Pak. J. Bot., 21(1): 158–169, 1989.

A CLADISTIC ANALYSIS OF *CALANDRINIA* (PORTULACACEAE)

SYEDA SALEHA TAHIR AND PETER S. ASHTON

Arnold Arboretum of Harvard University,
Cambridge, Massachusetts 02138, U.S.A.

Abstract

The cladistic relationship among 34 species of the genus *Calandrinia* H.B. et. K. (Portulacaceae), endemic to Australia were analysed for 22 binary attributes, by using "PHYSYS" computer program. The criteria used to assign evolutionary polarity of attribute state is discussed in detail. In all the Phenograms four main groups come out fairly clearly. The major difference in the trees produced by PHYSYS are the changes in the position of a few taxa, within the major group. The present paper provides data on variation and correlations in seed and pollen characters, and also synthesized detailed morphological relationships. The species having questionable position in some groups are discussed in the light of their unique characters.

Introduction

The genus *Calandrinia* H.B. et. K. belongs to family Portulacaceae, with about 100 species, distributed in Australian and American continents. All the 34 species endemic to Australia (Syeda, 1979) were analysed, for 22 binary attributes, and the cladistic analysis proved to be a powerful tool, that enabled us to sort out complex species with relative ease.

Cladistic technique combining the features of "PHYSYS" and Wagner (1961) were used to construct Phenograms (Alves & Stock 1986, Carpenter, 1987). Some of the terms used in this study, and the criteria used to decide whether a given attribute state is primitive or derived is also described.

Attributes: Attributes are abstract entities consisting of one or more states, which are used as a basis for comparing or identification of different taxa e.g., the attribute "capsule deheisence" can assume one of the two states; by pore and by valves.

Binary attributes: A binary attribute is one, in which attribute have only two states, for example seed surface may be dull or glossy, or the sepal lobes persistent or deciduous.

Criteria used to assign evolutionary polarity to attribute states: Various criteria have been used in recent literature to decide, whether a given attribute state is primitive or derived. The most satisfactory method for assigning evolutionary polarity of attribute state is out-group analysis (Stevens, 1980). In the out-group analysis some idea of the relationship of three (or more) taxa is needed – the taxon being examined, its sister groups, and at least one taxon that is cladistically more primitive (the latter two taxa are the out-groups). An attempt was made to do the out-group analysis, but the generic limits in Portulacaceae are not clear (Carolin, 1987), therefore the out-group analysis was not possible for this study.

Unfortunately, the task of estimating attribute 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. The character state that occurs most frequently with in group studied, the common state, is taken as the primitive state. Many botanical workers have used this criterion, although, often in conjunctin with others, (Thorne, 1958; Crowson, 1970; Judd, 1979; Takhtajan, 1969, Wagner 1961, Kluge & Farris, 1969). In general, except where otherwise indicated, the more common state is considered as primitive and a numerical code "0" is given, whereas less common state is considered as derived or advance, and a numerical code "1" is given.

Details of the attributes used in the computer analysis.

Roots: The roots are based on the tap root system, which are usually unthickened and non-tuberous but in a few species like *C. schistorrhiza*, the roots have several tubers. The non-tuberous roots are considered as a primitive condition, as it is frequently found among the species of *Calandrinia*. According to Carolin (1987), tuberous root is an advance condition.

1. Roots non-tuberous (0): Roots tuberous (1).

Stem: The basic architecture of the members of Portulacaceae is much the same. The stem is defined here as the short basal sterile portion of the plant which usually has short internodes and is mostly erect. It carries a rosette or fascicle of leaves in the axils of which scapes arise. The branched stem is considered as primitive and unbranched stem system is considered as an advance state.

2. Stem branched (0): Stem unbranched (1).

Only one species in *Calandrinia (C. volubilis)* has a twining stem and is considered as an advance condition, whereas all the rest of species have straight stems, and is considered as a primitive state.

