EMBRYOLOGICAL STUDIES ON THE HALORAGIDACEAE

II. *Laurembergia brevipes* Schindl. and a Discussion of Systematic Considerations

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Laurembergia brevipes is a small, glabrous herb. The inflorescence is a dichasial cyme and bears bisexual and pistillate flowers. The ovary is tetracarpellary, syncarpous, inferior and tetralocular, and contains a single pendulous ovule in each locule. The fruit is a ribbed nut. The anther is 4-lobed. It consists of an epidermis, fibrous endothecium, a middle layer and glandular tapetum with uninucleate cells. Cytokinesis is simultaneous. The tetrads are tetrahedral or decussate. The pollen grains are usually 5-porate and shed at the 3-celled stage. The ovules are anatropous, bitegminal and crassinucellar. The development of the embryo sac conforms to the Polygonum type. Fertilization is porogamous. The remnants of the antipodal cells persist up to the early stages of endosperm development. The endosperm is Nuclear, and embryogeny conforms to the Myriophyllum-variation of the Caryophyllad type. Like other members of the Haloragidaceae, the embryo shows prominent suspensor haustorium. The seed coat is thin and derived from the outer epidermis of the outer integument. The pericarp is thick and hard due to the presence of sclerenchymatous and tannin-filled cells. On the basis of embryological data, it is concluded that since *Haloragis*, *Laurembergia* and *Myriophyllum* differ substantially from *Callitriche*, *Gunnera* and *Hippuris*, the last three genera should be excluded from the Haloragidaceae.

Introduction

In the first paper of the series, Kapil and Bawa (1968) described the embryology of *Haloragis colensoi*. The present communication deals with the life history of *Laurembergia brevipes* and systematic position of the investigated genera of the family.

L. brevipes is a common weed found in wet places in the Western Ghats, Nilgiris and Pulney hills (altitude 1,800–2,100 m). Except for the work of Bley (1925) on *L. javanica*, there is no significant contribution on the embryology of this genus. Moreover, none of the previous investigators has studied fully the structure and development of the seed and fruit. All these aspects are discussed in detail in this paper.

Material and Methods

The material for this investigation was fixed in formalin-acetic-alcohol by Dr. R. N. Kapil of the Department of Botany, University of Delhi, from Kodaikanal, Madras, in June 1962. It was stored in 70 per cent ethanol,

dehydrated through the usual alcohol-xylene series and imbedded in paraffin wax of 56–58 °C melting point. Young and old fruits were softened in 20 per cent hydrofluoric acid (diluted in 70 per cent ethanol) for 8–10 days, and passed through the tertiary butyl-ethyl alcohol series before infiltration. Sections were cut 7–18 microns thick and stained with safranin and fast green. Erdtman's (1960) schedule was employed for making acetolysed preparations of pollen grains.

Observations

External morphology

L. brevipes is a small, glabrous herb. The stem is usually reddish and bears opposite or sub-opposite leaves with serrate margins. The inflorescence is a dichasial cyme and 2 such cymes develop in the axils of 2 leaves at each node so that the nodal complex gives the appearance of a false verticillaster (Fig. 1 A). It bears a couple of bisexual and a cluster of 11 (or sometimes less) pistillate flowers at each node. The former have long pedicels whereas the latter are short-stalked.

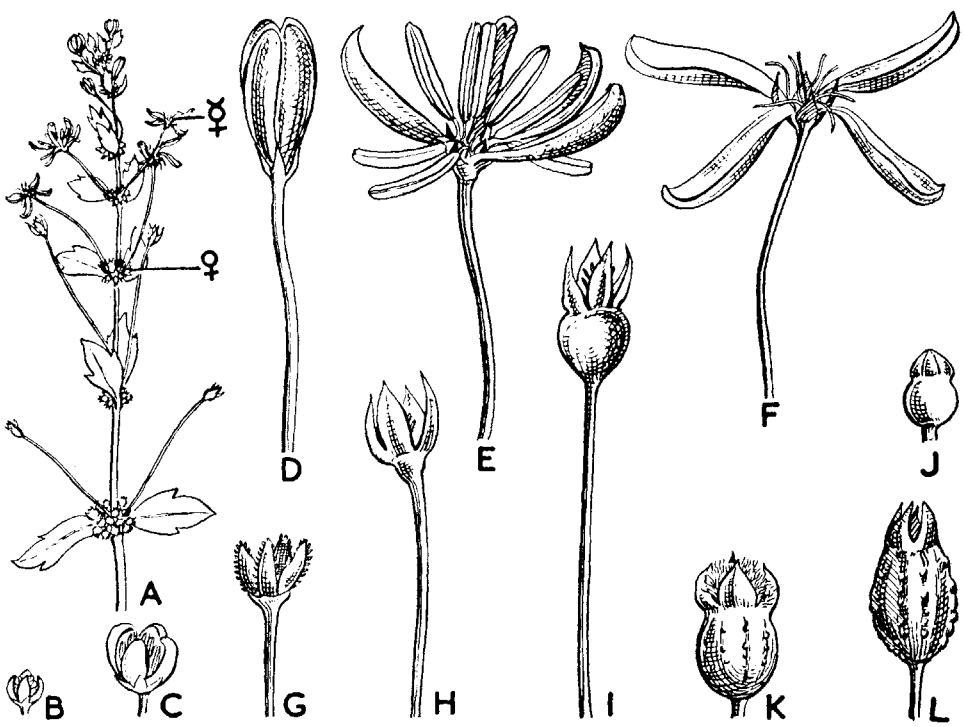

Fig. 1. External morphology (♀, pistillate flowers; ☿, bisexual flowers). A, branch bearing bisexual and pistillate flowers. ×1·3. B–E, stages leading to the development of bisexual, long-pedicellate flower. ×5. F, mature flower, anthers have been shed. ×5. G–I, stages in the formation of fruit from bisexual flower; calyx is persistent. ×5. J–L, formation of fruit from short-pedicellate, apetalous pistillate flower. ×5.

The bisexual flowers (Fig. 1 B–E) are complete, tetramerous and protandrous. Near the tip of the shoot these flowers are composed of 4 sepals, 4 cucullate petals and 8 stamens arranged in 2 whorls. The sepals are united at the base whereas the petals remain free. At a slightly lower level of the stem, besides sepals, petals and stamens, the flowers also show tetracarpellary pistil; the anthers are mature whereas the ovary contains young ovular primordia. Still lower down the anthers fall off (Fig. 1 F), and this is followed by the shedding of the petals so that they look like the female flowers which gradually develop into fruits (Fig. 1 G–I).

The pistillate flowers (Fig. 1 J, K) are bracteate, bracteolate and incomplete. The 4 lobes of the calyx project beyond the ovary which is tetracarpellary, syncarpous, tetralocular and inferior. Each locule contains a single pendulous ovule, although at an early stage a small sterile protuberance is also seen above the fertile ovular primordium. The styles are free and the stigma is plumose. The fruit is a ribbed nut with a persistent calyx (Fig. 1 L).

Since these flowers did not exhibit any differences in the gametogenesis and seed development, a common description is presented for both.

