

EVOLUTION AND IMPROVEMENT OF CULTIVATED AMARANTHS

I. BREEDING SYSTEM AND INFLORESCENCE STRUCTURE

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An investigation of inflorescence structure and the composition of glomerules revealed a basal plan which is somewhat modified in different species. This affects the mating system, of which there are 3 types : (i) obligate cross pollination through wind in dioecious group of amaranths (erstwhile genus *Acnida*), (ii) relatively more outcrossing by wind and insects in Sect. *Amaranthus* with very prominent colourful terminal inflorescences containing 0.4–1.0 per cent male flowers per glomerule coupled with protogyny, and (iii) relatively greater self pollination in Sect. *Blitopsis* having small, generally axillary inflorescences with 10–25 per cent male flowers per glomerule. Dioecious amaranths are very restricted in distribution in comparison to other groups, since for successful colonization outside their range, they need at least two propagules (male and female) to disperse together. The other two sections have a very wide distribution, but Sect. *Blitopsis* has rather narrow ecological preferences than the Sect. *Amaranthus*.

INTRODUCTION

The genus *Amaranthus* is widely distributed in the tropical and temperate regions, and some of the species are noxious weeds (notably *A. spinosus* L.), others are cultivated. Besides carotene-rich pot herbs (*A. tricolor* L., *A. lividus* L., etc.) domesticated in the old world from time immemorial and attractive ornamentals (*A. caudatus* L., *A. tricolor* L. var. *salicifolius* (veitch) Aellen.), there are highly nutritious grain-yielding species (*A. hypochondriacus* L., *A. caudatus* L., *A. edulis* Speg. and *A. cruentus* L.) which constituted the staple food of Central and South American people in the historical past and, presently, of the people inhabiting the valleys in the north-west Himalayas, particularly the Sotlej valley.

Except for the painstaking and brilliant ethnobotanical studies of Sauer (1950, 1967) on the grain amaranths, no integrated evolutionary study aimed at improving this group of cultivated plants has been undertaken. It is increasingly felt that the amaranths, especially the grain types, although considerably overshadowed by the cereals, could still play, together with vegetable amaranths, a much larger role than they now do in feeding the hungry world.

The present study is based on 17 species of the genus, and aims at unravelling the genetic-evolutionary dynamics of the cultivated amaranths with a view to affect genetic improvement. This communication deals with inflorescence structure and breeding system. To an evolutionist, such a study helps in working out genetic composition, and evolutionary potentialities together with their taxogenetic implications,

and to a breeder it is helpful not only in formulating the exact breeding procedures and objectives for production of new and improved forms, but also in their subsequent maintenance. The genus *Amaranthus* has not been studied from these aspects, although there is a prevailing impression that the entire Amaranthaceae, together with Chenopodiaceae, are predominantly wind-pollinated.

OBSERVATIONS

The two sections of the genus *Amaranthus* are *Amaranthus* Sauer (= *Amaranthotypus* Dumort.), and *Blitopsis* Dumort. The three chief differences between the two sections are given in Table I.

TABLE I
Differences between the two sections within the genus Amaranthus

Character	Sect. <i>Amaranthus</i>	Sect. <i>Blitopsis</i>
Inflorescence	Terminal, very prominent and variously coloured	Mostly axillary, small when terminal
Flower	Usually pentamerous	Usually bi- or tri-merous
Dehiscence of utricle	Usually circumscissile	Usually irregular

The main inflorescence in Sect. *Amaranthus* is a dense spike or panicle, which is usually profusely branched (Fig. 1). These panicles or spikes may be either drooping (*A. caudatus*), semidrooping (*A. spinosus*, *A. cruentus*, etc.), or erect (*A. edulis*). The growth of the terminal inflorescence and its branches is indeterminate (racemose) and, thus, it may reach a length of one metre or even more. However, *A. edulis* is the only exception in which the inflorescence is determinate due to the presence of a terminal polymorous male flower and, therefore, the elongation of the inflorescence in this species is due to intercalary growth of the axis.

Individual flower clusters or glomerules develop alternately along the axis of the main inflorescence. In Sect. *Amaranthus* glomerules develop chiefly on the terminal inflorescences, and are rather feebly developed in the axils of the branches. In the Sect. *Blitopsis*, due to the absence of prominent terminal inflorescence, axillary glomerules are well developed (Fig. 2), and resemble glomerules in the terminal inflorescence of Sect. *Amaranthus*.