3. Nature of the stem straight (0): Stem twining (1).

Inflorescence: Generally the inflorescence are misinterpreted in floras and treatments of individual genera. Troll (1922) examined the inflorescence of *Montia sibirica*, and described it as a cincinnus and indeed the basic form of infloresence in the family Portulacaceae is a cyme. Occasionally in *Calandrinia*, the inflorescence is reduced to a solitary flower. Rickett (1944) and Troll (1964) considered cymose inflorescence as primitive and reduced inflorescence i.e., solitary flower as an advance condition.

4. Cyme infloresence (0): Reduced (solitary flower) inflorescence (1).

Sepals: In this investigation the outer floral whorl are referred as sepals. However there is a general disagreement, as to the homology of the outer floral whorl in family Portulacaceae (Von Prolliitz, 1934; Legrand, 1972; Geesink, 1969; Eckhardt, 1976).

Most of the *Calandrinia* species have persistent sepals, but in some cases, they are deciduous, and this character was used in the past in the identification of a few *Calandrinia* species (Syeda, 1979). Carolin (1987) indicated that the persistent sepals are primitive and deciduous are advance conditions.

5. Sepals persistent (0): Sepals deciduous (1).

Sometimes sepals shows prominent longitudinal folds on the upper surface, and this distinction has proved to be very useful in discriminating between species. Sepal lobes without longitudinal folds is considered as primitive because they are more widely distributed in taxa, related to *Calandrinia.*

6. Sepal lobes without longitudinal folds (0): Sepal lobes with longitudinal folds (1).

Petals: There are functional reasons to belove that primitive angiosperms have polymerous flowers (Leppik, 1977). Therefore petals more than 5 is accepted as primitive and petals 5 or less as an advance condition.

7. Petals more than 5 (0): Petals 5 or less (1).

Stigma: Stigmatic branches 4 or more is considered as a primitive, and stigmatic branches 3 is considered as an advance condition.

8. Stigmatic branches 4 or more (0): Stigmatic branches 3 (1).

Carolin (1987) indicates that in family Portulacaceae connate condition of stigmatic branches is primitive, therefore stigmatic branches free to the base is considered as an advance condition.

9. Stigmatic branches connate at the base (0): Stigmatic branches free to the base (1).

Fruit: In most cases the fruit is a capsule dehiscing through valves from the apex, but in a few species the fruit circumcissile from the base and splits into short valves from the base. Regarding the polarity of attributes for fruit character, the more general condition is considered as primitive, and attributes are coded as follows:

10. Fruit dehiscent (0): Fruit indehiscent (1).

11. Dehiscence not circumcissile (0): Dehiscence circumcissile (1).

12. Fruit dehiscence by valves (0): Fruit dehiscence by pores (1).

13. Opening of fruit by terminal valves (0): Opening of fruit by basal valves (1).
14. Fruit valves persistent (0): Fruit valves deciduous (1).

Seeds: Syeda & Carolin (1987) and Carolin (1987) have shown that the seed type, in particular is useful at the generic level in this family. Many types of seed surface pattern and seed shapes are recognised within the species of *Calandrinia*. As multistate disordered attributes are not taken into considereation, therefore seed surface pattern and seed shapes are not included in this investigation. Seed characters taken into consideration are: number of seeds per capsule; seed type (monomorphic vs. diamorphic); seed surface whether glossy or not; seed size (widest part is measured); and seed lusture (coppery vs. non coppery lusture). The polarity of the seeds attributes was determined following the principle outlined in the beginning, and attributes are coded as follows:

15. 3-many seeds per capsule (0): 1-2 seeds per capsule (1).
16. Seed monomorphic (0): seed dimorphic (1).
17. Seed surface non-glossy (0): Seed surface glossy (1).
18. Seed without coppery lusture (0): Seed with coppery lusture (1).
19. Seed size less then 1 mm (0): Seed size more then 1 mm (1).

Pollen: Three pollen attributes are included in this systematic investigation. In *Calandrinia* species both aperturate and inaperturate (without any apertures) pollen are found. The spores of lower plants including the Pteridophytes, do not possess apertures, however, the spores of Pteridophytes, do have analogous, weakened areas on the proximal pole called tetrad scars, by which they often open (Walker & Doyle, 1975). Undoubtedly the inaperturate pollen grains are primitive (ancestral) as they are found in lower plants (Walker, 1974) and aperturate pollens are considered as advance type.

