EMBRYOLOGICAL STUDIES IN THE BROMELIACEAE


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ABSTRACT

Embryological characters of *Lindmania penduliflora* is presented. The tapetum is of the secretive type and the cells are binucleate. Microspore mother cells divide in a successive manner resulting in isobilateral, tetrahedral or linear tetrads. Mature pollen grain is two-nucleate. Division of the single hypodermal archesporial cell results in a primary parietal cell and a megaspore mother cell. Meiotic division of the latter results in a linear tetrad. The chalazal megaspore of the tetrad develops into a normal type of eight-nucleate embryo-sac.

Endosperm is of the helobial type. The chalazal endosperm nucleus may divide, with or without wall formation, either synchronised with the division of the micropylar endosperm nucleus or else earlier.

ZUSAMMENFASSUNG


Embryological literature on the family Bromeliaceae is neither very plentiful nor detailed enough to allow thorough discussion. Since the treatise of Schnarf (1931) two more papers have been published. The report of Beck and Horton (1932) deals mainly with the cytology and adds a few embryological data on some species of *Bromus*. The work of Guttenberg and Riebe (1957) pertains to embryogeny of certain species of *Pitcairnia*. Since the available data are either contrary to each other or incomplete, the embryological investigation of the family will here be taken up: the present contribution is the first of a series.

*Lindmania penduliflora*, native of Peru, was in flowering during the month of April in the Botanical Gardens of the Freie Universität, Berlin-Dahlem. Material was collected in May 1965 and fixed in FPA (Formalin-Propionic-Acid-Alcohol). The slides were prepared following the customary microtechnical methods using haematoxylin stain.

**Observations**

*Microsporogenesis and male gametophyte.*—In the anther some of the cells of the hypodermal layer divide periclinally giving rise to the outer primary parietal layer and the inner primary sporogenous tissue. The former, by further divisions in a similar plane, results in two (sometimes three) wall layers limited internally by the tapetal layer (Pl. III, Fig. 1). The cells of the tapetal layer are larger in size and have dense cytoplasm. While the microspore mother cells are in diakinesis stage, the tapetal cells become binucleate (Arrow in Pl. III, Fig. 2) and degenerate as such at the time the microspores are separating from the tetrad configuration. At about this stage the wall subjacent to epidermis develops fibrous thickening.

The primary sporogenous cells divide and function as microspore mother cells. These cells divide meiotically in a successive manner (Pl. III, Fig. 3). Bilateral as well as decussate arrangements of tetrads are common. Very occasionally linear tetrads are also observed (Pl. III, Figs. 4, 5, 6).

In the development of the microspore into a two-nucleate mature pollen grain (Pl. III, Fig. 7), no significant variation is found from that which has been described for other Members of Bromeliaceae (1932).

*Megasporogenesis and female gametophyte.*—As the microspore mother cells are in diakinesis stage, the ovular primordia make their appearance on the placenta. The primordium arises as a small knob, bending down as it grows. Slightly away from the apex of the young primordium the inner integument makes its appearance. The outer integument arises below the inner integument.
A single hypodermal cell can easily be distinguished as the archesporial cell by its large nucleus and dense cytoplasm. It divides periclinally to form the primary parietal cell and the megaspore mother cell (Pl. III, Fig. 8). At this stage the ovule is anatropous; the outer and the inner integuments are each of two layers; in longissection the parietal cells appear as two by virtue of anticlinal division of the primary parietal cell. The megaspore mother cell divides meiotically resulting in a linear tetrad (Pl. III, Fig. 9). The chalazal functioning megaspore increases in size, divides (Pl. III, Fig. 10) and develops into a normal type of eight-nucleate embryo-sac.

Endosperm.—The primary endosperm nucleus divides before the zygote. The division of the nucleus is immediately followed by wall formation. It results in a small chalazal endosperm chamber and a large micropylar endosperm chamber (Pl. IV, Fig. 11). The nucleus of the latter undergoes repeated free nuclear divisions. The nuclei, embedded in a thin film of cytoplasm, occupy the periphery of the chamber.

Even at an early stage there is an accumulation of cytoplasm and few nuclei at the chalazal end. These nuclei do not divide synchronously with the divisions of the nuclei in the upper half of the same micropylar endosperm chamber. Soon partition walls are laid, resulting in uninucleate cells with dense cytoplasm, which top over and around the chalazal endosperm cell (Pl. IV, Fig. 12). These cells can be observed even at a very late stage. Cell wall formation in the rest of the micropylar endosperm takes place when the proembryo is spherical in shape.

The chalazal endosperm cell remains about the same size and without any division of the nucleus. It degenerates earlier than in many of the taxa which show helobial type of endosperm.

Although what has been described above is the norm, one can observe variations. Just prior to the division of the micropylar endosperm nucleus, the chalazal endosperm nucleus divides and exhibits two-nucleate condition (Pl. IV, Fig. 13). In a few cases it is present as two distinct cells in longissection (Pl. IV, Fig. 14). Whatever may be the number of nuclei or cells that constitute the chalazal endosperm chamber, neither the nuclei nor the cells exhibit the morphological changes that have been observed in the basal apparatus of Hydrocharitaceae (1963). Text-Figure 1 shows a schematic representation of the ontogenetic variability in the formation of the helobial endosperm.