Microsporangium, microsporogenesis and male gametophyte

The cross-section of a young anther shows 4 groups of microspore mother cells, each surrounded by a tapetum, a middle layer, endothecium and epidermis (Fig. 2 A, E). A few crystals are distributed in the connective. The cells of the epidermis undergo anticlinal divisions and become stretched at maturity. There is a uniform deposition of tannin in the epidermal cells as well as the tissue around the vascular bundle. The cells of the endothecium also contain tannin and develop fibrous thickenings at maturity (Fig. 2 H). The middle layer starts degenerating after the formation of the tetrads so that by the time uninucleate pollen grains are formed it becomes disorganized at places (Fig. 2 C, G). The tapetal cells are uninucleate and full of dense cytoplasm, but soon they enlarge and become vacuolate (Fig. 2 B, F). They degenerate *in situ*. At the uninucleate stage of the pollen grains, the anther locule becomes filled with a mucilaginous substance (Fig. 2 C, G) which, however, disappears soon. In a mature anther, the partition walls between the adjacent microsporangia break down and they become confluent. The dehiscence occurs by a longitudinal slit. The wall of the dehisced anther shows flattened epidermis, fibrous endothecium and remnants of the glandular tapetum (Fig. 2 D, H).

The microspore mother cells undergo simultaneous reduction divisions (Fig. 2 I–N), and the microspores are arranged in a tetrahedral or decussate manner (Fig. 2 O, P). They are surrounded by mucilaginous sheath which develops in early stages of division. The sheath soon disappears and the

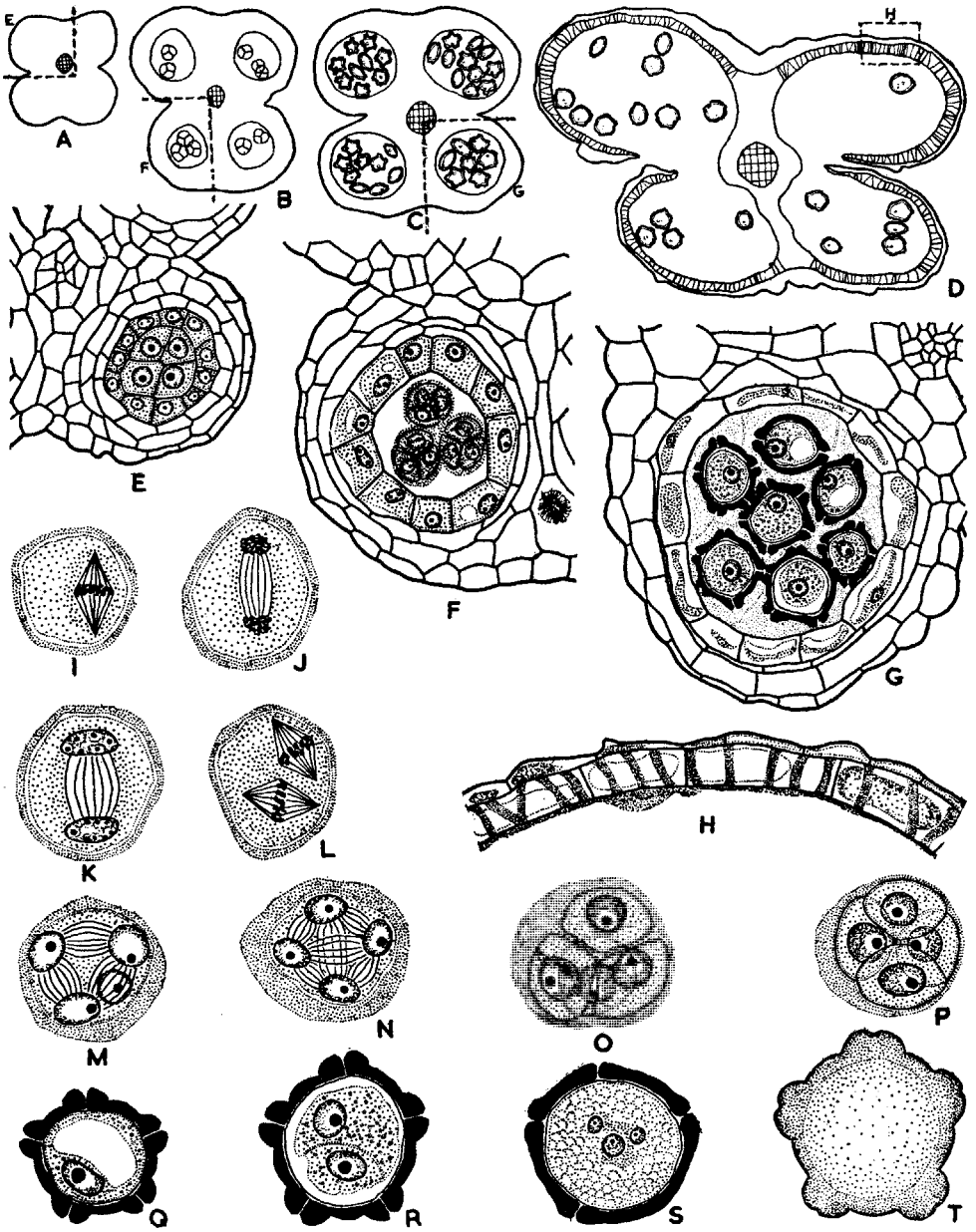

FIG. 2. Microsporangium, microsporogenesis and male gametophyte. A–D, outline diagrams of cross-sections of anthers at various stages of development. ×114. E, enlarged view of portion marked *E* in A to show microspore mother cells and wall layers. ×411. F, G, sectors *F* and *G* magnified from B and C to show enlargement and subsequent degeneration of middle layer and tapetal cells. ×411. H, part of anther wall at the time of dehiscence enlarged from region *H* marked in D; endothecium shows fibrous thickenings. ×411. I–N, microspore mother cells showing meiosis I and II. ×1234. O, P, tetrahedral and decussate tetrads. ×1234. Q–S, 1-, 2- and 3-celled pollen grains. ×822. T, palynogram. ×822.

microspores separate. They increase in size and acquire a thick exine and a thin intine (Fig. 2 Q). The pollen grains are packed with starch grains, their cytoplasm shows vacuolation and the nucleus is pushed to one side where it divides to cut off a small lenticular generative cell (Fig. 2 R). During subsequent development the wall between the generative and vegetative cells dissolves so that the former lies free in the cytoplasm of the vegetative cell. Finally, the generative cell divides to give rise to 2 gametes (Fig. 2 S). The mature pollen grains are 5-porate (Fig. 2 T) and shed at the 3-celled stage.

Megasporangium

Longitudinal section of a young flower shows that initially in each locule 2 ovular primordia arise as small, mound-shaped protuberances (Fig. 3 A). The one towards the pedicel subsequently develops into a mature ovule and is fertile, whereas the other towards the stigma aborts (Fig. 3 B, C).