20. Pollen inaperturate (0): Pollen aperturate (1).

Family Portulacaceae have been the subject of some classical studies on pollen morphology e.g., Franz (1908), Nilsson (1967). Van Campo (1976) has described a phylogenetic series of aperture changes which she called successiform is the characteristic of the caryophyllales. Carolin (1986) while reviewing the family Portulacaceae indicated that pantocolpate and non-operculate type of apertures are primitive, and hence, the pantoporate and operculate type of apertures are considered as an advanced type.

21. Aperture pantocolpate (0): Aperture pantoporate (1).
22. Aperture non-operculate (0): Aperture operculate (1).

In order, that the characters may be referenced in a convenient manner, they are listed in Appendix-I, and coding of the attributes for each species of *Calandrinia*, used in the computer analysis is given in Appendix-II.

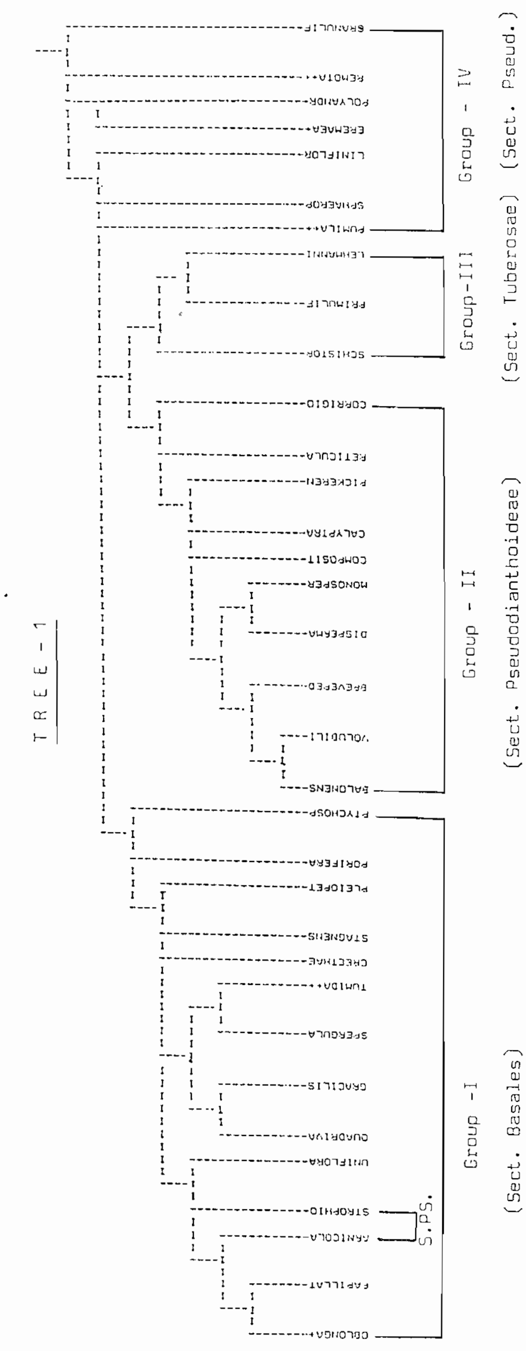

Fig. 1. Phenogram computed by PHYSYS, showing 4 groups in *Calandrinia* (S. PS = Sect. Pseud).

Results and Discussion

Using DWAGNER command, (Wagner-ground-plan analysis) three different Trees or Phenograms were computed and plotted. The phenograms are branching diagrams depicting the phenetic relationships of the included taxa. By "phenetic relationships" is meant the degree of phenetic similarity, a measure of over all similarity, based on all available attributes without any weighting (Cain & Harrison, 1960).

