BULL. BOT. SURV. INDIA
Vol. 46, Nos. 1-4 : pp. 139-150, 2004

CONTRIBUTION TO THE EMBRYOLOGY, SPORODERM AND SPERMODERM PATTERN OF *BOTHRIOCHLOA PERTUSA* (L.) A. CAMUS, *CAPILLIPEDIUM FILICULME* (HOOK.F.) STAPF AND *DICHANTHIUM ANNULATUM* (FORSSK.) STAPF WITH A BRIEF DISCUSSION ON ITS TAXONOMIC STATUS

C.A. Nikhade and V.A. Ghaisas

Post Graduate Department of Botany, Nagpur University Campus, Nagpur

ABSTRACT

Embryological features in *Bothriochloa pertusa, Capillipedium filiculme* and *Dichanthium annulatum* have been studied. The male reproductive characters are constant as evidenced by anther wall development and it corresponds to Monocot type. At maturity the pollen grains are 3-celled. Embryo sac development and embryogeny conforms to *Polygonum* type and Asterad type respectively. Endosperm, seed coat and pericarp have been studied and data on SEM investigation on pollen wall and seed coat of these taxa are added.

The three taxa *viz., Bothriochloa, Capillipedium* and *Dichanthium* were considered under Andropogoneae of Panicoideae as separate genera by Bor (1960). De Wet and Harlan (1970) merged them in *Dichanthium*. The evidences given by them are intergeneric hybridization and production of fertile hybrids between these three genera. Clayton (1977) also followed the concept of merger taking priority. The authors assessed the possibility of merger into *Dichanthium* on the basis of embryology, sporoderm and spermoderm pattern.

INTRODUCTION

The Poaceae is one of the largest and most widely distributed family of the Angiosperm which account for 24% of earth's vegetation. The opinions differ with respect to the number of genera and species to be included in the taxon. The taxon is known for its structural diversity both in vegetative and reproductive characters. The division of the Poaceae into two subfamilies *viz.* Pooideae and Panicoideae as proposed by Brown (1814) is being maintained even today.

The embryological studies on grasses have been strictly descriptive with a little attempt to correlate them in systematics. The embryological characters have been successfully utilized for understanding the interrelationship at different taxonomic levels, *e.g.* at subfamily level (Reeder, 1957, 1962; Venkateshwarlal and Devil 1984; Nikhade, 1996), at tribes level (Maze and Bohm,1977; Bhanwara,1984), at generic level (Mahlenbacher,1970; Maze and Bohm, 1973, 1974; Bhanwara, 1981; Ghaisas, 1991) at species level (Tateoka, 1964; Aulbuch Smith Herr Jr., 1984) and even at variety level (Ghaisas, 1991).

In the present investigation authors worked out the embryology, sporoderm and spermoderm pattern in three taxa *viz. Bothriochloa pertusa, Capillipedium filiculme* and *Dichanthium annulatum* and they have discussed the taxonomic status on the basis of these characters.

MATERIALS AND METHODS

The taxa *Bothriochloa pertusa* and *Dichanthium annulatum* were collected from various localities around Nag pur (M.S.) India, while that of *Capillipedium filiculme* was collected from Salekasa (Bhandara district (M.S.) India). Voucher specimens were deposited in the herbarium of Botany Department, Nagpur University Nagpur.

Mature spikelets become very hard due to the impregnation of silica. Such spikelets were first treated with a 40% solution of hydroflouric acid in 70% alcohol for a period of 4 to 8 hours. Similarly, from the older spikelets hardened glumes, were removed mechanically. The young spikelet, ovaries and developing seeds separated from the glumes were processed through customary methods of dehydration, infiltration and embedding. The sections were cut at 8-10 μm thick and stained with Delafield's hematoxylin. The sections were mounted in canada balsam.

RESULTS

Microsporogenesis and male gametophytes

The anthers are tetralocular. However; the septum separating the two adjoining lobes, gets dissolved prior to anthesis In *C. filiculme* and *D. annulatum,* the septum breaks down much earlier when the pollen grains are 2-celled. The pollen dissemination in all the three taxa is accomplished by formation of a longitudinal slit, which constitutes the stomium. A single archesporial cell differentiates hypodermally at each corner of the young anther. The anther wall composed of four layers including epidermis, endothecium, middle layers and tapetum. The development corresponds to the Monocot type (Davis, 1966).

