

Comparative Embryology of Some Grasses

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Comparative embryology of 15 taxa belonging to the tribes Andropogoneae, Paniceae, Aristideae, Arundinelleae, Arundinae and Glycerieae, has been studied. The species belonging to the tribes Andropogoneae, Paniceae and Arundinelleae are very closely related and show a cluster of features not met within the tribes Aristideae, Arundineae and Glycerieae.

Key Words: Embryology, Grass, Andropogoneae, Paniceae, Aristideae, Arundinelleae, Arundineae

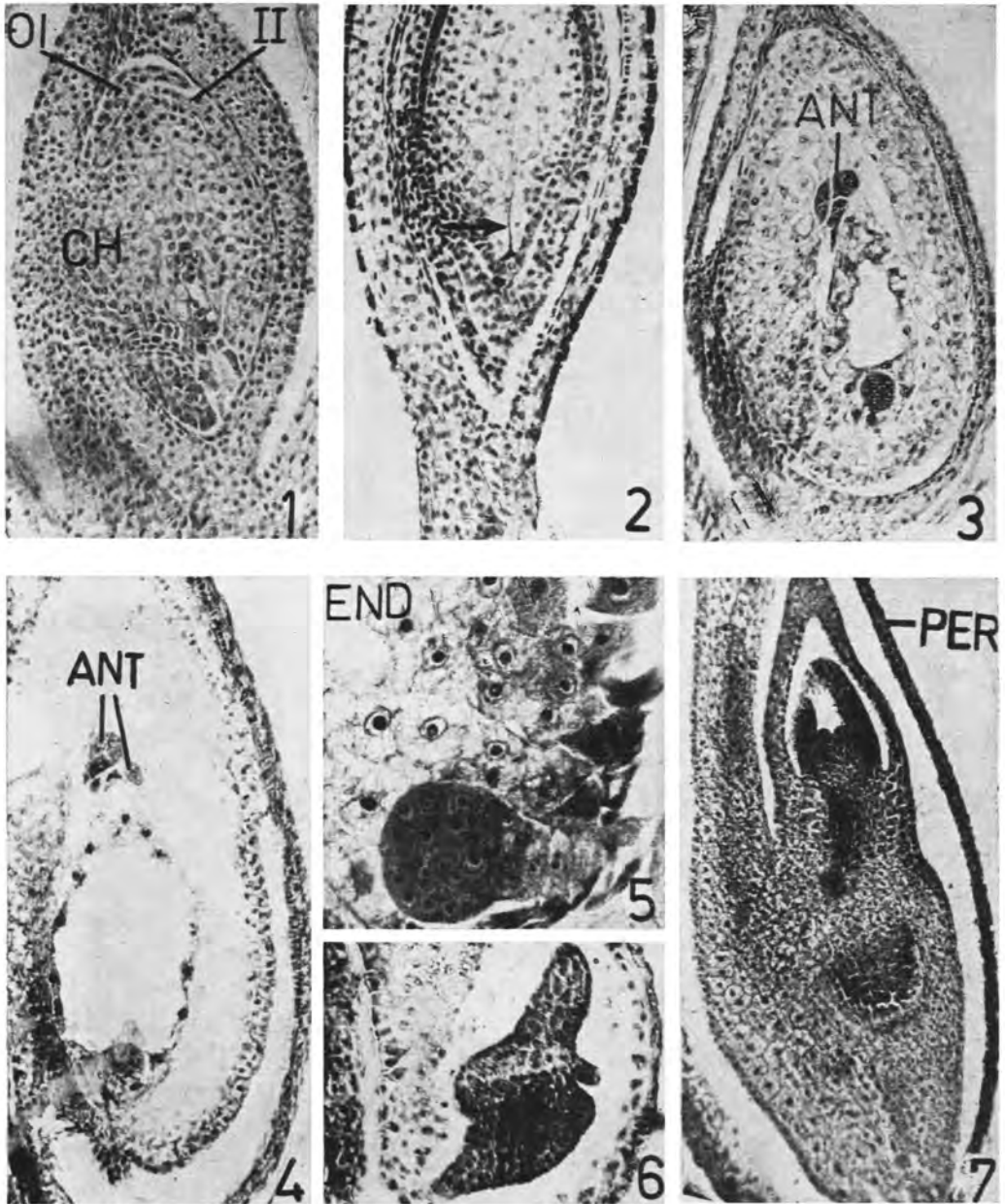
Introduction

The embryological studies in the Gramineae have revealed that some of the features can be of considerable taxonomic interest (see Chandra 1963, Venkateswarlu & Devi 1964, Kam & Maze 1974, Maze & Bohm 1977, Bhanwara & Choda 1980 and Bhanwra et al. 1981). In a previous paper (Bhanwra et al. 1981), the authors have utilized these features to clarify the relationships among some of the festucoid grasses. The present investigation is an attempt to elucidate further the relationships between the tribes Andropogoneae, Paniceae, Aristideae, Arundinelleae, Arundineae and Glycerieae, and deals with the embryology of 15 taxa. Except for the structure of the mature embryo (Reeder 1957), embryological information is lacking for the tribes Aristideae, Arundinelleae, Arundineae and Glycerieae but many species have been investigated from the tribes Andropogo-

neae and Paniceae from the point of view of apomixis or otherwise (see Artschwager et al. 1929, Artschwager & McGuire 1949, Narayanaswami 1953, 1954, 1955a, 1956, Brown & Emery 1958, Chandra 1963, Venkateswarlu & Devi 1964).