The phenograms show some interesting departures from expectation, although the major groups come out fairly clearly. In all the phenograms I, II, and III (Fig. 1-3), four major groups are developed, the details of which are given below:

Group I. This group includes 14 species (*C. oblonga, C. papillata, C. arnicola, C. strophiolata, C. uniflora, C. quadrivalvis, C. gracilis, C. spergularinia, C. tumida, C. creethae, C. stagnensis, C. pleiopetala, C. porifera* and *C. ptychosperma*), belonging to Section Basales and section Pseudodianthoideae which were recognised by Von Poellnitz (1934) and Syeda (1979). The main attributes which held the species of this group together are:- Stigmatic branches 4, Free to the base; capsule 4-valved, mostly opening by terminal valves. Out of 14 species in this group, 12 belongs to sect. Basales and remaining 2 species (*C. arnicola* and *C. strophiolata*) belongs to sect. Pseudodianthoideae.

The position of *C. arnicola* and *C. strophiolata* is questionable in this group. As both *C. arnicola* and *C. strophiolata* has many unique characters, which are not found in other *Calandrinia* species. *C. strophiolata* has 6-valved capsule, 6-stigmatic branches, and the seeds with large strophiole. According to Bentham (1963), strophiolate seeds is the characteristic feature of the genus *Talinum*. But on the other hand, according to Pax & Hoffman (1934), Talinum has a 3-valved capsule, and does not occur in Australia and New Zealand.

Group-II. This group includes 10 species of *Calandrinia* (*C. balonensis, C. volubilius, C. brevipedata, C. disperma, C. monosperma, C. composita, C. calyptrata, C. pickerengi, C. reticulata,* and *C. corrigiloides*), and they all belongs to section Pseudodianthoideae which was recognized by Von Poellnitz (1934) and Syeda (1979). The main attrributes which held the species of this group together are:- Stigmatic branches 3, and capsule 3-valved, opening mostly by terminal valve or terminal pore or indehiscent. *C. disperma* and *C. monosperma* which are included in this group, have some unique characters which are not found in other species of *Calandrinia.*

C. monosperma has only a single seed in the capsule, which is indehiscent, and the fruit wall surface has a prominent colliculate-verrucate pattern. *C. disperma* has always two seeds in the capsule, which are superposed, one is broad and ca. sub-rhomboid in

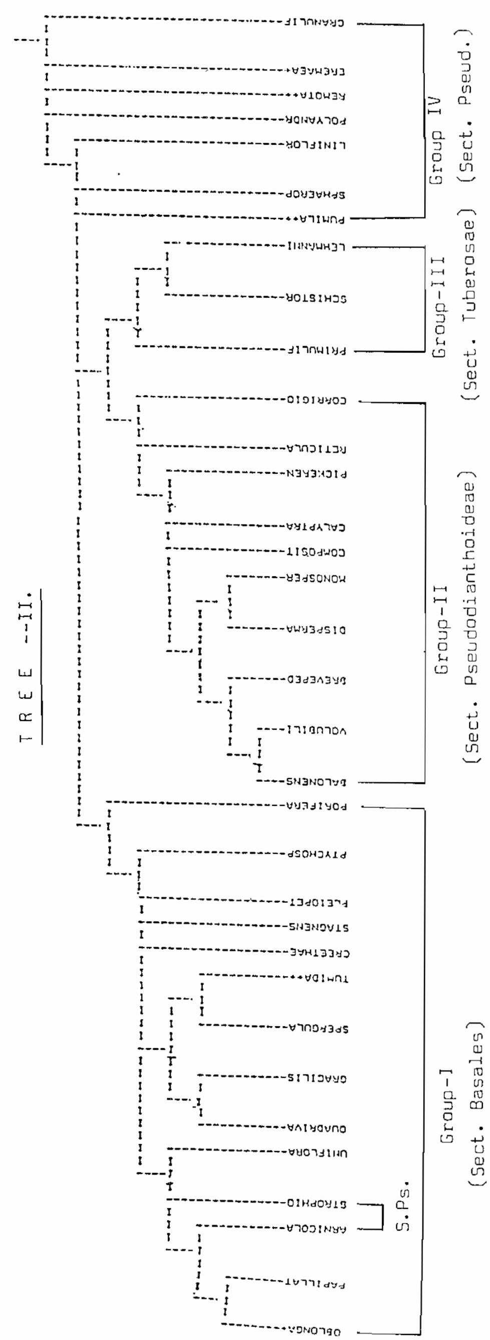

Fig. 2. Phenogram computed by PHYSYS, showing 4 groups in *Calandrinia* (S. Ps. = Sect. Pseud).

shape, and retained in the lower swollen portion of the capsule, and other narrower, but larger contained in the upper part of the capsule, more over the capsule has a terminal opening.

