

## THE FUNCTIONAL SIGNIFICANCE OF POLLEN AGGREGATES IN ANGIOSPERMS

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### Abstract

Functional significance of pollen aggregates in Angiosperms is discussed with reference to the number of ovules per ovary, number of seeds per fruit, polyad stigma relationship and correlation with the pollen type. Information regarding the pollination and breeding systems is also presented. It is shown that pollen aggregates have repeatedly evolved in Angiosperms.

### Introduction

In most of the plant groups in Angiosperms, at maturity, all the pollen grains are free from each other. As the prime function of the pollen grains is to provide the male gametes to the female counter part, in order to facilitate fertilization and ultimately the formation of the seed, such a strategy seems logical. However, it is also well known that in some plant groups, the pollen grains do not separate at maturity and remain associated together. The term pollen aggregate is used in the present paper to include all types of compound pollen grains, and for various types of situations where pollen grains are dispersed in groups. Char, Swamy & Cheluviah (1973) reviewed the evolutionary trends in pollen organization and discussed their adaptive significance.

In the present paper the functional significance of pollen aggregates is discussed with reference to the number of ovules per ovary, fruit seed number, polyad stigma relationship and correlation with the pollen type (bi or trinucleate). Information regarding the pollination and breeding systems is also presented.

### Observations & Results

#### (i) *Range of Morphological Variation*

In some cases, for instance in *Datisca* (Datiscaceae) the pollen grains are free or loosely united. Loose assemblage of pollen grains are met with in those cases also where viscin threads and other pollen connecting threads are present. According the definition adopted by Waha (1984) viscin threads are  $\pm$  long exinous processes which consist of exinous material and connect pollen grains and tetrads. Such viscin threads are met with in Onagraceae, Caesalpinaceae, Ericaceae and Mimosaceae only. These threads always consist of sporopollenin and exhibit very stickiness even after all viscid substances have been

removed by acetolysis. Thus they are different from pollen connecting scleroprotein threads of Orchidaceae and cellular threads of *Strelitzia reginae* (Musaceae) (Hesse & Waha, 1983). Nevertheless, these structures facilitate the movement of a group of pollen grains at a time (Cruden & Jensen, 1979; Kress, 1981; Waha, 1984). The presence of sticky pollen grains are also likely to remain together, thereby resulting in comparable genetic implications.

The regular production of dyads is known only in the Podostemaceae and Scheuchzeriaceae (Walker & Doyle, 1975), though occasionally dyads are also reported from some other families e.g. Pyrolaceae (Erdtman, 1952).

Permanent tetrads are met with in 44 families of Dicotyledonous plants and 12 families of Monocotyledonous plants (Table 1). In 13 families pollen grains are present entirely or almost entirely in tetrads, six families have significant number of genera with permanent tetrads, four have several genera with pollen in tetrads and rest of the families (27) rarely have permanent tetrads (Walker & Doyle, 1975). In Cyperaceae pseudomonads (cryptotetrads) are present. Here 3 of the 4 pollen grains fail to develop and the wall of the apparently solitary pollen grain is formed by the pollen mother cell.

In *Rollinia*, *Rolliniopsis* and the advanced West Indian species of *Annona* and in 3 species of *Zygonium* (Winteraceae) there is evidence to indicate the formation of secondarily evolved solitary pollen from tetrads (Walker, 1971; Sampson, 1981).

According to spatial arrangement of the individual pollen grains within the tetrad, two fundamentally different types of tetrads may be recognised, i.e. Uniplanar — with all the grains in the same plane and multiplanar with grains in more than one plane (Walker & Doyle, 1975). Uniplanar tetrads may be tetragonal (square, isobilateral), rhomboidal, linear or T-shaped, while multiplanar tetrads may be tetrahedral or decussate. As a rule, the monosulcate pollen of magnoliid dicots and monocots occur in tetragonal tetrads, while the tricolpate pollen of the non-magnoliid dicotyledons are generally found in tetrahedral tetrads.