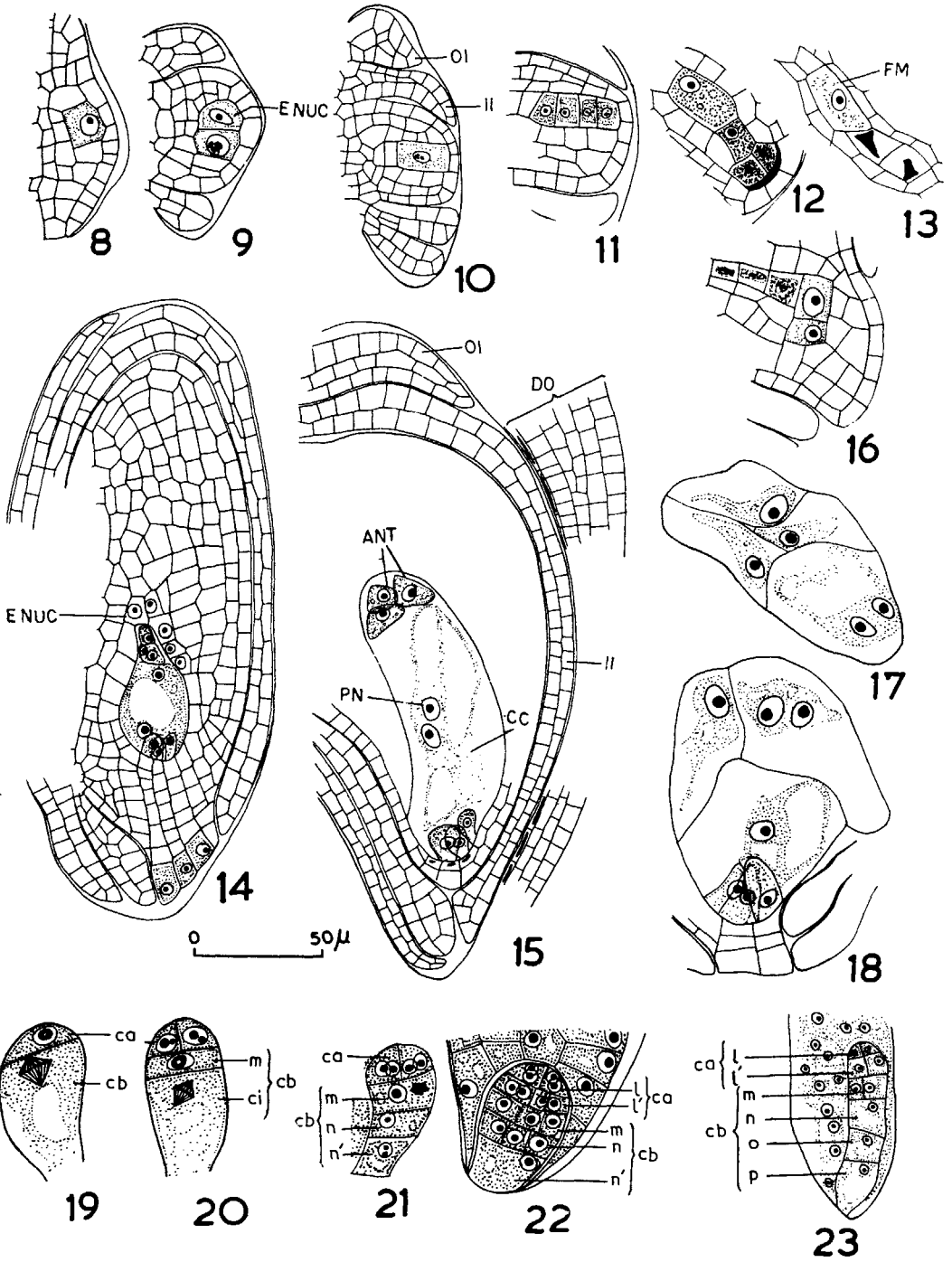
Materials and Methods

The investigated taxa include *Cappillipedium parviflorum* (R. Br.) Stapf, *Imperata cylindrica* (L.) P. Beauv., *Trilema prostratum* (L.) Andress, *Sacciolepis bengalense* Retz. (diploid, tetraploid and hexaploid cytotypes), and *Vetiveria zizanioides* (L.) Nash (tribe Andropogoneae), *Brachiaria distachya* (L.) Stapf, *Cenchrus biflorus* Roxb., *Paspalidium flavidum* (Retz.) A. Campus, *Setaria glauca* (L.) Beauv. (tetraploid and octoploid cytotypes), *S. intermedia* (Roxb.) Kunth and *S. verticillata* (L.) P. Beauv. (tribe Paniceae), *Aristida adscensionis* L. (tribe



Figures 1-7 Structure of the ovule, embryo, endosperm and pericarp. 1, *Cenchrus biflorus*; 2, *Arundo donax*; 3, *Setaria intermedia*; 4, 6, *Setaria verticillata*; 5, 7, *Setaria glauca*; (ANT, antiopodal cell; CH, chalaza; END, endosperm; II, inner integument; L. S. longitudinal section; OI, outer integument; PER pericarp).

1, 2. L. s. of the mature ovule passing through the chalaza; 3-7, L. s. of the caryopses at different stages of development. 1($\times 120$), 2, 3, 4, 6 ($\times 160$); 5($\times 400$); 7($\times 90$)



Aristideae), *Arundinella nepalensis* Trin. (tribe Arundinelleae), *Arundo donax* L. (tribe Arundineae) and *Glyceria tonglensis* C. B. Clarke (tribe Glycerieae). The material was collected from the Chandigarh plains (North-West India) except for *C. parviflorum* and octoploid *S. glauca* (collected from Kasauli and Solan hills) and *G. tonglensis* which was collected from Gulmarg (Kashmir). The inflorescences at different stages of development were fixed in FAA. The spikelets were dehydrated in ethyl alcohol tertiary butyl alcohol series and embedded in paraffin wax. Sections were cut varying in thickness from 6-10 μm . The safranin-fast green combination and Heidenhain's Hematoxylin were used for staining purposes. Voucher specimens have been deposited in the herbarium of the Department of Botany, Panjab University, Chandigarh.

Observations

Ovary and Ovule

The ovary has a long stalk in *A. donax* (figure 2), *A. adscensionis* (figures 24, 26) and *G. tonglensis* (figure 25) but it is sessile in other taxa. In *A. adscensionis*, the ovary shows a bulge due to asymmetrical position of the stalk (figures 24, 26). The ovary is obovate in *A. donax* and *G. tonglensis* while it is ovoid in other species. The ovary encloses a

