

## SOME RECENT EXAMPLES OF THE VALUE OF EMBRYOLOGY IN RELATION TO TAXONOMY

R. N. KAPIL

Department of Botany, University of Delhi, Delhi-6

## ABSTRACT

Embryological evidence indicates that *Schisandra* does not belong to the Magnoliaceae. Its inclusion in a separate family Schisandraceae is quite justified. Moreover, the Schisandraceae do not seem to be related to the Illiciaceae.

The genus *Haloragis* is quite distinct from *Gunnera* and *Hippuris* and only the former should be included in the family Haloragaceae.

The Malaysian genus *Pentaphragma*, although somewhat aberrant, is correctly assigned to the Campanulaceae and need not be removed from this family.

## INTRODUCTION

The classification of angiosperms is based mainly on exomorphic characters. However, for attaining a truly phylogenetic system it is essential to analyse and harmonize evidences from various other disciplines of botany. While anatomy and cytology have long been used to verify the affinities of certain disputed genera and families, during recent years the embryologist has also contributed significantly towards an improvement of the existing schemes of classification. Many such examples have been discussed by Maheshwari (1962). This paper deals with some additions to his account.

According to Maheshwari (1950, 1962) the following embryological characters are of taxonomic significance: (i) structure and development of anther, especially the behaviour of tapetum; (ii) mode of quadripartition of microspore mother cell; (iii) structure and development of pollen grain; (iv) structure and development of ovule; (v) megasporogenesis; (vi) development and organization of embryo sac; (vii) fertilization; (viii) development and fate of endosperm; and (ix) embryogeny. He has also suggested the need of taking into account certain abnormalities like parthenogenesis, apogamy and polyembryony.

While dealing with problems of relationships it has been felt that one more character needs to be added to the above list, viz. the development of the seed coat and the contribution made by the integuments in its organization especially when structures like aril, caruncle, operculum and sarcotesta are present. In evaluating the systematic position of *Schisandra grandiflora*, *Haloragis colensoi* and *Pentaphragma horsfieldii*, discussed in this paper, all the above mentioned features have been considered.

## OBSERVATIONS AND DISCUSSION

*Schisandra*: Several systematists (Bentham & Hooker, 1862; Engler & Prantl, 1889-1897; Hutchinson, 1926) include the genus *Schisandra* along with *Kadsura* in a subfamily or special tribe of the Magnoliaceae. Recently, Hayashi (1960) has also

followed this classification. In 1959 Hutchinson raised this tribe to family rank and assigned it a position under the order Magnoliales. From the point of view of vegetative anatomy, Bailey & Nast (1948) include *Schisandra* and *Kadsura* in the family Schisandraceae without any close relationship with the Magnoliaceae. Erdtman (1952) gives it the status of a family under the Ranales on the basis of pollen morphology.

The material of *Schisandra grandiflora* was collected from Kedarnath. The flowers are solitary and unisexual, and are borne in the axils of leaves. There are numerous carpels and stamens arranged spirally on an elongated receptacle (Fig. 1 A, B). The stamens are monadelphous and well differentiated into a filament, anther and connective. A single vascular strand traverses each stamen (Fig. 1 C). The carpels are essentially conduplicate with a conspicuous ventral stigmatic crest (Fig. 1 I, J). Each carpel is bilocular and contains a single ovule in each locule (Fig. 1 J).

The primary wall layer is cut off from the hypodermal archesporial cells which differentiate at the four corners of a young anther. Tetrahedral and decussate tetrads are formed as a result of reduction divisions in the microspore mother cells. Both the endothecium and the secretory tapetum are irregularly 2-layered in the mature anther wall (Fig. 1 D). The tapetal cells (Fig. 1 E-G) frequently contain polyploid nuclei. Prior to dehiscence the endothecium develops fibrous bands. The mature pollen is hexacolpate with reticulate exine. Three of the furrows are longer and meet at one pole to form a triradial mark while the other three are short and do not reach the poles (Fig. 1 H).

The ovules are anatropous, crassinucellar and bitegminal (Fig. 1 J). A single (sometimes two) archesporial cell differentiates in the young nucellus. It cuts off a primary parietal and the primary sporogenous cells (Fig. 1 K). The female gametophyte is monosporic (Fig. 1 L-N). So far no antipodal cells are found but they may be very ephemeral. The endosperm is Cellular and the development of the embryo conforms to the Onagrad

