



Infrageneric relationships within *Pogostemon* Desf. (Labiatae)

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Received January 1998; accepted for publication May 1998

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,

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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) | |
| Gynoecium | C34 | filament bases | (glabrous(1)/ villous(2) | |
| | 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) | |
| Gynoecium | 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) | |

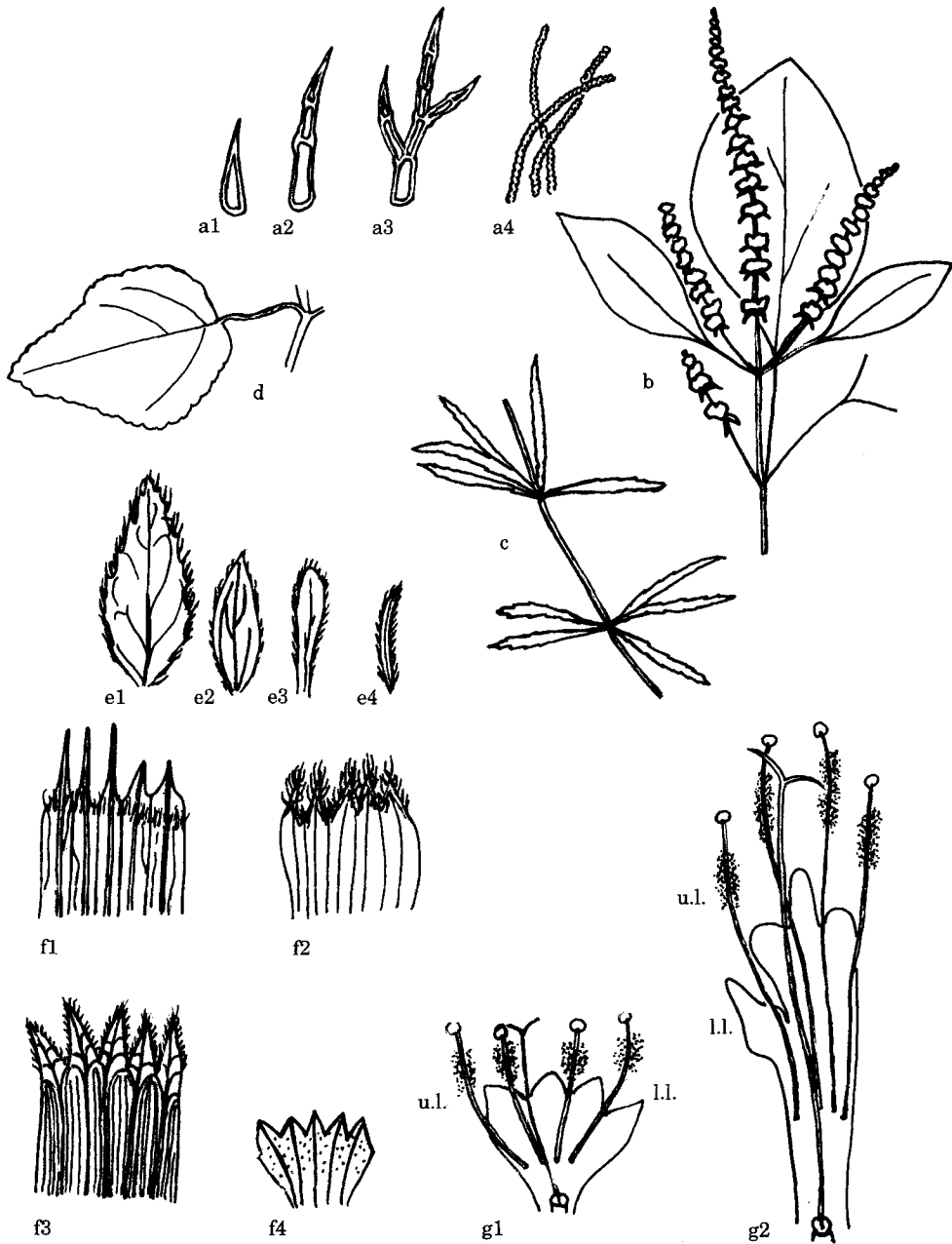


Figure 1. Qualitative characters used in cladistic and phenetic analysis: trichomes, a1 – simple, unicellular, a2 – simple, multicellular, a3 – branched, multicellular, a4 – moniliform hairs; b – inflorescence with unbranched laterals, lax throughout, leaves in pairs; c – 5 leaves at each node, sessile, 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