Glomerule

The structure of an individual glomerule is basically the same in both sections. It is a dichasial cyme where the first flower is terminal on the branch and, at its base, on either side, develop, on two secondary branches, the second and third flowers (Fig. 3). Both the flowers are terminal on the secondary branches, and at their base develop the next two flowers. This process continues till the plants mature. In the last stages the process not only slows down considerably, but the flowers are also

as many as 250 flowers, while completely pollinated flowers tend to have significantly lesser number. This number is far exceeded in the grain amaranths which seem to have been selected for this character, obviously to obtain an increase in the grain production. According to Murray (1940), the apparently opposite branching in the flower cluster is probably produced by the shortening of the axis of an essentially alternate branching system. Only developmental studies can confirm such a view.

In Section *Blitopsis*, the glomerules are very compact because of the shortening of the axes of the flowers. Thus, it is rather difficult to analyse such glomerules which have a large number of flowers that absciss with slight pressure and, in these cases, a glomerule was studied in relatively younger condition.

Development of a dichasium is very symmetrical in some species like *A. edulis* and *A. caudatus* where the dichasial character of the glomerule is maintained up to the end (Figs. 3, 4). However, in all the remaining species investigated by us, the dichasial branching gradually changes over to monochasial type (Figs. 5, 6). Murray (1940) is of the view that the symmetry is upset after the third or fourth series of flowers due to seed-setting. However, the present investigations do not support this view, and this character seems to be distinctive to a species and very likely under a genetic control. For instance, in *A. caudatus* and *A. edulis* there is a perfectly regular behaviour and a set pattern which remains unchanged. Moreover, in the unfavourable season when there is little or no seed-set, the species maintain their specific arrangements. Another point, not in line with Murray's view, is afforded by a study of the sterile interspecific hybrids (*A. spinosus* × *A. dubius* and *A. edulis* × *A. hypochondriacus*). These, according to him, should have shown a regular dichasium, because there is very little or no seed set, but the dichasial branching in reality changes to monochasial after the third or fourth order in the "former, and after fifth or sixth order in the latter hybrid. The prolongation of the dichasial pattern in the latter case is perhaps due to the influence of *A. edulis* which has a regular dichasial arrangement.

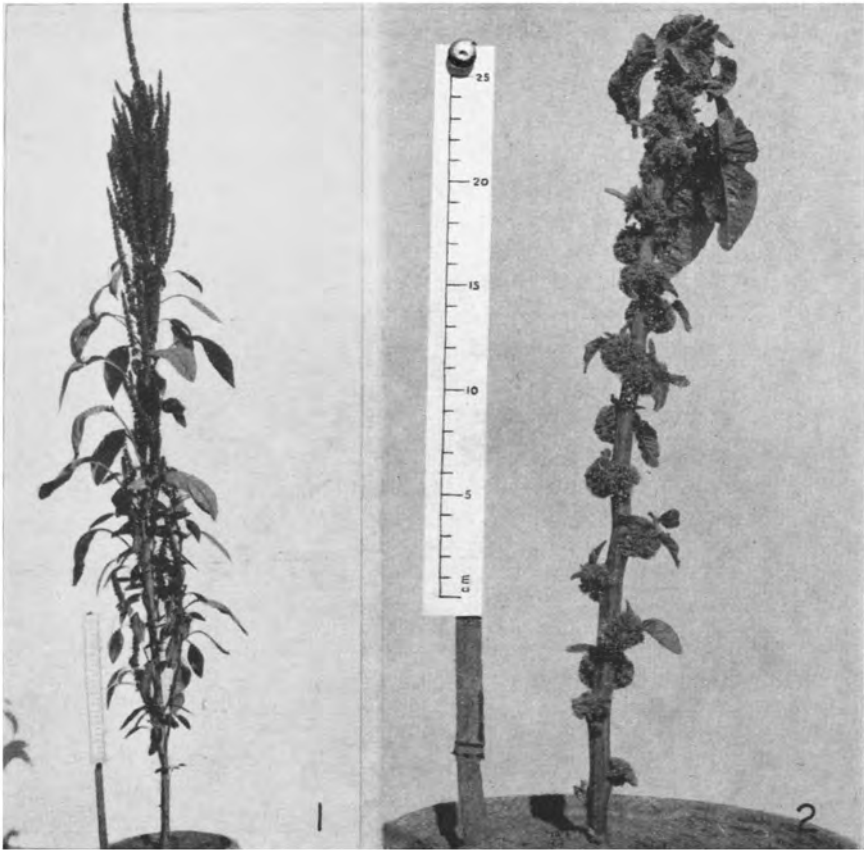
The eventual outcome of these two types of arrangements is interesting in as much as these impart different but definite shapes to the glomerules. Globular shape of the individual glomerules seen in *A. caudatus* (Fig. 3) and *A. edulis* (Fig. 4) is due to the maintenance of the dichasial branching. In other species, like *A. hypochondriacus* (Fig. 5), *A. hybridus*, *A. cruentus*, *A. dubius*, some hybrids (Fig. 8), etc., due to initial 2 to 3 successive dichotomies, 4-8 branches are formed. However, these, as a consequence of repeated monochasial branching result in 4-8 finger-like processes (Fig. 8), which sometimes, are rolled on themselves. Of the two types of glomerule structures, it is difficult to say which one is basic or ancestral, although the latter condition is not only more common but is also dominant in the interspecific hybrids involving parents with these two types.