The epidermal cells in *B. pertusa* and *D. annulatum* show stretched appearance. However, in *C. filiculme,* they are papillate. A uniform character which has been observed in these taxa is the development of spiny projections on the outer tangential walls of epidermis at maturity forming echinulate epidermis. The outer secondary parietal layer, situated below the epidermis, differentiates into a endothecium, in which develops spiral thickenings. The orbicules (ubisch granules) are observed on inner tangential wall of endothecial cells. A single middle layer is ephemeral and get crushed during anther development. Tapetum the inner most wall layers ambients the sporogenous tissue comprises uninucleate cells. The tapetal cells degenerate with the onset of meiosis *in situ* showing secretory nature. In *B. pertusa* the tapetal cells remain persistent which leads to the pollen sterility.

The primary sporogenous cells undergo few mitotic divisions and form microsporocytes. The pollen output is comparatively low in these taxa. The meiotic divisions in the pollen mother cells are normal resulting in microspore tetrads of isobilateral type. The microspore get separated from each other and individual microspore starts increasing in size. The young microspores have dense cytoplasm and centrally placed nucleus. Later, the nucleus undergoes first mitotic division forming generative cell and vegetative cell. The generative cell later divides, and forms two male gametes. The generative cell becomes lenticular in *C. filiculme*. The mature pollen grains are thus 3-celled at maturity.

SEM study shows that the mature grains are monoporate, with granular surface, sometimes columellate and showing uniformity in these features in all the taxa with few differences.

Ovule: The ovules are campylotropous, tenuinucellate and bitegmic. Both the integuments are two layered. In *D. annulatum* towards micropylar end the integument become 3-4 layered. The micropyle in all the three taxa, appears to be organised by inner integument alone which is rather wide due to formation of nucellar cap.

Megasporogenesis and female gametophytes

The female archesporium differentiates hypodermally comprising single cell but sometimes 2-3 cells were also noticed in the taxa studied here. The archesporium further enlarges in size and directly functions as megaspore mother cell. Meanwhile, the cells of the nucellar epidermis divide anticlinally as well as periclinally to form a well organised nucellar beak. The cells of inner layer of nucellar beak undergo degeneration at the time of organization of embryo sac. The megaspore mother cell undergoes meiosis followed by successive cytokinesis. The meiosis I results in dyad cells. A twin dyad is observed in *D. annulatum*. Meiosis II in each dyad cell results in a linear row of four megaspores.

Twin tetrads are of common occurrence in *C. filiculme* and *D. annulatum*. In all taxa, chalazal megaspore alone functions and remaining 3 megaspores degenerate. The functional megaspore is provided with dense cytoplasm, its nucleus lies almost in the centre. The nucleus undergoes three successive mitotic divisions to produce eight nuclei which organise into *Polygonum* type of embryo sac which is rather broad in *B. pertusa* broader at the micropylar end and tapering towards chalazal end in *D. annulatum* or may be spindle shaped in *C. filiculme*. The egg apparatus comprises two synergids which degenerate soon after fertilization. The polars move to the centre of the embryo sac, i.e. close to each other the polars may migrate to the vicinity or may remain away from egg at the time of fertilization. They fuse prior fo fertilization to form secondary nucleus.

The behaviour of the antipodals is rather interesting in these taxa. In *B. pertusa*, a complex of 21 cells is seen, in *C. filiculme*, there are 9 cells while in *D. annulatum*, there are 4-8 cells. This complex is prersistent during early embryogeny. However, due to excessive lateral and downward growth of embryo sac, the antipodal complex appears to be lateral. The twin embryo sacs have also been observed in *B. pertusa* and in *D. annulatum*.

Fertilization : Fertilization is porogamous. The pollen tube penetrates one of the synergids and breaks open to discharge its contents in it. The syngamy and triple fusion occurs in a normal way.

Embryogeny : The fertilized egg is almost spherical in *C. filiculme,* flask shpaed in *B. pertusa* and *D. annulatum.* The cytoplasm is vacuolated and nucleus is situated in the centre.

The first transverse division in zygote results in formation of two superposed cells, *viz.* terminal cell *ca* and basal cell *cb* are of equal size, whereas in *D. annulatum ca* is smaller than *cb*. The terminal cell *ca* divides vertically whereas basal cell *cb* transversely to form *m* and *ci* The resulting proembryonic tetrad is 'T' shaped.