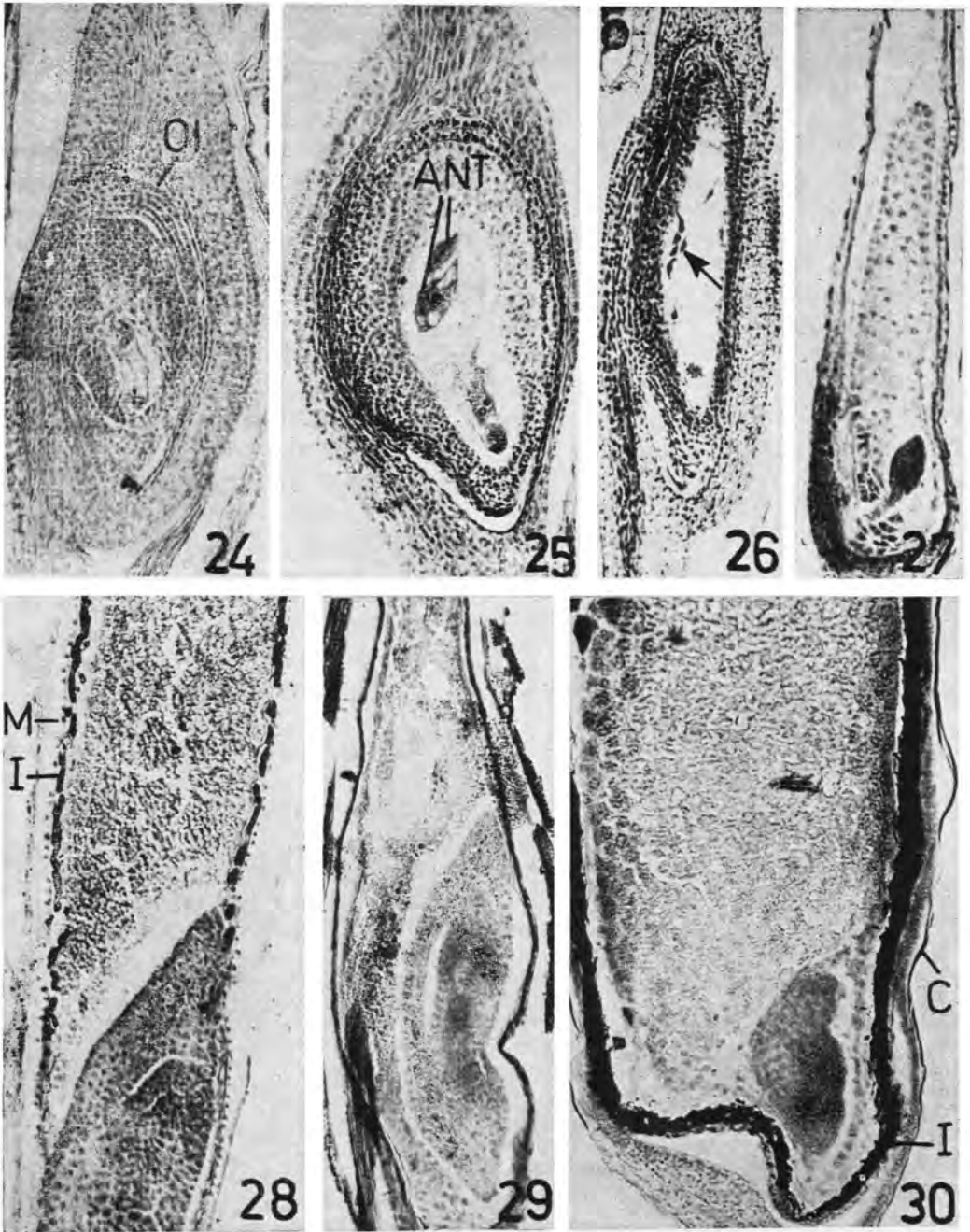
sessile, bitegmic, pseudo-crassinucellate and hemianatropous ovule (figures 1, 2, 24, 25). The ovule generally has a shape corresponding with that of the ovary.

The inner integument is formed first and it grows fast as compared with the outer integument (figures 9, 10). At the time of pollination it is 2 cell-layers thick except at the chalaza and micropylar region in *A. donax* (figure 2) and *A. adscensionis* where it has 3-5 layers of cells. The micropyle is formed by the inner integument in *A. donax*, *A. adscensionis*, *G. tonglensis*, *S. bengalense* and *S. glauca* but in other taxa it fails to grow beyond the level of the nucellus (figure 14). The inner integument degenerates after fertilization in species belonging to the tribes Andropogoneae, Paniceae and in *A. nepalensis* (figures 3,4,27, 29). In *A. adscensionis* (figure 28) and *G. tonglensis* (figure 30), the outer layer of the inner integument degenerates after fertilization but the cells of the inner layer show deposition of a darkly staining material and this layer persists in mature caryopsis.