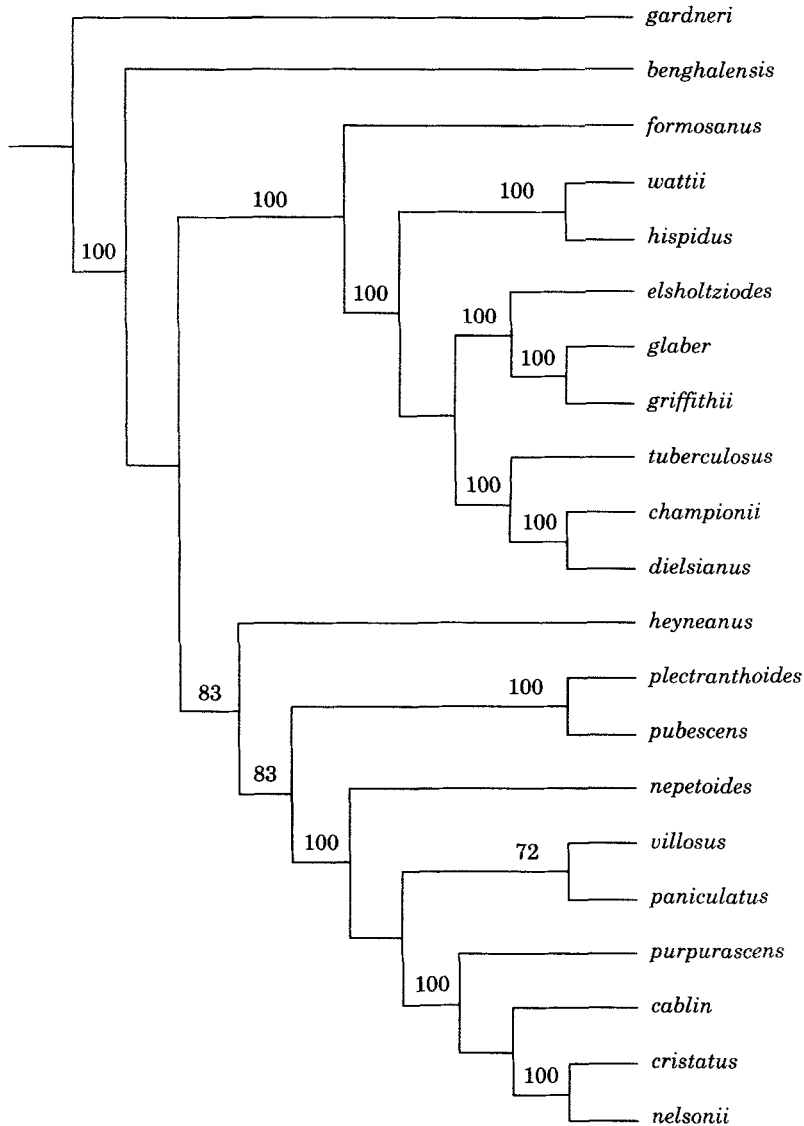


Figure 2. Cladogram of *Pogostemon* subgenus *Pogostemon* 50% majority consensus cladogram produced from 87 shortest trees rooted on *P. amaranthoides* and *P. williamsii*. Percentage of trees agreeing with branches indicated.