The cell *ca* undergoes vertical division resulting in quadrant *q*. The cells m next divides vertically to form two juxtaposed cells, while *ci* undergoes transverse division to form cells *n* and *n'* At the end of 3rd cell generations 8 cells are formed which are disposed of in 4 tiers. This is obseved in *D. annulatum.* However, in *B. pertusa* and *C. filiculme* synchrony in division of *ca* , *m ci* is not observed during third cell generation. In *B. pertusa* soon after the quadrant stage transverse partition occurs to form tiers *I* and *I.* The later undergoes vertical division soonafter its formation. Further division in tiers *I, I* and m do not follow a regular sequence, but occurs in different planes resulting in a massive globular embryo. The dermatogen generally differentiates atmost simultaneously in the tiers and *I'* and later to tier *m*. The cell *n* segments vertically forming two juxtaposed cells while cell *n'* divides transversely forming a suspensor of 2-3 cells.

The globular embryo which is organised consists of a small region having 3-4 layers constituting *I* a little broader region of 5- 7 layers composing of *I'*. 4-5 layers of *m*, 2-4 layers of *n*. However, in *C. filiculme* the derivatives of *n* undergoes vertical division to form a broad suspensor. The repeated mitotic divisions in the epidermal cells of tier *I* and *I'* but situated on side of the proembryo, result in the notch which appears at the junction of tiers *I* and *I*. The notch deepenes further, the derivatives of tier engender a single cotyledon called the scutellum (sc.). The epidermal cells of tier I, bordering the notch, however, grow downwards to differentiate into upper lip of the coleoptile (Cl") situated below the upper lip of the coleoptile and differentiated from the epidermal cells of tier I' are present the primordium of stem tip *pvt.* first leaf and lower lip of coleoptile *CI"* respectively.

The hypocotyledonary region (*phy*) along with the central cylinder of root (iec) is engendered from the elements of tier *m*. The superior derivatives of tier *n* produce a sheath called coleorhiza (*cor*). A layer of cells situated between the central cylinder of root (*iec*) and root sheath (*cor*) give rise to root cap (*co*).

The plumule and radicle is slightly curved and shows distinct provascular strand. The vascular strand of scutellum is joined to that of embryo axis. The three histogenic layers are clear in mature embryo. The cells of scutellum show starch grains. In *D. annulatum* the two embryos at globular stages have been reported.

Endosperm : The endosperm development in these taxa is *ab initio* free nuclear manner. Repeated free nuclear divisions produce large number of endosperm nuclei. The micropylar nuclei aggregate around the developing embryo, while in the other regions lie embedded in peripheral layer of cytoplasm. In *C. filiculme* degenerating remains of antipodals also seen during endosperm development. The endosperm becomes cellular, first around the proembryo. The endosperm becomes completely cellular, as the embryo attains globular stage. The meristematic in the cells of peripheral and to some extent hypodermal layers increases the bulk of endosperm.

In *B. pertusa* starch deposition is uniform and that too in all the cells below the aleurone layer. However, in *C. filiculme* the terminal and basal part of endosperm show uniform distribution of starch but in the middle region peripheral 2-3 layers are devoid of starch. The protein grains also deposit in the endosperm cells. In *D. annulatum* starch deposition is similar to that of *B. pertusa.*

In all these species the outermost layer of endosperm in mature grain constitutes the aleurone layer. The embryo during development, consumes starch from neighbouring cells. In the mature caryopsis the 70% portion of the grain is occupied by the endosperm. The mature grain thus is endospermic.

Seed coat and Pericarp : The ovule in these taxa is bitegmic and each integument is uniformly two layered thick for its major part, though at micropylar end becomes three layered. The outer integument, takes no part in the construction of a mature seed coat. It starts degenerating .early and process of degeneration is rather fast along the distal side. The first sign of degeneration is noticeable at zygote stage. Its *disiecta membra* however persists for sometime and are visible at globular and mature state of the embryo.

The inner integument is generally involved in the formation of seed coat. In all the three taxa stuided here, both layers of inner integument get highly stretched during early embryogeny. The inner integument in *B. pertusa* persists in a degenerated conditon till flaps of coleoptile and stem tip appear, but is lost during subsequent development. In *C. filiculme* the stretched cells of inner integument persists for a longer time. Similar is the situation in *D. annulatum.* Thus, the mature seed coat in *B. pertusa* is made up of a single layer of cells derived from the inner layer of inner integument. In *C. filiculme* and *D. annulatum* the seed coat may show presence of two layers.