Group-III. This is the only group which seems to be natural. This group includes 3 species (*C. schistorhiza, C. primuliflora* and *C. lehmannii*), belonging to section Tuberosae. The species of this group are characterized by tuberous roots, 3 stigmatic branches, capsule 3-valved and seeds rugose-tuberculete or verrucate. Sect. Tuberosae was recognised by Von Poellntz (1934) and Syeda (1979).

Group-IV. It includes the members of section Pseudodianthoideae which was recognised by Von Poellnitz (1934) and Syeda (1979). Group-IV includes 7 species (*C. pumila, C. sphaerophylla, C. liniflora, C. eremaea, C. polyandra, C. remota* and *C. granulifera*). The members of these putative taxa left out of groupings and are not included until after Group-I, Group-II and Group-III are merged.

The species of group-IV are separated from the members of group-II, which also includes the species of Sect. Pseudodianthoideae, mainly because of a few characters which are not present in the members of group-II. For example *C. polyandra* and *C. eremea* have non-aperturate pollen. Thus the species of group-IV, are separated, because they have unique characters. The strategy does not seem to be very satisfactory one for this type of data. It is difficult to recognize Group-IV as a distinct group from Group-II, because the attributes on which the members of Group-IV are separated from Group-II, have little significance.

During the examination and comparison of three Trees (phenograms), showing the cladistic relationships among the species of *Calandrinia* it has been noticed that four groups come out clearly in all the three Trees. Four main groups mainly represent the sections which were recognized by Von Pollentz (1934) and Syeda (1979). The only major difference in the three trees are the change in the positions of a few species within the major groups.

In group-I species *C. ptychosperma* and *C. porifera* are changing their positions. In Group-II, in all the three Trees, no change has been noticed. In Tree 1 and 3 the position of species belonging to Group-III are same. However, in Tree-2, the position of *C. primuliflora* and *C. schistorhiza* have changed. In Group-IV, the position of *C. polyandra* is same in Tree 2 and 3, but it has changed in Tree 1. Other species which have changed the position, within the group-IV are *C. remota* and *C. eremaea*.

In this computer analysis, the species of Sect. Pseudodianthoide has appeared in two places i.e., in Group-II and in Group-IV in all the three Trees. On these result there

