



Infrageneric relationships within *Pogostemon* Desf. (Labiatae)

M. INGROUILLE¹ AND G. RAZA BHATTI²

Department of Biology, Birkbeck College, University of London, London, WC1E 7HX

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Cladistic and phenetic analyses of the morphology of 79 species of *Pogostemon* Desf. *sensu lato* have been undertaken. The cladistic analysis included 135 character state differences encoded as 41 binary or multistate characters. The phenetic analysis included 52 metric variables and 54 binary variables. There is a very good correspondence between the results of cladistic and phenetic analyses based on different data sets. The existence of several clearly marked clades/clusters has been demonstrated. Some groups/clades are similar to those previously taxonomically recognized but the relationships and membership of infra-generic groups have been clarified by these analyses, validating a revised infra-generic classification which has been proposed.

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ADDITIONAL KEY WORDS:—cladistics—*Dysophylla*—*Eusteralis*—Lamiaceae—morphology—phenetics.

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INTRODUCTION

Pogostemon Desf. is a distinct genus in the Labiatae Juss. defined by exerted stamens and filaments usually bearing unilaterally densely arranged moniliform hairs (Bhatti, 1995). *Pogostemon* means 'with bearded stamen' (Stearn, 1992). *Pogostemon* is the largest genus in its sub-family tribe the Pogostemonoideae (Endl.) P.D. Cantino,

¹ Correspondence to: Dr M. Ingrouille. Email: m.ingrouille@biology.bbk.ac.uk.

² Present address: Botany Department, Shah Abdul Latif University, Khairpur, Sindh, Pakistan.

Harley & Wagstaff (Cantino *et al.*, 1992) but its relationship to other included genera such as *Anisomeles* R. Br., *Colebrookia* Sm., *Comanthosphace* S. Moore, based in part on the presence of bearded stamens, has been questioned (Bhatti & Ingrouille, 1995, 1996a,b, 1997). The centre of diversity of the genus is in the Indian subcontinent and there are other lesser centres of diversity in parts of south-east Asia. The genus is of moderate size with 80–90 species currently recognized. It includes diverse species ranging from tall sub-shrubs to slender aquatic herbs. This diversity has been recognized by the description of different infra-generic classifications or by the recognition of more than one genus, but these systems have not been stable (Table 1). For example different authors at various times have recognized two segregate genera, *Dysophylla* Benth. or *Eusteralis* Raf., or only one undivided genus, *Pogostemon sensu lato*. Others have recognized similar but slightly differently delimited groups at different infra-generic ranks.

Species have been transferred between groups. In particular the boundary between *Dysophylla* and *Pogostemon sensu stricto* has been difficult to establish with different authors including different species in each group. On the basis of sharing the characters “opposite, broad and petiolate leaves, presence of crystals in the calyx and absence of an aerenchyma tissue in the stem” El-Gazzar & Watson (1967) transferred the four species, *D. auricularia* (L.) Blume, *D. myosuroides* Benth. in Wallich, *D. rugosa* Hook.f. and *D. salicifolia* Dalz. ex Hook.f. to *Pogostemon*. Wu & Li (1975) also transferred *D. falcata* (C.Y.Wu) C.Y. Wu & Li to *Pogostemon* for similar reasons. Press (1982) maintained a single genus *Pogostemon* for all species including those described in *Dysophylla*.

Some workers have turned to multivariate techniques to try to elucidate the patterns of relationship. Khanam *et al.* (1994) carried out a cluster analysis on 13 species of *Pogostemon* from Bangladesh, using 34 characters, 27 of them morphological and seven chemical (presence or absence of different flavonoids). They identified two main groups, one of which included six species normally placed in *Dysophylla* plus *P. strigosus* (Benth.) Benth. in DC, and the other group containing species in *Pogostemon* sect. *Paniculatae* Benth. The flavonoid characters were not useful in defining the groups.

Press (1982) included 75 species of *Pogostemon sensu lato* in his phenetic analysis of tribe *Pogostemoneae* (Benth. ex Endl.) Briq. using 64 morphological characters. In a principal coordinates analysis *Pogostemon sensu lato* was clearly separated from other taxa. There was a transition between *Pogostemon sensu stricto* and species of *Dysophylla* sect. *Verticillatae* Benth. with several intermediate species, especially from *Dysophylla* sect. *Oppositifoliae* Benth. The results from cluster analyses were broadly in agreement with those from principal coordinates analysis. Press (1982) concluded that there was “a greater degree of unity between these groups than is generally acceptable between two genera”.

As the result of a detailed analysis of morphological and micromorphological variation a revised classification of the genus has been proposed (Bhatti & Ingrouille, 1997) with a more clearly defined hierarchy of infra-generic taxa. The revised classification is summarized in Table 2. It includes the recognition of a new subgenus and new sections. In this paper the cladistic and phenetic analyses of data, used in constructing the revised classification, are reported.

TABLE 1. History of the classification of *Pogostemon sensu lato*

Desfontaines (1815)					
<i>Pogostemon</i> described with Type <i>P. plectranthoides</i>					
Blume (1826)					
<i>Dysophylla</i> described with Type <i>D. auricularia</i> (= <i>M. auricularia</i> L.)					
Bentham (1832)					
<i>Dysophylla</i> sect. <i>Oppositifoliae</i> (with opposite leaves)		<i>Dysophylla</i> sect. <i>Verticillatae</i> (with verticillate leaves)		<i>Pogostemon</i> sect. <i>Paniculatae</i> (with a panicle)	
				<i>Pogostemon</i> sect. <i>Racemosae</i> (with a raceme)	
Hasskårl (1842)					
<i>Pogostemon</i> (includes <i>Dysophylla</i>)					
Rafinesque-Schmaltz (1837)					
<i>Eusteralis</i> Rafinesque-Schmaltz (= <i>Dysophylla</i> sect. <i>Verticillatae</i> Benth.)					
Miquel (1859)					
<i>Pogostemon</i> (includes <i>Dysophylla</i>)					
Kuntze (1891)					
<i>Pogostemon</i> (including <i>Dysophylla</i>)					
Briquet (1897)					
<i>Dysophylla</i>			<i>Pogostemon</i>		
sect. <i>Rhabdocalicinae</i> Calyx tube cylindrical and rounded or very indistinctly pentagonal		sect. <i>Goniocalicinae</i> Calyx tube prominently five angled		sect. <i>Paniculatae</i> branched inflorescence	
sect. <i>Racemosae</i> simple inflorescence					
subject. A. Perennial species		subject. B. Annual species		subject. Interrupted verticils	
				subject. Continuous verticils	
				subject. <i>Glabriuscula</i> naked filaments	
				subject. <i>Barbata</i> hairy filaments	
Kudo (1927)					
<i>Dysophylla</i>					
sect. <i>Eudysophylla</i> stem indumentum tomentose to hirsute and leaves opposite, broad, ovate – lanceolate, margin serrulate			sect. <i>Chotekia</i> stem glabrous to pubescent and leaves verticillate, narrow, linear to linear – lanceolate with an entire margin.		

TABLE 1. History of the classification of *Pogostemon sensu lato*—continued

Keng (1978)	
<i>Pogostemon</i> (including <i>Dysophylla</i>)	
Press (1982)	
sect. <i>Verticillati</i> (including sect. <i>Eusteralis</i> (Rafin.) H. Keng = <i>Dysophylla</i> sect. <i>Verticillatae</i> Benth.)	sect. <i>Pogostemon</i> (including <i>Dysophylla</i> sect. <i>Oppositifoliae</i> Benth.)

TABLE 2. A summary of a revised infrageneric classification of *Pogostemon* Desf.

Subgenus	Section	Subsection
<i>Pogostemon</i>		
<i>Allopogostemon</i> Bhatti & Ingr.	<i>Racemosus</i> (Benth.) Bhatti & Ingr.	<i>Racemosus</i> <i>Glabriusculus</i> (Briq.) Bhatti & Ingr.
	<i>Zygocalyx</i> Bhatti & Ingr.	
<i>Dysophyllus</i> (Blume) Bhatti & Ingr.	<i>Dysophyllus</i> <i>Verticillatus</i> (Benth.) Bhatti & Ingr.	

MATERIAL AND METHODS

Details of the 79 species of *Pogostemon sensu lato* analysed are listed in Appendix 1. Of the probably distinct species only *Pogostemon brevicorollus* Y.Z. Sun, *P. reticulatus* Merrill, *P. falcatus*, *P. szemacensis* (C.Y. Wu & Hsuan) Press and *P. tsiangii* (Y.Z. Sun) Press have been excluded because specimens at a comparable state of floral development were not available.

About 400 specimens were examined. Specimens are listed in Bhatti & Ingrouille (1997). Some other specimens were rejected because they were incomplete or had no information about their geographical origin. Herbarium material of *Pogostemon* has been obtained from the herbaria of the Natural History Museum (BM), the Royal Botanic Gardens, Kew (K) and the Royal Botanical Garden Edinburgh (E). More than half of the total number of species come from India. A field excursion to India was undertaken in 1991. The following herbaria of the Botanical Survey of India were visited: Poona (BSI), Calcutta (CAL), Coimbatore (MH), Dhera Dune (BSD), and Rabinath Herbarium, St. Joseph College (RHT). A few species have been observed in nature in India. These included *P. paniculatus* (Willd.) Benth. in Wallich, *P. purpurascens* Dalz. in Hook.f., *P. quadrifolius* (Benth. in Wallich) Kuntze, *P. heyneanus* Benth. in Wallich, *P. auricularius* (L.) Hassk. and *P. plectranthoides* Desf.

Species were treated as operational taxonomic units (OTUs) or terminal taxa. In 85% of species it was possible to include at least one type specimen in the analysis. Cultivated material of *P. plectranthoides* and *P. quadrifolius* was available and used to check, for the characters scored, that dried material accurately represented the living

state. In order to minimize the confusion arising from developmental plasticity, every effort was made to use mature organs for each feature. The majority of characters come from the flowers.

Both cladistic and phenetic analyses were carried out. This dual approach was chosen because at specific rank both qualitative characters used in cladistics and metric characters used in phenetics are useful. It has been recognized by many workers that cladistic analysis works best where there are a large number of characters with variable but distinct character states. Methods have been proposed to convert metric characters to discrete character states (Almeida & Bisby, 1984; Chappill, 1989; Morton *et al.*, 1995). However at species rank, in the zone between phylogenetic and tokogenetic studies, there may be relatively few morphological characters with sharply contrasting character states or characters are polymorphic. Many specific differences are expressed as differences in mean value of continuously varying characters.

