PHYLOGENETIC STUDY OF *DAMPIERA* SPECIES BY WAGNER TREE ALGORITHM

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Abstract

The Wagner Tree algorithm was used as an aid in estimating the phylogeny. Using 15 multistate attributes, 66 species of Dampiera were analysed in a numerical phylogenetic study. During the construction of the Wagner Tree or network no weighting of attributes was undertaken. The polarity of attribute states was also not determined, except for 6 attributes in which primitive states were suggested. However, in most cases, the attribute states were arranged in possible logical transformation series. A diagram showing the probable phylogenetic relationship of Dampiera species has been developed, in view of primitive characters, found in the species. It is suggested that the root of the phylogenetic tree is somewhere at the junction of Sect. Dicoelia and Sect. Dampiera.

Introduction

The genus *Dampiera* R. Br. (Goodeniaceae), includes 66 species. It is an Australian taxa, with greatest concentration of species in Western Australia, which are arranged into 5 sections (Benth; 1868, Krause, 1912). In this contribution Carolin's computer program "KLADI" was used to construct a Wagner Tree or network, and this was used as a basis for the phylogeny.

The study of phylogeny has been greatly altered by the theories of Hennig (1966) and their developments by workers such as Farris (1970). Although Hennig derives a systematic arrangement from his phylogenies by a series of rigid rules, this is not necessary and in no way detracts from the phylogenies derived using his rules. These methods are called cladistic analysis and algorithms are now developed for the derivation of phylogenetic trees using computers. Basically all these algorithms attempt to find a minimum span network or tree. Prim networks use extent taxa as nodes whilst Wagner networks do not necessarily do so.

Some algorithms require that primitive and advance states of every attribute be known. The Wagner network algorithms of Farris (1970), and Nelson & Von Horn (1975), and the Prim network algorithm of Farris (1970) do not have these constraints. These methods are used to develop a minimum span tree connecting the extant taxa, in which each unit represents an evolutionary step from one attribute state to another. Each node on a minimum span tree represents a taxon extent or hypothetical, while each branch is interpreted as a lineage, sub-terminal nodes are interpreted as hypothetical ancestral taxa, while the terminal nodes or branch tips represent extant taxa. These networks are undirected, which may be given an evolutionary interpretation (i.e., turned into a directed tree) by selecting one of the nodes as a likely root of the tree, at which to locate a group ancestor.

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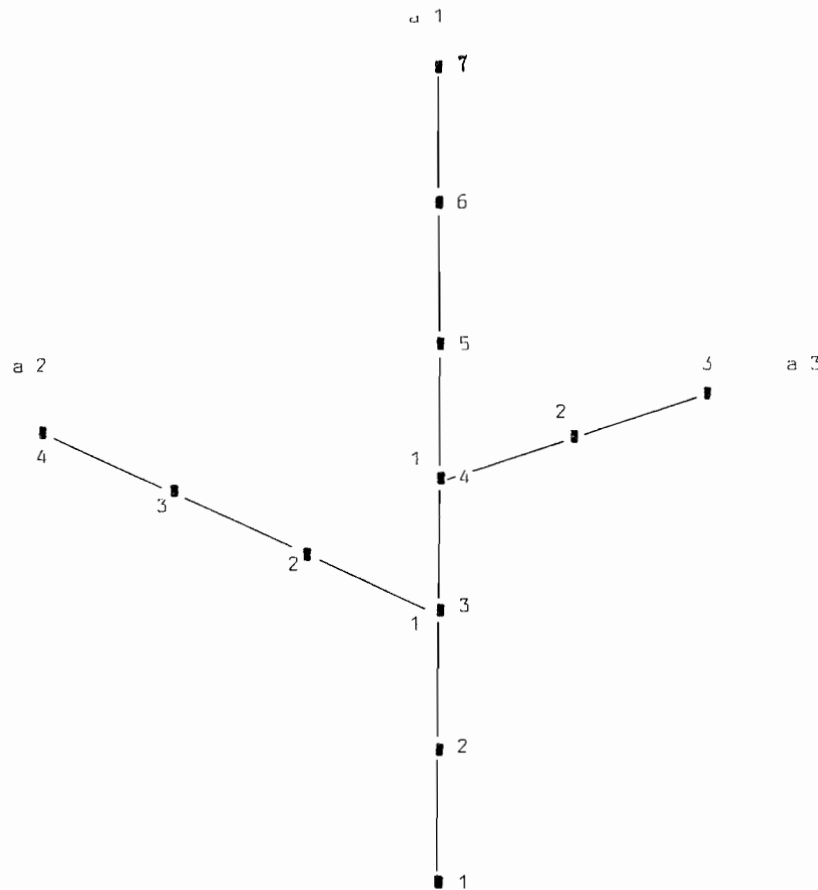
Fig.1. Branching attributes (for explanation see text).