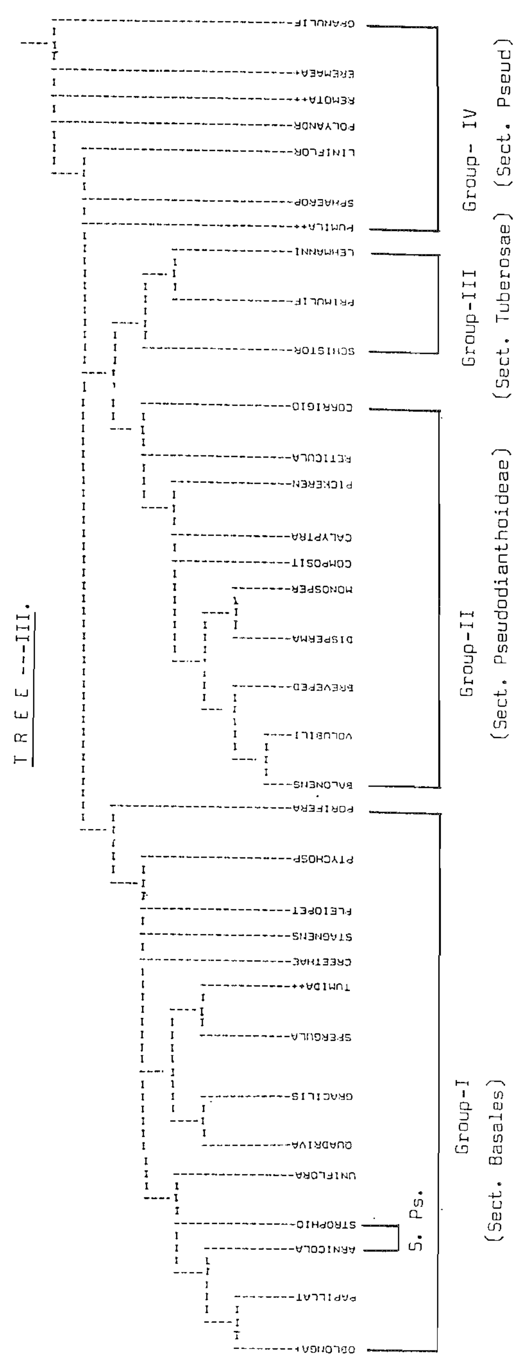

Fig. 3. Phenogram computed by PHYSYS, showing 4 groups in *Calandrinia* (S. Ps. = Sect. Pseud).

seems to be a little basis for separating Group-II, Group-III and Group-IV. But in fact if type of roots and the seed surface pattern is considered which is rugose-tuberculate or verrucate, Sect. Tuberosae (Group-III) can be separated from the members of Sect. Pseudodianthoideae (Group-II and Group-IV). The main reason for overlaping the members of Sect. Tuberosae (Group-III) with the members of Sect. Pseudodianthoideae (Group-II and Group-IV) is because PHYSYS analysis has put much emphasis on the number of stigmatic branches and the number of capsule valves.

Acknowledgements

We are greatly indebted to Dr. Peter Stevens, Roger Carolin, Tahir Rajput, for extensive discussion, numerous suggestions throughout review and criticisms of both the concept and presentation of this paper. It is a great pleasure to acknowledge the help of Dr. J.M. Carpenter, of Museum of Comparative Zoology, Harvard University, in computer analysis. Travel grant from the Council for International exchange of Schorars Washington D.C., through the United States Educational Foundation in Pakistan to the senior author is thankfully acknowledged.

References

Alves, B.I. and M. Stock. 1986. *The new user's Guide to VAX/VMS*, 5th. Edition. Harvard Univesity, Cambridge, U.S.A.

Bentham, G. 1863. *Flora Australiansis*. Vol. I. Lovell Reeve & Co., London.

Cain, A.J. and G.A. Harrison, 1960. Phyletic weighting. *Proc. Zool. Soc.*, London, 135: 1-31.

Carpenter, J.M. 1987. *Notes for Harvard Users, PHYSYS documentation*. Harvard Arts and Sciences Computer Services (HASCS), Harvard University, Cambridge, M.A., U.S.A.

Carolin, R.C. 1987, A review of the family Portulacaceae. *Aust. J. Bot.*, 35: 383-412.

Crowson, R.A. 1970. *Classification and Biology*. New York, Atherton Press.

Eckhardt, T. 1976. Classical morphological features of Centrospermous families. *Plant Syst. & Evol.*, 126: 5-25.

Farris, J.S. and M. Mickevich. 1985. *Physys documentation*. Harvard Arts and Sciences computer Services, Harvard University, U.S.A.

Franz, E. 1908. Beitrage Zur Kenntnis Der Portulacaceen und Basellaceen. Beibt. *Bot., Jahrb.* No. 97: 42, 2 and 3 Leipzig.

Geesink, R. 1969. An account of the genus *Portulaca* in Indo-Australia and the pacific (Portulacaceae). *Blumea*, 17: 275-307.

Kluge, A. and J.S. Farris. Quantative phyletics and evolution of Anurans. *Syst. Zool.*, 18: 1-32.

Legrand, C.D. 1962. Las especies americanas de *Portulaca*. *Anal. Mus. Hist. Nat. Montevideo.*, 29: 1-47.

Leppik, E.E. 1977. *Floral evolution in relation to pollination Ecology*. Today & Tomorrow Publ. Co. New Delhi.

Nilsson, O. 1967. Studies in *Montia* L. *Claytonia* L. and allied genera. III. Pollen Morphology. *Grana Palyn.*, 7: 279-363.

Pax, F. and K. Hoffman. 1934. *Portulacaceae*, in Die Naturlichen Pflanzenfamilien, (Eds.) F. Pax & H. Harms) Edn. 2. Band 16C, 234-62. Englemann, Berlin.