Flower

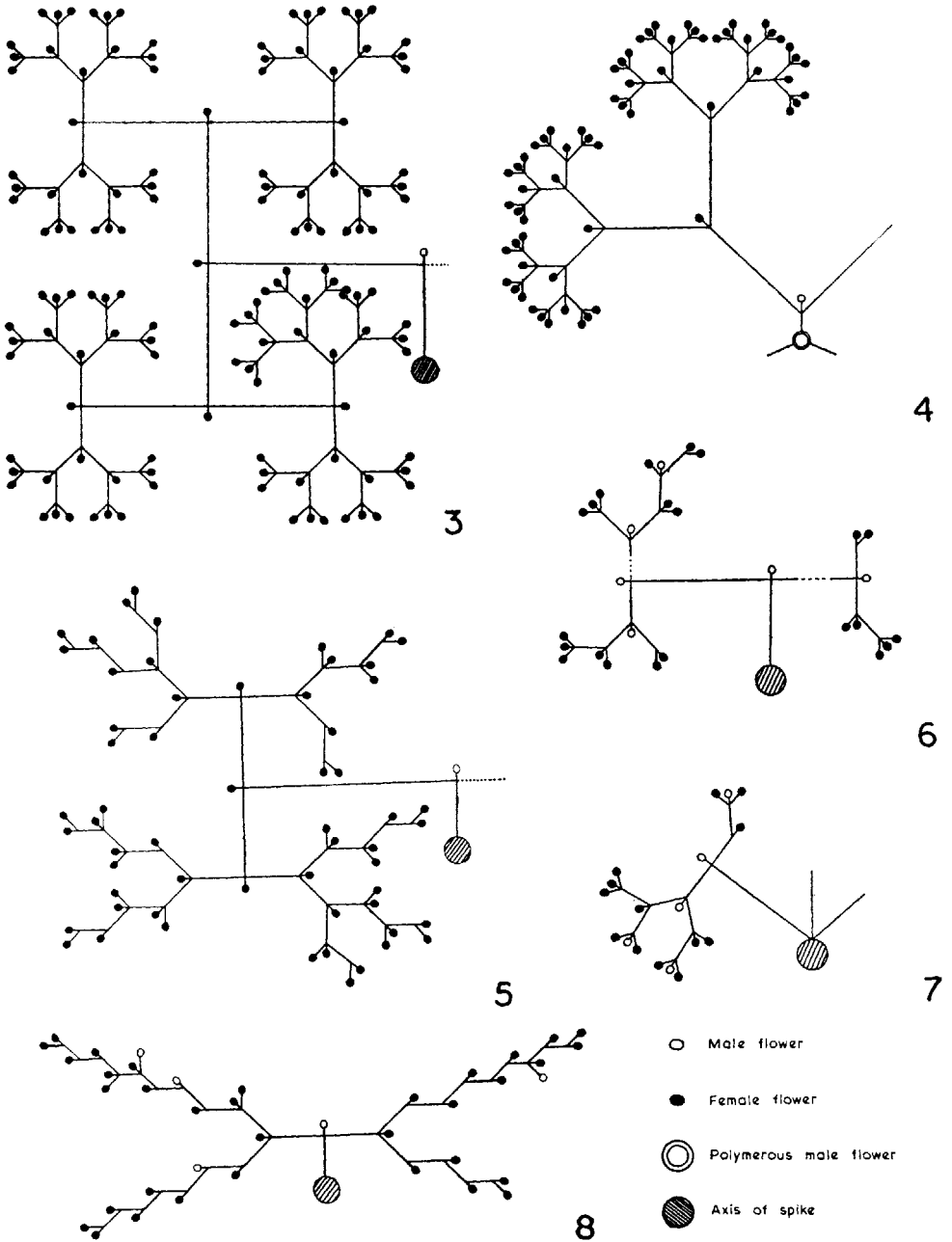
In *Amaranthus* there are both dioecious and monoecious species. The growth pattern of the individual dichasia, as described above, is common to all species irrespective of the sex. As expected in dioecious species, all the glomerules on a plant feebly developed and are sterile. Incompletely pollinated glomerules may develop