The outer integument usually consists of 2-3 layers of cells but it becomes massive near the micropyle or near the chalaza in certain species, such as *A. adscensionis*, *C. biflorus* (figure 1) and *S. bengalense*. It covers about one-third of the ovule in species of the tribes Andropogoneae, Paniceae, *A. nepalensis* and

Figures 8-23 Development of ovule, female gametophyte and embryo. 8, 9, 14, *Arundinella nepalensis*; 10, 13, 23; *Aristida adscensionis*; 11, 15, *Glyceria tonglensis*; 12, *Setaria verticillata*; 16-18, *Capillipedium parviflorum*; 19, 20, *Saccharum bengalense*; 21, *Setaria glauca*; 22, *Setaria intermedia*

8, Ovule at archesporial cell stage; 9, 10, Megaspore mother cell stage; 11, 12, Megasporogenesis; 13, Functioning megaspore; 14, 15, Ovule structure at the organized embryo sac stage; 16, Degenerating sporogenous tissue and 2 aposporic embryo sac initials; 17, One binucleate and 3 uninucleate aposporic embryo sacs; 18, Three aposporic embryo sacs; 19-23, Stages in the development of embryo (ANT, antipodal cell; CC, central cell; DO, dorsal ovary wall; ENUC, enlarged nucellar cell; FM, functioning megaspore; II inner integument; OI, outer integument; PN, polar nucleus; cb, basal cell; ca terminal cell; 1, 1', tiers of the terminal cell; m, ci, n, n', o, p, products of the basal cell)



Figures 24-30 Ovule structure, embryo, endosperm and pericarp. 24, 26, 28, *Aristida adscensionis*; 25, 30, *Glyceria tonglensis*; 27, 29, *Arundinella nepalensis*; ANT, antipodal cell; C cuticle; I' inner layer of the inner integument; L. s., longitudinal section; M, meristematic layer); 24, 25, L. s. of the mature ovule passing through the chalaza ($\times 160$); 26-30, L. s. of the caryopses at different stages of development. 26, 28 ($\times 160$); 27, 29, 30 ($\times 120$)

G. tonglensis (figures 1, 14, 15), about half of the ovule in *A. adscensionis* (figure 24) while it is fully developed in *A. donax* (figure 2). The outer integument degenerates after fertilization in all the taxa studied here.

The nucellar epidermis near the micropyle undergoes 2-3 periclinal divisions and forms a parietal tissue in species of Andropogoneae, Paniceae and in *A. nepalensis* (figure 1, 14). The apical cells in *A. nepalensis* (figure 14), *C. biflorus* (figure 1), *C. parviflorum*, *S. glauca* and *V. zizanioides* become conspicuous owing to their large size, dense contents and prominent nuclei. There is usually only one periclinal division in the nucellar epidermis in *A. donax* while there is one or rarely two periclinal divisions in *A. adscensionis* and *G. tonglensis* (figure 15). After fertilization, the embryo and endosperm grow at the expense of the nucellus and in mature caryopsis the nucellus gets completely absorbed (figures 3-7, 26-30).

At the time of pollination, the ventral ovary wall is thicker than the dorsal ovary wall (figures 1, 2, 24, 25). The dorsal ovary wall has an outer epidermis, an inner epidermis lining the loculus and a variable number of middle layers in the distal region, in the region opposite to the chalaza and near the base (figures 1, 2, 24, 25, table 1). In *A. donax*, the cells of the outer epidermis show deposition of a darkly staining material (figure 2). The dorsal ovary wall is generally thicker at the top and near the base than in the region opposite to the chalaza in species of Andropogoneae, Paniceae and in *A. nepalensis*. In *A. adscensionis* (figure 24), *A. donax* (figure 2) and *G. tonglensis* (figure 25), the dorsal ovary wall is thick at the distal end and becomes narrow towards the base of the ovary. The dorsal ovary wall is, however, thicker in

A. adscensionis than in *A. donax* and *G. tonglensis*. The locular epidermis of the ovary wall starts disorganizing when the ovule is mature (figures 2, 15). The innermost middle layer shows meristematic activity keeping pace with the increasing size of the caryopsis. Except this meristematic layer, the cells of which develop thick walls, other middle layers undergo degeneration (figure 28). In mature caryopsis only the compressed remains of the meristematic layer and the outer epidermis are traceable (figure 7). The outer walls of the cells of the

