

Investigations on the Post-Fertilization Development and Seed and Fruit Wall of *Prenanthes brunoniana* Wall. (Asteraceae)

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Prenanthes brunoniana の胚・胚乳および種皮形成

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Investigations on the post-fertilization development and seed and fruit wall in embryologically unknown taxon, *Prenanthes brunoniana* Wall. (Asteraceae) have been described. Fertilization is porogamous. Endosperm development is of the Nuclear type. Cellularisation occurs after the two-nucleate stage. Proembryonal tetrad is T-shaped and the embryogeny corresponds to the Senecio variation of the Asterad type. Cells of the endothelium degenerate in the mature seed. Seed coat is represented by the outer epidermis, hypodermal layer and the degenerated remains of the integument. It lies compressed between the pericarp and the persistent layer of endosperm. Pericarp is 4–6 layered and shows an apical plate and a nectary disc at the upper end of the fruit. Dermal originated pappus is biseriate, thick-walled and shows pits in the lower portion of its central canal.

The only embryological study on the genus *Prenanthes* is that of Sood and Thakur (1985) who described the development of male and female gametophytes and integument initiation in *Prenanthes brunoniana*. So far there exists no work on the study of post-fertilization events and seed and fruit wall of *Prenanthes*, and the present investigation was undertaken to fill this gap.

mature achenes of *Prenanthes brunoniana* Wall. were collected from Fagu and Summer Hill (Shimla District) and fixed in formalin-acetic-alcohol. Customary methods of dehydration in tertiary butyl alcohol series and embedding in paraffin wax were followed. Microtome sections cut between 10–14 μ m thickness were stained in safranin-fast green combination.