Rickett, H.W. 1944. The classification of infloresences. *Bot. Review*, 10: 187-231.

Stevens, P.F. 1980. Evolutionary polarity of character states. *Ann. Rev. Ecol. Syst.*, 11: 333-358.

Syeda S.T. 1979. *Calandrinia in Australia*, Sydney University, M.S. Thesis.

Syeda, S.T. and R.C. Carolin. 1988. Seed type and seed surface pattens in of *Calandrinia* Sens. Lat. (Portulacaceae). *Proc. Linn. Soc. N.S.W., Australia* 110: 307-316.

Takhtajan, A. 1969. *Flowering plants: Origin and dispersal* (Transl. C. Jeffrey), Edinburgh., Oiver and Boyd.

Thorne, R.F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants, *Aliso*, 6: 57-66.

Troll, K. 1964. *Die Infloreszenzen*, Erster Band. Gustav, Fischer Verlag, Jena.

Van Campo, M. 1976. Pattern of pollen morphological variation within taxa. In: *The evolutionary significance of the exine*. (Eds.) I.K. Ferguson and J. Muller, Linn. Soc. London, Symposium Series No. 1. Academic Press, London.

Von Poellnitz, K. 1934. Die *Calandrinia* - Arten Australiens. *Feddes Rep.*, 35: 161-173.

Wagner, W. 1961. Problems in the classification of ferns. In: *Recent advances in Botany*, (Ed.) W.B. Turrill, Toronto, Univ. Toronto Press.

Walker, J.A. 1974. Aperture evolution in the pollen of primitive angiosperms. *Amer. J. Bot.*, 61: 112-136.

Walker, J.A. and J.A. Doyle. 1975. The basis of angiosperms phylogeny; *Ann. Missouri. Bot. Gard.*, 62: 644-723.

(Received for publication 30 October 1988)

APPENDIX-I

Summary of the characters used in the PHYSYS analysis. These are discussed in detail in the text. The state given first is considered as the primitive and is coded as "O". Second state is considered as derived or advance, and is coded as "1". Information when not available for a particular state is coded as "9".

Character	Primitive	Advance
1. Roots	Non-tuberous	Tuberous
2. Stem	Branched	Unbranched
3. Stem nature	Straight	Twining
4. Inflorescence	Cyme	Solitary
5. Sepal lobes	Persistent	Deciduous
6. Longitudinal folds on sepal lones	Without folds	With folds
7. Petal number	More than 5	5 or less
8. No. of stigmatic branches	4 or more	3
9. Nature of stigmatic branches	Connate at the base	Free to the base
10. Fruit type	Dehiscent	Indehiscent
11. Nature of fruit dehiscence	Not circumcissile	Circumcissile
12. Fruit opening	By valves	By pores
13. Position of valves	Terminal	Basal
14. Fruit valves	Persistent	Deciduous
15. No. of seeds per capsule	3-numerous	1-2
16. Seed type	Monomorphic	Dimorphic
17. Seed surface	Non-glossy	Glossy
18. Seed lusture	Without coppery lusture	With coppery lusture
19. Seed size	Less than 1 mm	More than 1 mm
20. Pollen apertures	Inaperturate	Aperturate
21. Aperture type	Pantocolpate	Pantoporate
22. Apertures	Non-operculate	Operculate

APPENDIX-II

```
$ YPE CALAN. DAT
CALANDRINIA DATA
022     034     001     0009
(11F1. 0, 1X, 2A4)
0000001110000000100099    POLYANDRA
0000001100000000001100    BALONENSIS
0000001110000000100111    REMOTA
0100001110000000100100    RETICULATA
1000011100000000100101    PRIMULIFLORA
1100001100000000000101    SCHISTORIZA
0100000010000000101111    STROPHIOLATA
0100001111909910101100    MONOSPERMA
0000001110019911101110    DISPERMA
0100001110000090100100    CORRIGIOLOIDES
0000001100000000101100    BREVEPEDATA
0100901110001000100111    PUMILA
0100001110000000100111    SPHAEROPHYLLA
0000000110000000100100    COMPOSITA
```