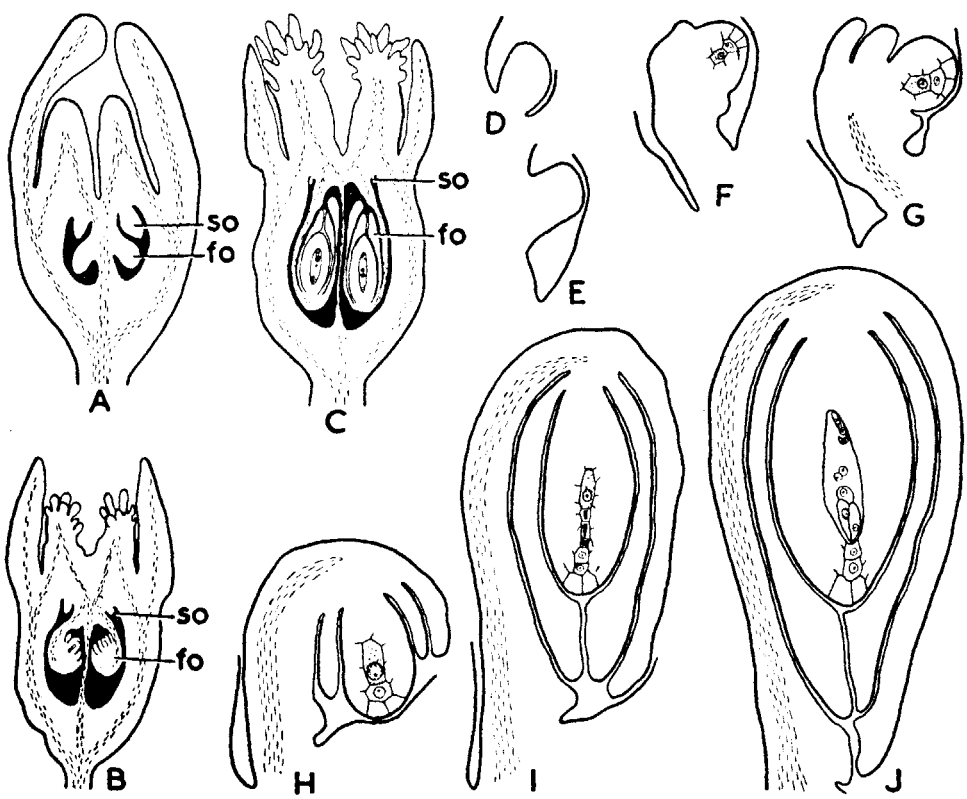

FIG. 3. Megasporangium (*fo*, fertile ovular primordium; *so*, sterile ovular primordium). A, l.s. female flower showing 2 ovular primordia in each locule. ×100. B, C, same; fertile ovular primordium has matured into an ovule, whereas the sterile one has aborted. ×56. D–J, median longisections of ovules during progressive stages of development and curvature. ×250.

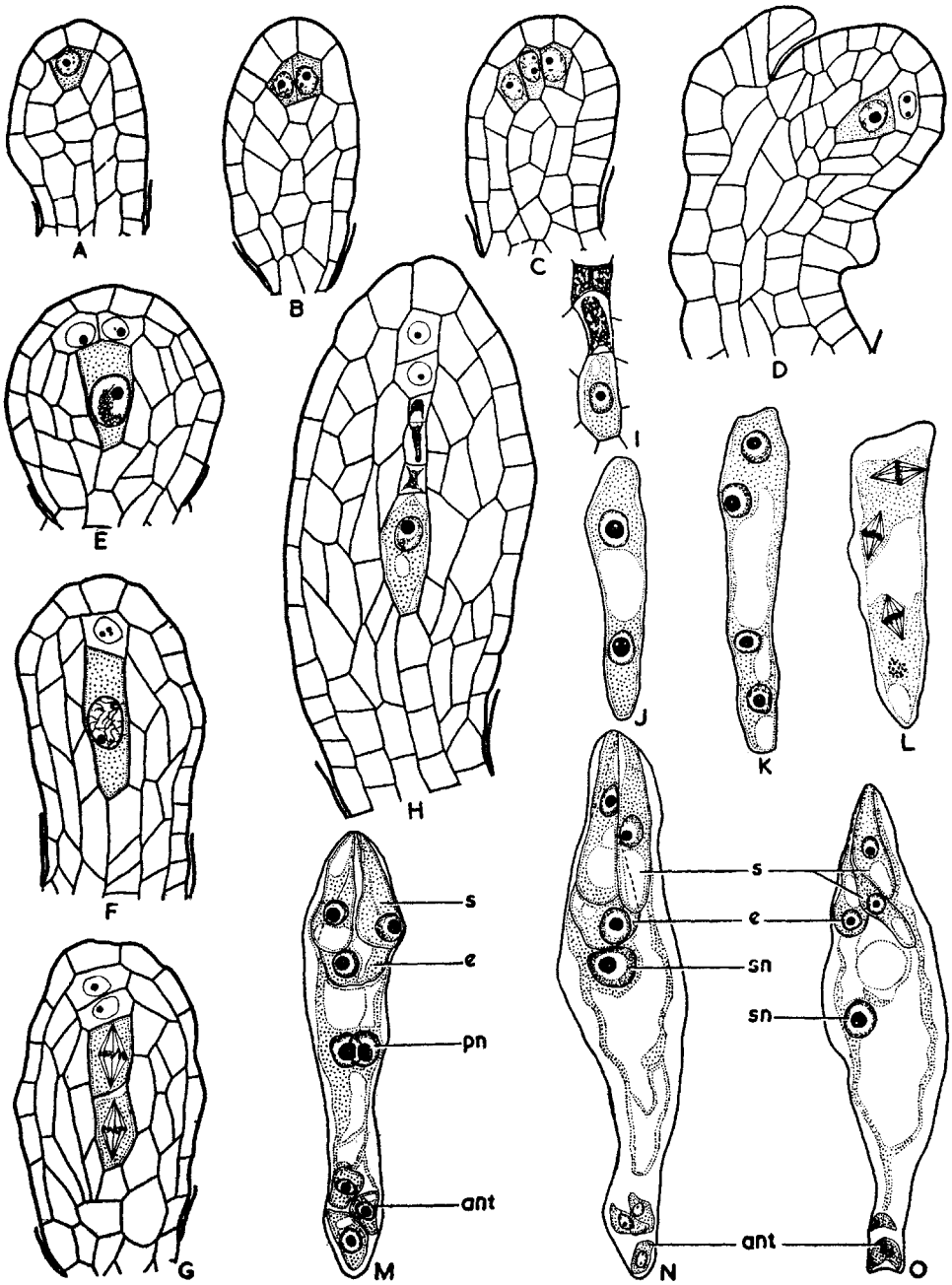

FIG. 4. Megasporogenesis and female gametophyte (*ant*, antipodal cells; *e*, egg; *pn*, polar nuclei; *s*, synergid; *sn*, secondary nucleus). A–C, longitudinal sections through young nucelli showing 1-, 2- and 3-celled archesporium. ×650. D, l.s. nucellus showing sporogenous and parietal cells. ×650. E, F, same with megaspore mother cell and parietal cells. ×650. G, dyad cells in division. ×650. H, I, linear and T-shaped tetrads. H, ×650; I, ×837. J–N, stages in the formation of mature embryo sac; the polar nuclei have fused to form secondary nucleus in N. ×837. O, embryo sac showing laterally disposed egg. ×837.