A Wagner tree is a more likely depiction of th phylogeny of a group than a Prim tree, mainly because, a Wagner tree admits nodes which need not be extant. In the case of phylogenetic trees distances between taxa are calculated as Manhattan distances, that is the sum of the attribute differences, i.e., the number of putative phylogenetic changes between each pair of taxa.

Material and Methods

Wagner trees for this data were developed using the method of Nelson & Von Horn (1975), written into a computer program by R.C. Carolin (1979). This program "KLADI" is written in BASIC at University of Sydney computing center. The first scan through the data produced 14 pairs of taxa showing the same distance between each other. The trees based upon these 14 pairs were developed, each subsequent addition to each tree being the first closest discovered in each scan. The shortest of these trees was taken as the most likely representation of the phylogeny as illustrated in (Fig.4). For the construction of Wagner tree following steps were followed:

Step 1: All the major attributes were listed and their states arranged in logical transformation series. The states of each attribute are given a numerical code (Appendix-I). The logical transformation series A----A'----A", would be coded as A = 1, A' = 2, A" = 3. The number of evolutionary steps between A" and A is thus 3 -- 1 = 2. Branching transformation series are split into a number of attributes. For example the logical transformation series in Fig.1, is split into three attributes (a.1) with states 1,2,3,4,5,6 and 7 (a 2) with states 1,2,3 and 4; and (a 3) with states 1,2 and 3. A taxon with state 4 is coded 4 for attribute (a 2) and 3 for attribute (a 1) and 1 for attribute (a 3). This coding method preserves the evolutionary step relationships between the states of a branching attribute, while expressing the states in a linear order, suitable for the calculation of a Man-hattan distance.

Step 2: All the species and associated attributes states are listed in a data matrix (Appendix-I).

Step 3: The computer program "KLADI" was used to construct minimum span tree.

Step 4: A tree was constructed by joining all the taxa according to the computer outprint result.

The states coded for a particular attribute in a particular species does show some variation with the descriptions of the species. For example leaves of *D. discolor* are entire or dentate, only entire state is coded, since KLADI at present does not permit alternative states of a particular attribute, only one state can be encoded. Therefore a state which was more frequent in a particular attribute was coded, and alternative less frequentstates of the attributes were ignored. The attribute states and their numerical code used in this study are given in Appendix-I, data and matrix are summarised here.

Fifteen attributes were selected to analyze the cladistic of the members of *Dampiera*. Detailed description of the attributes and their respective states are given below. During the construction of the network no weighting of attributes was undertaken.

APPENDIX-I

Attributes:

Hairs on the outside of the corolla:

These are arranged into 3 possible logical transformation series, as shown in (Fig.2).

1. Line 1. Which is now considered as attribute 1, has 7 states (see Fig.2), only names of the exemplar secies are given, for the shape of their hairs see Rajput *et al.,* (1985).