Polyads, the pollen units of a definite number greater than four are present only in six families: Annonaceae, Leguminosae (Mimosoideae), Celastraceae (including Hippocrataceae), Gentianaceae, Asclepiadaceae and Orchidaceae. In some polyads the identity of the individual tetrads may be recognised, whereas in others it is not possible to do so. Bigger pollen-units known as massulae, where the number of pollen grains is not ascertainable due to large number of grains or as a result of large amount of pollen fusion, are present in Asclepiadaceae and Orchidaceae. By definition, 2 polyads or massulae must be present in each locule, if only one such unit is present, it is designated as a pollinium. Like massulae, pollinia are also met with in only 2 families, Asclepiadaceae and Orchidaceae (Walker & Doyle, 1975).

Table 1. Taxa with compound pollen grains.

Taxa	Compound pollen grains	Flowers	Pollination	Breeding system	Pollen type	Ovules/locule
1	2	3	4	5	6	7
<b>Dicotyledons</b>						
Magnoliiflorae <i>Annonales</i>						
1. Annonaceae	c. 1/3 of 130 genera have tetrad pollen (Sampson, 1981); also polyads	Bisexual	Beetle Pollination (Faegri & van der Pijl, 1971)	Outbreeding	binucleate	1- $\alpha$
<i>Rafflesiales</i>						
2. Rafflesiaceae	Tetrads very rare ( <i>Cytinus dioecus</i> ; <i>C. baroni</i> )	Unisexual	Sapromyophily (Faegri & van der Pijl, 1971)	Outbreeding	binucleate (not studied in <i>Cytinus</i> )	$\alpha$
<i>Magnoliales</i>						
3. Winteraceae	Tetrads in overwhelming majority of the family. <i>Drimys</i> , <i>Zygogonium</i> (3 species have secondarily evolved solitary pollen (Sampson, 1981)	Unisexual, bisexual	Cleoptera and others (Thien, 1980)	Outbreeding	binucleate	1- $\alpha$

(Table 1. Contd.)

1	2	3	4	5	6	7
<i>Lactoridales</i>						
4. Lactoridaceae	Tetrads in overwhelming majority of the family	Polygamomonoecious		Outbreeding		6
<i>Laurales</i>						
5. Monimiaceae	Tetrads very rare ( <i>Hedyocarya arborea</i> , <i>H. cunninghamii</i> )	Usually unisexual		Outbreeding (not studied in <i>Hedyocarya</i> )	binucleate	1- $\alpha$
<i>Nymphaeiflorae</i>						
6. Nymphaeaceae	Tetrads very rare ( <i>Victoria regia</i> )	Bisexual	Dynastid pollinator (van der Pijl, 1971)		binucleate (not studied in <i>Victoria</i> )	1- $\alpha$
<i>Ranunculiflorae</i>						
<i>Ranunculales</i>						
7. Berberidaceae	Tetrads very rare ( <i>Podophyllum emodi</i> )	Bisexual	Entomophily, long-tongued insects (Grant, 1950)	Generally outbreeder (Rendle, 1959); Protogyny (van der Pijl, 1971)	binucleate	$\alpha$ -few

(Table 1. Contd.)

1	2	3	4	5	6	7
Papaverales						
8. Papaveraceae	Tetrads very rare	Bisexual			binucleate	$\alpha$
Caryophylliflorae						
Caryophyllales						
9. Didiereaceae	Possibly tetrads present	Unisexual or rarely ( <i>Decaryia</i> ) bisexual, female				1
Malviflorae						
Malvales						
10. Tiliaceae	Tetrads very rare ( <i>Neotessmannia</i> spp.)	Generally bisexual			binucleate	1- $\alpha$
11. Sarcolaenaceae	Tetrads occur in overwhelming majority of the family	Bisexual				2 or more

(Table 1. Contd.)