The fertile ovular primordium grows rapidly on one side and begins to curve downward. The inner integument differentiates first and is followed by the outer. Progressive stages of curvature are shown in Fig. 3 D–J. The micropyle is formed by both the integuments. The ovule is anatropous, bitegminal and crassinucellar. Some cells of the funicular epidermis elongate and probably form a feeble obturator. The vascular supply extends up to the base of the integuments. After fertilization a few cells of the nucellus below the embryo sac become slightly prominent and take red stain with safranin. They constitute a poorly defined hypostase.

Megasporogenesis and female gametophyte

A single hypodermal archesporial cell differentiates in the young nucellus (Fig. 4 A). However, occasionally 2 or even 3 cells may be seen in the juvenile ovule (Fig. 4 B, C). Of these only one functions. It cuts off a parietal cell (Fig. 4 D, F) which divides transversely to form 2 cells (Fig. 4 G, H). Rarely, the parietal cell may divide anticlinally to produce 2 juxtaposed cells (Fig. 4 E). The megaspore mother cell enlarges and undergoes meiosis to give rise to a dyad (Fig. 4 G) and finally a linear tetrad of megaspores (Fig. 4 H). Sometimes T-shaped tetrads are also met with (Fig. 4 I). The upper 3 megaspores degenerate while the chalazal one forms an 8-nucleate gametophyte of the Polygonum type (Fig. 4 J–O). A similar kind of development was also observed by Bley (1925) in *L. javanica*. The egg is usually situated between the synergids but rarely it may be laterally placed (Fig. 4 O). One of the synergids degenerates immediately after fertilization whereas the other remains healthy for some time (Fig. 5 E), its remnants persist up to the 5-celled stage of proembryo. In two preparations healthy synergids were observed even at the 3-celled stage of proembryo (Fig. 6 B). The polar nuclei fuse in the middle of the embryo sac to form a secondary nucleus (Fig. 4 M–O). There are 3 antipodal cells which may or may not remain healthy, but can be recognized up to the 12-celled stage of endosperm (Fig. 6 F).

Fertilization

The pollen tube enters the micropyle, pierces through the nucellus and reaches the embryo sac (Fig. 5 A, D). In Fig. 5 B, although the pollen tube has reached the embryo sac, the polar nuclei have not yet fused. Figure 5 C shows one of the male gametes (semi-lunar) lying close to the egg nucleus while the other is approaching the fusing polar nuclei. The remnants of the pollen tube are visible up to 3- (Fig. 5 F) or even 4-celled stage of proembryo.

Endosperm

The primary endosperm nucleus divides later than the zygote (Fig. 6 A, B) which is an unusual feature among the angiosperms. The division of the

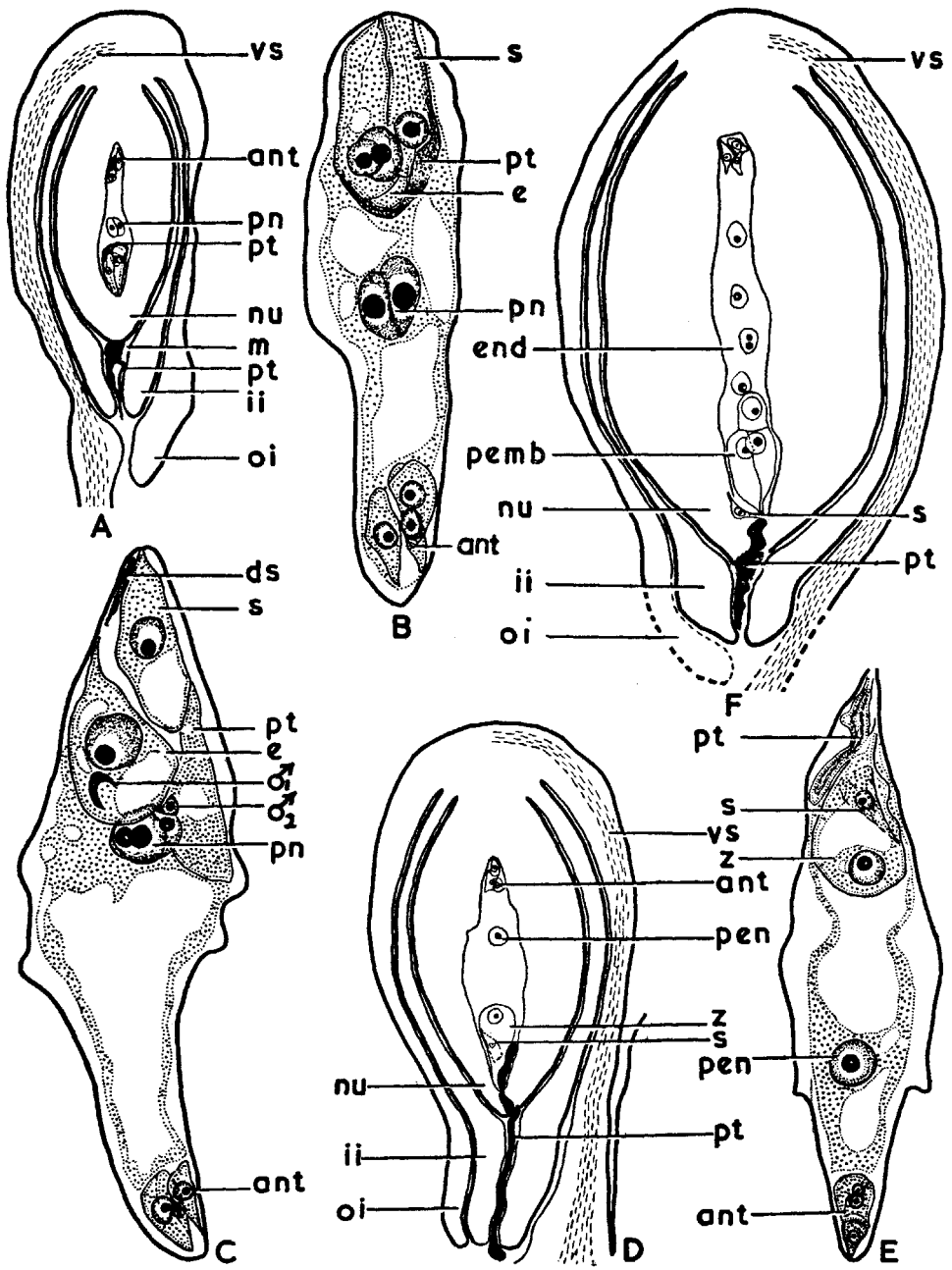
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FIG. 5

primary endosperm nucleus and its derivatives are free nuclear (Fig. 6 C, D). The cytoplasm shows intense vacuolation all over except around the nuclei. Wall formation sets in after 8 endosperm nuclei have been formed. In *L. javanica* (Bley 1925) wall formation occurs at the 16-nucleate stage. The first-formed walls are transverse (Fig. 6 E) and these are followed by both vertical as well as transverse walls (Fig. 6 F). Gradually the entire endosperm becomes cellular. To begin with, the cells are large, thin-walled, vacuolate and their nuclei are quite prominent (Fig. 6 G, I). At maturity, however, they become packed with reserve food materials so that the nuclei of some of the cells are scarcely visible (Fig. 6 H, J). A portion of the endosperm in the immediate vicinity of the mature embryo is absorbed by the developing embryo, whereas the rest of it persists in the mature seed.