2. Line 2. Which is now considered as attribute 2, has 4 states (Fig.2), which starts from line 1 at state number 3.

3. Line 3. Which is now considered as attribute 3, has 3 states (Fig.2), and it starts from line 1 at state number 4.

4. Stem shape. (for further details see Rajput & Carolin, 1983).

1. Terete, 2. Ribbed, 3. Triangular, 4. 3-winged and 5. 2-winged or flat.

5. T.S. morphology of leaf blade.

1. Flat, 2. Recurved and 3. Revolute,

6. Leaves on plant.

1. Fasciculate, 2. Foliage leaves on the entire plant, 3. Foliage leaves present on the lower portion of the plant, upper leaves mostly scaley or reduced to bracts and bracteoles and 4. Foliage leaves radical only.
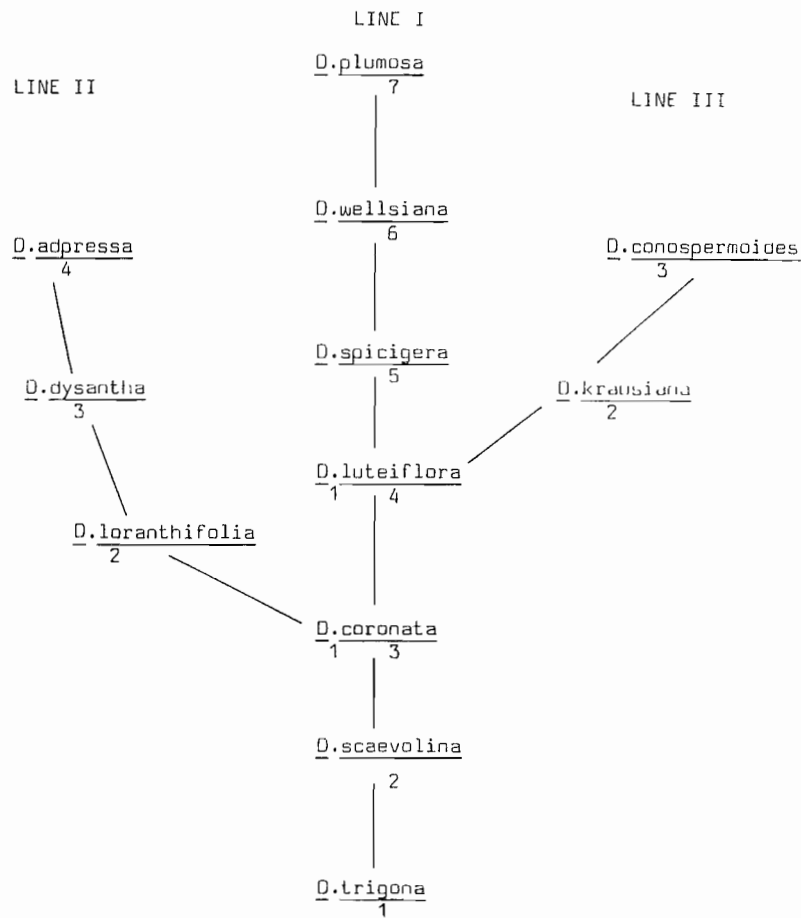
LINE I

D.plumosa
7

LINE II   LINE III

D.wellsiana
6

D.adpressa   D.conospermoides
4   3

D.spicigera
5

D.dysantha   D.krausiana
3   2

D.luteiflora
1   4

D.loranthifolia
2

D.coronata
1   3

D.scaevolina

2

D.trigona
1

Fig.2. Diagram showing possible logical evolutionary transformation series of hairs of Dampiera. The species names are examples of the hair type. This figure must not be interpreted as the phylogeny of the species concerned.

7. Leaf margin
1. Entire, 2. Slightly dentate, 3. Deeply dentate, 4. Dentate to lobed and 5. Lobed,
8. Leaf base.
1. Cordate, 2. As wide as stem (in case of flat stem, e.g., *D. deltoidea*).3. Narrowing towards base, 4. Sub-sessile and 5. Petiolate.
9. Leaf surface.
1. Tomentose on both surfaces, 2. Glabrescent on both surface, 3. Glabrous on the upper surface, tomentose on the lower surface. 4. Glabrescent on the upper surface, tomentose on the lower surface and 5. Glabrous on the both surface.