Table 1 Structure of the dorsal ovary wall

Tribe, genus and species	No. of middle layers in the distal region	No. of middle layers in the region opposite to the chalaza	No. of middle layers near the base
ANDROPOGONEAE			
<i>Capillipedium parviflorum</i>	4	2	3
<i>Imperata cylindrica</i>	3	2	3
<i>Iseilema prostratum</i>	5	3	6
<i>Saccharum bengalense</i>	6	5	4
<i>Vetiveria zizanioides</i>	7	4	6
PANICEAE			
<i>Brachiaria distachya</i>	4	2	3
<i>Cenchrus biflorus</i>	6	3	4
<i>Paspalidium flavidum</i>	5	3	4
<i>Setaria verticillata</i>	3	2	4
<i>Setaria intermedia</i>	3	2	4
ARISTIDAE			
<i>Aristida adscensionis</i>	9	6	5
ARUNDINEAE			
<i>Arundinella nepalensis</i>	3	2	3
ARUNDINELLEAE			
<i>Arundo donax</i>	4	3	2
GLYCERIEAE			
<i>Glyceria tonglensis</i>	6	2	3

outer epidermis develop a thick cuticle in *G. tonglensis* (figure 30).

Megasporogenesis and female gametophyte

There is a hypodermal archesporial cell in the nucellus which increases in size and behaves as the megaspore mother cell (figures 8-10). In 2 plants of *A. donax* grown in the Panjab University Botanical Garden, the megaspore mother cell fails to divide leading to seed sterility (figure 2, arrow). Two megaspore mother cells have been occasionally observed in *S. bengalense* but they are of frequent occurrence in *V. zizanoides*. The megaspore mother cell undergoes meiosis so as to form a linear or T-shaped tetrad of megaspores (figures 11, 12) except in *A. nepalensis*, where the upper dyad degenerates as such. With the exception of *C. parviflorum*, the chalazal megaspore function and forms an 8-nucleate Polygonum type of embryo sac (figures 13-15). In *C. parviflorum*, the products of meiosis degenerate in most of the ovules and 4-nucleate unreduced embryo sacs are formed from the nucellar cells (figures 16-18) as in other aposporous apomicts of the tribe Andropogoneae. Due to the occurrence of 2 megaspore mother cells in *V. zizanoides* many ovules show 2 megaspore tetrads, one of which, however, degenerates. Enlargement of a nucellar cell adjoining the megaspore mother cell or many cells near the chalazal end of the embryo sac, has been observed in *A. nepalensis* (figures 9, 14). Due to the functioning of many nucellar cells in *C. parviflorum* a number of ovules possess multiple embryo sacs. Twin embryo sacs have also been occasionally observed in *A. nepalensis*, *I. cylindrica* and *V. zizanoides*.

The mature embryo sac consists of an egg, 2 synergids, a binucleate central cell and 3 antipodal cells (figures 14, 15).

The antipodal cells do not proliferate further in *S. glauca* and *G. tonglensis* (figure 25) but they become hypertrophied and in *S. glauca* each cell contains 1-4 nuclei. Secondary multiplication of the 3 antipodal cells leads to the formation of 5-8 cells in *B. distachya*, *I. cylindrica*, *I. prostratum*, *P. flavidum*, *S. bengalense*, *S. verticillata* (figure 4) and *V. zizanoides*, about 18 cells in *A. nepalensis* and *A. adscensionis*, 22-25 cells in *C. biflorus* and 23-27 cells in *S. intermedia*. The antipodal cells do not show any change in position after fertilization in species of the tribes Andropogoneae, Paniceae and in *A. nepalensis* (figures 3, 4) but in *A. adscensionis* (figure 26, arrow) and *G. tonglensis* they get displaced to a lateral position near the chalaza. The antipodal cells degenerate at 2 or 4-celled stage of the proembryo in *A. nepalensis*, *A. adscensionis* and *V. zizanoides* but they persist even up to the early globular proembryo stage in other species (figure 3).

The embryo sac before fertilization is oblong or spindle-shaped and it lies parallel to the longitudinal axis of the ovule except in *S. intermedia* where it shows a prominent curvature towards the chalaza. Before initiation of wall formation in the endosperm, the embryo sac has a maximum diameter in the middle or in the micropylar half in members of the tribes Andropogoneae, Paniceae and in *A. nepalensis* (figures 3, 4); it is oblong in *A. adscensionis* but is obovate in *G. tonglensis*.