Embryo

The zygote (Fig. 7 A) is divided by a transverse wall giving rise to a small terminal (*ca*) and a large basal cell (*cb*) (Fig. 7 B). The latter undergoes a single vertical division to form 2 juxtaposed cells (Fig. 7 C–L), whereas the former divides transversely to form 2 superposed cells *cc* and *cd* (Fig. 7 D). The cell *cc*, by two vertical and one transverse division, gives rise to an octant (Fig. 7 E–H). Tangential walls are now laid down in these tiers which result in the formation of a globular proembryo (Fig. 7 I, J). Subsequent development leads to the differentiation of a dicotyledonous embryo (Fig. 7 K, L), the cells of which are rich in food materials.

The tier *cd* undergoes a transverse division to form *m* and *ci* (Fig. 7 E, F). Some of the derivatives of *ci* close to *cb* organize into a short suspensor.

The two daughter cells formed by the vertical division of the basal cell (*cb*) enlarge considerably and occupy the entire space in the micropylar part of the embryo sac. The cytoplasm in these cells is highly vacuolate and the nuclei are conspicuously large (Fig. 7 C–J). They, however, start degenerating after the formation of the cotyledons, and in the ripe seed only their remnants are seen at the micropylar end.

Bley (1925) described two types of development in *L. javanica* after the 4-celled stage of proembryo. In one case there is a large embryo hanging from a short suspensor, whereas in the other a small embryo is attached to a long

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FIG. 5. Fertilization (*ant*, antipodal cells; *ds*, degenerating synergid; *e*, egg; *end*, endosperm; *ii*, inner integument; *m*, micropyle; *nu*, nucellus; *oi*, outer integument; *pemb*, proembryo; *pen*, primary endosperm nucleus; *pn*, polar nuclei; *pt*, pollen tube; *s*, synergid; *vs*, vascular supply; *z*, zygote; σ'_1, σ'_2, male gametes). A, l.s. ovule after the entry of pollen tube. ×252. B, embryo sac enlarged from A; the pollen tube is adpressed to egg apparatus. ×1124. C, l.s. embryo sac at the time of fertilization; one male gamete (σ'_1) is lying close to egg nucleus and the other (σ'_2) adjacent to fusing polar nuclei. ×1124. D, l.s. ovule after fertilization. ×252. E, fertilized embryo sac; remnants of pollen tube and synergid are also seen. ×686. F, longisection of ovule showing 3-celled proembryo and persistent pollen tube. ×287.

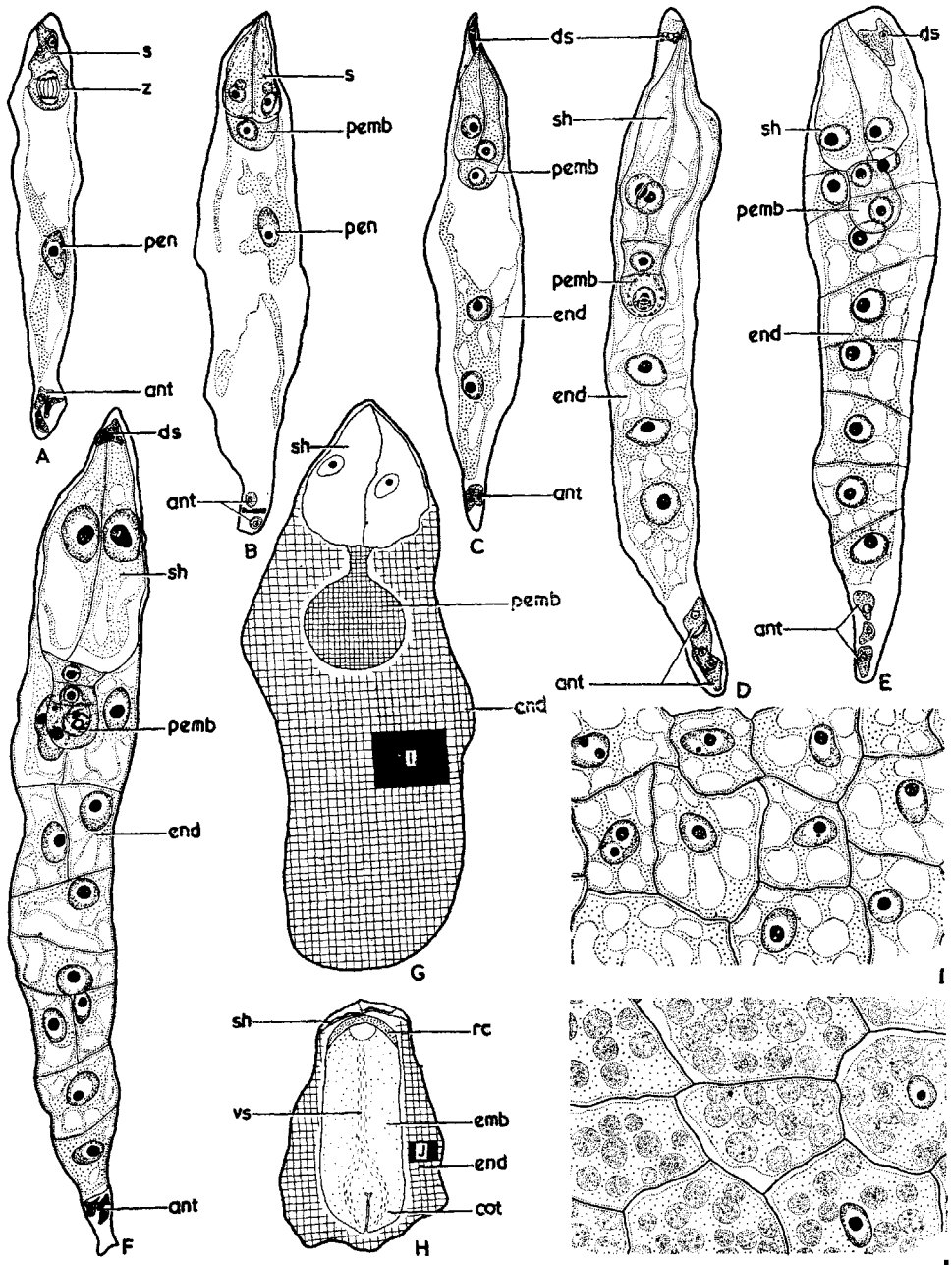
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FIG. 6

suspensor. It appears that he observed embryos at different stages of development. As the embryo matures, the suspensor starts degenerating and naturally looks smaller in older stages.

Seed coat

In a young ovule the outer as well as inner integument consists of 2 layers of parenchymatous cells (Fig. 8 A, F). At the megaspore tetrad stage, the cells of both the integuments elongate and show vacuolation (Fig. 8 B, G). By the time a mature embryo sac is formed, the outer integument may become 3-layered whereas the inner remains 2-layered (Fig. 8 C, H).