The layer which constitutes the seed coat, with increase in bulk of endosperm and embryo, gets pushed towards the periphery so as to lie in close proximity with the pericarp. However, the former does not show fusion with the later at any stage during development and is present as an independent entity.

Pericarp : At mature embryo sac stage the ovary wall consists of 4-6 layers. During post fertilization development, there is a tendency towards gradual elimination in ovary wall layers. When the organization of mature embryo takes place, silica deposit in the intervening layers of pericarp in all the three species. Silica deposition usually starts at 2nd or 3rd cell generation of embryo development.

The thickness of the pericarp is on decline, from the indentation stage of embryo onwards as some of its middle layers collapse. In *B. pertusa* the outer tangential walls of outer epidermis develop spiny outgrowths. However, in remaining two taxa the pericarp is smooth at maturity.

SEM study shows uniform characters *viz.* uneven surface, with blunt ridges and furrows with minor differences which are unaccountable in all the three taxa.

DISCUSSION

The male reproductive features tend to remain constant at the family level. The taxonomic significance of anther wall development was overlooked by earlier workers (Davis, 1966). The four layered anther wall is conforming to monocotyledonous type (Davis, 1966). This is true for the taxa studied here. The only report of presence of 2 middle layers i.e. anther wall to be 5-layered, in the forage grasses studied by Seshavatharam and Satyamurti (1976).

The male archesporium is hypodermal and consisting of a single cell in all the three taxa, unicellular archesporium is reported earlier by Cannon (1900) in *Avena fatua;* Untawale and Sharma (1969) in *Eragrostis unioloides;* Raju (1980) in wheat; Bhanwara and Choda (1986) in *Echinochola.* Multicellular condition has been reported in *Pennisetum typhoideum* by Rangaswamy (1935) and Raju (1980) in *Oryza sativa* and *Zea mays*. The earlier workers Narayanswami (1956); Chandra (1963a); Venkateshwarlu and Oevi (1964); Godbole (1968) Kaul (1970 a, 1970 b); Bhanwara (1988) however, failed to report on this aspect.

Echinulate epidermis is a constant feature in all the taxa. These outgrowths according to authors are perhaps siliceous in nature. The echinulate nature of epidermal cells has earlier been reported by Batygina (1974 b), Oiwanji (1976) and Gawli (1977). Earlier Narayanswami (1953), made mention of bristle like hairs in *Pennisetum typhoideum.* Raju (1980) on the basis of position, nature and persistance nature till dehiscence, feels that they serve as an organ of defence.

The hypodermal endothecium develops fibrous thickenings and this is true for the taxa studied here. However, thickening does not develop in the sterile anthers. A review by Gerenday and French (1988) reveals that whenever the dehiscence of anther is porate the fibrous thickenings are absent. The 'Ubisch' granules (Orbicules) in the taxa studied here appear on the inner tangential walls of endothecium. However, Bhanwara (1985, 1988) did not mention about these granules in the plants studied by him.

The cells of glandular tapetum are mostly uninucleate in all the three species. The male sterility is related to the abnormal behaviour of tapetum (Artschwager, 1949; Zenkteler, 1962; Dubey and Singh, 1965; Singh , 1965; Kaul and Singh, 1966; Chauhan and Singh, 1966; Godbole, 1968). This is also true in the present study.

The number of sporogenous cells in each anther lobe is variable. Bhanwara (1988) pointed out that they are very high in Bambusoideae, Poaceae and in some taxa of Andropogoneae. They are less in Aveneae and Chloridoideae. In the taxa studied here they are less which speaks of the low output of pollen grain. The dissolution of callose leads to the formation of functional pollen grains. Normal meiosis in pollen mother cells, followed by successive cytokinesis results in isobilateral tetrads of pollen grains which is perhaps the rule in Poaceae.

The family is characterised by 3-celled pollen grains at anthesis (Davis, 1966), substantiated by present study.