The approach used here was to subject the data to the most appropriate kinds to analyses: cladistics for qualitative characters and cluster analysis and principal components analysis for mainly metric data. Where congruent results are produced, by different methods of analyses and when using different data sets, more confidence can be placed on a revised classification based upon them.

CHARACTER CODING

A mean number of five specimens was examined for each species. Only one specimen was available for 17 of the 79 species but in most species this was a type or isotype. All stems on each specimen were examined and 5–10 calyces and corollas were examined from each specimen, but, if there was any doubt about identity, or there was a large degree of variation, the number of the samples was increased. Nutlets were obtained from fruiting calyces. Details of character variation are listed in Bhatti & Ingrouille (1997).

Two data sets were prepared, one for cladistic analysis and one for phenetic analysis. 135 character states were scored and encoded as 41 multistate characters for cladistic analysis (Table 2, Fig. 1). Metric variables were screened following the methods recommended by Tabachnick & Fidell (1989). Some pairs of variables were very highly correlated. In this case, if it was possible that the variables were logically correlated so that inclusion of both variables would positively weight a feature of the plant, one of each pair of variables correlated at $r > 0.85$ was excluded from the phenetic analyses. Six metric variables were excluded in this way leaving 52 metric variables (Table 4). The distribution of metric characters was examined and 18 with high skewness or kurtosis were transformed to their log value to normalize them. In addition, 54 binary variables from characters not otherwise measured as a metric variable, were included by recoding multistate characters from the cladistic analysis.

Metric data can be found in Bhatti & Ingrouille (1997) and the cladistic data set is provided in Appendix 2.

CLADISTIC ANALYSIS

Character states were treated as unordered. Cladistic analysis was carried out by a combination of HENNIG86 (Farris, 1988), PAUP 3.1.1 (Swofford, 1993) and

TABLE 3. Cladistic characters (character states in parenthesis)

Plant	C1	form	herb(0)/ hydrophyte or helophyte (1)/shrub(2)	
	C2	trichomes	glabrous(0)/simple-unicellular(1)/simple-multicellular(2)/branched(3)/simple and branched(4)	
Leaf	C3	petiole	petiolate(0)/sub-sessile(1)/ sessile(2)	
	C4	phyllotaxis	2(0)/3(1)/4(2)/5(3)/6-10(4) leaves at each node	
	C5	shape	simple(0)/compound(1)	
	C6	shape	linear-linear lanceolate(0)/lanceolate(1)/elliptic to elliptic-oblong(2) /ovate(3)/orbicular(4)	
	C7	apex	obtuse(0)/acute(1)/acuminate(2)	
	C8	base	rounded(0)/cuneate(1)/truncate(2)/cordate(3)	
	C9	margin	dentate(0)/double-dentate(1)/crenate(2)/double-crenate(3)/serrate(4)/inciso-serrate -crenate(5)/entire-revolute(6)	
	Inflorescence	C10	branching	single terminal(0)/spike/terminal spike with 2 laterals(1)/with more than 2 laterals(2)
		C11	density	lax(0)/lax below and dense above(1)/dense(2)
C12		bracts	membranous and caducous(0)/not membranous and persistent(1)	
C13		bract shape	filiform(0)/spathulate(1)/narrow lanceolate(2)/broad ovate(3)	
C14		bract tothing	entire(0)/entire(1)	
Calyx	C15	circumference	wide(1)/equal to tube length(2)/narrow(3)	
	C16	shape	cylindrical(1)/tubular-inflated(2)/infundibular(3)	
	C17	shape	symmetrical(1)/asymmetrical(2)/zygomorphic(3)	
	C18	venation	5-veined(1)/5 main veins with multiple parallel secondaries at sinus(2)/5 main veins with a variable number of extra weaker primary veins between(3)/10-veined(4)	
	C19	teeth	broadly triangular(0)/narrowly-triangular(1)/lanceolate (2)	
	C20	margin	glabrous(0)/ hairy(1)/bristly(2)	
	C21	exterior	glabrous(0)/sparsely hairy(1)/densely hairy(2)	
	C22	interior of teeth	glabrous(0)/tips hairy(1)/densely hairy(2)	
Corolla	C23	interior tube	glabrous(0)/hairy(1)	
	C24	glands	obscure(0)/obvious(1)	
	C25	tube to limb	length ratio $< 1(1) = 1(2) > 1(3)$	
	C26	shape	length diameter ratio $\leq 1.6(1)/1.7-1.8(2) / \geq 1.9(3)$	
	C27	tube shape	infundibular(1)/tubular(2)	
	C28	upper lip length	middle lobe \cong lateral lobe length(1)/middle $>$ lateral (2)	
	C29	upper lip width	middle lobe \cong lateral lobe (1)/middle $<$ lateral (2)	
	C30	upper lip shape	lateral lobes with parallel sides(1)/ winged(2)	
Stamens	C31	lip length	lower $<$ upper(1)/ lower \cong upper(2)/ lower $>$ upper(3)	
	C32	lip width	lower $< \frac{1}{2}$ upper(1)/ lower $\cong \frac{1}{2}$ upper(2)/ lower $> \frac{1}{2}$ upper(3)	
	C33	moniliform hairs	absent(0)/ present(1)	
	C34	filament bases	(glabrous(1)/ villous(2)	
Gynoecium	C35	insertion	arising at the same height in tube(1)/ at two heights(2)	
	C36	disc	symmetrical(1)/ asymmetrical(2)	
	C37	stigma	smooth (0)/ hairy(1)	
	C38	nutlet surface	scales(0)/ spinulose(1)/ truncate(2)/ reticulate-foveate with secondary reticulations(3)/ reticulate-foveate(4)/ reticulate(5)/ granulate(6)/ reticulate-punctulate(7)/ punctulate(8)/ smooth (9)	
	C39	hairs	absent(0)/ present(1)	
	C40	nutlet shape	oblong with angular upper end(0)/ ovate(1)/orbicular(2)/ oblong(3)/ obovate(4)/ lanceolate-linear-lanceolate(5)/ elliptic-elliptic-oblong(6)/ elliptic-fusiform(7)/ D-shaped(8)	
	C41	glands	absent(0)/ present(1)	

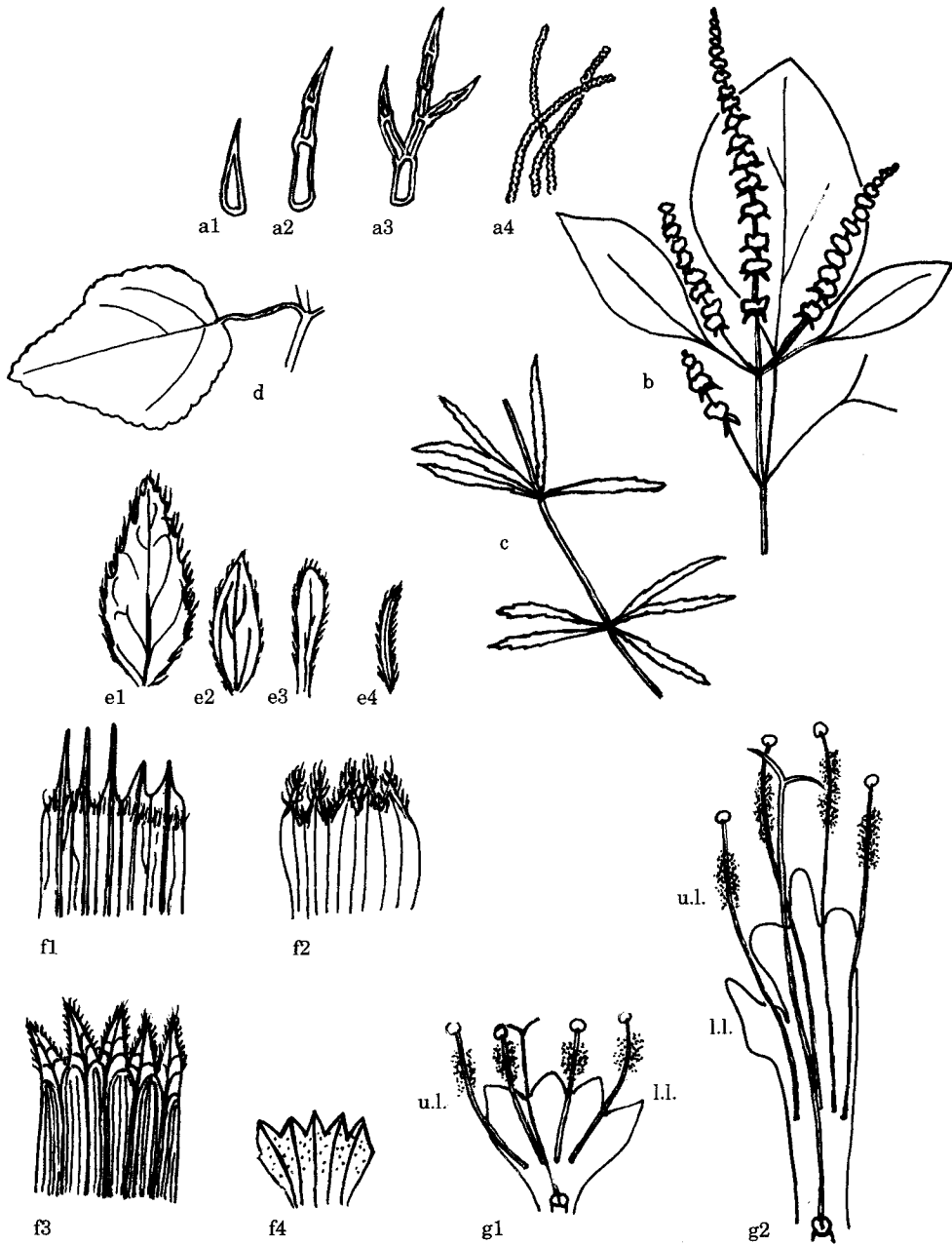


Figure 1. Qualitative characters used in cladistic and phenetic analysis: trichomes, a1 - simple, unicellular, a2 - simple, multicellular, a3 - branched, multicellular, a4 - moniliform hairs; b - inflorescence with unbranched laterals, lax throughout, leaves in pairs; c - 5 leaves at each node, sessile, linear-shaped and toothed; d - petiolate, ovate with crenate margin; e - bracts, e1 - broadly lanceolate, toothed, e2 - narrowly lanceolate, even, e3 - spatulate, e4 - filiform; f - calyx (dissected), f1 - asymmetrical, tubular, ring of hairs, teeth narrowly lanceolate, 5 main veins plus others, f2 - tubular, inflated, teeth triangular margin bristly 10-veined, f3 - tubular 5 main veins and multiple parallel secondaries, f4 - infundibular, 5-veins with obvious glands; g - corolla (dissected), g1 - infundibular, upper lip (u.l.) with \pm equal lateral lobes and equal to lower lip (l.l.), g2 - tubular, upper lip (u.l.) longer than lower lip (l.l.) and with lateral lobes shorter, broader than middle lobe.