After fertilization, the cells of the inner epidermis of inner integument become tangentially stretched, their nuclei show signs of degeneration, and they completely disorganize at the 4-celled stage of the proembryo. The outer epidermis of inner integument also begins to show unhealthy signs (Fig. 8 D, I). The nucellar cells increase in size considerably, show scanty cytoplasm and develop a thick cuticle on the epidermis. The disorganization of the nucellus sets in from the centre to the periphery. As the embryo grows older, the cells of the outer integument also start disintegrating; the degeneration is initiated in the inner epidermis and proceeds towards the outside. At maturity, the seed coat is represented by the outer epidermis of outer integument whose cells become flattened and compressed. The remaining layers of the outer integument, inner integument and nucellus (except the cuticle) disorganize on the sides, whereas their remnants can still be demarcated near the micropylar region (Fig. 8 E, J).

Pericarp

In a young carpel when the ovules are at the archesporial cell stage, the ovary wall consists of 9 or 10 layers. The outermost and 1 or 2 middle layers are filled with tannin, whereas the cells of the hypodermis and 4 or 5 inner layers are vacuolate (Fig. 9 A, E). The nuclei in the tannin-filled cells appear as darkly stained irregular bodies. Prior to fertilization the epidermal cells become radially elongated, the hypodermal cells show chloroplasts, the middle layers increase in number and become impregnated with tannin, and the

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FIG. 6. Endosperm (*ant*, antipodal cells; *cot*, cotyledon; *ds*, degenerating synergid; *emb*, embryo; *end*, endosperm; *pemb*, proembryo; *pen*, primary endosperm nucleus; *rc*, root cap; *s*, synergid; *sh*, suspensor haustorium; *vs*, vascular supply; *z*, zygote). A, fertilized embryo sac showing first division of zygote, whereas the primary endosperm nucleus is still undivided. ×469. B, same, showing 3-celled proembryo, healthy synergids, undivided primary endosperm nucleus and degenerated antipodal cells. ×469. C, D, 2- and 4-nucleate endosperm. ×469. E, 8-celled linear endosperm. ×469. F, 12-celled endosperm; some cells have divided vertically. ×469. G, H, diagrams of longisections of seeds (testa removed) at globular and dicotyledonous stages of embryo. G, ×170; H, ×68. I, J, magnified views of portions *I* and *J* from G and H showing young and mature cells of endosperm. ×768.

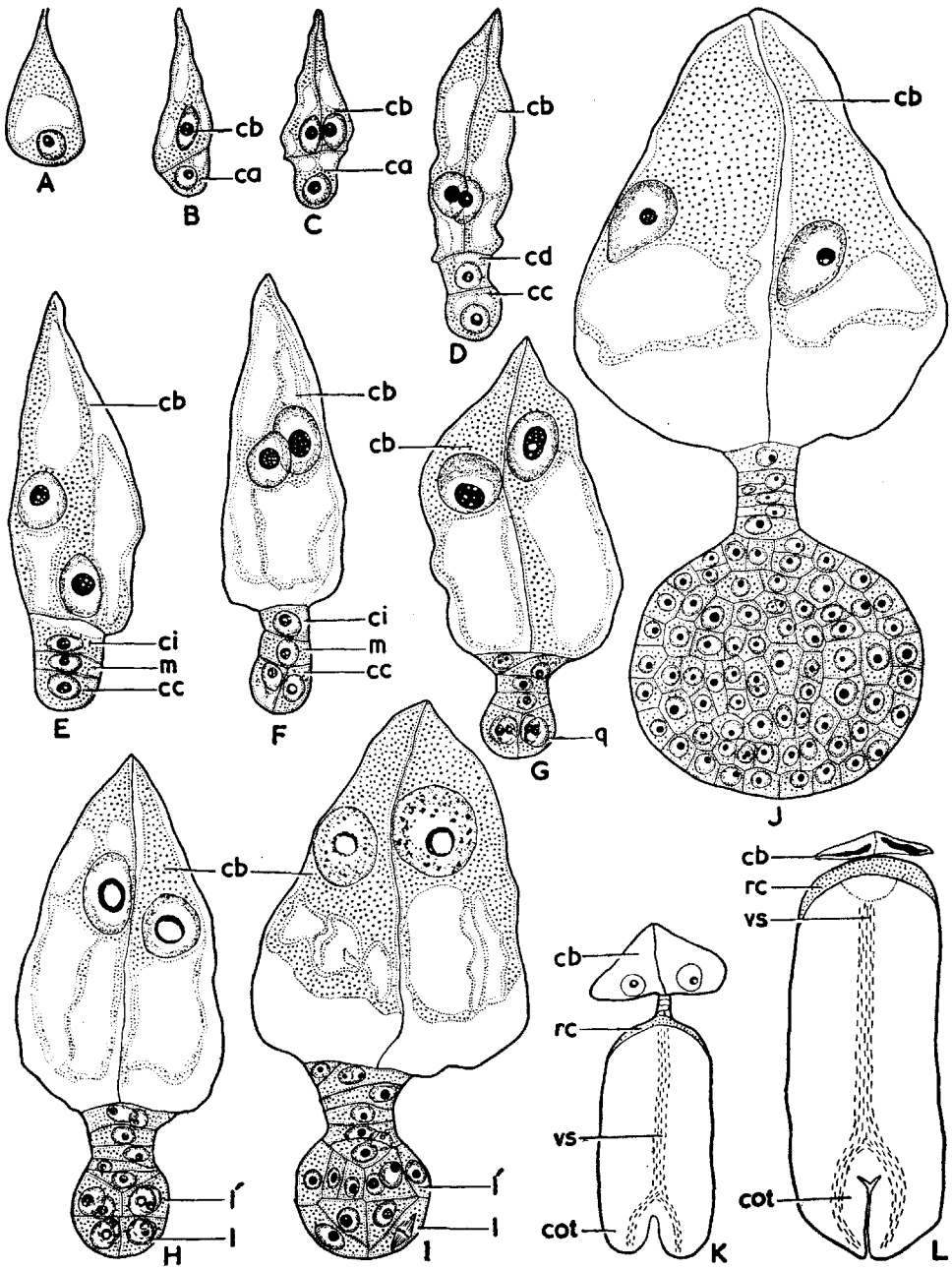

FIG. 7. Embryo (*cot*, cotyledon; *rc*, root cap; *vs*, vascular supply). A, zygote. ×470. B, C, 2- and 3-celled proembryos. ×470. D–H, stages leading to the formation of octant proembryo; cells of suspensor haustorium have considerably enlarged and contain hypertrophied nuclei. ×470. I, J, formation of globular proembryo. ×470. K, L, young and mature dicotyledonous embryos; haustorial cells (*cb*) have degenerated in L and their remnants are seen above the root cap. ×130.