have the flowers of the same sex. The monoecious species, on the other hand, exhibit three types of arrangements of male and female flowers.

A. caudatus Type—Here the initial flower in each glomerule is staminate, and all the succeeding flowers are pistillate. Thus, there is only one male flower in each glomerule which abscises immediately after shedding pollen (Figs. 3–5). All the species of the Sect. *Amaranthus*, except *A. spinosus*, exhibit this type of arrangement. A slightly different condition is met with in a closely related species, *A. edulis*, which is distinctive inasmuch as, in addition to the normal pentamerous male flower, it also produces a terminal polymerous male flower (Figs. 4, 9). The latter renders the inflorescence axis of this species determinate, perhaps because the growing point is used up in the formation of the polymerous flower. Rarely, in place of one polymerous male flower, there are two incompletely-fused pentamerous male flowers indicating that the polymerous flower may have arisen by the fusion of two primordia. This can be confirmed only through a detailed developmental study.



FIGS. 1–2. *A. hypochondriacus* (Sect. *Amaranthus*) and *A. tricolor* var. *salicifolius* (Sect. *Blitopsis*) showing prominent terminal and axillary inflorescences, respectively.



FIGS. 3-8. Diagrammatic representation of the ground plan of half or full glomerule. 3, *A. caudatus* (half glomerule); 4, *A. edulis* (half glomerule); 5, *A. hypochondriacus* (half glomerule); 6, *A. tricolor* var. *viridis* (full glomerule); 7, *A. tricolor* var. *salicifolius* (half glomerule); 8, F_1 *A. hybridus* \times *A. hypochondriacus* (The initial dichasium is followed by four monochasial branches, and origin of male and female flowers is disturbed).

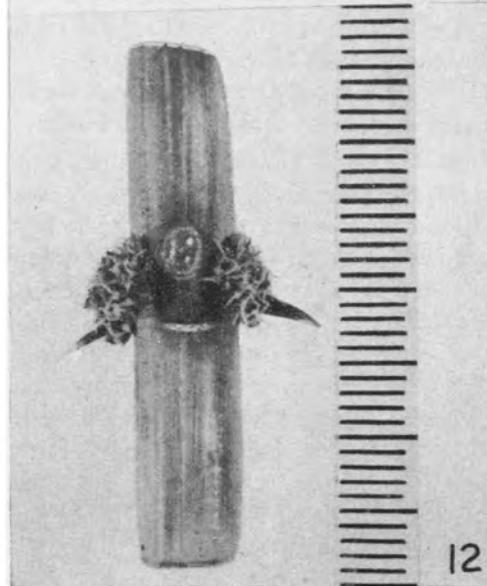
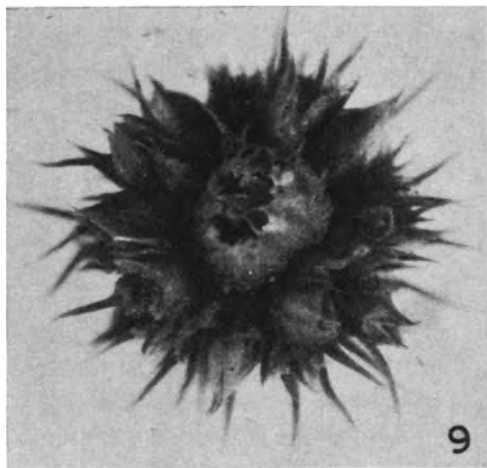
A. spinosus type—It represents an intermediate condition between the dioecious and monoecious species as well the flowers in a glomerule are of the same sex. The pistillate glomerules develop only in the axils of the branches and at the base of the terminal inflorescence, while the male glomerules develop only on the terminal portions of the inflorescences (Fig. 10). *A. spinosus* is the only species with this arrangement out of the 17 species investigated here.