Materials and methods

The materials consisting of developing and

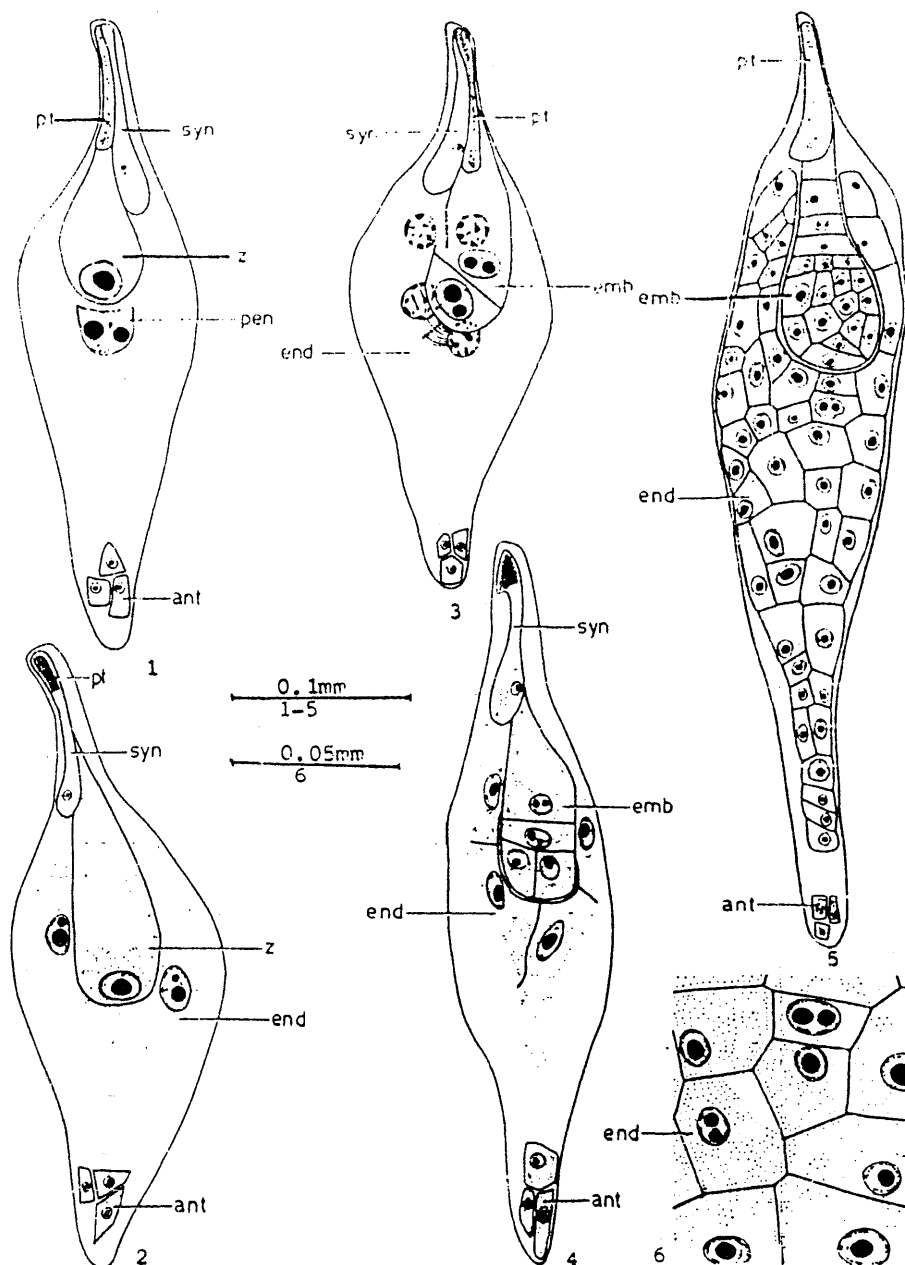
Observations

Fertilization and endosperm. The pollen tube

enters the embryo sac through the micropyle (Fig. 1) and discharges the two male gametes. One male gamete fuses with the secondary nucleus and the

other with the egg nucleus.

The primary endosperm nucleus divides earlier than the zygote (Fig. 2). The first division results