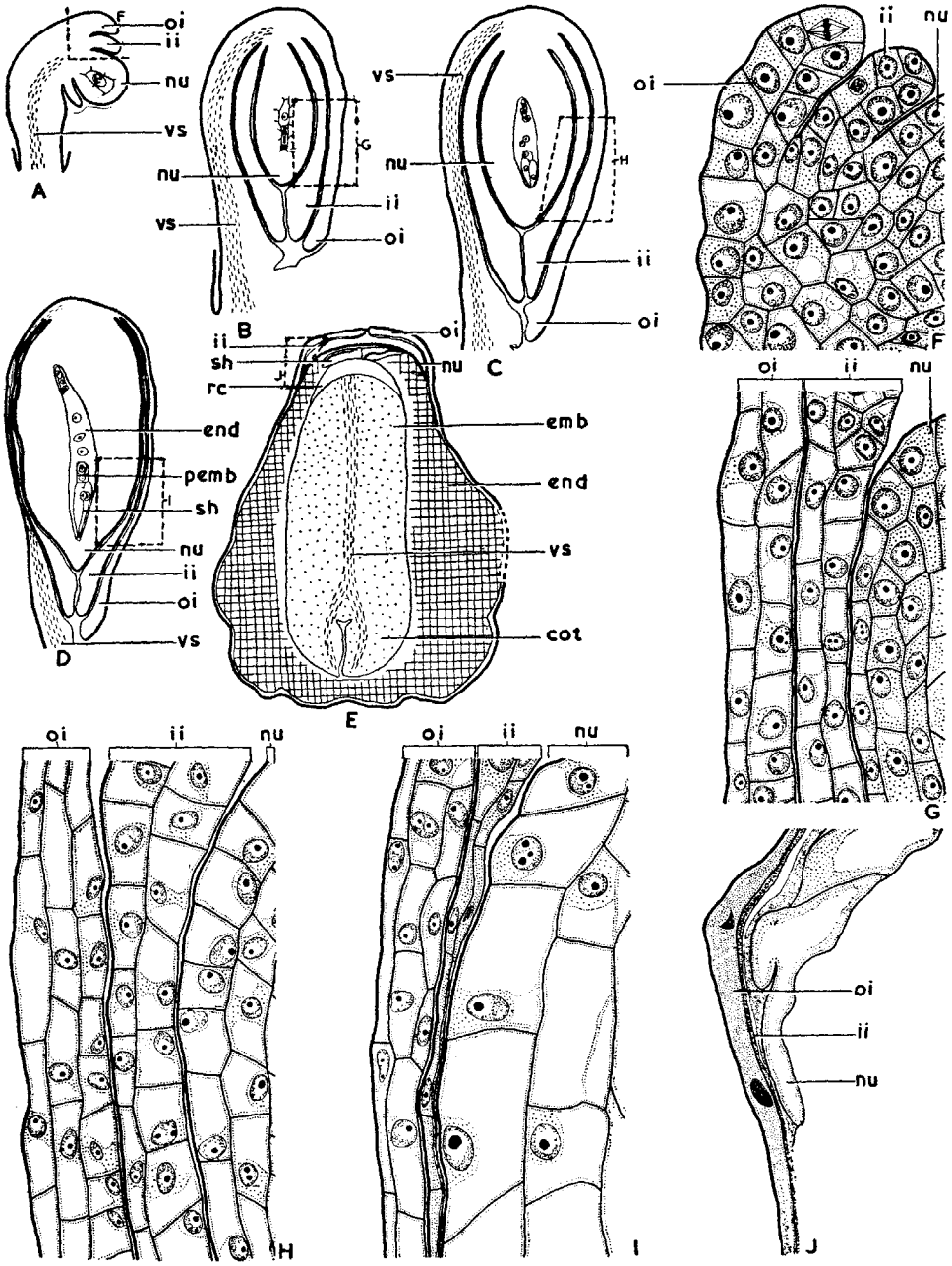

FIG. 8. Seed coat (*cot*, cotyledon; *emb*, embryo; *end*, endosperm; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *pemb*, proembryo; *rc*, root cap; *sh*, suspensor haustorium; *vs*, vascular supply). A–E, longitudinal sections of ovules at megaspore mother cell, megaspore tetrad, mature embryo sac, 4-celled proembryo and dicotyledonous embryo stages respectively. A–C, × 169; D, E, × 106. F, magnified view of portion *F* marked in A; the outer as well as inner integument is 2-layered. × 762. G, portion *G* enlarged from B; cells of both the integuments show scanty cytoplasm and conspicuous vacuoles. × 762. H, enlargement of sector *H* from C; outer integument is 3-layered. × 762. I, magnified view of portion *I* from D; the inner layer of inner integument has degenerated but nucellar cells have considerably enlarged. × 762. J, mature seed coat enlarged from E. × 762.

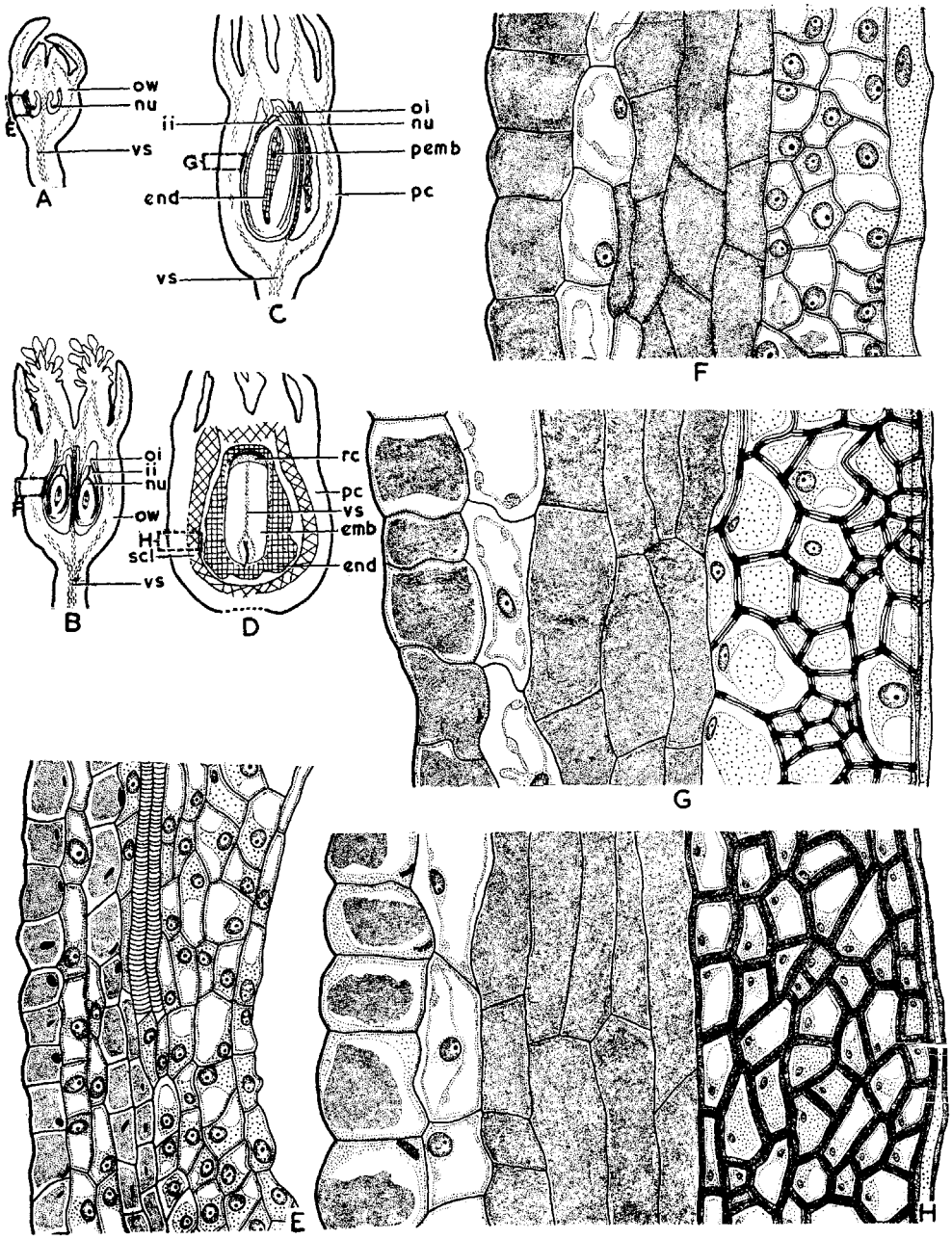
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FIG. 9

cells of the inner epidermis become stretched (Fig. 9 B, F). At the 4-celled stage of proembryo, the inner epidermis is further stretched and the cells of 5 or 6 layers outside it develop thickenings (Fig. 9 C, G). Subsequently these cells become sclerenchymatous, have wide lumen and small nuclei, and constitute the stony part of the fruit wall (Fig. 9 D, H).