Inflorescence:

Diagram shown in Fig.3, shows the possible logical arrangements of the inflorescences within the genus *Dampiera*.
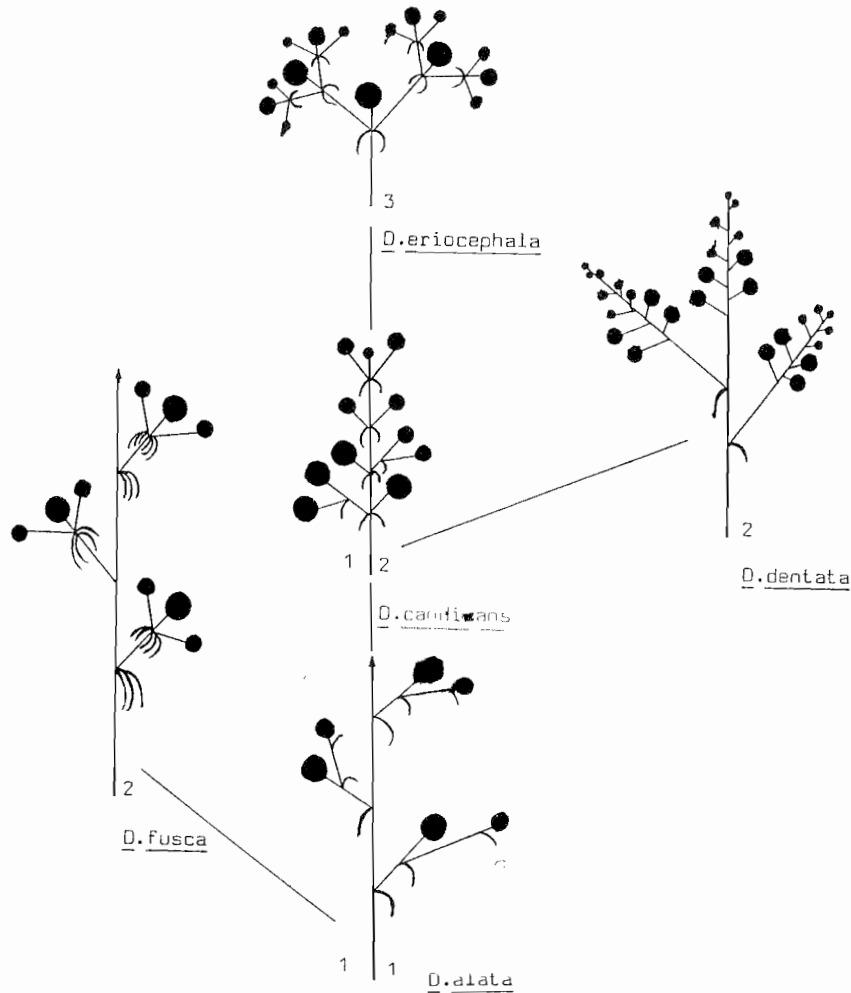
Fig.3. Diagram showing possible logical transformation series of inflorescence. The specific names are exemplar. and the diagram is not intended to be interpreted as a phylogeny of the species.

10. Line 1. This line shows the decrease in the length of the internodes, and increase in branching of dichasial partial inflorescence i.e., formation of a complex dichasium.

1. *D. alata* type: internodes long, flowers are mostly arranged in monochasia, 2. *D. candicans* type: internodes condensed or very short and 3. *D. eriocephala* type: complex dichasia are formed, and flowers are arranged in a loose head.

11. Line 2. This line shows the development of false dichotomous branching with development of many sterile bracts. This attribute has 2 states.

1. *D. alata* type, (same as in line 1), 2. *D. fusca* type, (see Fig.3).