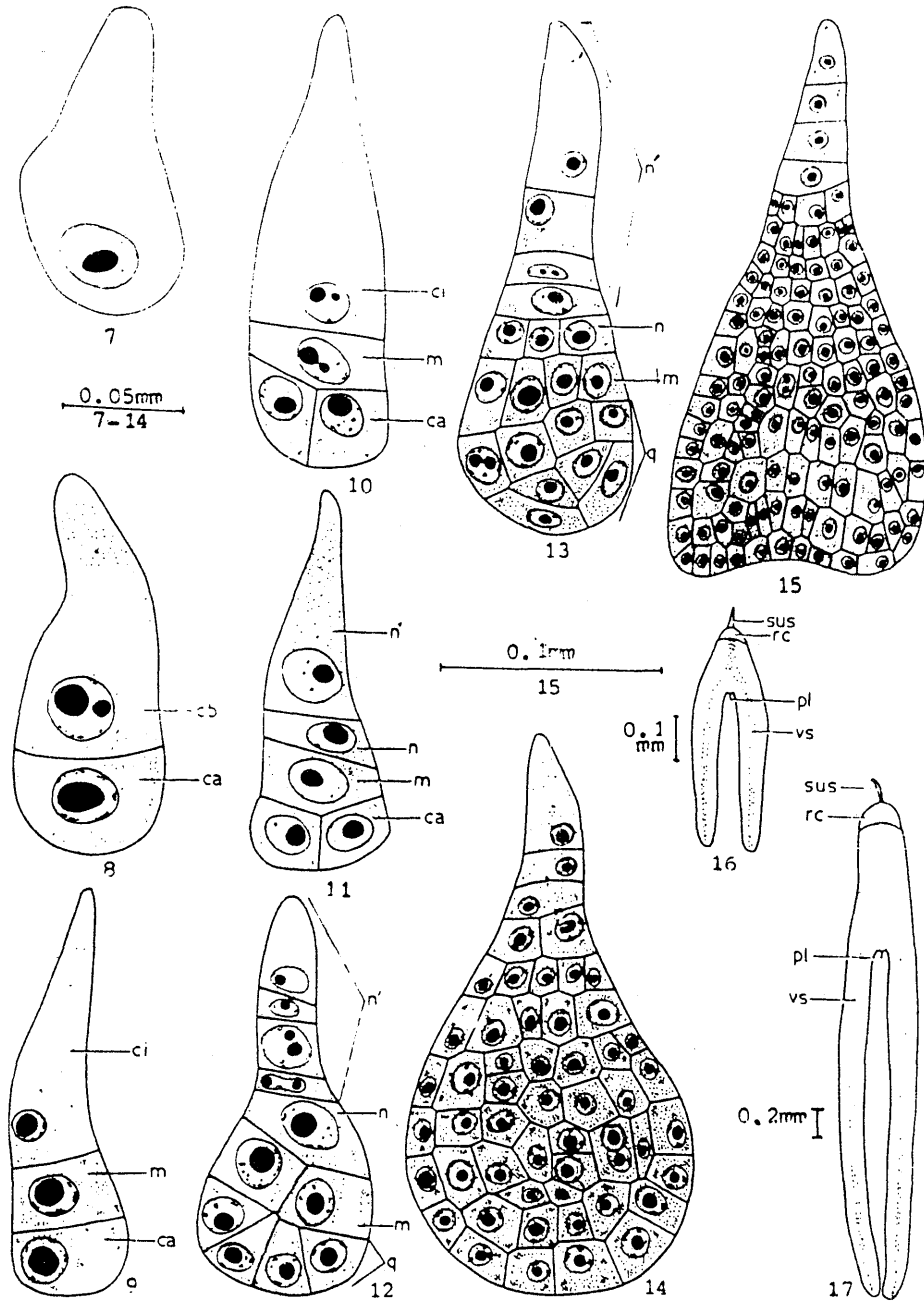


Figs. 1-6. *Prenanthes brunoniana*, endosperm (ant, antipodal cell; emb, embryo; end, endosperm; pen, primary endosperm nucleus; pt, pollen tube; syn, synergid; z, zygote). 1: Fertilized embryo sac showing zygote, primary endosperm nucleus, persistent pollen tube and antipodal cells. 2, 3: Same, showing the earlier free nuclear divisions of primary endosperm nucleus. 4, 5: Stages in the development of cellular endosperm. 6: Magnified portion of a part of endosperm tissue at globular embryo stage.

in the formation of two free nuclei (Fig. 2). Division of the two free nuclei is followed by cell wall formation (Fig. 3) giving rise to four-celled endosperm (Fig. 4). Subsequent divisions are

regularly followed by wall formation (Fig. 5).

In the beginning the endosperm cells are large, vacuolated and contain prominent nuclei (Fig. 6) but in the later stages most of the endosperm tissue



Figs. 7-17. *Prenanthes brunoniana*, embryogeny (pl, plumule; rc, root cap; sus, suspensor; vs, vascular supply). 7: Zygote. 8: Two-celled proembryo. 9: Three-celled proembryo. 10: T-shaped proembryonal tetrad. 11: Five-celled proembryo. 12: Quadrant stage. 13: Octant stage. 14: Globular embryo stage. 15: Heart-shaped embryo. 16: Small dicot embryo. 17: Mature dicot embryo.

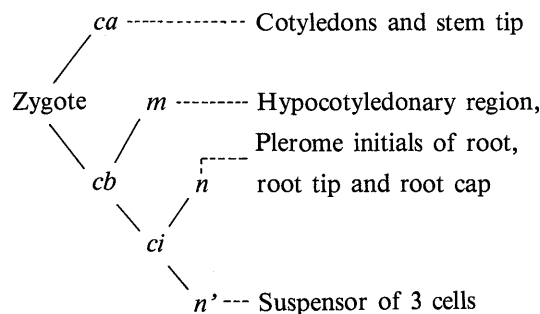
is absorbed by the developing embryo leaving only one or two layers of it in the mature seed (Figs. 22, 24).

Embryo. The zygote (Fig. 7) divides transversely resulting in a small terminal cell *ca* and a large basal cell *cb* (Fig. 8). *ca* divides vertically (Fig. 10) whereas *cb* undergoes a transverse division to form a suspensor initial cell *ci* and middle cell *m* (Fig. 9). The resulting proembryonal tetrad is T-shaped (Fig. 10).

The derivatives of tier *ca* divide by vertical division at right angles to the first to form a quadrant which then divide obliquely to form an octant (Fig. 13). The tier *m* divides vertically to form two cells (Fig. 12) which undergo another vertical division to give rise to four cells (Fig. 13). *ci* divides transversely into *n* and *n'* tiers (Fig. 11) of which the latter by further transverse divisions ultimately results in the 4-celled suspensor (Figs. 12–15).

Subsequent longitudinal and transverse divisions in the tiers *ca*, *m* and *n* result in the formation of mature embryo with two cotyledons, stem tip, a hypocotyle, a root cap and a suspensor (Figs. 14–17).

Destination of the individual cells of the proembryonic tetrad is given below in the schematic representation:



Embryo development conforms to the Senecio variation of the Asterad type of Johansen (1950).