A. tricolor type—Here the initial flower in the glomerule is male, but the succeeding female flowers are interspersed by male flowers. However, there is no regularity regarding the emergence of male flowers. Obviously, a glomerule comprises both male and female flowers, though the number of female flowers is much more than the male flowers (Figs. 6, 7). This type of arrangement is characteristic of the members of the Sect. *Blitopsis* studied here, and the percentage of the male flowers per glomerule varies from 10 (*A. gracilis*) to 25 (*A. tricolor*) in different species, in contrast to 0.4 to 1.0 per cent in Sect. *Amaranthus*.

Abnormalities—Ordinarily, a species maintains a particular constitution of a glomerule. This may, however, be disturbed sometimes. For instance, in *A. caudatus* (Fig. 11) and *A. hypochondriacus*, instead of the usual unisexual flowers, there are produced bisexual flowers, and the tendency is usually towards the femaleness of the first male flower. However, in all cases the perianth and other characters remain the same. The number of stamens is reduced from 5 to either 3, 2 or even 1. In one such bisexual flower in *A. hypochondriacus* even seed formation was observed. Perhaps, the production of seed by such flowers depends on the extent of conversion. Similarly, a stamen may develop in a female flower though the other floral characters remain essentially like the female flower. Such abnormalities are not restricted only to the members of the Sect. *Amaranthus* but also appear in the species of Sect. *Blitopsis* and, in fact, are more common in the latter.

Probably, such abnormal behaviour regarding the sex of several species of the genus may have resulted in the disagreement between different authors (Duke 1961; Hooker 1885). Often the flowers in several species have been described as polygamous, and this observation may have been based on such abnormal flowers.

The occurrence of female parts in otherwise male flowers, found infrequently in Sect. *Amaranthus* but frequently in Sect. *Blitopsis* may be explained on the basis of auxin imbalance. The presence of unisexual flowers must be under some regulatory effect of the respective auxins. Since the female flowers immediately succeed male flower, it is easy to comprehend that the switch over in auxin production has to be very precise, and may have to be almost abrupt. Any irregularity in such switch over is likely to result in the types of abnormalities described earlier. Since the position of male flowers is not definite in *Blitopsis*, there is a greater incidence of such abnormalities in this Section than in the other. This is supported by the fact that such abnormalities are located in the transitional region as seen in *A. caudatus* and *A. hypochondriacus*. These disturbances, especially in the transitional zones, are also known in a number of monoecious species like *Cucurbita pepo* and *Cleome spinosa* (Van Nigtevecht 1966). The latter example is particularly instructive because the zones of the male and female flowers alternate in the inflorescence. Between these zones of pure male and pure female flowers, there occur



transitional forms gradually proceeding towards the other sex from the preceding one.

An interesting feature in the old plants of *A. hypochondriacus*, during unfavourable seasons, is the sudden emergence of male flowers in the glomerules. The pollen is fertile, and some selfed seed is produced in the female flowers of glomerule. This may be a sequel to the large number of unpollinated female flowers in such glomerules because male flowers absciss early.

The type of arrangement of the male and female glomerules in *A. spinosus*, described earlier, is of common occurrence (*see also* Murray 1940; Aellen 1961). However, several interesting natural variations were observed in Lucknow populations during August–September, 1966. An analysis of 307 plants of *A. spinosus*, from a small area, is presented in Table II.