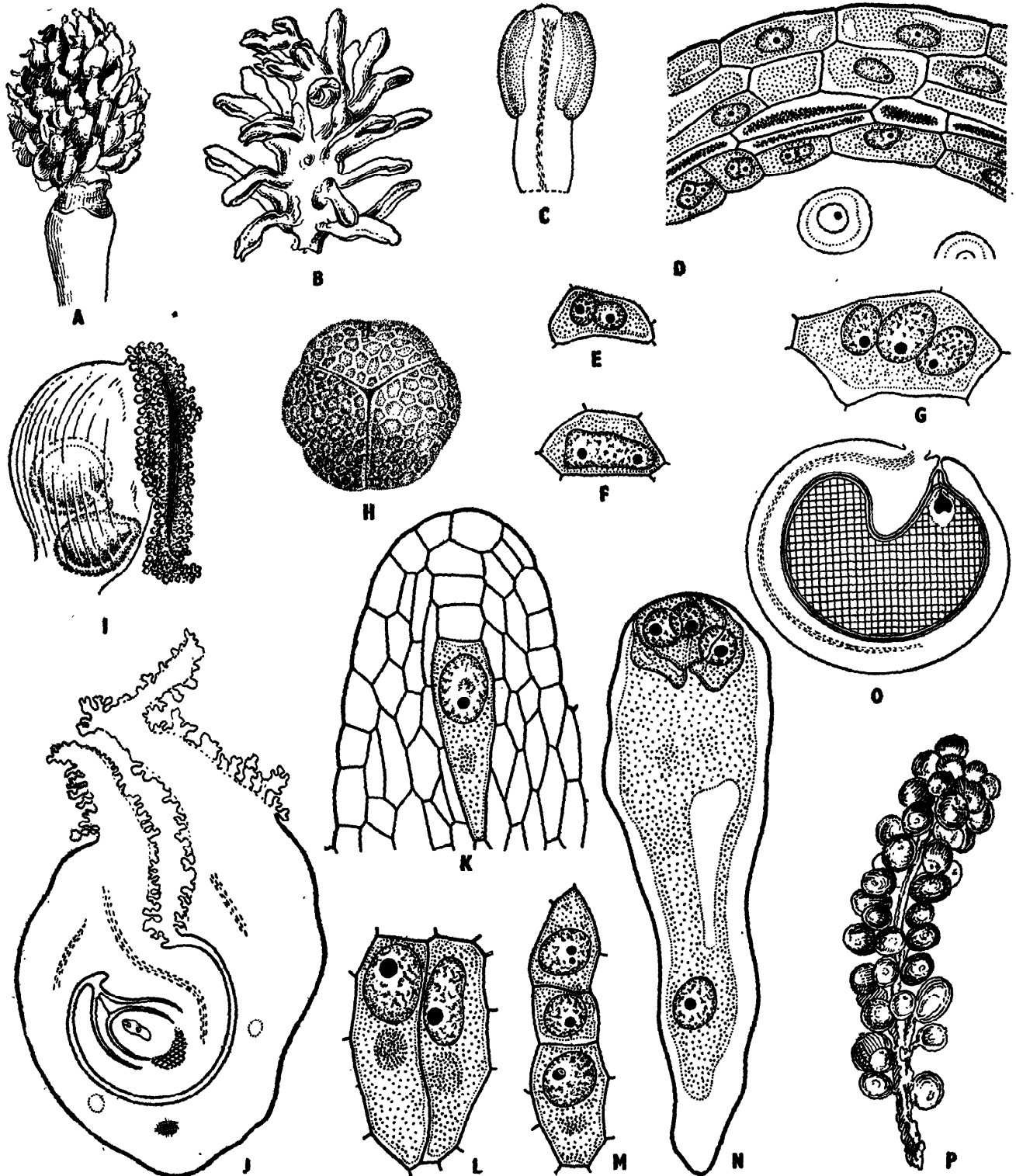


FIG. 1A-P—*Schisandra grandiflora*. A. Carpels arranged spirally on floral axis.  $\times 5$ . B. Male flower without perianth lobes.  $\times 3$ . C. Stamen showing protuberant anthers.  $\times 6$ . D. Portion of anther wall at the 1-celled stage of pollen grain.  $\times 647$ . E-G. Tapetal cells.  $\times 805$ . H. Hexacolpate pollen grain.  $\times 912$ . I. Carpel showing ventral stigmatic crest.  $\times 36$ . J. Same in t.s. showing stigmatic papillae and laminar placentation.  $\times 36$ . K. Primary parietal and sporogenous cells.  $\times 647$ . L. Two megaspore mother cells lying side by side.  $\times 805$ . M. Megaspore triad.  $\times 805$ . N. Organized embryo sac.  $\times 805$ . O. L.s. seed at the late heart-shaped stage of the embryo.  $\times 8$ . P. Baccate fruit.  $\times 1.5$ .

type. The mature embryo is minute with a short and inconspicuous suspensor. The seeds are albuminous (Fig. 10) and are characterized by a hard and stony testa formed only by the outer integument. The fruit is a berry with a succulent pericarp (Fig. 1 P).