Fertilization, Endosperm and Embryo

The egg apparatus consists of a globular egg, and 2 synergids which are usually narrow at the micropylar end but broad at the chalazal end. The 2 polar nuclei meet somewhere in the middle of the central cell but come to lie just above the egg apparatus before fertilization.

The synergids show signs of disorganization before the entry of the pollen tube into the embryo sac. The pollen tube seems to enter through the micropyle into one of the synergids as evidenced by its denser contents. Syngamy and triple fusion have been observed in *S. glauca* and *B. distachya* and result in the formation of zygote and the primary endosperm nucleus. In *C. parviflorum*, as the mode of reproduction is mostly aposporic, the unreduced egg develops parthenogenetically but the fertilization of the polar nucleus is essential for the formation of endosperm.

The primary endosperm nucleus divides earlier than the zygote and the first few divisions are free nuclear. The endosperm nuclei arrange themselves along the periphery of the embryo sac (figures 3, 4). Wall formation in the endosperm takes place first around the proembryo and then progresses towards the chalazal end. The endosperm becomes completely cellular at globular stage of the proembryo (figure 27). There is a single aleurone layer and aleurone transfer cells get differentiated in the region of ovular attachment (figures 5, 6, 27).

The early development of the embryo could not be studied in *A. donax*, *A. nepalensis*, *I. cylindrica* and *I. prostratum* because of a poor seed set. The development of the embryo in other taxa (figures 19-25) is essentially similar to that described in other members of the family. However the octant proembryo is filamentous in *A. adscensionis* (figure 23) as compared with other species, where it is globular in shape. Another feature which seems to be of interest is the shift in the attachment region of the globular proembryo towards the chalaza as a result of which the proembryo temporarily comes to lie at right angles to the longitudinal axis of the caryopsis in *C.*

blflorus, *P. flavidum*, *Setaria* spp. (figures 5, 6) and in *A. nepalensis* (figure 27). The formation of nucellar embryos near the micropyle has been occasionally observed in *B. distachya*. The mature embryo is more than half the length of the caryopsis in members of the tribes Andropogoneae, Paniceae and in *A. nepalensis* (figure 29) and it is of the Panicoid type. In *A. adscensionis* and *G. tonglensis*, the mature embryo is less than half the length of the caryopsis and it is of the Arundinoid-Danthonioid type and Festucoid type respectively.

Caryopsis

The mature caryopsis is a short biconvex structure (figure 29), 1.5-2.0 mm long except in octoploid *S. glauca* where it is about 3.0 mm long. In *A. adscensionis* (figure 28), the caryopsis is long and slender and about 4.0 mm long.

Discussion

Table 2 presents a comparison of embryological features of the tribes Andropogoneae, Paniceae, Arundinelleae, Aristideae, Arundineae, Glycérieae, Stipeae and tribes of the subfamilies Eragrostoidae and Festucoideae. The available data suggests that the tribes Andropogoneae, Paniceae and Arundinelleae are very closely related to each other as they show a cluster of features not met within the tribes Aristideae, Arundineae, Glycérieae, Stipeae, and Agrostideae, Aveneae, Brachypodieae, Bromaeae, Festuceae, Phalarideae, Triticeae (subfamily Festucoideae) as well as Chlorideae, Eragrostaeae, Sporoboleae and Zoysiaceae (sub-family Eragrostoidae). These features are lack of differentiation in the inner layer of the inner integument, poorly developed outer integument, occurrence of 2-3 periclinal divisions in the nucellar epidermis near the micropyle, mature

embryo sac mostly lying parallel to the long axis of the ovule, no change in the position of antipodal cells after fertilisation, the embryo sac, before initiation of wall formation in the endosperm, having a maximum diameter in the middle or in the micropylar half, the dorsal ovary wall at the time of pollination being

thicker at the top and near the base of the ovary than in the region opposite to the chalaza, presence of a cytoplasmically dense layer subjacent to the locular epidermis of the ovary wall, the mature embryo being more than half the length of the caryopsis and of the Panicoid type of Reeder (1957). The above data are

