A REVIEW

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A Criticism of Sareen and Wadhwa's (1981) paper entitled, 'Embryological studies in Papilionaceae, the genus *Alysicarpus* Neck'

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In Alysicarpus vaginalis the male archesporium is multi-cellular and hypodermal. The anther wall is four-layered and its development confirmed to the Dicotyledonous type. The tapetum is uni-nucleate, uni-seriate and secretory type. The endothecium forms fibrous thickenings at maturity. Simultaneous cytokinesis results in tetrahedral and isobilateral tetrads. Pollen grains are shed at bi-nucleate and bi-celled stage. Some pollen grains show the sign of germination before anthesis and had three-nuclei. However, Sareen and Wadhwa (1981) reported uni-cellular archesporium, Monocotyledonous type of anther wall development and decussate microspore tetrads. They also failed to report three-nucleate pollen and their germination *in situ.* The ovule is bitegmic, crassinucellate and campylotropous. The female archesporium which is uni- or bi-cellular is hypodermal in origin. A linear tetrad of megaspores is formed. The development of the megagametophyte is confirmed to the Polygonum type. Some abnormalities were observed during the development of the megagametophyte, indicating that the nuclear divisions in the megagametophyte are not always simultaneous resulting in three-, five- and six-nucleate megagametophytes. At one instance in the eight-nucleate an anomalous megagametophyte, polar nuclei were missing and two extra antipodals were found arranged in two series (3+2). However, Sareen and Wadhwa (1981) were not aware of any type of anomaly in the megagametophyte. Fertilization is porogamous. Though double fertilization is a rule occasionally single fertilization that is syngamy occurred without triple fusion. Very often the zygotic nucleus was found to divide prior to the primary endosperm nucleus. The endosperm development follows the nuclear type. Sareen and Wadhwa (1981) were unaware of such anomalies. In *Alysicarpus vaginalis* six different Megarchtypes (A_1, A_2, B_1, B_2, C_1, C_2) were noted. The embryo development follows the Alysicarpus variation of the Onagrad type of Johansen (1950) or First Period, Series A, Megarchtype IV of Soueges and Crete (1952). In fact Sareen and Wadhwa (1981) could not go beyond Onagrad type. The structure of the testa agrees in general with the Papilionaceous type of Corner (1951). Thus it is confirmed that the observations of Sareen and Wadhwa (1981) on the embryology of *Alysicarpus vaginalis* are superficial and misleading.

Key words : Embryology of angiosperms.

The embryogeny of the Papilionaceae is full of interest. In this family, so well characterized by the structure of its flower and fruit, the degree of homogenity is apparently so great that the systematist hesitates in setting the limits of the various genera within the family. However, from the embryogenic point of view these genera can be as clearly distinguished as those of the Papaveraceae. The Papilionaceae has long been an object for embryological studies on account of considerable variation that exists in the mode of embryonal development so much so that even two different Megarchtypes may occur in the same species as is reported by Rau (1954) in *Desmodium laevigatum* (Hedysareae), Goursat (1969) in *Astragalus glycyphyllos* (Astragaleae) and *Baptisa australis* (Podalyrieae). However, Salgare (1973e,74a,97c) has observed three different Megarchtypes in *Phaseolus aconitifolius* (Phaseoleae), out of these three, the first two could be placed in Soueges and Crete (1952) embryogenic classification, but the third could not be placed in their system and seems to be a type by itself. In addition to the transverse division of the Oospore either vertical (Piperad type) or an obliquely transverse divisions were observed by Salgare (1975p) in *Sesbania aegyptiaca* (Galegeae). In *Alysicarpus vaginalis* (Hedysareae) six different Megarchtypes (A_1, A_2, B_1, B_2, C_1, C_2) were noted by Salgare (1986b). Two different Megarchtypes were noted by Salgare (unpublished) in *Phaseolus aureus* (Phaseoleae).