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

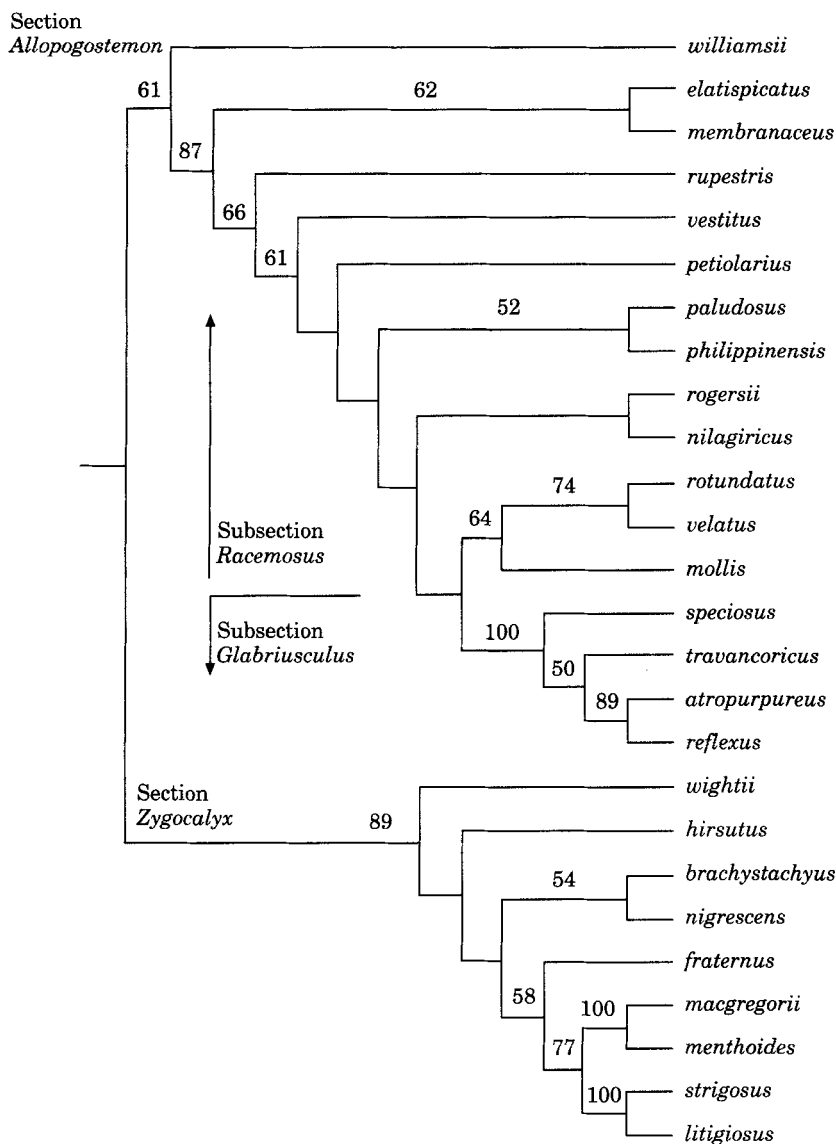


Figure 3. Cladogram of *Pogostemon* subgenus *Allopogostemon* 50% majority consensus cladogram produced from 571 shortest trees rooted on *P. amaranthoides* and *P. gardeneri*. Percentage of trees agreeing with branches indicated.