TABLE 4. Variables measured for phenetic analysis, metric characters in full, binary/ordered multistates recoded from cladistic data set (explanation in text)

P1	Plant	Stem trichome length
P2		Max. no. of cells in the stem trichome
	and C1, C4 recoded as binary variables	
P3	Leaf	Petiole length
P4		Max. number of leaves at each node
P5		Max. length of lamina
P6		Max. length of lamina at widest point
P7		Max. width at widest point
P8		Max. width at mid point
P9		Ratio of total length and width of the lamina
P10		Ratio of total length of lamina and the length of lamina where lamina has widest point
P11		Leaf trichome length
P12		Max. no. of cells in the leaf trichome
	and C5, C6, C7, C8 recoded as binary variables	
P13	Inflorescence	Length of the terminal spike without stalk
P14		No. of verticils per terminal spike
P15		No. of the flowers on the lowermost verticil on the terminal spike
P16		No. of the flowers on the uppermost verticil on the terminal spike
P17		Length in between first 2-verticil on the terminal spike
P18		Length in between last two verticils on the terminal spike
P19		Internode trichome length
P20		Internode trichome max. no. of cells
P21		Peduncle trichome length
P22		Peduncle trichome max. no. of cells
	and C12, C13, C14 recoded as binary variables	
P23	Calyx	Length of calyx in mm.
P24		Circumference
P25		Calyx circumference to length ratio
P26		Length of longest tooth
P27		Length of shortest tooth
P28		Length of the calyx tube without teeth
P29		Calyx tube and teeth length ratio
P30		Length difference in between longest and shortest tooth
P31		Max. width of tooth at the base
P32		Min. width of tooth at the base
P33		Width difference in between max. and min. width of teeth
P34		Max. length of trichome
P35		Max. no. of cells in trichome
	and C15, C16, C17, C18, C20, C21, C22, C23, C24 recoded as 15 binary variables	
P36	Corolla	Total length of the corolla
P37		Length of the lower lip of the corolla
P38		Width of the lower lip of the corolla
P39		Width of the upper lip at the sinus of the lower and upper lip
P40		Length of the central lobe of the upper lip
P41		Width of the central lobe of the upper lip
	and C27, C29, C30, C31, C32 recoded as binary variables	
P41	Stamens	Height of the corolla tube where filaments attached
P42		Length of the longest filament
P43		Length of shortest filaments
p44		Length difference between the longest and the shortest filaments
P45		Length exerted part of the longest filament out of the corolla
	and C33, C34, C35 recoded as binary variables	
P46	Gynoecium	Length of the style
P47		Length of the longest lobe of the stigma
P48		Length of the shortest lobe of the stigma
P49		Length of the disc
P50		Length of the nutlet
P51		Width of nutlet
P52		Length and width ratio
	and C36, C37, C39, C41 and C38 and C40, C41 recoded as binary variables	

McCLADE 3.04 (Maddison & Maddison, 1992). Tree searching was carried out in HENNIG86 by a combination of mhennig* followed by bb* procedures. Successive weighting was carried out using the xsteps procedure for 5 or 6 iterations. A strict consensus tree was computed by the procedure Nelsen. Tree searching on PAUP * was carried out by heuristic search using the TBR routine. Analysis was carried out to the limits of the memory of the computer. This meant, that in some analyses not all shortest trees could always be retained. Polytomous trees were retained only if a more highly resolved compatible tree did not exist. Strict and majority rule consensus trees were constructed.

PHENETIC ANALYSES

Phenetic analyses were carried out using SPSS-PC FOR WINDOWS version 6.0 (Norusis, 1985) and NT-SYS (Rohlf, 1990). Cluster analysis and principal components analysis was carried out on a data set including both metric and binary data. Characters were standardized as Z-scores to have the same range. A distance matrix of Squared Euclidean distance was calculated. This distance was used as a measure of phenetic difference.

Clustering was carried out by Ward's method of minimum variance clustering. Grouping of OTUs by Ward's method has the potential disadvantage that large clusters have a high gravity and 'attract' distinct OTUs or small groups so that they can be included in the larger cluster in a rather spurious fashion. Various other kinds of clustering of subsets of the data, for example analysing metric and binary characters separately, or using different similarity coefficients and clustering methods were also carried out but are not reported here. They produced essentially similar results to clustering by Ward's method but clusters did not correspond as well to the clades produced in the cladistic analysis.

Principal Components Analysis was also carried out because it has the advantage of abstracting factors, one of which may represent some underlying variable like overall size which may affect many characters. There were 40 significant factors but only the first four were extracted. Factor scores were calculated for each OTU and the first two plotted in a scatter diagram.

RESULTS AND DISCUSSION

Cladistic analysis of all species together revealed three major clades which were present in all shortest trees saved. The same clades were resolved using HENNIG86 with successive weighting and using PAUP 3.1.1. These clades were taxonomically recognized as the subgenera *Pogostemon*, *Allopogostemon* and *Dysophyllus*. Characters which distinguish them are listed in Table 4. Each clade was then subjected to separate analysis and rooted using the closest sister species from the other major clades/subgenera. The resulting cladograms of these separate analyses are shown

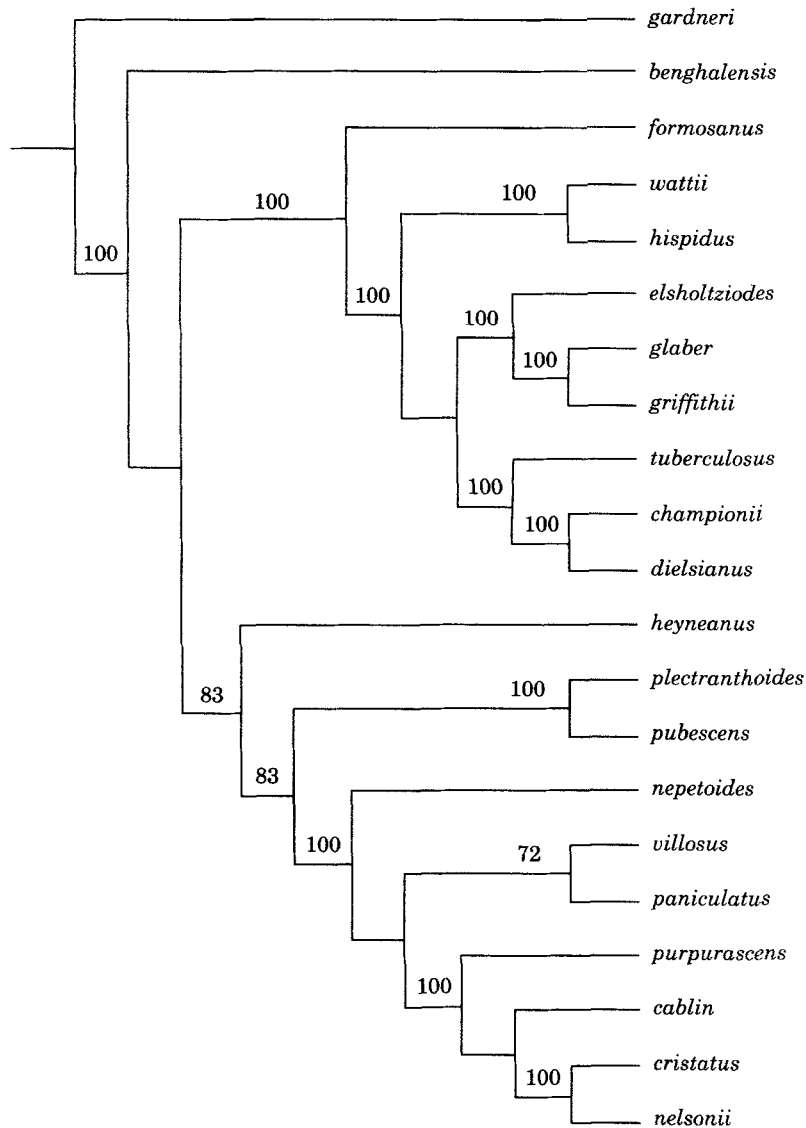


Figure 2. Cladogram of *Pogostemon* subgenus *Pogostemon* 50% majority consensus cladogram produced from 87 shortest trees rooted on *P. amaranthoides* and *P. williamsii*. Percentage of trees agreeing with branches indicated.

in Figures 2–4. Character state distributions for these cladograms can be scanned in Appendix 2 where species have been ordered in the same sequence as the cladograms. It is clear that although there are relatively few unambiguous synapomorphies, both major and minor clades have distinct suites of character states.

Analysis of major clade/subgenus *Pogostemon* (Fig. 2) produced 87 shortest trees. The 50% majority rule consensus tree divides the species into two groups but places *P. benghalensis* and *P. gardneri* as sister taxa to the rest.