In *Alysicarpus vaginalis* the male archesporium is multi-cellular and hypodermal. The anther wall is four-layered and its development confirmed to the dicotyledonous type. The tapetum is uni-nucleate, uni-seriate and secretory type. The endothecium forms fibrous thickenings at maturity. Simultaneous cytokinesis results in tetrahedral and isobilateral tetrads. Pollen grains are shed at bi-nucleate and bi-celled stage (1975d,76d). Similar condition was also observed by Salgare in *Phaseolus aureus* (1970,73d,75f,86a), in *Phaseolus aconitifolius* (1974a,75q,76p,97d), in *Dumasia villosa* (1975aa), *Cyamopsis psoralioides* (1975as), in *Sesbania*

aculeata (1975ab,76a,s), in *Sesbania aegyptiaca* (1976b,r). Howeveer, Sareen and Wadhwa (1981) reported uni-cellular archesporium, Monocotyledonous type of anther wall development and decussate microspore tetrads. They also failed to report three-nucleate pollen. Salgare (1975d,76d) observed *in situ* germination of polloen in *Alysicarpus vaginalis*. It was the failure of Sareen and Wadhwa (1981) to report such an interesting observations. Salgare (1975d,76d) stated that in *Alysicarpus vaginalis* the ovule is bitegmic, crassinucellate and campylotropous. The female archesporium which is uni- or bi-cellular is hypodermal in origin. A linear tetrad of megaspores is formed. The development of the megagametophyte is confirmed to the Polygonum type. Some abnormalities were observed during the development of the megagametophyte, indicating that the nuclear divisions in the megagametophyte are not always simultaneous resulting in three-, five- and six-nucleate megagametophytes. At one instance in the eight-nucleate an anomalous megagametophyte, polar nuclei were missing and two extra antipodals were found arranged in two series (3+2). Similar condition was also observed by Salgare in *Phaseolus aureus* (1970, 73d, 75f,ah, 76e,j,k,t, 78a, 80a,86a,97a,b,2000a), in *Phaseolus aconitifolius* (1974a,75q,ac-ag,76e-k,p,77a,b,78a,80a,b,81,97a-c, 2000a), in *Dumasia villosa* (1975v-aa,ai,aq,76e-k,t, 77a,b, 78a, 80a,b, 97a,b, 2000a), *Cyamopsis psoralioides* (1973b,75a,m,n,ai,aq,as,76e-h,j,k,q,t, 77a,78a, 80a,b, 97a,b, 2000a), in *Sesbania aculeata* (1973a,c,75c,e,ab,aq,76a,e-j,k,s,t, 77a,b,78a,80a,b,97a,b,2000a), in *Sesbania aegyptiaca* (1974d,75r-u,ai,aq,76b,c,e-k,r,t, 77a,b, 78a, 80a,b, 97a,b, 2000a) with a large number of very interesting anomalies. However, Sareen and Wadhwa (1981) were not aware of any type of anomaly in the megagametophyte.

In *Alysicarpus vaginalis* fertilization is porogamous. Salgare (1975b,d,o,aj,ar,76n,78b,86b) stated that though double fertilization is a rule in *Alysicarpus vaginalis*, occasionally single fertilization that is syngamy occurred without triple fusion. Very often the zygotic nucleus was found to divide prior to the primary endosperm nucleus. The endosperm development follows the nuclear type. Sareen and Wadhwa (1981) were unaware of such anomalies. Salgare (1975b,d,ar,76n,86b) observed six different Megarchtypes (A_1, A_2, B_1, B_2, C_1, C_2) in Alycarpus vaginalis. The embryo development follows the Alysicarpus variation of the Onagrad type of Johansen (1950) or First Period, Series A, Megarchtype IV of Soueges and Crete (1952). In fact Sareen and Wadhwa (1981) could not go beyond Onagrad type. The structure of the testa agrees in general with the Papilionaceous type of Corner (1951). Thus it is confirmed that the observations of Sareen and Wadhwa (1981) on the embryology of *Alysicarpus vaginalis* are superficial and misleading.