12. Line 3. This line shows the reduction of the partial inflorescence to a single flower, and subsequent loss of bracts and bracteoles. This attribute has 2 states.

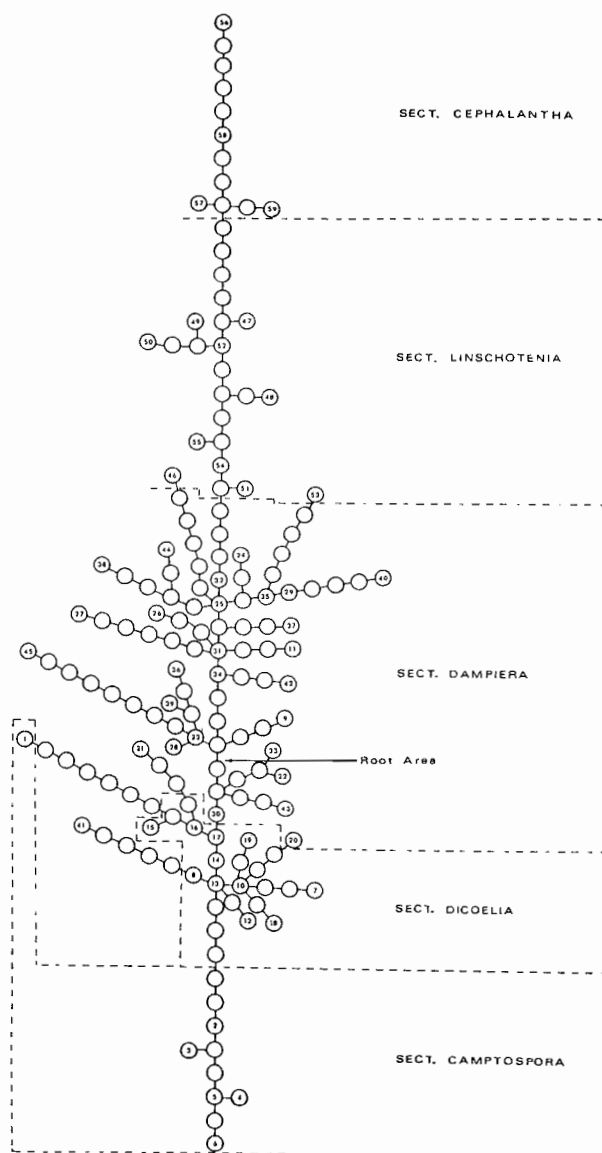1. *D. candicans* type, (same as in line 1), 2. *D. dentata* type, (see Fig. 3).

Fig. 4. Key to the species shown in the Wagner Tree or network.
1. D. alata, 2. D. angulata, 3. D. carinata. 4. D.deltoidea, 5. D.lindleyi 6. D. coronata, 7. D.decurrens, 8. D fasciculata. 9. D. fusca. 10. D. galbraithia, 11. D.glabrescens, 12. D. latealata, 13. D. leptoclada, 14. D. loranthifol, 15. D. obliqua, 16. D. parvifolia, 17. D.stricta, 18.D.triloba, 19. D.trigona, 20. D. altissima, 21. D. adpressa, 22. D. carolinii, 23. D. dysantha, 24. O. eriantha, 25. D. haematotricha 26. D. hederacea, 27. D. incana, 28. D. lavandulacea. 29. D. lanceolata. 30. D. linearis 31. D. marifolia, 32. D.oligophylla, 33. D. pedunculata 34. D.pritzelii 35. D.purpurea, 36. D. rodwayan 37.D. rogerana, 38.D. roycei, 39. D. rosma rinifoli 40. D. salehae, 41. D. scaevolina, 42. D. stenophylla, 43. D. tenuicaulis 44. D. tomentosa, 45. D. tephrea, 46. D. atriplicina, 47. D. candicans. 48. D. cinerea, 49. D. conospermoide, 50. D. discolor. 51. O. krausian 52. D. ramosa, 53.D. spicigera 54.D.stenos 55. D. teres. 56. D. dentata. 57. D. eriocephala, 58. D. plumosa, 59. D. wellisiana.