1	2	3	4	5	6	7
Violiflorae						
<i>Cucurbitales</i>						
12. Datiscaceae	Tetrads very rare. In <i>Datisca</i> , pollen grains free or loosely united	Unisexual, (plant dioecious) rarely bisexual ( <i>Datisca</i> )	Anemophily (Willis, 1973)	Outbreeding	binucleate	α
13. Begoniaceae	Tetrads very rare. (In <i>Begonia evansiana</i> , grains occasionally united in tetrads (Erdtman, 1952)	Unisexual (plant monoecious)	Entomophily inferred (Rendle, 1959) Bird flower (Grant, 1950)	Outbreeding	binucleate	α
14. Cucurbitaceae	Tetrads very rare ( <i>Gurania</i> sp.)	Unisexual (plant monoecious)	Entomophily (Gant, 1950) and ornithophily (Grant, 1950)	Outbreeding	binucleate (not studied in <i>Gurania</i> )	α
Theiflorae						
<i>Theales</i>						
15. Marcgraviaceae	Tetrads very rare ( <i>Marcgravia polyantha</i> )	Bisexual	Cheropteroiphily (Faegri & van der Pijl, 1971; Proctor & Yeo, 1973)		binucleate	α

(Table 1. Contd.)

1	2	3	4	5	6	7
16. Nepenthaceae	Tetrads present in overwhelming majority of the family	Unisexual (Plant dioecious)		Outbreeding	binucleate	$\alpha$
17. Lecythidaceae	Tetrads very rare	Bisexual	Entomophily (Vogel, 1978)		bi and trinucleate	1- $\alpha$
18. Clusiaceae	Tetrads very rare ( <i>Kielmeyera coriacea</i> , <i>K. variabilis</i> )	Bisexual			binucleate (not studied in <i>Kielmeyera</i> )	$\alpha$ or 1
Rosiflorae						
<i>Hamamelidales</i>						
19. Myrothamnaceae	Tetrads in almost all members	Unisexual (plant dioecious)		Outbreeding		$\alpha$
<i>Saxifragales</i>						
20. Saxifragaceae	Tetrads very rare	Bisexual			binucleate	$\alpha$
<i>Droserales</i>						
21. Droseraceae	Tetrads present in most of the genera, except in <i>Drosophyllum</i> and <i>Pusitanicum</i>	Bisexual	<i>Drosera</i> usually selfed and often cleistogamous; <i>D. capensis</i> large showy flowered is insect pollinated. (Proctor & Yeo, 1973)		bi and trinucleate	3- $\alpha$

(Table 1. Contd.)

1	2	3	4	5	6	7
<i>Rosales</i>						
22. Rosaceae	Tetrads very rare, loose tetrads in <i>Sorbus</i> cf. <i>meinichii</i>	Bisexual			binucleate (not studied in <i>Sorbus</i> )	2 (2-5 loculed or partly partitioned ovary)
Podostemiflorae						
<i>Podostemales</i>						
23. Podostemaceae	Dyads, possibly polyads in significant number of genera	Bisexual	Entomophilous in <i>Dicraca</i> and <i>Mourera</i> (Rendle, 1959)		binucleate	$\alpha$
Myrtiliflorae						
<i>Myrtales</i>						
24. Onagraceae	Tetrads in several genera of the family	Bisexual	Ornithophilily, entomophilily (Grant, 1950; Protor & Yeo, 1973)	Outbreeding	binucleate	$\alpha$ -1



(Table 1. Contd.)

1	2	3	4	5	6	7
Fabiflorae						
<i>Fabales</i>						
25. Mimosaceae	Tetrads and polyads in significant number of genera	Bisexual	Entomophily	Outbreeding	bi and trinucleate	$\alpha$
26. Caesalpinaceae	Tetrads very rare ( <i>Afzelia</i> spp.)	Bisexual			binucleate (not studied in <i>Afzelia</i> )	$\alpha$ (in <i>Afzelia</i> )
Rutiflorae						
<i>Sapindales</i>						
27. Sapindaceae	Tetrads very rare ( <i>Magonia</i> sp.)			Outbreeding	binucleate (not studied in <i>Magonia</i> )	1-3
Sanatiflorae						
<i>Celastrales</i>						
28. Celastraceae (including Hippocrataceae)	Tetrads and polyads very rare. ( <i>Campylostemon</i> )	Bisexual			bi and trinucleate (not studied in <i>Campylostemon</i> )	2

(Table 1. Contd.)