In *Magnolia*, on the contrary, the flowers are solitary, terminal, regular, bisexual, actinomorphic and hypogynous (Fig. 2 A). There is no distinction into calyx and corolla and the perianth consists of 9-14 petaloid lobes. The stamens are numerous and free. They are arranged spirally and have long, slender, embedded sporangia (Fig. 2 D). The gynoecium is polycarpellary, apocarpous with the carpels arranged spirally on an elongated floral axis. They are 1-celled and biovulate (Fig. 2 B, C).

At the microspore mother cell stage the anther wall in *M. stellata* consists of an epidermis, single-layered endothecium, three or four middle layers and the glandular tapetum (Fig. 2 E). Concurrent with the meiotic divisions in the microspore mother cells the tapetum becomes 2-layered and binucleate (Fig. 2 F) while the endothecium develops reticulate thickenings. The pollen grains are monocolpate (Fig. 2 G) and are shed at the 2-celled stage.

The ovules are bitegminal, crassinucellar and anatropous. The archesporial initial cuts off a parietal cell which divides anti- as well as periclinally to produce two or three rows of 6 to 8-layered parietal tissue (Fig. 2 H). Meiotic divisions in the

megaspore mother cells result in linear or T-shaped tetrads (Fig. 2 I). The chalazal megaspore functions to form a Polygonum type of embryo sac (Fig. 2 J).

The endosperm is Cellular in *Magnolia stellata* as well as in *M. obovata*. After triple fusion the primary endosperm nucleus divides and a transverse wall is laid to give rise to the micropylar and chalazal chambers. Further divisions in the two chambers are usually transverse and produce a linear row of cells. Rarely, however, the chalazal chamber may divide vertically (Fig. 2 L). In *M. obovata*, at the late zygote or early 2-celled stage of the proembryo, two or three cells in the chalazal region of the endosperm elongate considerably to form the chalazal haustorium while the rest of them divide in all planes and constitute the endosperm proper (Fig. 2 M). The embryogeny is of the Onagrad type.

In the mature seed the inner integument is crushed while the outer differentiates into an inner stony and outer fleshy layers. After fertilization the funicular vascular supply extends into the outer integument and is prominent in the sarcotesta of the ripe seeds.

A comparison of the embryological characters of *Schisandra* and Magnoliaceae shows significant differences as tabulated below (for literature see Padmanabhan, 1960; Hayashi, 1960):

	<i>Schisandra</i>	Magnoliaceae
Flower	Unisexual	Bisexual (rarely unisexual) <sup>1</sup>
Stamen	Monadelphous, well differentiated into filament, anther and connective; single traced and without a sclerenchymatous sheath	Free, usually poorly differentiated into filament, anther and connective; 3 to 5-traced and with sclerenchymatous sheath
Anther	Protuberant, dehiscence extrorse	Embedded, dehiscence introrse
Tapetum	Parietal in origin, secretory, cells multinucleate	Parietal or sporogenous in origin, secretory, cells binucleate
Microspore tetrad	Tetrahedral, decussate	Isobilateral
Pollen	Hexacolpate with reticulate exine	Monocolpate with smooth exine
Carpel	With a ventral stigmatic crest	Without a ventral stigmatic crest
Ovary	Bilocular with a single ovule in each locule	Unilocular, bi- to multiovulate
Endosperm	Cellular	Cellular <sup>2</sup> , rarely with chalazal haustorium
Embryo	Minute with a short and inconspicuous suspensor	Minute with a massive suspensor
Seed	Albuminous, testa undifferentiated, hard, formed only by the outer integument	Albuminous, testa differentiated into an outer fleshy and an inner hard layer, formed by the outer integument alone
Fruit	Berry with succulent pericarp	Follicle or capsule with hard pericarp

<sup>1</sup> *Kmeria*, *Michelia* sp.

<sup>2</sup> The report of the occurrence of Nuclear endosperm in *Magnolia grandiflora* by Earle (1938) requires confirmation.