Analysis of major clade/subgenus *Allopogostemon* produced 5200 trees. A 50% majority consensus tree is presented in Figure 3. One subclade, present in 89% of

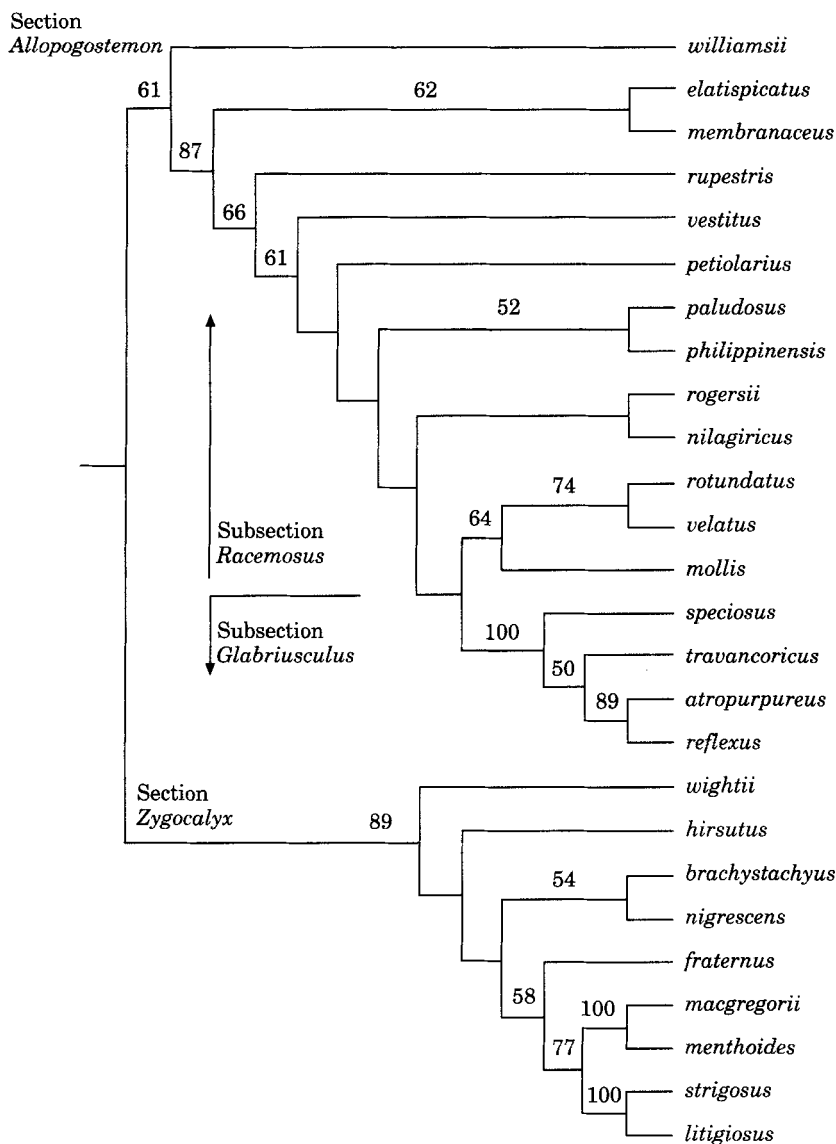


Figure 3. Cladogram of *Pogostemon* subgenus *Allopogostemon* 50% majority consensus cladogram produced from 571 shortest trees rooted on *P. amaranthoides* and *P. gardeneri*. Percentage of trees agreeing with branches indicated.

all trees, was taxonomically recognized as section *Zygocalyx* and another, present in 100% of all trees, as Subsection *Glabriusculus*. The remaining species were placed in a paraphyletic Subsection *Racemosus* sister to Subsection *Glabriusculus*.

Analysis of major clade/subgenus *Dysophyllus* (Fig. 4) produced two shortest trees which differ only in the placement of *P. crassicaulis* and *P. trinervis* either as a monophyletic clade or as a paraphyletic clade sister to a clade including *P. erectus*, *P. stellatus*, *P. koeheanus*, *P. stocksii* and *P. deccanensis*. The taxonomic treatment was to recognize one large subclade as section *Verticillatus* but exclude *P. tisserantii* and *P.*

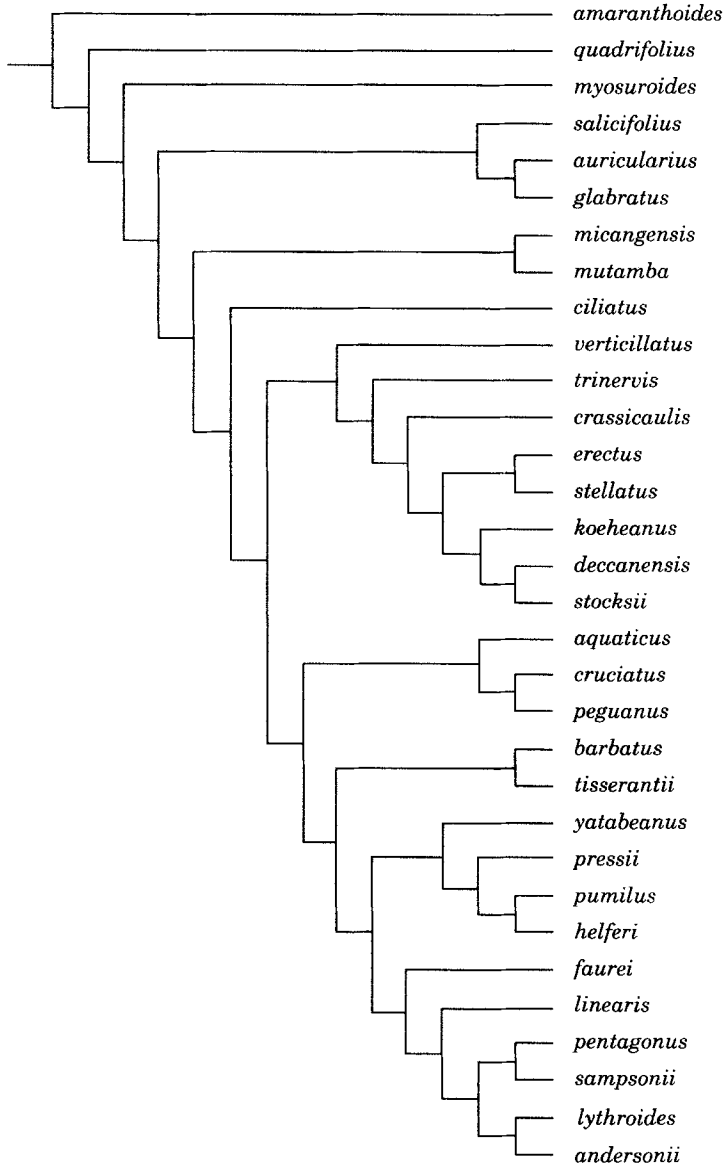


Figure 4. Cladogram of *Pogostemon* subgenus *Dysophyllus* 50% majority consensus cladogram produced one of 2 shortest trees rooted on *P. williamsii* and *P. gardeneri*.

barbatus which differ from the others in phyllotaxy or leaf shape. They were placed in section *Dysophyllus* which is here shown to be a paraphyletic group.

Results of the cluster analysis and principal components analysis correspond very closely with those from the cladistic analysis except for the placement of a few individual species. The dendrogram is shown in Figure 5. Two main clusters are produced.

The first cluster (*P. erectus*–*P. micangensis*) is nearly perfectly congruent with the *Pogostemon* subgenus *Dysophyllus*. Only *P. amaranthoides* is clustered elsewhere. Similarly

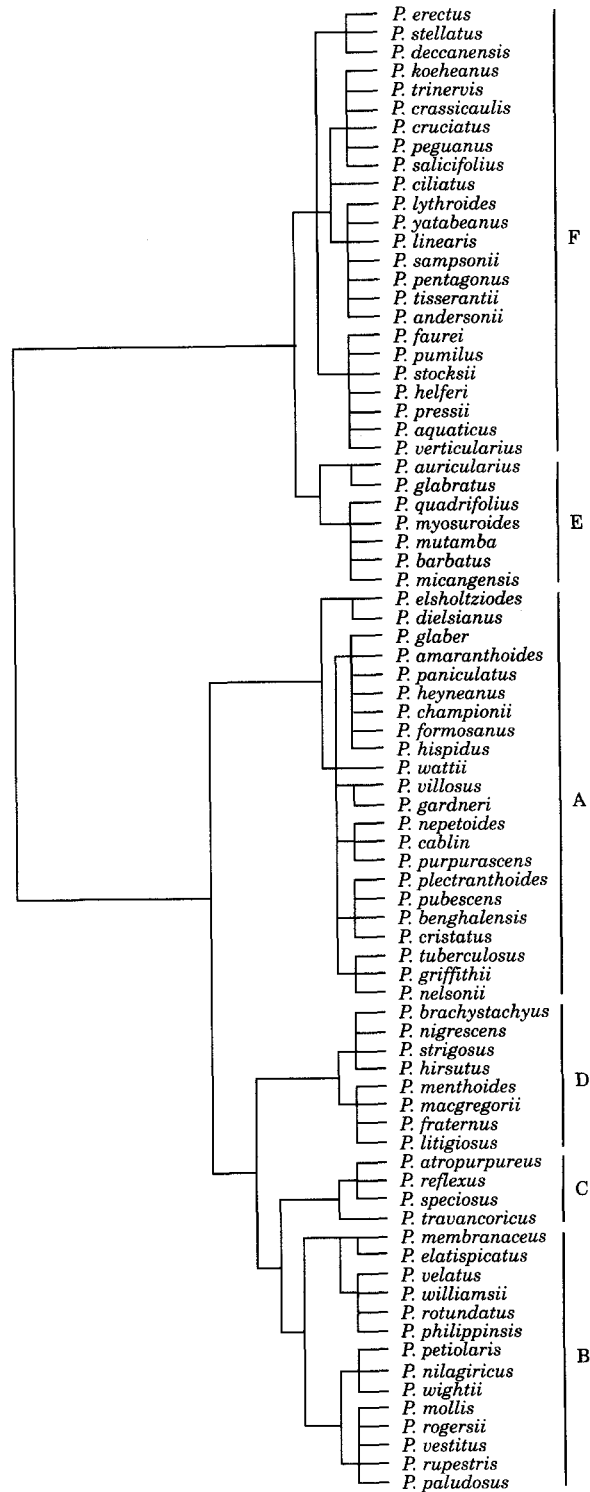


Figure 5. Phenogram of cluster analysis by Ward's method of 79 *Pogostemon* species. Excluding four mis-clustered species (*P. salicifolius*, *P. barbatus*, *P. amaranthoides* and *P. wightii*) clusters are A=Subgenus *Pogostemon*, B=Subgenus *Allo-pogostemon* Section *Racemosus* Subsection *Racemosus*, C=Subgenus *Allo-pogostemon* Section *Racemosus* Subsection *Glabriusculus*, D=Subgenus *Allo-pogostemon* Section *Zygocalyx*, E=Subgenus *Dysophyllus* Section *Dysophyllus*, F=Subgenus *Dysophyllus* Section *Verticillatus*.