The three antipodal cells remain for sometime as uninucleate cells which later degenerate,
Seedcoat.—At the time of fertilization each integument is two layered. As the development proceeds, the inner integument becomes three-layered. The hardened nature of the seed is mainly due to the thickening of the outer layer of the inner integument; the two inner layers degenerate. The inner layer of the outer integument gradually disintegrates while in the persisting outer layer the radial and inner walls develop thickenings.

DISCUSSION

As pointed out earlier, the embryological literature on the family Bromeliaceae is incomplete. Although microsporogenesis and development of male gametophyte follow more or less a similar pattern in the taxa so far investigated, there are variations in megasporogenesis and female gametophyte.

The primary archesporial cell gives rise to the primary parietal cell and the megaspore mother cell. The division of the latter results in a linear tetrad. Of the four megaspore mother cells thus formed, the chalazal one develops into the normal type of eight-nucleate embryo-sac. As reported by Beck and Horton (1932), the parietal cell is absent in Bromus rubens; in the three megaspores of the linear tetrad in B. marginalis, the apical megaspore is binucleate. There are 5–8 antipodal cells.

After fertilization the primary endosperm nucleus divides earlier than the zygote. The work of Billings (1904) as interpreted by Schnarf (1931) has led Wunderlich (1959) and Hamann (1964) to conclude that Tillandsia usneoides exhibits helobial type of endosperm. After a decade, Birge (1911) reported nuclear endosperm in T. recurvata. Swamy and Parameswaran (1963), after having discussed the observations of Billings (1904), Birge (1911) and Tischler (1913), came to the conclusion that "only a thorough reinvestigation should settle the issue". Beck and Horton (1932) describe that "the
endosperm nucleus divides rapidly and some of the resulting nuclei pass around the antipodals to the chalazal end of the embryo-sac". From this account it may be inferred that, in *Bromus*, nuclear type of endosperm, with accumulation of its contents, at the chalazal end, is present. Their Fig. 28 strengthens this view.

In *Lindmania* the development of endosperm is of the normal helobial type. The micropylar endosperm exhibits accumulation of free nuclei and dense cytoplasm at the chalazal end which overtops and surrounds the chalazal endosperm chamber. This accumulation soon becomes cellular, whereas the rest of the micropylar endosperm chamber remains nuclear till the embryo attains more or less the spherical shape. The chalazal endosperm chamber remains as a uninucleate cell.

There are, however, deviations from the norm. The nucleus in both the chambers divides simultaneously or division may be earlier in the chalazal endosperm chamber. In other cases still, the early division of the chalazal endosperm nucleus is followed by wall formation. The 5–8 antipodal cells, described by Beck and Horton (1932), may be the three antipodal cells and the cells of the chalazal endosperm chamber. What they have narrated as "the resulting nuclei pass around the antipodals" may be the chalazal accumulation of the micropylar endosperm chamber.

Attention may be drawn to another genus of Bromeliaceae, *Pitcairnia funkiana* (a detailed account of which is under preparation) where the helobial type of endosperm is met with too. The division of the chalazal endosperm nucleus is earlier than that in the micropylar endosperm chamber.

In literature there are cases available where the nucleus of the chalazal endosperm chamber divides, with or without wall formation, prior to nuclear division in the micropylar endosperm chamber. As early as 1922, Brenner reported such a case in certain species of Juncaceae. He mentioned about the basal endosperm with distinct nuclei, probably due to amitosis, in *Juncus compressus* (His Plate Fig. 24).

It will not be out of place to mention the helobial type of endosperm reported in Philydraceae (1961, 1962, 1963, 1964 and 1966). Division of the chalazal endosperm nucleus, with or without wall formation, occurs prior to the division of the nucleus in the micropylar endosperm chamber. According to Kapll and Walia (1965) the cell formation commences at the chalazal end of the micropylar chamber, becomes partitioned into 2–6 cells, which then degenerate. Hamann, in his personal communication, observed that in *Philydrella* also the chalazal endosperm chamber becomes cellular.
earlier than the micropylar endosperm chamber. Swamy and Parameswaran (1963), on the other hand, feel that if wall formation occurs in the chalazal endosperm cell, it is significantly belated.

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FIGS. 1-10
FIG. 11-14
EXPLANATION OF PLATES

PLATE III

FIG. 1. Differentiation of wall, tapetal and sporogenous layers, ×1,200.
FIG. 2. Binucleate tapetal cell (shown by arrow) and microspore mother cell, ×1,200.
FIG. 3. Meiotic division of the microspore mother cells, ×1,300.
FIGS. 4–6. Tetrads of microspores. Fig. 4, ×1,300; Figs. 5, 6, ×860.
FIG. 7. Two-nucleate microspore. (Figs. 3–7. Same magnification), ×1,400.
FIG. 8. Young ovule with the primary parietal cell and the sporogenous cell, ×800.
FIG. 9. Linear tetrad, ×1,200.
FIG. 10. Four-nucleate embryo-sac, ×1,200.

PLATE IV

FIG. 11. After the first division of the primary endosperm nucleus, ×800.
FIG. 12. Nuclei in the chalazal accumulation of the micropylar endosperm in division, ×850.
FIG. 13. Binucleate chalazal endosperm cell, ×1,250.
FIG. 14. Two-celled chalazal endosperm, ×3,900.