Seed coat. At the four-celled proembryo stage the integument comprises 14–16 layers of cells including the endothelium (Figs. 18, 19). As development proceeds, the cells of the integument near the endothelium start degenerating and as a result endothelium gets detached from the rest of the integument (Fig. 22). Thus, the seed coat consists of the outer epidermis, hypodermal layer and the degenerated remnants of the integument (Fig. 22). It lies compressed between the pericarp and persistent layer of the endosperm (Fig. 22). Cells of the endothelium degenerate in the mature seed. The developing embryo consumes most of the endosperm and pushes it outward so that its peripheral layer comes to lie close to the remaining 2 or 3 layers of the integument (Figs. 20, 22–24).

Pericarp. At four-celled embryo stage the pericarp consists of 10–12 layers of cells (Figs. 18, 19). The outer epidermis is followed by a layer of large rectangular cells constituting the hypodermis. The remaining layers are parenchymatous, some of which disorganise at maturity to form schizogenous cavity (Figs. 23, 24).

In the mature fruit, the pericarp is 4–6 layered and cells of the outermost layer become highly cutinised (Fig. 22). In the region of ridges, the outermost layer and the underlying 4 or 5 layers become sclerotic (Fig. 24).

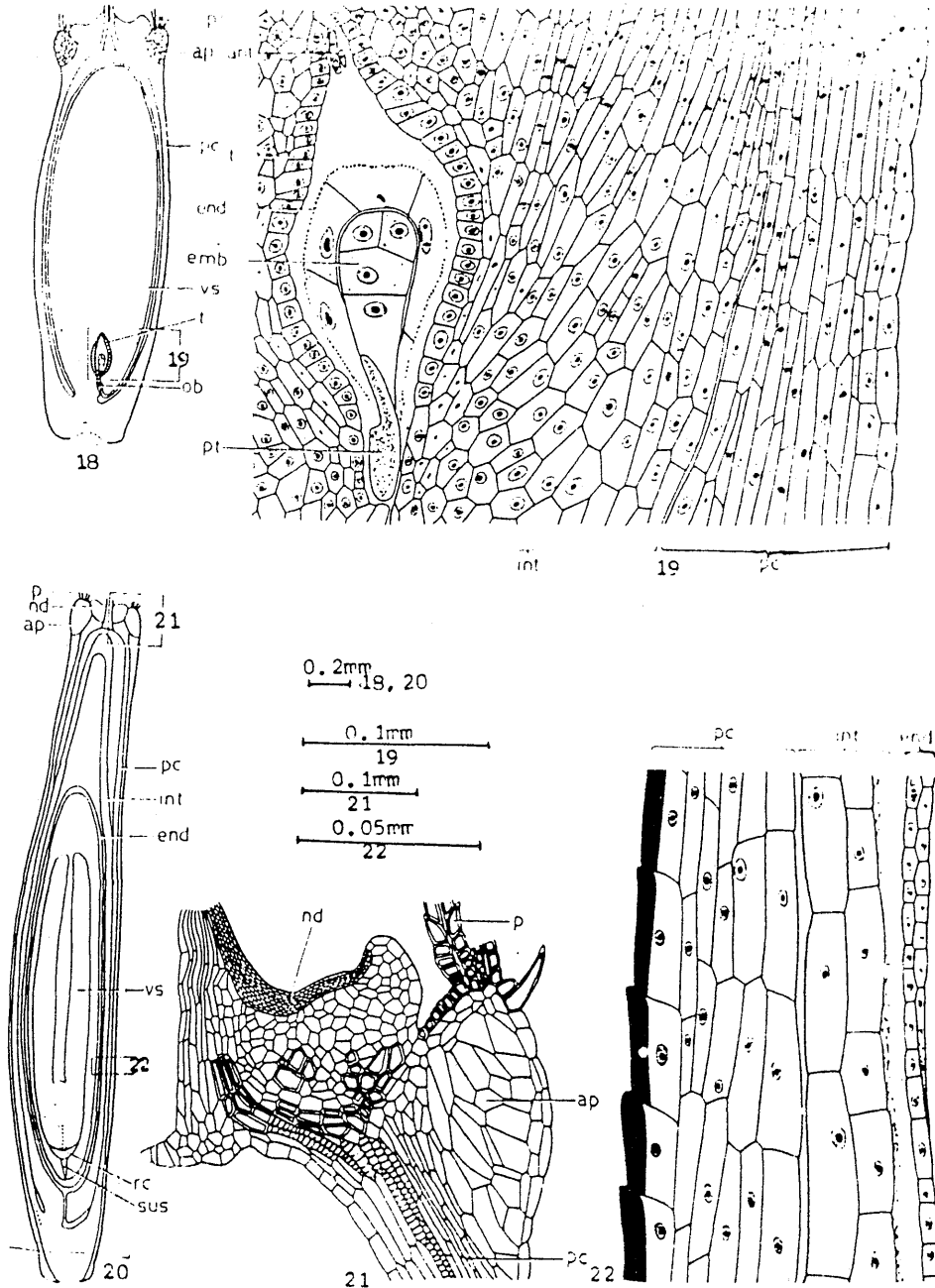
The pericarp has an apical plate and a nectary disc at the upper end of the fruit (Figs. 20, 21).