1	2	3	4	5	6	7
Solaniflorae						
<i>Solanales</i>						
29. Solanaceae	Tetrads very rare ( <i>Salpiglossis</i> )	Bisexual			binucleate (not studied in <i>Salpiglossis</i> )	$\alpha$
Comiflorae						
<i>Ericales</i>						
30. Ericaceae	Tetrads present in over- whelming majority of the family	Bisexual except <i>Epigaea</i>	Ornithophily (Grant, 1950), entomophily (Faegri & van der Pijl, 1971; Proctor & Yeo, 1973)		bi and trinucleate	1- $\alpha$
31. Actinidaceae	Tetrads very rare ( <i>Saurauia elegans</i> )	Bisexual			binucleate	$\alpha$
32. Clethraceae	Tetrads very rare ( <i>Clethra spicigera</i> )	Bisexual			binucleate	2

(Table 1. Contd.)

1	2	3	4	5	6	7
33. Empetraceae	Tetrads present in overwhelming majority of the family	Unisexual, rarely bisexual	Outbreeder		binucleate	1
34. Pyrolaceae	Tetrads present in overwhelming majority of the family	Bisexual			binucleate	$\alpha$
35. Epacridaceae	Tetrads present in overwhelming majority of the family. In Tribe Stypheleae usually only one microspore per tetrad is functional and 3 microspores persist as relics in permanent tetrad	Bisexual	Honey eaters of Australia and Pacific together with parrakeets are main pollinators	Outbreeding <i>Epacris</i> , <i>Styphelia</i> (Grant, 1950)	binucleate	1- $\alpha$
<i>Eucommiales</i>						
36. Eucommiaceae	Tetrads very rare	Unisexual, plant dioecious		Outbreeding	binucleate	2
<i>Cornales</i>						
37. Cornaceae	Tetrads very rare ( <i>Melanophylla humblotii</i> )	Bisexual			binucleate	1 (not studied in <i>Melanophylla</i> )

(Table 1. Contd.)

1	2	3	4	5	6	7
38. Escalloniaceae	Tetrads very rare ( <i>Carpodetus</i> sp.)	Bisexual			trinucleate	$\alpha$
Gentianiflorae						
<i>Goodeniales</i>						
39. Goodeniaceae	Tetrads very rare ( <i>Leschenaultia</i> sp.)	Bisexual	Protandry (Rendle, 1959); Ornithophily in <i>Scaveola</i> (Grant, 1959). Entomophily (Willis, 1973)		binucleate	1, 2- $\alpha$
<i>Gentianales</i>						
40. Rubiaceae	Tetrads in several genera of the family	Bisexual	Entomophily (Willis, 1973; Rendle, 1959); Ornithophily (Grant, 1950)		bi and trinucleate (binucleate in <i>Casasia</i> , <i>Gardenia</i> , <i>Oxyanthus</i> , <i>Randia</i> )	1- $\alpha$

(Table 1. Contd.)

1	2	3	4	5	6	7
41. Gentianaceae	Tetrads and polyads in significant number of genera	Bisexual	Entomophily (Willis, 1973; Grant, 1950); Dimorphic heterostyly (Faegri & van der Pijl, 1971)		bi and trinucleate	Usually $\alpha$
42. Apocynaceae	Tetrads in significant number of genera	Bisexual	Entomophilous (Rendle, 1959)		bi and trinucleate	2- $\alpha$
43. Asclepiadaceae	Tetrads, polyads, massulae and pollinia in overwhelming majority of the family	Bisexual	Entomophilous	Outbreeding	bi and trinucleate	$\alpha$
Lamiiflorae						
<i>Scrophulariales</i>						
44. Bignoniaceae	Tetrads in several genera of the family	Bisexual	Bird flowers (Grant, 1950) Chiropterophily (Faegri & van der Pijl, 1971), Ornithophily		binucleate	$\alpha$

(Table 1. Contd.)