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.*

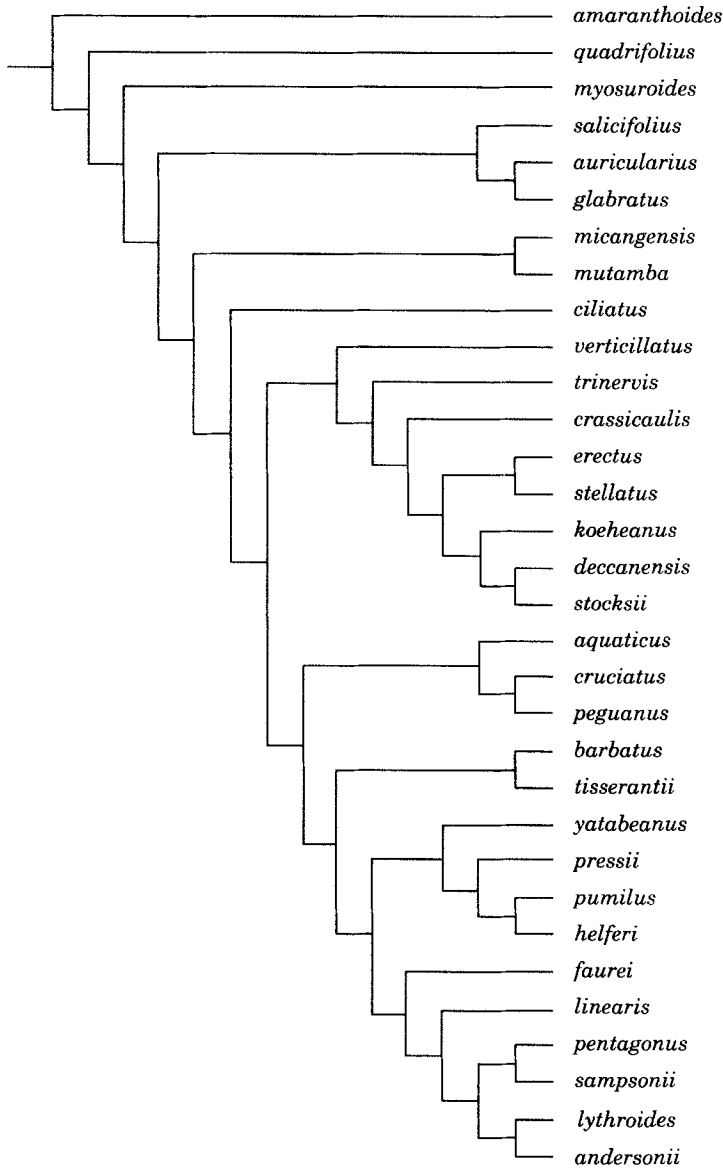


Figure 4. Cladogram of *Pogostemon* subgenus *Dysophyllus* 50% majority consensus cladogram produced one of 2 shortest trees rooted on *P. williamsii* and *P. gardeneri*.

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

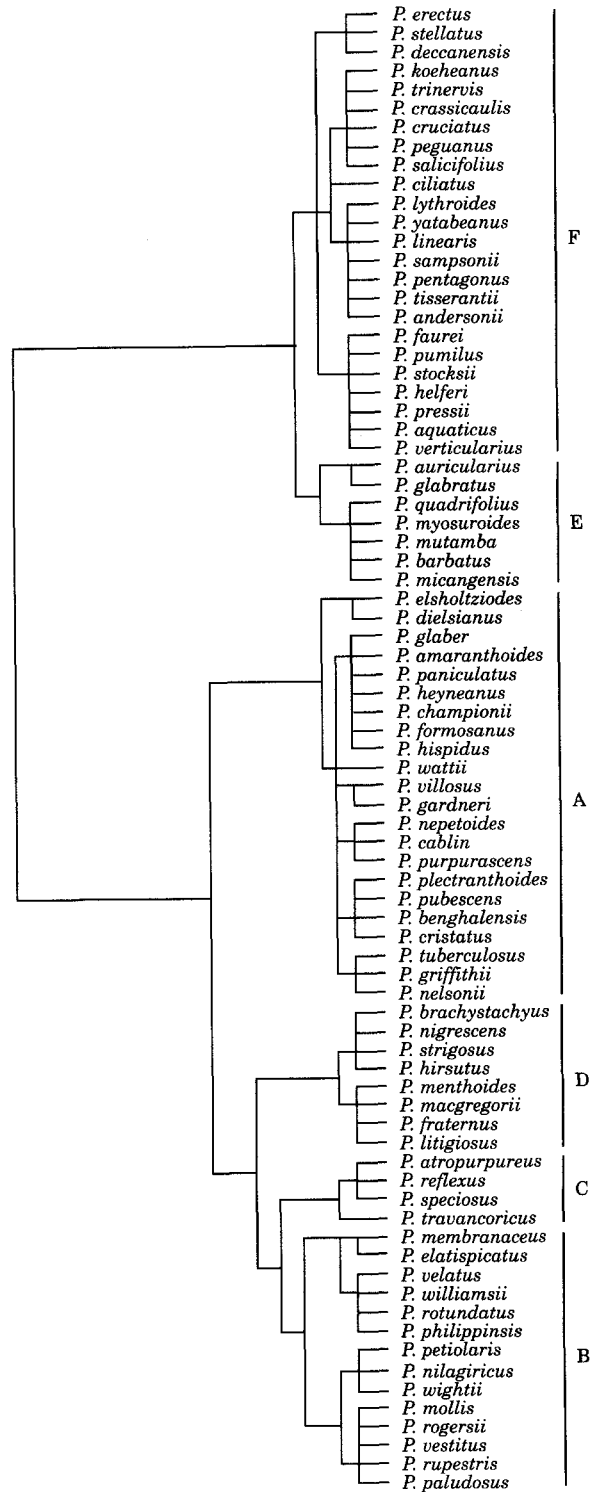


Figure 5. Phenogram of cluster analysis by Ward's method of 79 *Pogostemon* species. Excluding four mis-clustered species (*P. salicifolius*, *P. barbatus*, *P. amaranthoides* and *P. wightii*) clusters are A=Subgenus *Pogostemon*, B=Subgenus *Allopogostemon* Section *Racemosus* Subsection *Racemosus*,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