The ovule is tenuinucellate. According to Davis (1966) this condition is found in taxa belonging to Pooideae, while in Panicodeae, nucellar epidermis at the tip in the micropylar region divide periclinally and forms a cap of variable numbers of layers. Such ovules where periclinal divisions occur in the nucellar epidermis are described as crassinucellar (Maheshwari, 1950) or Psedocrassinucellar according to Davis (1966). Though the distinction between Pooideae and Panicoideae on the basis of this character is also made by Bhanwara (1988) who studied 59 species of grasses together, the details regarding structure, origin and the development of nucellar cap are not given. The nucellar cap is the distinctive character of the two subfamilies and has considerable taxonomic value. This was earlier mentioned by (Narayanswami, 1953, 195~a 1956; Kaul, 1970a ; Diwanji, 1976; Gawli, 1977 and Bhuskute, 1990). Present study shows that there are 2-5 layers where the cells are quite emerged and densely cytoplasmic.

The megaspore tetrads of varying pattern are described in Poaceae. Twin linear tetrads have been reported by Muniamma (1969), which is also corroborated by the present work. The embryo sac development conforms to *Polygonum* type (Maheshwari, 1950). Twin embryo sacs showing different state of development in *B. pertusa* and *D. annulatum*. The origin of these two embryo sac cannot be traced due to non-availability of sequential stages.

According to Ambegaonkar and Johri (1977) in Triticales one synergid enlarges and persists upto 2-celled stage of proembryo. However, Cass and Jensen (1970), Chao (1971) and Maze and Lin (1975) emphasised that pollen tube penetrates one of the synergids which degenerate. The present work also testify to this.

The antipodals in family are unique. They present great variation in respect of their number, position and behaviour, a multiple antipodale tissue is a feature noticeable in the family Poaceae (Hector, 1936) and is true for all the three taxa investigated by the authors.

The antipodals enlarge and become glandular after fertilization, offer a close analogy to the anther tapetum according to Maheshwari (1950). Beaudry (1951) assigned a secretary role to antipodals and the hypertrophy in them to be associated with the degeneration of endosperm. Hoshikawa and Higuchi (1960-61) on the other attribute, haustorial role to one of the antipodal cells located at the chalazal end. The haustorial nature of antipodals has also been accepted by Rangaswami (1935), Chikkannaiah and Mahalingappa (1976 a) and Bhuskute and Makde (1986).

In Pooideae, according to Chandra (1963 b), Venkateshwarlu and Devi (1964) and Davis (1966) they are housed in a lateral diverticulum of the embryo sac. Among the Panicoideae they occupy chalazal position (Percival, 1923 ; Beck and Horton, 1932;

Narayanswami, 1955 c; Deshpande, 1976; Diwanji, 1976; Gawli, 1977; Raju, 1980; Bhanwara, 1988; Bhuskute, 1990). The position of antipodals has not been given much importance by several authors, but the available data suggest that the same can safely be used as a taxonomic character. The antipodals eventually degenerate completely. They however, are reported to persist in the mature grain of maize (Weatherwax, 1926) and *Euchlaena mexicana*, (Cooper, 1937; Kaul, 1959). In *C. filiculme* author reported persistent antipodals at proembryonic tetrad.

The fertilization is normal and porogamous. The embryo development in all the three species follows the Astered pattern of Johansen (1950) or Soueges (1951) system of classification corresponds to grand period 1, series A, Proembryonic tetrad of A2 category but varies in Megarchetypes. Similar pattern of embryo development reported by (Soue'ges, 1924; Guignard, (1962). Terezski and Kharistov, 1973; Chikkanniah and Mahalingappa, 1976 a; Johri and Ambegaonkar, 1976; Seshavatharam and Satyamurti (1976).

Batyagina (1968, 1969, 1974 b) demonstrated the "Graminad type" of embryo development in the grass family on the basis of oblique division in early embrogeny Gerasimova Navashina (1972); Raju (1980); Makde (1994); Nikhade and Makde (1997) criticised the stand taken by Batygina. The minor differences during early development do not warrant the creation of new variations of Graminad type.

The free nuclear endosperm development, becomes cellular at the end of globular phase. Meristematic activity in peripheral layer and the aleurone layer has been the universal feature of the Gramineae (Gordon, 1922; Chandra, 1963a; Davis, 1966; Maze and Bohm 1974; Deshpande, 1976; Johri and Ambegaonkar, 1976; Sapre, 1964; Diwanji, 1976; Sudhir Chandra, 1976; Bhanwara *et al* 1983, 1985; Raju, 1980 and Bhuskute, 1990).