1	2	3	4	5	6	7
45. Pedaliaceae	Tetrads very rare <i>Sesamothamnus</i> , <i>Sigmatosiphon</i> )	Bisexual	Entomophily (Grant, 1950)		binucleate (not studied in <i>Sesamothamnus</i> )	1- $\alpha$
Alismatiflorae			Monocotyledons			
<i>Hydrocharitales</i>						
46. Hydrocharitaceae	Tetrads very rare ( <i>Elodea</i> )	Bisexual and unisexual; polygamous in <i>Elodea</i>	Hydrophily	Outbreeding	binucleate	1- $\alpha$
<i>Zosterales</i>						
47. Scheuchzeriaceae	Dyads in overwhelming majority of the family	Bisexual			trinucleate	2 or few
Ariflorae						
<i>Arales</i>						
48. Araccae	Tetrads very rare ( <i>Cladium</i> , <i>Xanthosoma</i> )	Unisexual in <i>Cladium</i> , <i>Xanthosoma</i>		Outbreeding	bi and trinucleate	1- $\alpha$

(Table 1. Contd.)

	1	2	3	4	5	6	7
Liliiflorae							
<i>Asparagales</i>							
49. Agavaceae		Tetrads very rare ( <i>Fourcroya</i> , <i>Beschorneria</i> )	Bisexual	Chiropterophily (Faegri & van der Pijl, 1971)		binucleate (not studied in <i>Fourcroya</i> , <i>Beschorneria</i> )	α
<i>Orchidales</i>							
50. Orchidaceae		Tetrads, polyads, mas- sulae and pollinia in the overwhelming majority of the family	Bisexual	Entomophilous, ornithophilous, sometimes autogamous	Mostly Outbreeding	binucleate	α
Bromeliiflorae							
<i>Velloziales</i>							
51. Velloziaceae		Tetrads in significant number of genera in the family	Bisexual	Bird flower (Grant, 1950)			α

(Table 1. Contd.)

1	2	3	4	5	6	7
<i>Bromeliales</i>						
52. Bromeliaceae	Tetrads very rare ( <i>Cryanthus</i> )	Bisexual	Entomophily inferred (Rendle, 1959); bird flower (Grant, 1950)		bi and trinucleate	$\alpha$
<i>Phylidrales</i>						
53. Philydraceae	Tetrads very rare ( <i>Philydrum lanuginosum</i> )	Bisexual				$\alpha$
<i>Typhales</i>						
54. Typhaceae	Tetrads in overwhelming majority of the family	Unisexual		Outbreeding	binucleate	1
<i>Commeliniflorae</i>						
<i>Juncales</i>						
55. Juncaceae	Tetrads in overwhelming majority of the genera	Usually unisexual	Anemophilous (Rendle, 1959);	Outbreeding	trinucleate	$\alpha$ or few



(Table 1. Contd.)

1	2	3	4	5	6	7
	in the family		Willis, 1973; Stebbins, 1974) Protogyny (Faegri & van der Pijl, 1971)			
56. Thurniaceae	Tetrads in overwhelming majority of the family	Bisexual				1- $\alpha$
<i>Cyperales</i>						
56. Cyperaceae	Pseudomonads or cryptotetrads in overwhelming majority of the genera in the family	Bisexual or unisexual	Anemophily (Faegri & van der Pijl, 1971)	Outbreeding	bi and trinucleate	1

1. Arranged according to Dahlgren (1983).

2. Information mostly based on Walker & Doyle (1975).

3. Information extracted from Brewbaker (1967).

Empty spaces in the table indicate non-availability of authentic data.