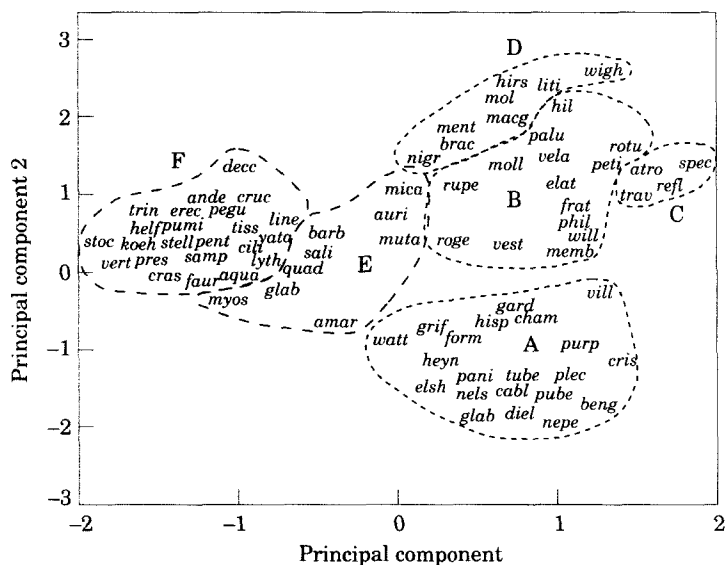


Figure 6. Scatter diagram of first (X-axis) and second (Y-axis) principal component scores (comprising 28.5% and 8.2% of the variation). OTUs coded by first letters of specific name, groups as follows; A=Subgenus *Pogostemon*, E=Subgenus *Dysophyllus* Section *Dysophyllus*, B=Subgenus *Allopogostemon* Section *Racemosus* Subsection *Racemosus*, D=Subgenus *Allopogostemon* Section *Zygocalyx*, F=Subgenus *Dysophyllus* Section *Verticillatus*, C=Subgenus *Allopogostemon* Section *Racemosus* Subsection *Glabriusculus*.

the subclusters *P. auricularius*–*P. micangensis* and *P. erectus*–*P. verticillatus* are highly congruent with Sections *Dysophyllus* and *Verticillatus* except *P. salicifolius* and *P. barbatus* are clustered with species of Section *Verticillatus*.

The second main cluster (*P. elsholtzioides*–*P. paludosus*) has two very distinct subclusters (*P. elsholtzioides*–*P. nelsonii*), labelled A, and *P. brachystachyus*–*P. paludosus*), labelled B, C & D, which are highly congruent with subgenera *Pogostemon* and *Allopogostemon*. The only misclustered species is *P. amaranthoides* which is included in subcluster A. Within the *P. brachystachyus*–*P. paludosus* subcluster smaller clusters are congruent with Subsection *Racemosus* (*P. membranaceus*–*P. paludosus*) labelled B, but with the inclusion of *P. wightii*, Subsection *Glabriusculus* (*P. atropurpureus*–*P. travancoricus*) labelled C, and Section *Zygocalyx* (*P. brachystachyus*–*P. litigiosus*) labelled D.

P. salicifolius, *P. barbatus*, *P. amaranthoides* and *P. wightii* are mis-clustered because in the classification emphasis was placed on the arrangement determined by cladistics since it is based on more sharply marked character states. *P. salicifolius* and *P. barbatus* clustered with species of Section *Verticillatus* despite having leaves in opposite pairs rather than a whorl of leaves at each node. *P. amaranthoides*, in Subgenus *Dysophyllus*, is misplaced in cluster A. It is a very distinct species which has floral characters like other species in Subgenus *Dysophyllus* but is vegetatively a large and robust plant like some species of Subgenus *Pogostemon* with which it clusters. For similar reasons *P. wightii* was classified in Section *Zygocalyx* because of its calyx shape and hairiness but is misplaced in cluster B.

The first principal component accounts for 28.5% of the variation and the second for 8.2% of the variation. The scatter diagram of the factor scores for these two components clearly shows the three major clusters/subgenera and also other groups (Fig. 6). For clarity, lines separating the taxa have been superimposed on the diagram.

Character distributions of valuable characters, including mean values and standard errors for metric variables are summarized for important characters in Table 5.

A comparison of the extent of phenetic and cladistic variation in each subgenus is interesting. Phenetic variation within and between subgenera is shown graphically in Figure 7. Differences in the mean phenetic difference within each clade are highly significant (Subgenus *Dysophyllus* vs. Subgenus *Pogostemon* $t = 5.98^{**}$ df 704, Subgenus *Dysophyllus* vs. Subgenus *Allopogostemon* $t = 11.79^{**}$ df 846, Subgenus *Pogostemon* vs. Subgenus *Allopogostemon* $t = 7.43^{**}$ df 560). Mean phenetic distances between sections are recorded in Table 6.

These results indicate that species in Subgenus *Dysophyllus* are not as phenetically distinct as in those in the other subgenera. A similar finding is indicated by cladistic analysis because, although the mean number of character state changes on internal branches of each of the main clades/subgenera are not significantly different, the number of changes concentrated in terminal branches of Subgenus *Dysophyllus* is on average 2.3 compared to 3.1 for Subgenus *Pogostemon* and 3.3 for Subgenus *Allopogostemon*. Probabilities of a significant difference are $P = 0.07$ for the comparison *Pogostemon* versus *Dysophyllus* and $P = 0.03$ for the comparison *Allopogostemon* versus *Dysophyllus*.

Our results are broadly in agreement with those of Press (1982) but the inclusion of several new characters, especially from the calyx, has sharpened the definition of the various groups. There is a remarkable agreement between the results of the cladistic and phenetic analyses. Most of the taxa formally recognized in the classification are monophyletic according to the cladistic analysis, but some paraphyletic groups sister to monophyletic clades were also taxonomically recognized. Character state distributions of subspecies and sections are listed in Table 5.

There is a considerable degree of homoplasy in the genus. This may be related to convergence between species which have become adapted to the same habitat. For example in Section *Racemosus*, which has eleven species in southern India, five species from the Philippines and one from southern Africa, most species are dry habitat herbs with simple inflorescences and relatively narrow bracts. The flowers are relatively large and showy for the genus, and have long filaments. The base of the filaments is normally hairy. The calyx is clearly marked by 10 parallel veins.

Subsection *Glabriusculus* is unusual because moniliform hairs are absent from the filaments, though a few simple hairs can sometimes be found, and also the ovary/nutlets have stalked glands. *P. paludosus* Benth. in Wall., from the sister Subsection *Racemosus*, also has glands on its nutlets, but has moniliform hairs. This may indicate either parallel evolution of nutlet glands or that their presence is ancestral but they have been lost from most other members of their section.

In Section *Zygocalyx* the species have a two-lipped calyx, a condition which is seen at its most extreme in *P. litigiosus*. The teeth are often rather subulate and the interior of the calyx is fringed by a ring of hairs, which is either continuous or broken and is sometimes expressed as tufts of hairs at the sinus of each pair of teeth or inside the teeth. This section is centred geographically on the region of eastern Himalayas to Yunnan and Thailand but includes three endemics to Java, Borneo and Sri Lanka respectively. Parallel evolution is observed in *P. reflexus* and *P. speciosus* of Subsection *Glabriusculus*, which have a calyx with some teeth rather subulate and fringed by bristles rather like that in Section *Zygocalyx*. Alternatively, *P. menthoides* of Section *Zygocalyx* has relatively few moniliform hairs rather like species of Subsection *Glabriusculus*.

TABLE 5. Character states and means of clades/intra-generic taxa. Standard errors in parenthesis

Character	subg. <i>Allopagostemon</i>		subg. <i>Pagostemon</i>		subg. <i>Dysophyllus</i>	
	sect. <i>Racemosus</i>	sect. <i>Zygocalyx</i>	sect. <i>Pagostemon</i>	sect. <i>Dysophyllus</i>	sect. <i>Verticillatus</i>	sect. <i>Verticillatus</i>
number of species surveyed	17	9	21	10	22	22
Habit		herb	shrubby	herb	herb	herb
Phyllotaxis	2 leaves at each node		2 leaves at each node	2-4 leaves at each node	>2 at each node	
Petiole		petiolate	petiolate	sessile-petiolate	sessile	
Leaf length/width ratio	2.34 (0.14)	2.29 (0.20)	2.48 (0.24)	4.27 (0.80)	9.28 (1.42)	
Leaf margin		crenate or serrate	double dentate	dentate or serrate	dentate	
Inflorescence		unbranched verticillaster	branched verticillaster	unbranched verticillaster	unbranched verticillaster	
Calyx shape	tubular teeth triangular	± two-lipped teeth awl shaped	tubular inflated	usually campanulate	campanulate	
Calyx length	5.0 (0.3)	4.7 (0.3)	4.3 (0.2)	2.3 (0.2)	1.8 (0.1)	
Calyx throat circumf./tube length ratio	0.89 (0.04)	0.88 (0.05)	0.86 (0.03)	1.32 (0.04)	1.46 (0.05)	

continued

TABLE 5. Character states and means of clades/intra-generic taxa. Standard errors in parenthesis—continued

	5 main veins plus 5 parallel intercostal veins	5 main veins plus reticulate intercostal veins	5 main veins and multiple parallel intercostal veins	5 veins intercostal region thin and translucent
Number of calyx veins	8.5 (0.7)	5.6 (0.4)	6.4 (0.4)	3.6 (0.5)
Calyx interior indumentum	glabrous or with a ring of hairs around top of tube and teeth	throat ringed by hairs	glabrous or hairy but hairs not in a ring	± glabrous
Filament length mm	8.5 (0.7)	5.6 (0.4)	6.4 (0.4)	3.6 (0.5)
Corolla length mm	7.3 (0.4)	5.4 (0.5)	6.3 (0.4)	3.1 (0.4)
Corolla lower lobe length mm	3.2 (0.05)	3.0 (0.07)	2.7 (0.10)	2.3 (0.10)
Corolla upper lobe width mm	2.3 (0.18)	1.9 (0.17)	1.7 (0.09)	1.8 (0.15)
Corolla lower lip length/width	1.2 (0.02)	1.2 (0.04)	1.2 (0.02)	1.0 (0.01)
Style length mm	2.3 (1.0)	1.4 (1.5)	11.8 (0.7)	4.4 (0.3)
				5.0 (0.3)

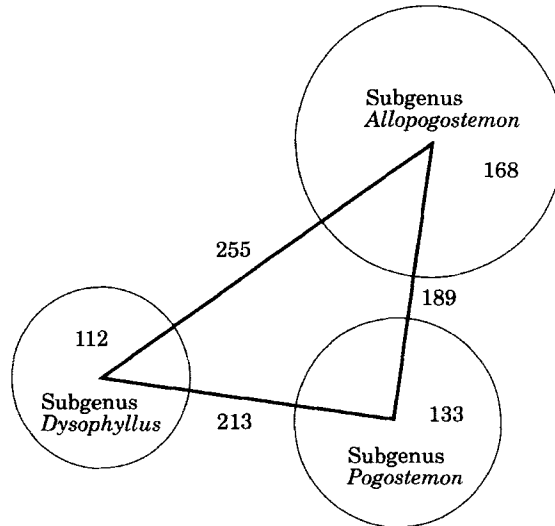


Figure 7. Cluster diagram showing mean phenetic distance (squared euclidean distance) within and between the three subgenera.

