruxelles, Institut national pour l'étude agronomique du Congo-Belge.
- WIRTH, M., G. P. ESTABROOK & D. J. ROGERS (1966). A graph theory model for systematic biology, with an example for the Oncidiinae (Orchidaceae). *Syst. Zool.* 15: 59-69.
- WISHART, D. (1975). *CLUSTAN 1C*. London, University College.