(ii) *Higher pollen units and correlation with ovule numbers*

As all the pollen grains present in a pollen unit are transferred to the stigma together, it is logical to expect, at least quite as many ovules per ovary. Out of 56 families where pollen units other than monads are present, large number of ovules per locule are consistently present in 25 families, in 19 families the number of ovules varies from 1, 2, 3, few to  $\infty$  and in only 12 families 1 (5 families), 2 (4 families), 2 or few (1 family), 1-3 (1 family) or 6 (1 family) ovules per locule (Table 1). From a survey of the genera and families of angiosperms having pollen tetrads and polyads, Walker (1971) also came to the conclusion that the evolution of these pollen units correlates significantly with a high ovule number per ovary. In Annonaceae, Walker (1971) has discussed the examples of closely related genera, *Anaxagorea* and *Xylopia*. The former has solitary pollen and 2 ovules per carpel, while the latter has pollen in tetrads or polyads and several to many ovules per carpel. He has pointed out similar situation between *Hexalobus* and *Cleistochlamys*; *Hexalobus* has tetrads and numerous ovules whereas in *Cleistochlamys* monads are present and there is only one ovule per carpel.

(iii) *Number of pollen grains per polyad/pollinium and the number of ovules per ovary*

The ratio of the number of pollen grains per polyad to the number of ovules per ovary varies from 0.71 to 1.18 in *Calliandra* (Cruden, 1977; Elias, 1981) from 1.1 to 4.0 in *Acacia* (Kenrick & Knox, 1982) and is reported as 1.3 and 1.45 in *Albizia lebbeck* and *Pithecellobium dulce* (Khatoun & Ali, unpublished) respectively in the family Mimosaceae. Whereas the ratio of the number of pollen grains per pollinium to the number of ovules per ovary varies from 1.99 to 2.13 in *Asclepias*, from 0.73 to 1.14 in *Matellea* and 1.46 in *Sarcostema clausum* (Cruden, 1977), 1.22 in *Calotropis procera*, 1.79 in *Pentatropis spiralis*, 3.31 in *Leptadenia pyrotechnica*, 3.81 in *Pergularia daemia* and 5.33 in *Caralluma edulis* in the family Asclepiadaceae (Ali, 1986). Cruden (1977) has stated that 2-6 pollen grains per ovule must reach the stigma to assure relatively high seed set, but not necessarily perfect seed set and that the pollen per polyad or pollinia/ovule per ovary ratio of Mimosaceae and Asclepiadaceae are not sufficient to give perfect but high seed set.

(iv) *Polyad grain number and maximum pod seed number*

Kenrick & Knox (1982) have demonstrated a correlation between polyad grain number and maximum pod seed number. In most of the cases the pod seed number does not exceed the polyad grain number. An exception to the rule was found in one pod of *Acacia mitchellii* which had 9 seeds, presumably the product of more than one polyad, since there are 10 ovules (Knox & Kenrick, 1983). Studies conducted on *Albizia lebbeck* and *Pithecellobium dulce* substantiate the above generalisation (Khatoun & Ali, unpublished).

In the case of Asclepiadaceae also on the basis of the available data (Table 2) a similar generalisation may be made, though there seems to be a tendency of the presence of larger number of pollen grains per pollinium as compared to Mimosaceae. More data about other groups is needed in this connection.

(v) *Polyad and stigma relationship*

Kenrick & Knox (1982) have demonstrated that there is 1:1 relationship between polyad and stigma in the case of *Acacia*. The stigma is cup-shaped having a diameter slightly bigger than the polyad, which neatly fits in the stigma cup. Same type of polyad stigma syndrome is met with in *Albizia lebbek* and *Pithecellobium dulce* also. The diameter of the polyads in *A. lebbek* is 114-136  $\mu\text{m}$  and the diameter of the stigma varies from 143-186  $\mu\text{m}$ , whereas in *P. dulce* the diameter of the pollen grain is 87-117  $\mu\text{m}$  and the diameter of the stigma varies from 133-196  $\mu\text{m}$  (Khatoon & Ali, unpublished). A post-pollination exudate is produced in the cup to facilitate adequate hydration for germination (Kenrick & Knox, 1982; Khatoon & Ali, l.c.). It is obvious that the information so far available is very limited; nevertheless it may stimulate further research on polyad stigma relationship in other groups of Angiosperms. However, judging by the information available, it can be generalised that in those cases where 1:1 relationship exists between the polyad and the stigma, the number of ovules have also been adjusted proportionate to the number of pollen grains per polyad/pollinium. Whereas in those plants where 1:1 relationship between the pollen unit and the stigma does not exist, generally large number of ovules per ovary are met with. This is in conformity with the observation of Kenrick & Knox (1982) who have demonstrated that generally the pod seed number is not more than the polyad grain number, whereas in Mimosaceae, the presence of monads is associated with high pod seed numbers.