Extensive work of Salgare (1973e,74a,75q,ac-ag,76e-k,m,p,t,77a,b,78a,80a,b,81,97a-d,2000a-d) on the embryology of *Phaseolus aconitifolius* proved that Bhasin (1971) and Deshpande and Bhasin (1974) were not aware of the fact that in addition to the uni-cellular male archesporium, bi-cellular archesporium and linear megaspore tetrad, in addition to T-shaped tetrads were also present. It was their failure to trace out the superimposed twin megagametophytes and superposed multiple megagametophytes and their further development into bisporic and trisporic development, respectively. Bhasin (1971) and Deshpande and Bhasin (1974) also failed to trace out the endosperm haustorium and the development of the barrier tissue. In addition to the category A_2 and C_2 of Soueges and Crete (1952) Salgare (1973e,97c) also recorded an additional tetrad of proembryoes which can fit in any of the categories of Soueges and Crete (1952) and forms the type by themselves. This proves that the observations of Bhasin (1971) and Deshpande and Bhasin (1974) on the embryology of *Phaseolus aconitifolius* are superficial and misleading.

In reinvestigation of the embryology of *Cajanus cajan*, it was noted that there are three different types of megaspore tetrads *viz*. linear, T-shaped and a third one where the lower dyad member divides by a transverse wall, while meiosis II proceeds in the upper dyad member without cytokinesis. This third pattern can not be accommodated under any of the Rembert (1969) megaspore tetrad patterns and thus would form an independent patterns (Salgare,1980c,95). Roy (1933) had failed to report this type of tetrad in *Cajanus indicus* syn. of *Cajanus cajan*. As a result of the non-simultaneous nuclear divisions of the megagametophyte a three-nucleate megagametophyte was also noted in *Cajanus cajan* which was escaped from the observations of Roy (1933). Nine-nucleate an anomalous megagametophyte was reported by Roy (1933) in *Dolichos lablab*. However, it was the failure of Roy (1933) to decide the fate of an additional nucleus. It was Salgare (1975am,80c) who proved that an additional nucleus in an anomalous megagametophyte of *Dolichos lablab* contributed to the formation of the secondary nucleus – resulting into triploid secondary nucleus in the Polygonum type of megagametophyte.

The ovule of *Phaseolus aureus* is bitegmic,

crassinucellate and campylotropous. Though the outer integument is initiated later it grows faster and by itself alone forms the micropyle (Salgare, 1970,73d, 75f, 76e, j,k,t, 78a,80a,86a,97a,b,2000a; Salgare and Dnyansagar, 1971). However, George *et al.* (1979) have stated that both the integuments are initiated simultaneously. This is an error due to their inability to get the earlier stages of integument development. The earliest stage which they have described (their Fig.14) is in fact, a more advanced stage and by 'no means the earliest. Hence, a degree of confusion and misinterpretation has inadvertantly been produced. The inner integument consists of two layers throughout its development and the outer integument which is bi-layered in the beginning becomes thicker. In one case it was observed that both the integuments were of the two layers. Normally outer integument reaches at the top of the nucellus at the megaspore mother cell stage. But in some cases it has been observed that even at the dyad and tetrad stage both the integuments are creeping at the base of the nucellus. Such a variability in the nature and behavior of the integuments in the same species of the Papilionaceae seems to be the first report. However, George *et al.* (1979) were unaware of it. In addition to linear tetrads, T-shaped ones and an oblique T-shaped tetrad of megaspores were also noted by Salgare (1970,73d,75f,76e,j,k,t,78a,80a,86a,97a,b,2000a) in *Phaseolus aureus*. George *et al.* (1979) failed to note T-shaped and an oblique T-shaped tetrads which proved their superficial and misleading observations. Further they stated that the chalazal dyad cell divides unequally such that D (chalazal functional megaspore) is much larger than the a, b or c megaspore (their Figs. 19, 41, 42). Once again, from their Figures 19, 41, 42 it appears that they have mistaken a later stage for an earlier one, where the functional megaspore is considerably increased in size which accounts for their error of interpretation. So far there is no report of an unequal division of dyad amongst the Papilionaceae. Further an abnormal case was observed by Salgare (1970,73d,75f,76e,t,78a,86a), where the megagametophyte was having an extra nucleus – 9-nucleate. George, George and Herr (1979) failed to take notice of such anomalies. With such a superficial observations they are comparing the development of ovule and megagametophyte in field-grown with the greenhouse-grown plants.