13. Shape of the ovary

1. Gibbous (e.g., *D. sacculata*), 2. Broad or ovoid (e.g., *D. incana*).3. Oblique (e.g., *D. obliqua*), 4. Straight (e.g., *D. leptoclada*).

14. Shape of the ovule

1. U-shaped (with both arms of U equal, e.g., *D. alta*), 2. U-shaped (with unequal arms of U, e.g., *D. incana*).

3. Erect but slightly bent near the base, e.g., *D. candicans.* and 4. Erect straight, e.g., *D. leptoclada*.

15. Indusium lips

1. Non-hairy and 2. Hairy.

Results and Discussion

The shortest network obtained is illustrated in (Fig.4). However, this is undirected and the problem of primitive characters must arise. Since it is difficult to decide about primitive and advance characters within the taxonomic units under study, there are problems in determining the root of this tree. The problem of ancestral character states, the directional component of the tree or any proposed phylogeny has only a small probability of being correct unless the trees of the individual attributes,upon which the final tree is based, are correct in terms of advance and primitiveness.

Unfortunately, the task of estimating character state phylogeny involves considerable guess work, as the fossil record is not known. Although numerous criteria for estimating ancestral states have been devised, there is no way to assess the reliability of these, and many of them rest on unwarranted assumptions.

Kluge & Farris (1969) briefly delineated three general criteria, which are outlined here:

(I). The primitive state of a character for a particular group is likely to be present in many representatives of closely related groups.

(II) A primitive state is more likely to be wide spread within a group than in any one advance state.

(III). The primitive state is likely to be associated with the states of other characters known from other evidence to be primitive.

On the other hand if the problem is approached by comparing supposedly related genera, Kluge & Farris's (1969) criteria do not necessarily hold up. Carolin (1967, 1977) suggested that the primitive ovary condition was 2-locular and this does not satisfy any of the criteria. Previous attempts at overall outgroup comparison by numerical means (Farris, 1969) have not been altogether satisfactory (Weston, 1978, and Carolin's pers. comm.). Thus we are reduced to the comparision of states, one by one of related taxa. The primitive states of some of the attributes are impossible to determine at this stage, e.g., hair type.

Of the 15 attributes, some of which are admittedly derivative of others, for only 6 we can suggest a primitive state. Mostly we consider these primitive because they are more widely distributed in taxa related to *Dampiera* unless indicated otherwise. They are as follows:

1. Terete-ribbed stem without cortical bundles and with 2/5 phyllotaxis.
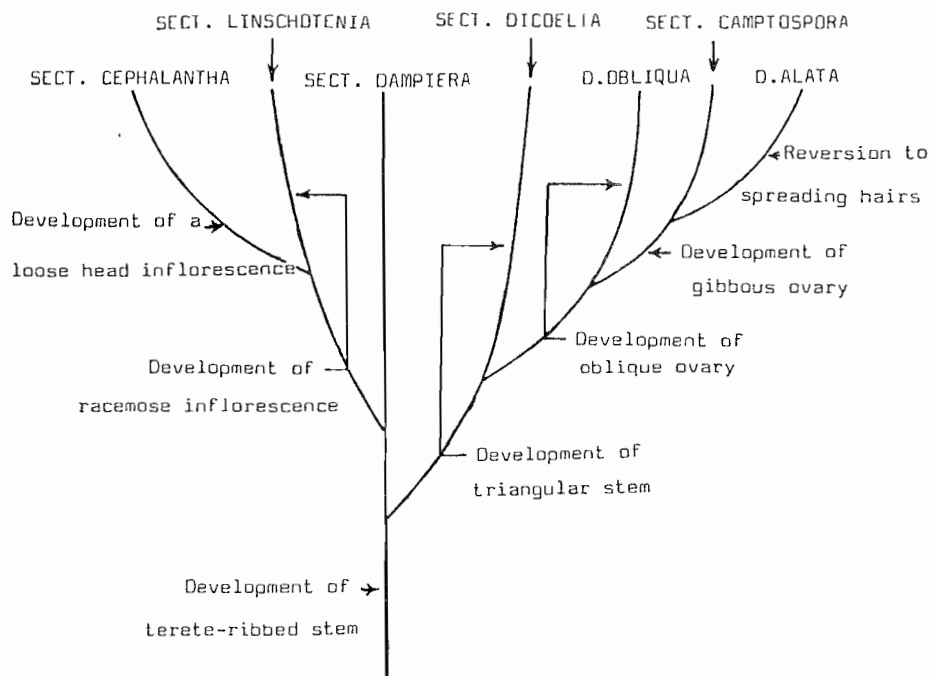2. Possibly flat leaves,
3. Foliage leaves scatterd all over the stem.