Pappus ontogeny. Two adjacent dermal cells become large and bulge outward (Fig. 25). Both these cells divide transversely (Fig. 26). These divisions continue resulting in the formation of a biseriate pappus (Fig. 27). At maturity the cells of pappus become thick-walled and elongated (Fig. 28) and the central canal in the lower portion of pappus shows pits (Fig. 28).

Discussion

Both Cellular and Nuclear types of endosperm are reported in Asteraceae but the reports of

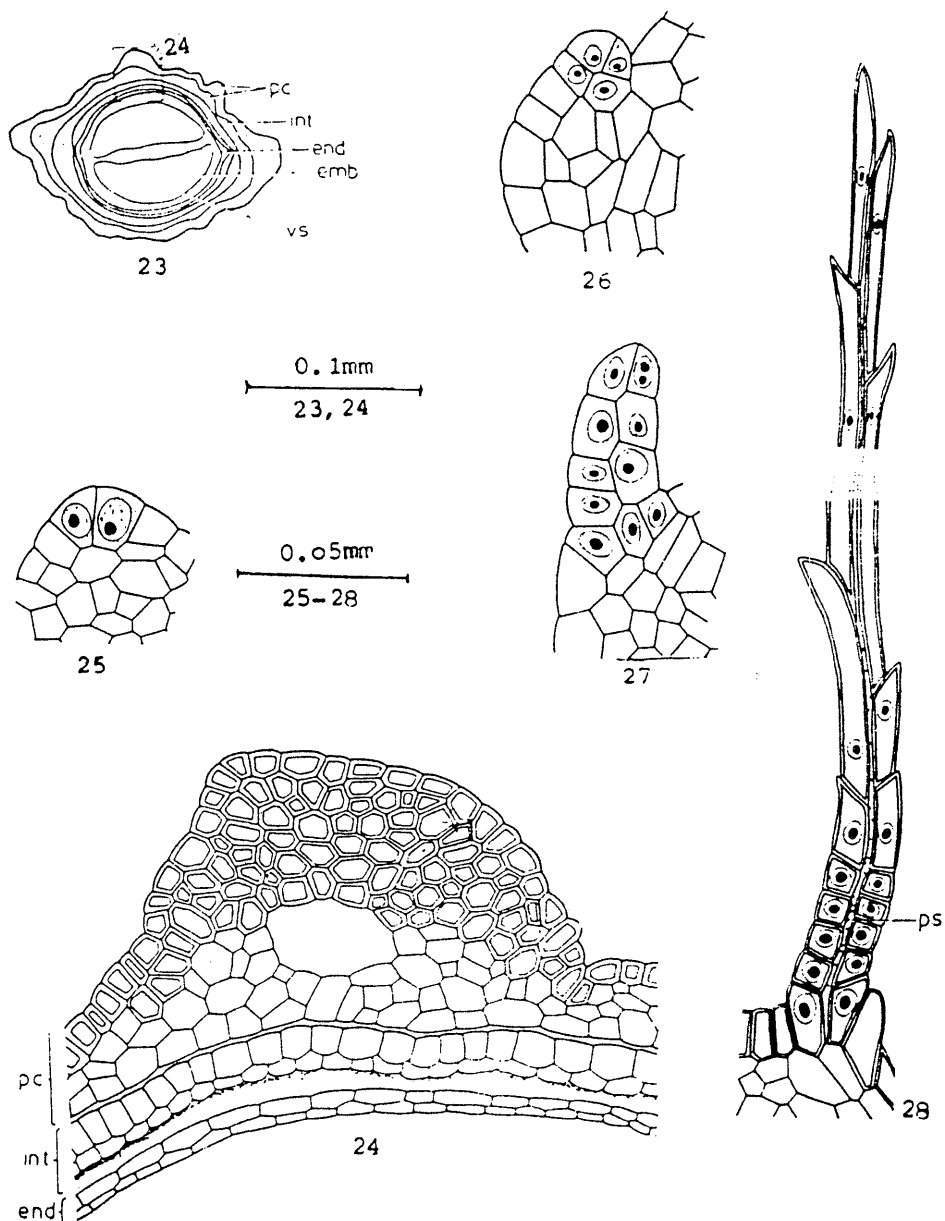
former type are more than the latter (Pullaiah 1984). In Nuclear type the process of cellularisation occurs at various stages of development. It