TABLE II
Sex polymorphism in Amaranthus spinosus

	Normal arrangement	Terminal entirely male		Pure male plants	Total
		Axillary female	Axillary male female		
Number	281	15	9	2	307
Percentage	91.53	4.89	2.93	0.65	100

In 0.65 per cent individuals there was a complete replacement of the normal axillary female flowers (Fig. 12) by male flowers (Fig. 13), with the result that the entire plant may be classified as pure male. This condition was not linked with any other morphological trait. However, such plants could be easily recognised, in a population, due to the abundance of yellow stamens. While the genetic basis of the sex polymorphism in this species has not been investigated, it may be mentioned that such male plants were normal diploids ($2n=34$). The size and fertility of pollen corresponded with plants having typical *A. spinosus* arrangement.

CONCLUSIONS

From the foregoing observations, it is clear that, broadly speaking, the genus *Amaranthus* possesses three types of mating system viz., (a) obligate outcrossing in dioecious species, (b) relatively greater outcrossing in monoecious members of Sect. *Amaranthus*, and (c) relatively greater self-pollination in members of Sect. *Blitopsis*.

All the dioecious species (about 10) are confined to a small area in North America (Sauer 1955, 1957) and, though sporadic occurrence of dioecious species

FIGS. 9–13. *A. edulis*, top view of spike showing polymerous male flowers. $\times 7$; 10, normal arrangement of male and female flowers in *A. spinosus*; 11, bisexual flower in *A. caudatus*. $\times 9$; 12–13, *A. spinosus* showing axillary female glomerule in a normal plant with prominent stigma (Fig. 12) and a branch with axillary glomerule of male flowers (Fig. 13). $\times 2$.

has been reported from time to time (Aellen 1961; Brenan 1961; Thakur 1964), these have never been able to establish themselves out of their native range. It appears to be yet another example in support of the Baker's Law (Baker 1955; Stebbins 1957). Naturally, the narrow geographic range of dioecious amaranths is due to the fact that, for any long-distance dispersal, at least two propagules (male and female) are necessary before a particular species can successfully establish and colonize the new area. Another reason for their restricted distribution may be that the few plants which happen to escape their native place are often involved in interspecific hybridization with monoecious amaranths, and the hybrids are totally sterile. This not only reduces their reproductive potential, but also eliminates them ultimately.

The monoecious species of *Amaranthus* are self-compatible, thereby falling in line with most other monoecious species (Godley 1955; Baker 1967). They are nearly cosmopolitan species, often weedy, and seem to have achieved a remarkable balance between immediate fitness and long-range flexibility.

All the monoecious species of *Amaranthus* studied by me exhibit protogyny, and the inflorescence structure ensures adequate cross pollination. The effectiveness may be judged from the fact that Walton (1968) observed 15.7–34.9 per cent cross pollination in *A. caudatus*. This estimate is in conformity with the author's observations in this and other species.

A. spinosus ($n=17$), with its specialised method for securing cross pollination, gave about 80 per cent hybrids with *A. dubius* ($n=32$) when the seeds were taken from the axillary inflorescences. Normally, the axillary inflorescences, which start developing earlier and are composed of only female flowers (Fig. 12), afford greater opportunities for cross pollination. With such a breeding system together with its being armed with spines, this species has become one of the most widespread and noxious weeds.

Though mainly wind-pollinated, the bees visit several species like *A. caudatus* and *A. dubius* (Sect. *Amaranthus*), especially in November and February, at Lucknow. Huge colourful inflorescences in this section (Fig. 1) appear to be suited both to wind and insect pollination. It is clear that there is a balance between self- and cross-pollination within Sect. *Amaranthus*. The balance may be affected by environmental factors like seasonal change, availability of insects, etc. Such a breeding behaviour ensures a balance between mutability and stability and, thus, makes them very successful.

In Sect. *Blitopsis* the species have a small terminal inflorescence (Fig. 2) which may even be absent altogether. The structure of the glomerules which are mostly axillary is peculiar in having more male flowers (Figs. 6, 7), besides, the frequency of hermaphrodite flowers is also relatively higher than Sect. *Amaranthus*. Moreover, the species belonging to this section have rather narrow ecological preferences, which perhaps makes them rely more on self pollination. However, cross pollination also occurs as is evident from a number of interspecific hybrids reported from time to time (Aellen 1961). Evidently, the two sections of genus *Amaranthus* differ in their breeding systems. The possible consequences of these differences in breeding system, in relation to cytogenetic differentiation, will be discussed elsewhere.

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