While monosporic development in megagametogenesis is the rule in Papilionaceae, bisporic development has occurred in Lathyrus odoratus (Jonsson, 1879-1880), in *Lupinus luteus* and *Lupinus polyphyllus* (Guignard, 1881), in *Laburnum anagyroides* (Rembert, 1966), in *Wisteria sinensis* (Rembert, 1967a) as well as in *Puereria lobata* (Rembert, 1969b), in *Canavalia ensiformis* (Salgare, 1975g-j,76g,77a,80a,b,,97a,b,2000a), in Canavalia gladiata (Salgare, 1975l, 76g, 77a, 80a, 97a,b, 2000a), in *Cyamopsis psoralioides* (Salgare, 1973b, 75m, as, 76g,q,t, 77a, 78a, 80a,b, 97a,b, 2000a), in *Dumasia villosa* (Salgare,1975z,aa,76g,77a,80a,b,97a,b,2000a), in *Phaseolus aconitifolius* (Salgare, 1973e ,74a, 75q,ad,76i,m,p,t,77a,b,80a,b,97a-c,2000a), in *Sesbania aculeata* (Salgare, 1975c, e, ab, 76a, i, 77b, 78a, 80a,b, 97a,b, 2000a), in *Sesbania aegyptiaca* (Salgare, 1975r,s, 76b,c,g,h,i,r ,77b, 80a,b,97a,b,2000a). It should be pointed out that all previous reports of bisporic development in Leguminosae have been challenged by Maheshwari (1955). Extensive work of Salgare make it very clear that the bisporic development in Leguminosae is a well established fact which invalid the challenge of Maheshwari (1955).

Salgare's (1970,73a-e,74a-d,75a-as,76a-t, 77a,b, 78a,b, 80a-c, 81,86a,b,95,97a-d,2000a-d) outstanding contribution in the field of embryology of Papilionaceae is as : (1) Tendency towards bi-layered tapetum, (2) Bi-nucleate microspore mother cells, (3) Giant pollen grains, (4) Twin megagametophytes, (5) Juxtaposed twin megagametophytes, (6) Superposed twin megagametophytes, (7) Superimposed twin megagametophytes, (8) Superposed multiple megagametophytes, (9) Superposed multiple megagametophytes, (10) Superimposed superposed multiple megagametophytes, (11) Juxtaposed superposed multiple megagametophytes, (12) Non-simultaneous formation of antipodals and egg apparatus, (13) Occurrence of additional nuclei in antipodals, (14) Reduction in the number of antipodal cells, (15) Failure of the development of antipodals, (16) Megagametophytes with increased number of antipodals, (17) Failure of cell formation amongst antipodal nuclei, (18) Separation of antipodals from the main body of megagametophyte, (19) Megagametophytes with reversed polarity, (20) Egg with an additional nuclei, (21) Avortion of cell formation by egg nucleus, (22) Megagametophyte with suppression of egg, (23) Synergids with additional nuclei, (24) Occasional omission of synergid nuclei from cell formation, (25) Suppression of synergids, (26) Formation of secondary nucleus by more than two nuclei in Polygonum type of megagametophyte, (27) Megagametophyte without development of polar or secondary nucleus, (28) Eight new Megaspore Tetrad Patterns in Papilionaceae, (29) New Megagametophyte type – Trisporic Development, (30) Occasional occurrence of a single fertilization, (31) Prior division of zygotic nucleus instead of primary endosperm nucleus, (32) More than one type of embryo

development in the same species, (33) Six different Megarchtypes in the same species and (34) New Megarchtypes. These are the first and only reports indicating that all the previous reports on the embryology of Papilionaceae are superficial and misleading.

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