The seed coat derived from the inner integument is a regular feature in the grasses. The fruit is described as 'Caryopsis' and has been defined as seed and adherant pericarp' by Lawrence (1951) or 'Pericarp adnate to the seed' by Hutchinson (1959). The present work indicates that pericarp and testa at no stage show fusion with each other, which is also reported by the earlier workers. Thus, on the basis of these characters and assessment, the merger of these genera *viz., Bothriochloa, Capillipedium* and *Dichanthium* into one i.e. *Dichanthium* appears sound as supported by De Wet and Harlan (1970) and Clayton (1977).

ACKNOWLEDGEMENT

The authors are grateful to Dr. K.H. Makde, Professor of Botany, Department of Botany, Nagpur University, Nagpur, for guidance and constructive criticism.

REFERENCES

Ambegaonkar, K.B. and B.M. Johri. Seed development in Triticale -1. *Phytomorph.,* 27 : 190-197. 1977.

Artschwager, E. and R.C. Mc Guirie. Cytology of reporoduction in *Sorghum vulgare. J. Agri. Res.* 78 : 659-673. 1949

BATYGINA, T.B. Embryogenesis in the genus *Triticum* L. as related to the problems of monocotyledony and remote hybridization in Gramineae. *Bot. Zh.* 53 : 480-490. 1969a.

BATYGINA, T.B. On the possibility of a new type of embryogenesis in angiosperms. *Rev. Cytol. Bioi. Veg.* 32 : 335- 341. 1969b

BATYGINA, T.B. Wheat Embryology "Kolos". Leningrad (In Russia). 1974.

BEAUDRY, J. R. Seed development following mating Elymus virginious × Agropyron repens. *Genetics,* 36 : 109-133. 1951.

BECK, P. AND J.S. HORTON. Microsporogenesis and embryology in certain species of *Bromus. Bot. Gaz.,* 93: 42-54. 1932.

BHANWRA, R.K. AND R. DEORI. Embryological studies in some grasses. *Proc. Indian Nat. Sci. Acad,* B, 47: pp. 408- 418. 1981.

BHANWRA, R.K. AND R. KUMAR. Comparative embryology of *Brachiaria ramosa* and *Poa annuua. Res. Bull. (Science) Punjab, Uni.* 36 : 245-253. 1985.

BHANWRA, R.K., SANJIV KUMAR AND RAJ KUMAR. Comparative embryology of *Brachiaria ramosa* and *Poa annua, Res. Bull (Sci.) of the Punjab Univ.,* (36), Parts III-IV : 245-253. 1985.

BHANWRA, R.K. Embryological studies in five species of *Eragrostis* Beauv. (Gramineae)" *Research Bulletin (Sci) of Punjab Univ.,* 37, Parts -I-II: 17-23. 1985.

BHANWRA, R.K. Embryology in relation to Systematics of Gramineae. *Annals of Botany,* 62 : 225-233. 1988.

BHANWRA, R.K. and S.P. CHODA, Comparative embryology of *Echinochloa colonum* and *Echinochloa crusgalli* (Poaceae). *Proc. Indian Aca. Sci.* (Plant Sci.), 96, No. (1) : 71-78. 1986.

BHUSKUTE, SUSHAMA, M. In vitro studies on *Dendrocalamus strictus* Nees and *Bambusa arundinacea* Mom. with some observations on their Embryology and Histochemistry. Ph.D. Thesis, Nag pur Uni., Nag pur. 1990.

BHUSKUTE S.M. AND K.H. MAKDE. Antipodal haustorium in *Braiza minor* L. *Curr. Sci.,* 55(7) pp. 364-367. 1986.

BOR, N.L. The Grasses of Burma, Ceylon, India and Pakistan. Pergamon Press, Oxford. 1960.

BROWN, R. In Mathew Flinders, "A voyage to Terra Australis" London. Eastern Canada, with discussions. *Can. J. Bot.* 56: 107-109. 1814.

CANNON, W.A. A morphological study of the flower and embryo of the wild Oat, *Avena fatua* L. Proc. Calif. Acad. Sci. III, 1 : 329-365. 1900.

CASS, D.D. AND W.A. JENSEN. Fertilization in Barley. *Amer. J. Bot.,* 53: 1051-1062. 1970.

CHANDRA, N. Morphological studies in Gramineae. IV. Embryology of *Eleusine indica and Dactyloctenium aegypticum. Proc. Indian Acad. Sci.* B, 58: 117-127. 1963a.