Table 2. Pollinium grain number and maximum fruit seed number in some Asclepiads\*.

Taxa	Pollinium grain number (Mean)	Maximum fruit seed number	Pollinium grain number**/maximum fruit seed number
1. <i>Calotropis procera</i>	350 $\pm$ 2.75	337	1.04
2. <i>Leptadenia pyriotechnica</i>	126 $\pm$ 1.52	50	2.52
3. <i>Pentatropis spiralis</i>	140 $\pm$ 1.52	98	1.43
4. <i>Pergularia daemia</i>	122 $\pm$ 3.01	30	4.06

\*Extracted from Ali (1986)

\*\*Mean values used in calculation.

(vi) *Correlation with binucleate and trinucleate pollen grains*

Brewbaker (1967) has shown that all phylogenetically primitive taxa are binucleate. The trinucleate trait has originated independently at many times during angiosperm evolution. In no instance must one infer the origin of binucleate taxa from trinucleate ancestors. In order to determine any possible correlation of this character with pollen aggregates the available information has been analysed. Out of the families known to have pollen units other than monads, information is available about 50 families. Thirty four of these families have binucleate pollen grains; 12 families have 2-3-nucleate pollen grains and only 4 have trinucleate pollen grains (Table 1). The frequency of binucleate pollen grain is higher than expected if there was no correlation ( $X^2 = 6.48$ ;  $p < 0.05$ ). Thus it is obvious that the presence of compound pollen grains is associated with the primitive binucleate pollen grains. As nearly all aquatic species with submerged flowers shed pollen in trinucleate stage (Brewbaker, 1967), the presence of trinucleate pollen grains in Hydrocharitaceae is not indicative of its advanced nature.

### Discussion

It is obvious that a number of strategies have been adopted in the plant world for achieving similar ends. The adaptive mechanisms operative in different taxa involve a flexible compensatory system of adaptation where a relative lack of fitness in one character may be compensated by special suitability in another character (Causen, Keck & Hiesey, 1948; Stebbins, 1950). Thus the dynamic processes of adaptive mechanisms operative in a population may be quite complicated and are generally effective at numerous stages involving many compromises (Clausen, Keck & Hiesey, 1948; Stebbins, 1950; Grant, 1963; Mather, 1966). These compromises, generally, involve a number of checks and balances. The pollen units other than monads are widely distributed and have repeatedly evolved in Angiosperms. Dyads are rare, present only in 2 families, Podostemaceae and Scheuchzeriaceae. Tetrads are the most common multipollen units, present in 46 families. The polyads are found in 7 families and the massulae and pollinia are met with in only 2 families, Asclepiadaceae and Orchidaceae.

Aglutination of pollen grains into tetrads seems to be the first step in the evolution of pollen aggregates in Angiosperms. As demonstrated by Levan (1942) in *Petunia* permanent tetrad formation may be controlled by a single gene difference. Gene(s) responsible for tetrad formation seems to be quite widely distributed both in Monocots and Dicots (Table 1). From the tetrad level two types of trends, one towards structural elaboration and the other towards structural reduction may be traced (Char, Swamy & Cheluviah, 1973). Trends in structural reduction from tetrads to dyads and monads are apparent in some cases. In several members of Podostemaceae and Scheuchzeriaceae, the microspores separate in pairs after the tetrad formation, whereas in *Pentochondra involucria* of Epacridaceae, two of the microspores of the tetrad degenerate, thus resulting in the formation of dyads

(Venkatarao, 1961). The rare occurrence of dyads in Cyperaceae is considered to be an abnormal feature (Shah, 1962).