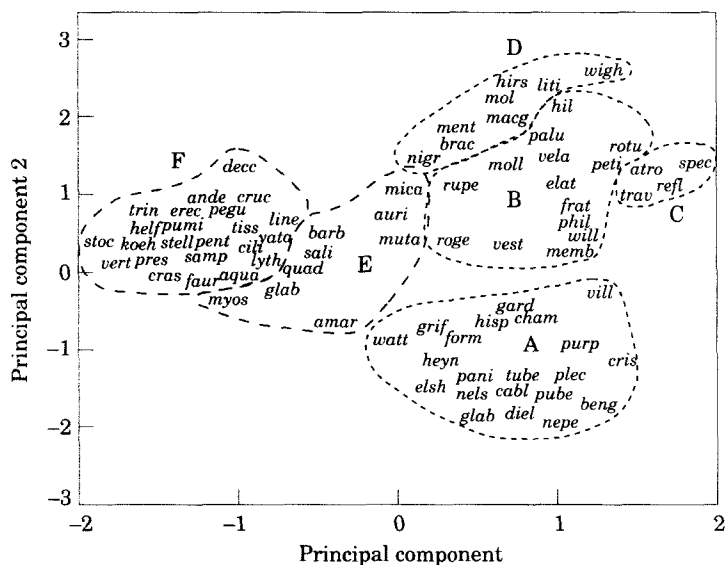


Figure 6. Scatter diagram of first (X-axis) and second (Y-axis) principal component scores (comprising 28.5% and 8.2% of the variation). OTUs coded by first letters of specific name, groups as follows; A=Subgenus *Pogostemon*, E=Subgenus *Dysophyllus* Section *Dysophyllus*, B=Subgenus *Allopogostemon* 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>Allopogostemon</i> | | subg. <i>Pogostemon</i> | | subg. <i>Dysophyllus</i> | |
|---|-----------------------------|-------------------------------|-------------------------|---------------------------|----------------------------|----------------------------|
| | sect. <i>Racemosus</i> | sect. <i>Zygocalyx</i> | sect. <i>Pogostemon</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 | herb | shrubby | herb | herb | herb |
| Phyllotaxis | 2 leaves at each node | 2 leaves at each node | 2 leaves at each node | 2-4 leaves at each node | >2 at each node | >2 at each node |
| Petiole | petiolate | petiolate | petiolate | sessile-petiolate | sessile | 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) | 9.28 (1.42) |
| Leaf margin | crenate or serrate | crenate or serrate | double dentate | dentate or serrate | dentate | dentate |
| Inflorescence | unbranched verticillaster | unbranched verticillaster | branched verticillaster | unbranched verticillaster | unbranched verticillaster | unbranched verticillaster |
| Calyx shape | tubular teeth triangular | ± two-lipped teeth awl shaped | tubular inflated | usually campanulate | campanulate | campanulate |
| Calyx length | 5.0 (0.3) | 4.7 (0.3) | 4.3 (0.2) | 2.3 (0.2) | 1.8 (0.1) | 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) | 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 | | | | |
| 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) |

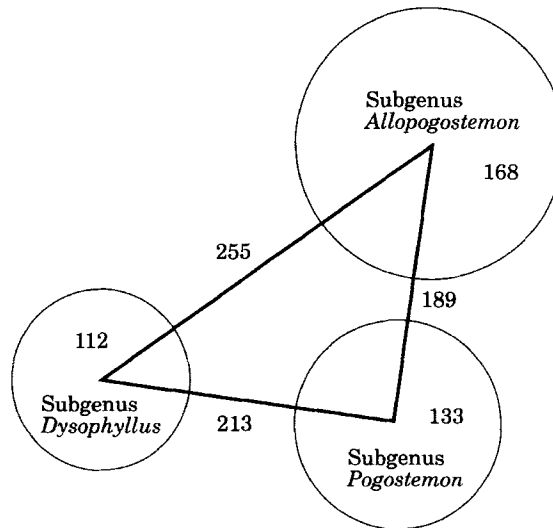


Figure 7. Cluster diagram showing mean phenetic distance (squared euclidean distance) within and between the three subgenera.

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

This work was supported by a Pakistan Government scholarship to G.R. Bhatti.

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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 Hooev. & 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 Bataviae* 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.

Section *Vérticillatus* (Benth.) Bhatti & Ingr. *Bulletin of the Natural History Museum. London. (Botany)* 27(2): 111 (1997).

- 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 *Reprum 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 *Reprum 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 |