TABLE 6. Variation within and between groups. Phenetic distance calculated from squared euclidean distance between all pairs of species

	Subgenus <i>Allopogostemon</i>		Subgenus <i>Pogostemon</i>	Subgenus <i>Dysophyllus</i>	
	Section <i>Racemosus</i>	Section <i>Zygocalyx</i>		Section <i>Dysophyllus</i>	Section <i>Verticillatus</i>
Number of species	17	9	21	10	22
mean phenetic distance within and between sections (SE)					
Section <i>Racemosus</i>	154 (4.5)				
Section <i>Zygocalyx</i>	191 (4.0)	125 (7.4)			
Subgenus <i>Pogostemon</i>	189 (2.9)	188 (2.8)	133 (3.2)		
Section <i>Dysophyllus</i>	222 (5.7)	192 (5.2)	183 (3.2)	121 (3.2)	
Section <i>Verticillatus</i>	269 (4.1)	233 (4.2)	226 (2.5)	133 (2.4)	91(2.5)

Subgenus *Pogostemon* includes most of the shrubby species of *Pogostemon* including the type species of the genus *P. plectranthoides*. Many are of economic importance as the source of Patchouli, the pungent oil extracted from dried plants. The shrubby Patchouli species include several rather poorly defined taxa around *P. benghalensis* (Burm.f.) Kuntze, *P. plectranthoides*, *P. cablin* (Blanco) Benth. and *P. heyneanus*. Patterns of variation are complicated by the cultivation of variants which rarely flower and are maintained vegetatively, and by the introduction of cultivars into areas outside their native distribution. New data from a range of populations of each species are required to ascertain whether currently recognized species should be considered as infra-specific variants of one or more polymorphic species.

Similarly, a population based study is needed to evaluate the relationships of species in Subgenus *Dysophyllus*, many of which are adapted as aquatic or semi-aquatic herbs. The taxonomic status of geographically narrowly restricted endemics like *P. erectus* (Kuntze) Press from Bombay, *P. koehneanus* (Muschler) Press from Thailand and *P. andersonii* (Prain) Press from Sikkim, to geographically widespread taxa like *P. stellatus* (Benth.) Bhatti and Ing., *P. crassicaulis* (Benth. in Wallich) Press and *P. cruciatus* (Benth. in Wallich) Kuntze would be especially valuable.

Placing the boundary between Subgenus *Dysophyllus* and the rest of the genus has taxed previous workers but here emphasis has been placed on calyx characters so that, for example, *P. amaranthoides* is placed within the subgenus as sister to the rest of the subgenus, because it too has a broadly conical and translucent calyx. Nevertheless a taxonomic problem remains because a number of very distinct taxa have been lumped together rather artificially in Section *Dysophyllus* which is paraphyletic to Section *Verticillatus*. These include the type species of the subgenus, *P. auricularius*. Different species of Section *Dysophyllus* have different combinations of character states found in Section *Verticillatus* and in the other subgenera. *P. mutamba* and *P. micangensis*, the African species, have normally been placed in *Pogostemon sensu stricto*. They have the normal zygomorphic corolla of other *Pogostemon* species but although they also have a calyx with intercostal veins it is very strongly conical/campanulate like other species of Subgenus *Dysophyllus*. Another problematical African species is *P. tisserantii* from Chad. It is unique in *Pogostemon* in having a pinnatifid leaf.

Most species of Subgenus *Dysophyllus* have a small corolla in which the separate lobes of the upper lip and the single lobe of the lower lip are approximately equal in size and shape so that the corolla has a symmetry which is nearly actinomorphic. The evolution of this kind of corolla is also found as a parallelism in other genera of Labiatae which have many aquatic or marsh species, like *Mentha* L. Many species in Subgenus *Dysophyllus* have weak stems and most have several linear to linear-lanceolate leaves arranged in a whorl at each node.

Part of the taxonomic difficulty experienced in placing the boundary between infra-generic groups in *Pogostemon* is because of the lack of a reasonable outgroup to establish where the root of the cladogram is and to establish ancestral states. The absence of a good outgroup makes it difficult to translate directly the cladogram into a phylogeny for *Pogostemon*.

Other genera of subfamily *Pogostemoideae* do not have moniliform hairs on the filaments and are unlikely to be phylogenetically related (Bhatti & Ingrouille, 1995). A proper outgroup for *Pogostemon* may not be found in the Labiatae but in the Verbenaceae Jaume St-Hil. where very similar moniliform hairs have been recorded, not on the filaments, but on other floral parts (Endress, 1994). If the shrubby Verbenaceae contain the most recent ancestors of *Pogostemon* it seems likely that it is the subshrubs of subg. *Pogostemon* which are sister to the other clades in the genus. The other subgenera include representatives with various specializations, many involving reductions or loss. For example the aquatic and marshland herbs of Subgenus *Dysophyllus* have weak stems, narrow leaves and small campanulate flowers. It is also possible that evolutionary convergence, especially in marshland and aquatic species, has given rise to group of heterogeneous taxa which share some characters. The dry habitat herb species of Subgenus *Allopogostemon* have pollination and nutlet dispersal adaptations such as the loss of moniliform hairs, a zygomorphic corolla with subulate teeth and the evolution of glands on the nutlets.

ACKNOWLEDGEMENT

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APPENDIX 1

A revised classification of *Pogostemon* (Bhatti & Ingrouille, 1997) with species studied and including synonymy and geographical origin.

Pogostemon Desf.Subgenus *Pogostemon*

- P. atropurpureus* Benth. in A. DC. *Prodromus* 12: 154. Paris (1848). (*P. imberbe* Wright, ex Hook. f. Fl. Brit. Ind. iv. 637 (1885). India.
- P. benghalensis* (Burm.f.) Kuntze, *Revisio generum plantarum* 2: 529 (1891). (*Origanum benghalense* Burm. f. Fl. Ind. 128: 38 (1768), *Pogostemon parviflorus* Benth. in Wall., 1: 31 (1830), *P. intermedius* Benth. in Wall. Cat. n.2327 (1830), *P. frutescens* Graham Cat. Bomb. Pl. 149, (1839) *pro parte*, *P. purpuricaulis* Dalz. *pro parte* in Hook. *Kew Journal* 2: 337 (1850), *P. plectranthoides auct. pro maj.*, non Desf.). Nepal, India, Bangladesh, Burma, Thailand and Sri Lanka.
- P. cablin* (Blanco) Benth. in A. DC., *Prodromus* 12: 146. Paris (1848). (*Mentha cablin* Blanco Fl. Philip. 473 (1837), *Mentha auricularia* Blanco, op. cit. ed. 2 (1845) non Linn., *P. patchouly* Pellet. in Mém. Soc. Sci. Orléans, v. 277.t.7 (1845) *pro parte*, *P. suavis* Ten. in Parl. *Giornale Botanico Italiano. Firenze.* ii, 56 (1847) *pro parte*). Widespread in the Asian Tropics to Fiji. Introduced into many places as one of the sources of Patchouli oil.
- P. championii* Prain in *Kew Bull.* 254 (1908). Hong Kong.
- P. cristatus* Hassk. in Hce. & De Vriese, *Tijdschr.* 10: 127 (1843). Timor, Lesser Sunda Islands.
- P. dielsianus* Dunn in *Notes of the Royal Botanic Gardens Edinburgh* 8: 159 (1913). Western China.
- P. elsholtzioides* Benth. in A. de Candolle, *Prodromus* 12:153. Paris (1848). The Himalayas.
- P. formosanus* Oliver in Hook.f. *Icones* 25, Pl. 2440 (1896). Taiwan.
- P. gardneri* Hook.f. in *Flora of British India* 4: 632. (1885). Western India.
- P. glaber* Benth. in Wall. *Plantae Asiaticae Rariores* 1:31.(1830). North-western India and Nepal to Yunnan and Thailand.
- P. griffithii* Prain in *Kew Bull.* 181, (1908). Burma.
- P. heyneanus* Benth. in Wall. *Plantae Asiaticae Rariores* 1: 30. (1830). (*P. patchouly* Pellet. in Mém. Soc. Sci. Orléans, 277: 7 (1845) *pro parte*, *P. suavis* Tenore in Parl. *Giornale Botanico Italiano. Firenze.* ii, 56 (1847) *pro parte*). Widespread in southern Asia from Sri Lanka to Indonesia. Introduced into many areas including the Seychelles as a source of Patchouli oil.
- P. hispidus* Prain in *Kew Bull.* 254, (1908). Thailand to Bangladesh.
- P. nelsonii* Doan in Humbert, *Fl. Gen. Indo-Chine* 4: 975 (1936). Southern India, Kerala.
- P. nepetoides* Stapf. in *Kew Bull.* 116 (1908). The Philippines, Luzon.
- P. paniculatus* (Willd.) Benth. in Wall. *Plantae Asiaticae Rariores* 1: 30. (1830). (*Elsholtzia paniculata* Willd. *Sp. Pl.* 3: 59. (1800)). Southern India and Thailand.
- P. plectranthoides* Desf. in *Mem. Mus. Natl. Hist. nat. Paris* 2: 154.t.6 (1815). (*Mentha secunda* Roxb. *Hortus Bengalensis* 44. Serampore (1814)). India, Bangladesh.
- P. pubescens* Benth. in A. DC., *Prodromus* 12: 152. Paris (1848). South-east Asia.
- P. purpurascens* Dalz. in *Hooker's J. Bot.* 2: 337 (1850). India from Bombay to Assam.
- P. tuberculatus* Benth. in Wall. *Plantae Asiaticae Rariores* 1: 31 (1830). Eastern Himalayas.
- P. villosus* Benth. in Wall., *Plantae Asiaticae Rariores* 1: 30 (1830). India, Bengal and Bangladesh.
- P. wattii* C.B. Clarke, *J. Linn. Soc.* 25: 59. (1889). (*P. battakianus* Ridl. in *Journal of the Asiatic Society. Calcutta.* 1: 85). India, in western Assam near Burma.