(Table I. Contd.)

	1	2	3	4	5	6	7
<i>Bromeliales</i>							
52. Bromeliaceae		Tetrads very rare ( <i>Crytanthus</i> )	Bisexual	Entomophily inferred (Rendle, 1959); bird flower (Grant, 1950)		bi and trinucleate	α
<i>Philydrales</i>							
53. Philydraceae		Tetrads very rare ( <i>Philydrum lanuginosum</i> )	Bisexual				α
<i>Typhales</i>							
54. Typhaceae		Tetrads in overwhelming majority of the family	Unisexual		Outbreeding	binucleate	1
<i>Commeliniflorae</i>							
<i>Juncaceae</i>							
55. Juncaceae		Tetrads in overwhelming majority of the genera	Usually unisexual	Anemophilous (Rendle, 1959);	Outbreeding	trinucleate	α or few

with outbreeding. Apparently it is not likely to have any significance for inbreeding. In view of this, the information available for 55 families has been analysed. In 14 families unisexual flowers are met with. In 12 families, self-incompatibility systems have been demonstrated, whereas in 14 families the pollination systems investigated indicate outcrossing (Table 1). The case of Droseraceae is, however, very interesting. Except in the genera *Drosophyllum* and *Pusitanicum*, the pollen grains are united in tetrads. According to Proctor & Yeo (1973) *Drosera* is usually selfed and often cleistogamous. Though entomophily has been demonstrated in large flowered and showy *Drosera capensis*, other species of *Drosera* seem to provide an exception to the generalisation stated above.

The amount of genetic variability present in the seeds of a single fruit is dependent on the number of male parents involved in fertilization. Random dispersal of monads characteristic of wind pollination tends to produce less closely related seeds in multiovulate ovaries (Kress, 1981).

Those plants where permanent tetrads are met with, pollen transfer in groups of fours is affected and each four ovules are likely to be fertilized by genetically similar pollen grains. Whereas in the plants where the polyads and pollinia are met with, the pollen grains from one plant may fertilize all the ovules of another carpel/flower located on a different plant. Though cross pollination is involved here, it is obvious that considerable restriction is imposed on the union of the genetic material as compared to a situation where random pollination through monads takes place. From the point of heterozygosity, this situation may therefore be said to be somewhat intermediate between selfing and outcrossing through monads. It is obvious that the genetic similarity of seeds within a single ovary is partially dependent on how many different paternal parents are involved in fertilization. As the situation present in pollinium and polyad producing plants is such where a single father is responsible for fertilizing all the ovules, the seeds will be full siblings, i.e., the degree of relatedness  $r$  is 0.5 (Hamilton, 1964). In those case where random pollination through monads takes place and every ovule is fertilized by a genetically different male parent, the seeds will be on the average half sibs:  $r$  approaches 0.25. Seeds produced apomictically and by cleistogamous and autogamous flowers will vary in their relatedness from being genetically identical to sharing most alleles in common:  $r$  approaches unity (Kress, 1981).

However, in terms of pollinator energetics, all the pollen grains (in the form of a pollinium) are delivered in one trip, thus the situation may be compared with placing all the eggs in one basket. If the pollination is affected, all the ovules are fertilized, alternatively there may not be any seed formation. The floral structure is also considerably modified and the pollination can take place, only through the intervention of insects or other animals. According to Cruden (1977) the reproductive biology of groups like Asclepiadaceae and Mimosaceae where pollinia or polyads are present are comparable to the gam-

bling lottery i.e., minimal energetic investment in each pollen packet, low reproductive return on each pollinia or polyad, but large reproductive return when pollination is successful. He has suggested the name "sweepstakes" reproduction for this strategy. Plants in these families are exceptions in xenogamous group. These plants invest minimal energy in pollen production and their fecundity is low, but when pollination is successful, the reproductive return is relatively high (Cruden, 1977).

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