Table 2 Comparison of embryological features of the various tribes

Feature	Andro	Pani	Arund	Arist	Arund	Glye	Stip	Era	Fest
Differentiation in the inner layer of the inner integument after fertilization]	-or R ⁺	-	-	+	+	+	-or+	+	+or-
Poorly developed outer integument	+	+	+	+	-	+	-	-	-
Two to three periclinal divisions in the nucellar epidermis near the micropyle	+	+	+	-	-	-	-	-	-
Mature embryo sac showing a prominent curvature towards the chalaza	-	-or R ⁺	-	-	-	-	-	+or R ⁻	-or R ⁺
Displacement of antipodal cells to a lateral position after fertilization	-	-	-	+	×	+	+	+or R ⁻	+
Embryo sac having a maximum diameter in the middle or in the micropylar half before initiation of wall formation in the endosperm	+	+	+	-	×	-	-	-	-
Dorsal ovary wall thicker in the distal region than in the region near the base of the ovary	-	-	-	+	+	+	+	+	+
Cytoplasmically dense layer subjacent to the locular epidermis of the ovary wall	+	+	+	+	+	+	+	-	+
Mature embryo more than half the length of the caryopsis	+	+	-	-	-	-	-	-	-
Epiblast of the embryo	-	-	-	-	-	+	-	+	+
Mature caryopsis long and slender	-	-	-	-	+	-	-	-	-

—, absent; R⁻, rarely absent +, present; R⁺, rarely present X, not known;

Andro, Andropogoneae; *Pani*, Paniceae; *Arundi*, Arundinelleae; *Arist*, Aristideae; *Arund*, Arundineae; *Glye*, Glyceriaceae; *Stip*, Stipeae; *Era*, Eragrostoideae; *Fest*, Festucoideae.

further supported by the fact that these tribes have small or medium size chromosomes (Setbbins 1956, Mehra et al. 1968), Panicoid underground organs of the seedlings (Hoshikawa 1969) and tropical or subtropical distribution. The tribes Andropogoneae, Paniceae and Arundinelleae, however, differ from each other in respect of the most common basic chromosome number i.e. $x=5$, 10 in Andropogoneae, $x=9$ in Paniceae $x=10$ (7.9) in Arundinelleae (cf. Mehra et al 1968).

Aristida, with about 209 species, is the only genus in the tribe Aristideae, distributed in the warmer regions of the world (Gould 1968). Aristideae has been regarded as a tribe of the subfamily Arundinoideae by Stebbins and Crampton (1961) while Gould (1968) has placed it in the subfamily Eragrostoideae. The Aristideae and Arundineae differ from each other in respect of the extent of development of the outer integument and thickness of the dorsal ovary wall in the distal region. However, the structure of the embryo in both these tribes is of the Arundinoid-Danthonioid type (Reeder 1957). The Aristideae share some important embryological features with tribes of the subfamilies Eragrostoideae and Festucoideae (see table 2). The tribe Aristideae can be distinguished from those of the subfamily Eragrostoideae in certain features, such as the presence of 1 or rarely 2 periclinal divisions in the nucellar epidermis near the micropyle, poorly developed outer integument, position of the embryo sac at the time of pollination, presence of a cytoplasmically dense layer subjacent to the locular

epidermis of the ovary wall and the number of middle layers in the distal region of the ovary wall. The structure of the embryo, long and slender fruit, leaf-anatomy, underground organs of the seedlings and size of chromosomes and basic chromosome number are other features by which Aristideae can be distinguished from the tribes of the subfamilies Eragrostoideae and Festucoideae (see Brown 1958, Hoshikawa 1969, Mehra et al. 1968, Reeder 1957, Stebbins 1956). *Arundo donax* of the tribe Arundineae has been found to be seed sterile. The tribe resembles other festucoid grasses in having the well developed outer integument, rare occurrence of periclinal divisions in the nucellar epidermis near the micropyle and structure of the dorsal ovary wall (see table 2). The members of this tribe have retained apparently primitive chromosomal condition of a basic number of $x=6$ or 12. The structure of the embryo is of the Arundinoid-Danthonioid type as in the Aristideae but the two tribe differ in respect of the internal structure of the leaf (Brown 1958).

The tribe Glycerieae has all the embryological features met within the true festucoid grasses except the poorly developed outer integument. The structure of the embryo, leaf-anatomy and underground organs of the seedlings are also of the Festucoid type (see Brown 1958, Hoshikawa 1969, Reeder 1957). The chromosomes are small with the basic number $x=10$ unlike the true festucoids where the chromosomes are large with the basic number $x=7$ (Mehra et al. 1968).

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