Systematic Considerations

Bentham and Hooker (1862–76) included the genera *Haloragis*, *Laurembergia* and *Myriophyllum* under the family Haloragaceae along with *Callitriche*, *Gunnera*, *Hippuris*, *Loudonia*, *Meionectes* and *Proserpinaca*. Engler and Prantl (1889–97) removed *Callitriche* and *Hippuris* to the families Callitrichaceae and Hippuridaceae, whereas the remaining genera were retained under the Haloragidaceae. Schindler (1905) divided the family Halorrhagaceae into two subfamilies, Halorrhagoideae and Gunneroideae. He included *Haloragis*, *Laurembergia*, *Loudonia*, *Meziella*, *Proserpinaca* (Halorrhageae) and *Myriophyllum* (Myriophylleae) in the subfamily Halorrhagoideae whereas *Gunnera* was assigned to the Gunneroideae. Wettstein (1935) as well as Rendle (1952) accepted Haloragaceae as distinct from the Hippuridaceae. Wettstein went a step further and segregated *Gunnera* into an independent and more advanced family, Gunneraceae. Schnarf (1931) has also treated the Haloragaceae, Gunneraceae and Hippuridaceae as separate families. Hutchinson (1959) has assigned *Gunnera* and *Hippuris* to the Haloragaceae, but *Callitriche* to a separate family, Callitrichaceae. In Engler's revised edition *Haloragis*, *Laurembergia*, *Loudonia*, *Proserpinaca* and two more genera have been placed in the tribe Halorageae, and *Myriophyllum* in the tribe Myriophylleae of the subfamily Haloragoideae of the Haloragaceae. The subfamily Gunneroideae of the Haloragaceae comprises only *Gunnera* (*see* Melchior 1964).

The morphological and embryological features of the Haloragidaceae, Hippuridaceae and Gunneraceae are summarized in the following table (for literature *see* Juel 1911; Samuels 1912; Schnarf 1931; Lawrence 1951; Erdtman 1952; Sethi 1964; Nagaraj and Nijalingappa 1967; Bawa 1968):

Fig. 9. Pericarp (*emb*, embryo; *end*, endosperm; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *ow*, ovary wall; *pc*, pericarp; *pemb*, proembryo; *rc*, root cap; *scl*, sclerenchyma; *vs*, vascular supply). A, B, longisections of carpels at archesporial cell and mature embryo sac stages of ovule respectively. ×35. C, D, longisections of young and mature fruits. ×35. E, portion of ovary wall enlarged from A; the cells of outer epidermis and 1 or 2 middle layers are filled with tannin whereas those of hypodermis and 4 or 5 inner layers are vacuolate. ×700. F, same, at mature embryo sac stage. There is an over-all increase in the size of cells and number of middle layers; the cells of inner epidermis have elongated. ×700. G, H, portions of pericarp enlarged from C and D to show further increase in the number and size of cells; inner epidermis and a few adjacent layers have become sclerenchymatous. ×700.

	Haloragidaceae (*Haloragis*, *Laurembergia*, *Myriophyllum*)	Hippuridaceae (*Hippuris*)	Gunneraceae (*Gunnera*)
Leaves	Exstipulate	Exstipulate	Stipules reduced to scales or an ochreate sheath
Flower	Bracteate, bracteolate, bisexual or unisexual, tetramerous; arranged in glomerules in leaf axils	Bracteate, bisexual, rarely unisexual; solitary; perianth forms a rim around the tip of the ovary	Ebracteate, bisexual, bimerous; crowded in large spikes or panicles
Androecium	4 or 4+4, obdiplostemonous	Single stamen placed medianly	2, antipetalous
Pollen	4 or 5 porate	4–6 colpate	3–5 colpate
Gynoecium	Tetracarpellary, tetralocular, with single pendulous ovule in each locule	Monocarpellary, unilocular, with single pendulous ovule	Bicarpellary, unilocular, with solitary ovule
Ovule	Anatropous, bitegminal, crassinucellar, with a feeble funicular obturator	Anatropous, naked or unitegminal, tenuinucellar, with a feeble funicular obturator	Anatropous, bitegminal, crassinucellar, without an obturator
Parietal cells	Present	Absent	Present
Embryo sac	Polygonum type	Polygonum type	Peperomia type
Fertilization	Porogamous	Pollen tube penetrates the embryo sac laterally	Porogamous
Endosperm	Cellular (*Haloragis colensoi*, *Myriophyllum intermedium*) or Nuclear (*Laurembergia brevipes*)	Cellular	Cellular
Embryo	Large, cylindrical, suspensor haustorium present	Large, cylindrical, suspensor haustorium absent	Minute, obcordate, without suspensor haustorium

These differences confirm and support the recognition of the Haloragidaceae as distinct from the Hippuridaceae and Gunneraceae. Apart from the aquatic habitat and the Polygonum type of embryo sac, *Hippuris* has hardly anything in common with the other members of the Haloragidaceae. Its separation from the latter is also supported on anatomical (Metcalfe and Chalk 1950) and palynological (Erdtman 1952) grounds. Similarly such characters as the Peperomia type of embryo sac, absence of suspensor haustorium and floral morphology uphold the segregation of *Gunnera* from the

Haloragidaceae. Since this view is also supported on the basis of chromosome number (Virkki 1962), Wettstein's classification appears to be fully justified.

The resemblance between the Callitrichaceae and the Haloragidaceae was first pointed out by Brown (1814; *cited* in Jørgensen 1923). He stated that *Callitriche* resembles *Myriophyllum* and *Serpicula* (= *Laurembergia*) in habit as well as the structure of the pistil. This view was accepted by several other taxonomists. However, Jørgensen (1923) stated clearly that *Myriophyllum* and *Callitriche* have nothing in common except for the aquatic habitat and 4-chamber fruit. The Callitrichaceae differ from the Haloragidaceae in the presence of (i) solitary flowers, (ii) single terminal stamen, (iii) non-aperturate pollen grains, (iv) bicarpellary gynoecium, (v) unitegminal and tenuinucellar ovules, (vi) well-developed endosperm haustoria; and the absence of suspensor haustorium (for literature *see* Jørgensen 1923; Maheshwari 1950; Erdtman 1952). Metcalfe and Chalk (1950), and Darlington and Wylie (1955) also treat the Haloragidaceae as distinct from the Callitrichaceae on anatomical and cytological grounds.

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