CHANDRA, N. Some ovule characters in systematics of the Gramineae. *Curr. Sci.,* 32: 277-279. 1963b.

CHAO, C.Y. A periodic acid Schiff's substance related to the directional growth of pollen tube into embryo sac in *Paspalum* ovules. *Amer. J. Bot.,* 58: 649-654. 1971.

CHIKKANAIH, P.S. AND M.S. MAHALINGAPPA. Embryological studies in *Eleusine,* Abst, In Embryology of crop plants. Indo- Soviet Symp. sponsored by INSA and Univ. of Delhi, pp. 7. 1976a.

CLAYTON, W.D. Studies in the Gramineae-42 new grasses from Eastern Africa. *Kew Bull.,* 25: 247-251. 1977.

COOPER, D.C. Macrosporogenesis and embyo sac development in *Euchlaena mexicana* and Zea mays. *J. Agric. Res.* 55 : 539-551. 1937.

DAVIS, G.L. Systematic Embryology of the Angiosperms. Wiley, New York. 1966.

DESHPANDE, P. K. Devélopment of embryo and endosperm in *Eragrostis unioloides* (Poaceae). *Pl. Sys. Evol.* 125: 253-259. 1976.

DESHPANDE, P.K. AND K.H. MAKDE. Embryo and Fruit in the Poaceae Advances in Plant Reproductive Biology, pp. 101- 116 (Eds. Y.S. Chauhan and A.K. Pandey). 1995.

DIWANJI, V.B. Embryological studies in the Gramineae, Ph.D. Thesis, Univ. of Indore, Indore. 1976.

DE WET, J.M.J. AND J.R. HARLAN. Morphology of the compilospecies of *Bothriochloa inter media. Am. J. Bot.* 53 : 94-98. 1966.

DE, WET, J.M.J. AND J.K. HARLAN. *Bothriochloa intermedia,* a taxonomic dilemma, *Biol. Sec. Argentina Bol.* 19: 339-340. 1970.

GAWLI, S.P. Embryological studies in the Gramineae. Ph.D. Thesis, Nagpur Uni, Nagpur India. 1977.

GERASSIMOVA NAVASHINA, H. Developmental determination of the embryo structure in Angiosperms. *Bot. Zh.* 57: 441-457. 1972.

GHAISAS, V.A. Morphological and Histochemical Investigations on some oil yielding grasses. Ph.D. Thesis, Nag pur Uni., Nag pur, India. 1991.

GUIGNARD, J.L. Researches surl embryogenie des Graminees; Rapports des Graminees avec les autres, Monocotyledonous. Thesis A la, Faculte des Sciences de l'niversite de Paris. 1962.

GERENDAY, A. AND J. FRENCH. Endothecial thickenings in anthers of porate Monocotyledons. *Amer. J. Bot.,* 75 (1) : 22-25. 1988.

GODBOLE, R.K. Embryological studies in some cultivated varieties of Sorghum. M.Sc. Disser. College of Agric. Nagpur. 1968.

GORDON, M. The development of endosperm in cereals. *Proc.Rov. Soc. Victoria,*34: 105-116. 1922.

HECTOR, J.M. Introduction to the Botany of Field Crops. Vol. I. *South African Agric. Series.* Vol.16. 1936.

HOSHIKAWA, K.A. AND A. HIGUCHI. Embryo sac formation in wheat. *Proc. Crop. Sci. Jap.,* 29: 256-257. 1960-61.

HUTCHINSON, J. The families of flowering plants. 2nd Vol. (2nd ed.) Monoctyledons Clarendon Press, Oxford. 1959.

JOHANSEN, D.A. *Plant Embryology.* Waltham, Mass U.S.A. 1950.

JUDD, W.S. CAMPBELL, C.S. E.A. KELLOGG AND P.F. STEVENS. Plant Systematics - A Phylogenetic Approach. Sinauer Associates Inc. Publishers Sunderland, Massachue's U.S.A. 1999.

JOHRI, B.M. AND K.B. AMBEGAOKAR. The antipodals in Triticales. *Phytomorph.,* 25: 211-217. 1975.

KAUL, A.K. Antipodals during the development of caryopsis in *Euchlaena mexicana. Agra Univ. J. Res.* (Sci.) 78:31-33. 1959.

KAUL, A.K. Cytoembryological studies in Oriental Maydeae I: *Coix acquatica* Roxb. *Proc. Nat. Acad. Sci.* 40: 163-178. 1970a.