Subgenus *Allopogostemon* Bhatti & Ingr. *Bulletin of the Natural History Museum. London. (Botany)* 27(2): 97 (1997). (*Pogostemon* section *Racemosa* Benth. *pro parte*).

Section *Racemosus* (Benth.) Bhatti & Ingr. *Bulletin of the Natural History Museum. London. (Botany)* 27(2): 97 (1997). (*Pogostemon* section *Racemosa* Benth., *Pogostemon* section *Barbata* Briq. *pro parte*).

Subsection *Racemosus*

- P. elatispicatus* Bhatti & Ingr. *Bulletin of the Natural History Museum. London. (Botany)* 27(2): 102 (1997). Philippines.
- P. membranaceus* Merr. in *Philippin Journal of Science (Botany)* 7: 347 (1912). Philippines.
- P. mollis* Benth. in *Labiatarum genera et species*, 155 (1832–6) London. Southern India in the western Ghats.

- P. nilagiricus* Gamble, *Fl. Madras*. 1134 (1924). Southern India, Nilagiri (Kunda Hills near Ootacamund).
P. paludosus Benth. in A. DC., *Prodromus* 12: 154. Paris (1848). India.
P. petiolaris Benth. in A. DC., *Prodromus* 12: 154. Paris (1848). Southern India in the western Ghats.
P. philippinensis S. Moore, *J. Bot.* 43 (1905). East Indies, Philippines and Marianas Islands.
P. rogersii N.E. Brown in *Kew Bull.* 379 (1909). Southern Africa.
P. rotundatus Benth. in Wall., *Plantae Asiaticae Rariores* 1: 31 (1830). Southern India.
P. rupestris Benth. *Labiatae genera et species*, 156 (1832–6) London. (non *Dysophylla rupestris* Dalz. in Hook. *Kew Journal* 3. 120 (1851)). Sri Lanka.
P. velatus Benth. in A. DC., *Prodromus* 12: 155. Paris (1848). Philippines.
P. vestitus Benth. in Wall. *Plantae Asiaticae Rariores* 1: 31 (1830). Southern India, western Tamil Nadu.
P. williamsii Elmer, *Leaflet. Philipp. Bot.* ix. 3197 (1934). Philippines.

Subsection *Glabriusculus* (Briq.) Bhatti & Ingrouille *Bulletin of the Natural History Museum. London. (Botany)* 27(2): 102 (1997).

- P. atropurpureus* Benth. in A. DC., *Prodr.* 12: 154 (1848) (*P. imberbe* C.H. Wright ex Hook. f. *Flora of British India* 4: 637).
P. reflexus Benth. in A. DC., *Prodromus* 12: 155. Paris (1848). Sri Lanka.
P. speciosus Benth. in Wall., *Plantae Asiaticae Rariores*, 1: 31 (1830). India, Nilagiri (Kunda Hills) on the border of Kerala and Tamil Nadu.
P. travancoricus Bedd., *Icones Plantarum Indiae Orientalis* 1: 34 (1869–1874). Southern India.

Section *Zygocalyx* Bhatti & Ingr. *Bulletin of the Natural History Museum. London. (Botany)* 27(2): 104 (1997).

- P. brachystachyus* Benth. in A. DC., *Prodromus* 12: 156. Paris (1848). Northern India to Burma.
P. fraternus Miq. *Flora Indiae Batavae* 2: 635 (1859). Northern India to China and Thailand.
P. hirsutus Benth. in *Labiatarum genera et species*, London. 155 (1832–6). Sri Lanka.
P. litigiosus Doan in Humbert, *Flora General of Indo-China*. 4: 972 (1936). Malaysia, Mt. Kinabalu only.
P. macgregorii W.W. Smith, in *Record of the Botanical Survey of India. Calcutta*. 6: 39 (1914). Northern Thailand.
P. menthoides Blume, *Bijdragen tot de Flora van Nederlandsch Indië* 3: 825 (1826). India and Burma to Indonesia and Vietnam.
P. nigrescens Dunn in *Notes of the Royal Botanic Gardens Edinburgh* 37: 159 (1918). Western China.
P. strigosus (Benth.) Benth. in A. DC., *Prodromus* 12: 155. Paris (1848). Assam, India and north-eastern Bangladesh.
P. wightii Benth. in *Labiatarum genera et species*, London. 156 (1832–6). Southern India.

Subgenus *Dysophyllus* (Blume) Bhatti & Ingr. (*Dysophylla* Blume (1826) *pro parte*).

Section *Dysophyllus*

- P. amaranthoides* Benth. in A. DC., *Prodromus* 12: 153. Paris (1848). Eastern Himalayas.
P. auricularius (L.) Hassk. *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie. Amsterdam* 10: 127 (1843). (*Mentha auricularia* L. *Mant. pl.* 81 (1767); *Dysophylla auricularia* (L.) Blume *Bijdr.*: 825 (1826)). Southern Asia from Sri Lanka to eastern China and New Guinea.
P. barbatus Bhatti & Ingr., *Bulletin of the Natural History Museum. London. (Botany)* 27: 108 Western China to Hong Kong.
P. glabratus Chermersir. ex Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982). Thailand.
P. micangensis G. Taylor in *Journal of Botany. London*. 69: Supp. 2, 166 (1931). Angola, Cameroon.
P. mutamba (Heirn) G. Taylor in *J. Bot. Lond.* 69, supp. 2 : 166 (1930). South-western Africa.
P. mysuroides (Benth.) Kuntze, *Revisio generum plantarum* 2: 530 (1891). Eastern India.
P. quadrifolius (Benth. in Wall.) Kuntze, *Revisio generum plantarum* 2: 530 (1890). (*Mentha stellata* Roxb. *nom. illegit.* in *Hortus Benghalensis*, Serampore (1814), *Dysophylla quadrifolia* Benth. in Wall. *Plantae Asiaticae Rariores* 1: 30 (1830), *D. velutina* Benth. in Wall. l.c., *D. rupestris* Dalz. in *Hooker's Journal of Botany* 3: 120 (1851)). Assam, Bangladesh and Kerala in southern India.
P. salicifolius (Dalz. ex Hook.f.) El-Gazzar & Watson in *Taxon*, 16: 187 (1967). (*Dysophylla salicifolia* Dalz. ex Hook. f. *Flora of British India* 4: 638 (1885)). Western India.
P. tisserantii (Pellegr.) Bhatti & Ingr. (*Dysophylla tisserantii* Pellegr. in *Compte Rendu Association Francaise Pour l'Avancement des Science* 49E Botanic session Grenoble 1925). Chad.

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- P. andersonii* (Prain) Press Bull. nat. Hist. Mus., bot., 10: 73–74 (1982). (*Dysophylla andersonii* Prain in *Journal of the Asiatic Society of Bengal. Calcutta.* 59: 298 (1891)). North-eastern India.
- P. aquaticus* (C.H. Wright in Dyer) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982). (*Elsholtzia aquatica* C.H. Wright in Dyer, *Flora of Tropical Africa* 5: 451 (1900)). East Africa.
- P. ciliatus* Bhatti & Ingr. *sp. nov.* New Guinea.
- P. crassicaulis* (Benth. in Wall.) Press in *Bulletin of the Natural History Museum. London. (Botany)*, 10: 73–74 (1982). (*Dysophylla crassicaulis* Benth. in Wall. *Plantae Asiaticae Rariores* 1: 30 (1830)). Bangladesh, India and south-eastern Asia.
- P. cruciatus* (Benth. in Wall.) Kuntze in *Revisio generum plantarum* 529: 2 (1891). (*Dysophylla cruciata* Benth. in Wall. *Plantae Asiaticae Rariores* 1:30 (1830)). The Himalayas, Assam to Thailand.
- P. deccanensis* (Panigr.) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73. (*Eusteralis deccanensis* Panigrahi in *Phytologia* 32(6): 475 (1978), *Dysophylla tomentosa* Dalz. in *Hooker's J. Bot.* 2: 337 (1850), non *Pogostemon tomentosa* Hassk. (1844)). Southern India.
- P. erectus* Kuntze in Bull. nat. Hist. Mus., bot. 10: 73–74 (1982). (*Dysophylla gracilis* Dalz. in *Hooker's Journal of Botany. London.* 2: 337 (1850), non *P. gracilis* Hassk. (1843)). India, Bombay.
- P. faurei* (Lév.) Press. in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982). (*Dysophylla faurei* Lév. in *Reprrium Species noae Regni vegetabile* 9: 248 (1911)). Korea.
- P. helferi* (Hook.f.) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982). (*Dysophylla helferi* Hook.f., *Flora of British India* 4: 640 (1885)). Bengal and Burma.
- P. koehneanus* (Muschl.) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982). (*Dysophylla koehneana* Muschl. in *Reprrium novae specie Regni Vegetabile* 4: 269 (1907)). Thailand.
- P. linearis* (Benth. in DC.) Kuntze, *Revisio generum plantarum* 529: 2 (1891). (*Dysophylla linearis* Benth. in A. DC., *Prodrum* 12: 157. Paris (1848)). Western China.
- P. lythroides* (Diels) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982). (*Dysophylla lythroides* Diels in *Notizblatt des Kgl. Botanischen Gartens und Museums zu Berlin.* 9: 1031 (1926)). Southern Asia.
- P. peguanus* (Prain) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10, 73–74 (1982). (*Dysophylla peguana* Prain in *Journal of the Asiatic Society of Bengal. Calcutta.* 59: 298 (1891)). South-eastern Asia.
- P. pentagonus* (C.B. Clarke ex Hook.f.) Kuntze, *Revisio generum plantarum* 2: 529 (1891). (*Dysophylla pentagona* C.B. Clarke ex Hook.f. *Flora of British India* 4: 641, (1885)). Southern India, Thailand.
- P. pressii* Panigrahi in *Taxon* 33: 1 (1989). (*P. griffithii* (Hook.f.) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982), *Dysophylla griffithii* Hook.f. *Flora of British India*, 4: 641 (1885)). India and China.
- P. pumilus* (Graham) Press in Bull. nat. Hist. Mus., bot., 10: 73–74 (1982). (*Mentha pumila* Graham in *Edinburgh New Philosophical Journal* 4: 393 (1828), *Dysophylla pumila* (Graham) Benth. in Wall., *Plantae Asiaticae Rariores.* 1: 30 (1830)). Nepal to Bangladesh.
- P. sampsonii* (Hance) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10, 73–74 (1982). (*Dysophylla sampsonii* Hance in *Annales des Sciences Naturelles. Paris.* 5: 284 (1866)). China.
- P. stellatus* (Lour.) Kuntze, *Revisio generum plantarum* 2: 429 (1891) (*Mentha stellata* Lour. in *Flora Cochinchinensis* 2 Ulyssipone (1790), *Dysophylla stellata* (Lour.) Benth. in Wall. *Plantae Asiaticae Rariores* 1: 30 (1830), non *Mentha stellata* Roxb. (1814)). India and Bangladesh, also collected in Hong Kong.
- P. stocksii* (Hook.f.) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10: 73–74 (1982). (*Dysophylla stocksii* Hook.f. *Flora of British India* 4: 642 (1885)). South-western India.
- P. trinervis* Chermisr. ex Press in *Bulletin of the Natural History Museum. London. (Botany)*, 10: 73–74 (1982). Thailand.
- P. verticillatus* (Roxb.) Bhatti & Ingr., comb. nov. (*Mentha verticillata* Roxb. in *Hortus Bengalensis.* Serampore (1814), *Dysophylla verticillata* (Roxb.) Benth. in Wall. *Plantae Asiaticae Rariores* 1: 30, (1830), *D. ramosissima* Benth. in Wall. Pl. As. Rar.i.30, (1830), *D. benthamiana* Hance in *Annales des Sciences Naturelles. Paris. Sér.* v. 234 (1866), *P. benthamianum* (Hance) Kuntze in *Revisio generum plantarum* 2: 530 (1891)). Bangladesh and India.
- P. yatabeanus* (Makino) Press in *Bulletin of the Natural History Museum. London. (Botany)* 10, 73–74 (1982). (*Dysophylla yatabeana* Makino in *Botanical Magazine. Tokyo.* 1: 55 (1898)). Honshu, Shikoku, Kyushu in Japan, Korea.