Figs. 18–22. *Prenanthes brunoniana*, Seed coat and pericarp (ant, antipodal cell; ap, apical plate; emb, embryo; end, endosperm; int, integument; nd, nectary disc; ob, obturator; p, pappus; pc, pericarp; pt, pollen tube; rc, root cap; sus, suspensor; t, integumentary tapetum; vs, vascular supply). 18: Outline (L.s.) of ovary at 4-celled proembryo stage. 19: Enlarged view of sector marked 19 in Fig. 17. 20: Outline (L.s.) of maturing fruit. 21: Enlarged view of sector marked 21 in Fig. 20. 22: Enlarged view of sector marked 22 in Fig. 20.

occurs after the first division of the primary endosperm nucleus in *Galinsoga ciliata*, *Siegesbeckia orientalis*, *Tridax lobata* (Harris 1935, Kapil and Sethi 1962b, Misra 1965) while in *Ainsliaea aptera*, *Guizotia abyssinica* (Chopra and Singh 1976, Kapil and Sethi 1962a) it occurs after the first

two free nuclear divisions. This is also true of *Prenanthes brunoniana* (present study). On the other hand, in *Blumea malabarica*, *Carduus acantoides*, *Carthamus tinctorius*, *Cirsium arvense*, *Crupina crupinastrum*, *Helianthus annuus*, *Onopordon acanthium* (Maheshwari Devi and Pullaiah



Figs. 23-28. *Prenanthes brunoniana*, pericarp and pappus ontogeny (emb, embryo; end, endosperm; int, integument; pc, pericarp; ps, pits). 23: T.s. (outline) of maturing fruit. 24: Enlarged view of portion marked 24 in Fig. 23. 25-28: Stages showing pappus ontogeny. Note the occurrence of pits in the central canal of pappus in Fig. 28.

1976, Newcomb 1973, Poddubnaya-Arnoldi 1931, Pullaiah 1979b) it commences at 16-nucleate stage.

Different views exist regarding the fate of integumentary tapetum (endothelium) and endosperm in the mature seeds of Asteraceae. Harris (1935), Jones (1927), Davis (1961), Maheshwari and Roy (1952), Pullaiah (1979a), Kapil and Sethi (1962a) and Padmanabhan (1962) recorded the occurrence of endosperm as 1 or 2 layers of cells in the mature seeds of *Lactuca sativa*, *Podolepis jaceoides*, *Tithonia rotundifolia*, *Tridax procumbens* and *T. trilobata*. The present study (*Prenanthes brunoniana*) also shows the same. Contrarily, Deshpande (1962a, b, 1964) reported that the endosperm is completely used up and the endothelium persists as a storage tissue in *Bidens biternata*, *Glossocardia bosvallia* and *Tridax procumbens*. Based upon the present study and the reports of earlier workers, it is clear that the observations of Deshpande (1962a, b, 1964) are incorrect.

The occurrence of schizogenous cavity in the pericarp has so far been reported in the tribes Eupatorieae, Helenieae and Heliantheae (Misra 1964, 1965, Pandey and Chopra 1979, Pullaiah 1982). *Prenanthes brunoniana* also shows this feature and forms the first report of its type for the tribe Lactuceae.

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要 旨

キク科フクオウソウ属の *Prenanthes brunoniana* の胚、胚乳、種皮形成を報告する。胚珠形成は Asterad type の *Senecio* variation である。胚乳形成は Nucled type であるが、2核の時期に細胞膜形成が始まり、4核期に膜形成が完成し、

その後は正常な細胞膜形成が繰り返される。種子が完成された時までの胚乳の行動には従来2説があった。ひとつは胚珠の成長に依って胚乳は完全に分解され、種皮の内層の endothelium が貯蔵組織の役割を持つという説と、もうひとつは種子

完成時にも胚乳は残り、貯蔵組織としての役割を保つという説である。*P. brunoniana* の場合や他の報告から判断して、胚乳が完全に消費されて、endothelium が貯蔵組織になるという説は誤りだと考えられる。