KAUL, A.K. Cytoembrological studies in Oriental Maydeae II: *Chionachne koenigii* Thu. *Proc. Nat. Acad. Sci.,* 40: 301 1970b.

LAWRENCE, G.H.M. Taxonomy of Vascular Plants. Mac Millan, New York. 1951.

MAHESHWARI, P. An introduction to the Embryology of Angiosperms. Mc Graw Hill, New York. 1950.

MAZE, J. AND L.R. BOHIM. *Embryology of Agrostis interrupta. Ibid.* 52: 365-379. 1974.

MAZE, J. AND S.C. LIN. A study of the mature megagametophyte of *Stipa elmeri. Ibid.* 53: 2958-2977. 1975.

MUNIAMMA, M. Occurrence of twin embryo sacs in *Themeda cymbaria.* Abst. *Proc. Ind. Sci. Cong.* 350. 1969.

NARAYANSWAMY, S. The strucutre and development of caryopsis in some Indian millets. I. *Pennisetum typhoideum* Rich. *Phytomorph.* 3: 98-112, 1953

NARAYANSWAMY, S. The structure and development of the caryopsis in some Indian Millets. VI. *Setaria italica. Bot. Gaz.* 118: 112-122. 1956

NARAYANSWAMY, S. The structure and development of the caryopsis in some Indian Millets. 111. *Panicum millare* Lamk. and *P. miliaceum* L. *Lloydia.,* 18: 61-73. 1955a.

NARAYANSWAMY, S. The structure and development of the caryopsis in some Indian Millets. V. *Eleusine coracana* Gaertn. *Mich. Acad. Sci. A.L.,* 40: 33-46. 1955c.

NIKHADE, C.A. Embryological Investigation on some members of Pooideae (Poaceae). Ph.D. Thesis Nag. Uni. Nagpur. 1996.

NIKHADE, C.A. AND K.H. MAKDE. A contribution to the embryology of *Perotis indica* (L.) O.Ktze, *J. Natl. Bot. Soc.* 51: 33-41. 1997.

RAJU, G. Embryological and Histochemcial studies on some crop plants (Gramineae) Ph.D. Thesis, Nagpur Uni., Nagpur. 1980.

RANGASWAMY, K. On the cytology of *Pennisetum typhoideum. J. Indian Bot. Soc.,* 14: 125-131. 1935.

SESHAVATHARAM, V. AND T.V. SATYAMARTI. Embryology of some forage grasses. Abst.: In Embryology of Crop plants. Indo-Soviet Symp. Sponsered by INSA and Univ. of Delhi, pp.39. 1976.

SOUEGES, R. Embryogenesis des Graminees Development de I'embryon chez. le Poa annua L.C.R. *Acad. Sci. France.* 178: 860- 862. 1924.

SOUEGES, R. Embryogenie et classification 4. Essaid' un systeme embryogenique. Partie specialoze periode due systeme. Paris, Hermann Cie. 1951.

SUDHIR CHANDRA. Post pollination development of wheat caryopsis. Abst. In : Embryology of crop plants. Indo-Soviet Symp. sponsored by INSA and Uni. of Delhi, pp. 46-47. 1976.

SAPRE, A.B. Embryological studies in the genus Oryza Ph.D. Thesis, Nagpur University, Nagpur. 1964.

TEREZSKI, D. AND M.A. KHRISTOV. Cytoembryonic study of *Festuca pratensis,* Huds., *Alopecurus pratensis* L., *Holcus lanatus* L. and *Agrostis vulgaris. Genet. Set.,* 6 : 45-57. 1973.

UNTAWALE, A.G., P.K. DESHPANDE AND K.B. SHARMA. Studies in the gramineae I. Male and female Gametophytes of *Eragrostis unioloides* (Retz.) Nees ex Steud. *J. Indian Bot. Soc.*, 48: 386-392. 1969.

VENKATESHWALU, J.AND P.I. DEVI. Embryology of some Indian grasses. *Curr. Sci.,* 33 : 104-106. 1964.

WEATHERWAX, P. Persistence of antipodal tissue in the development of the seeds of maize. *Bull. Torrey. Bot. Club* 53 : 381-384. 1926.

ZENKTELER, M. Microsporgenesis and tapetal development in normal and male sterile carrots (*Daucus carota*). *Am. J. Bot.* 49: 341-348. 1962.