APPENDIX 2

Data encoded for cladistic analysis. Columns ordered in sequence C1–C41. Species ordered in the same sequence as Figs 2–4.

<i>P. gardneri</i>	02000	32011	23012	12023	22113	22222	21111	00806	0
<i>P. benghalensis</i>	22000	32012	13121	12022	22113	32222	21112	00804	0
<i>P. formosanus</i>	22000	32012	22022	12022	21112	22222	21112	00404	0
<i>P. wattii</i>	22000	31212	22012	12022	22113	11222	21111	00401	0
<i>P. hispidus</i>	22000	11041	32022	12022	22113	12221	21111	00402	0
<i>P. elsholtzioides</i>	22000	22001	32022	12022	21112	21222	21111	00802	0
<i>P. griffithii</i>	22020	01001	32022	12023	21113	22222	22111	00203	0
<i>P. tuberculosus</i>	23000	31032	12021	12023	11112	21222	21111	00603	0
<i>P. championii</i>	22000	32031	12031	12023	21113	22221	22112	00402	0
<i>P. dielsianus</i>	22000	32022	12031	12023	21123	32221	21112	00205	0
<i>P. heyneanus</i>	22000	32042	23032	12023	22113	22222	11120	00802	0
<i>P. plectranthoides</i>	22020	01142	23022	12022	21112	21221	21111	00804	0
<i>P. pubescens</i>	22000	01142	23022	12022	22112	22222	21111	00804	0
<i>P. nepetoides</i>	22000	30222	23122	12022	22113	22222	21111	00806	0
<i>P. villosus</i>	22000	31022	23122	12023	22113	21222	22111	00803	0
<i>P. paniculatus</i>	22000	01062	33122	12023	22113	22221	22111	00806	0
<i>P. purpurascens</i>	22000	11040	33122	12022	22112	32222	22111	00706	0
<i>P. cablin</i>	22000	30012	23132	12023	22111	32222	22111	00406	0
<i>P. cristatus</i>	12000	31051	23022	12022	22113	32221	22111	00403	0
<i>P. nelsonii</i>	00000	31052	22122	12022	11123	32222	21111	00403	0
<i>P. williamsii</i>	04000	32020	20022	14022	11113	21222	21122	00106	0
<i>P. elatispicatus</i>	04000	12040	20021	14023	11113	22222	21122	00408	0
<i>P. membranaceus</i>	02000	31000	20031	14023	31113	32112	11122	00508	0
<i>P. rupestris</i>	12000	01200	30021	14022	11113	11221	21122	00402	0
<i>P. vestitus</i>	02000	31100	10021	14012	21113	31222	22122	00403	0
<i>P. petiolaris</i>	02000	31200	10021	14022	31113	22222	22122	00302	0
<i>P. paludosus</i>	02000	30210	20011	14022	11113	22222	22122	00502	1
<i>P. philippinensis</i>	02000	31110	20021	14022	21113	22221	22122	00503	0
<i>P. rogersii</i>	02000	41032	10021	14022	11111	22221	22122	00402	0
<i>P. nilagiricus</i>	02000	31130	10021	14023	11112	22221	22122	00302	0
<i>P. rotundatus</i>	02000	30100	10021	14023	11113	22222	21122	00003	0
<i>P. velatus</i>	04100	30100	10021	14023	11113	21222	21122	00103	0
<i>P. mollis</i>	02000	20100	30022	14123	11113	22222	22122	00402	0
<i>P. speciosus</i>	02000	00160	20031	14023	31112	23222	21022	00501	1
<i>P. travancoricus</i>	02000	32020	10021	14013	11113	23221	21022	00503	1
<i>P. atropurpureus</i>	12000	21130	10021	14023	31112	23221	21021	00503	1
<i>P. reflexus</i>	02000	21240	10021	14023	31113	23221	21021	00503	1
<i>P. wightii</i>	02000	31230	20022	33132	11213	13222	21122	00302	0
<i>P. hirsutus</i>	02000	31010	20022	33133	11213	22222	11220	00502	0
<i>P. brachystachyus</i>	02000	32000	20022	33133	11211	22221	22111	00502	0
<i>P. nigrescens</i>	02100	30021	10022	33133	11213	22222	21111	00504	0
<i>P. fraternus</i>	02000	31052	20032	33132	11211	32222	22112	00402	0
<i>P. macgregorii</i>	02000	31120	10022	33132	11221	22221	21121	00402	0
<i>P. menthoides</i>	02000	31040	30022	33132	11222	22222	21121	00402	0
<i>P. strigosus</i>	02120	01260	30032	33132	11213	22221	21111	00104	0
<i>P. litigiosus</i>	12020	01260	30022	33133	11211	22222	22112	00402	0
<i>P. amaranthoides</i>	02000	32011	22012	11022	11123	11221	21111	00803	0
<i>P. quadrifolius</i>	02120	32030	12013	11023	11123	11221	21111	00103	0
<i>P. myosuroides</i>	02100	31011	22013	11023	11123	11111	11111	00106	0
<i>P. salicifolius</i>	02100	01040	32023	11023	11123	11121	11111	00903	0

continued

APPENDIX 2—*continued*

<i>P. auricularius</i>	02100	11040	32013	11021	11123	11111	11111	00507	0
<i>P. glabratus</i>	02100	11000	22013	11021	11122	11112	11111	00407	0
<i>P. micangensis</i>	12100	31010	20013	21023	11123	22111	12112	00406	0
<i>P. mutamba</i>	02100	01102	30013	21023	11123	22111	22112	00403	0
<i>P. ciliatus</i>	02220	01060	30013	11021	11123	11111	22111	01613	0
<i>P. verticillatus</i>	12220	01202	31013	11023	11122	11111	12111	00606	0
<i>P. trinervis</i>	12210	40100	31013	11023	11122	11112	11111	00903	0
<i>P. crassicaulis</i>	12210	01001	31013	11023	11121	11111	11111	00903	0
<i>P. erectus</i>	12240	01200	31013	11023	21122	11111	11111	10903	0
<i>P. stellatus</i>	12240	02260	31012	11023	11122	11111	11111	10903	0
<i>P. koeheanus</i>	11210	01000	31013	11023	11122	11221	21111	00903	0
<i>P. deccanensis</i>	12240	11210	11013	11023	11211	12212	11111	00502	0
<i>P. stocksii</i>	12240	12240	20013	21023	11122	11221	21111	00903	0
<i>P. aquaticus</i>	12220	01062	31013	11022	11122	11111	11111	00903	0
<i>P. cruciatus</i>	12210	00060	30013	11022	11122	11111	11111	00903	0
<i>P. peguanus</i>	11220	00260	30013	11022	11112	11111	11111	00903	0
<i>P. barbatus</i>	12000	21020	32013	11021	11122	11111	11111	00403	0
<i>P. tisserantii</i>	12021	21060	32013	21023	11122	11111	11111	00402	0
<i>P. yatabeanus</i>	12210	01240	21012	11023	11123	11111	21111	00403	0
<i>P. pressii</i>	12220	31110	21012	11013	11122	11111	11111	00903	0
<i>P. pumilus</i>	12220	31210	21012	21023	11123	11111	11111	00703	0
<i>P. helferi</i>	12220	31210	21013	21022	11123	11111	11111	00903	0
<i>P. faurei</i>	12220	31050	21013	11022	11121	11111	11111	00703	0
<i>P. linearis</i>	12220	31010	20013	11023	11121	11111	11111	00406	0
<i>P. pentagonus</i>	12220	30210	10013	11023	11121	21111	11111	00404	0
<i>P. sampsonii</i>	12210	30230	11013	11023	11122	11111	11111	00403	0
<i>P. lythroides</i>	12220	31240	20013	10232	11221	11111	11110	00403	0
<i>P. andersonii</i>	12200	11200	30013	11023	21121	11111	11111	00403	0