Fig.5. Diagram showing the probable phylogenetic relationship of the major groups of Dampiera species and derivation of present day sections. This diagram is partially based on computer analysis.

4. Cymose inflorescence (see Rickett, 1944),
5. Straight ovary
6. Erect basifixed ovule.
7. 2-locular ovary (this attribute was not included in the analysis using KLADI).

Keeping in view the above mentioned primitive characters it is suggested that the root of the tree is somewhere at the junction of sect. Dicoelia and sect. Dampiera, because the members of sect. Dampiera mostly have terete-ribbed stem, with usually scattered foliage leaves, which are mostly flat, except in a few species which have recurved or revolute leaves. All the members of sect. Dampiera have cymose inflorescence, straight ovary, with single erect basifixed ovule. The main reason for suggesting the root area at the junction of sect. Dicoelia and sect. Dampiera, is that, the 3 members of sect. Dicoelia have 2-locular ovary, and 2-locular ovary is generally considered as a primitive feature.

Even now, however, it seems that some adjustment is necessary to the Wagner tee generated by KLADI. These methods are intended to generate hypothesis which must then be subjected to intellectual scrutiny. Merely because they have been developed by "numerical" means, does not mean that they should not be amended by "non numerical" means. In addition it was not possible to include all the attributes considered to be important since they could not be determined for some of the species e.g., phyllotaxis and internal stem anatomy. In this case it is possible that *D. alata* and *D. obliqua* are misplaced. *D. obliqua* indeed, appears to be a connecting link between sect. Dicoelia

and sect. Camptospora, because *D. obliqua* has oblique ovary, which can be considered as intermediate between straight and gibbous ovary.

D. alata has the characteristic ovary and ovule of sect. Camptospora and it appears to have been misplaced because it lacks the appressed T-shaped hairs on the outside of the corolla, which is the characteristic feature of that section. We think that the hair type has a greater chance of reversion than has the gibbous ovary. We have therefore moved *D. alata* to sect. Camptospora. On the other hand *D. obliqua* is kept within sect. Dicoelia, because of its triangular stem, and ovule which is not U-shaped.

Hair-type is also possibly the main reason for *D. fusca* and *D. glabrescens* being placed in sect. Dampiera. Also *D. fusca* has developed false dichotomous branching with development of many sterile bracts. Both *D. fusca* and *D. glabrescens* have the typical stem structure of sect. Dicoelia, we have therefore moved them to sect. *Dicoelia*.

D. spicigera and *D. atriplicina* are also somewhat displaced, from the members of sect. Linschotenia, and are placed with the members of sect. Dampiera, but infact they are pushed 6-7 steps away from the members of sect. Dampiera. Again possibly hair-type and leaf-surface are the main reasons for their displacement. We have placed them with the members of sect. Linschotenia, because of the inflorescence type and laterally attached ovule. The sect. Cephalantha comes out quite clearly in this network too. In Fig.5 a diagram is given to show the probable phylogenetic relationship of the major groups of *Dampiera* species.

Acknowledgements

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