While some features like the structure of the ovule, development of the embryo sac, Cellular en-

dosperm and Onagrad type of embryogeny are common to the Magnoliaceae and Schisandraceae,

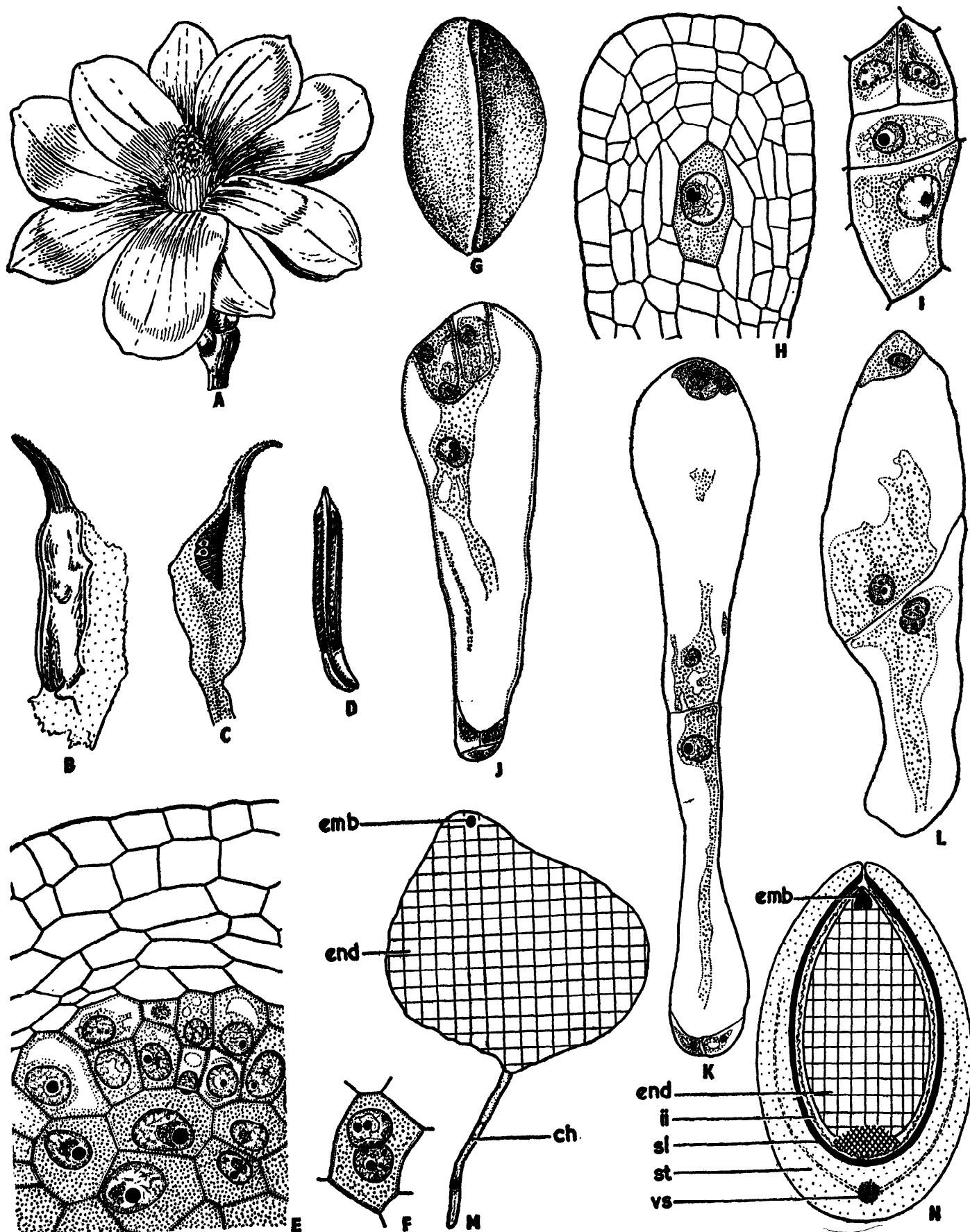


FIG. 2A-N— A-J. *Magnolia stellata*; K-N. *M. obovata* (ch, chalazal haustorium; emb, embryo; end, endosperm; ii, inner integument; sl, stony layer; st, sarcotesta; vs, vascular supply). A. Flower. x 1.5. B. Carpel. x 6. C. Same in l.s. showing two ovules. x 6. D. Single stamen. x 6. E. T.s. portion of anther having two-layered tapetum. x 560. F. Binucleate tapetal cell. x 560. G. Palynogram. x 1060. H. Megaspore mother cell. x 560. I. T-shaped tetrad. x 1090. J. Organized embryo sac. x 530. K. First division of endosperm. x 530. L. Three-celled endosperm; chalazal chamber has divided vertically. x 530. M. Cellular endosperm with chalazal haustorium (wholemount). x 53. N. L.s. mature seed (diagrammatic); outer integument differentiated into inner stony and outer fleshy sarcotesta. x 6.

there are significant differences in the flower, and structure of the carpel, stamen, tapetum, pollen, seed and fruit. Embryological data, therefore, do not support the inclusion of *Schisandra* in the Magnoliaceae.

During recent years the affinities of the Schisandraceae with the Illiciaceae have been frequently emphasized (see Ozenda, 1946; Smith, 1947; Bailey & Nast, 1948; Erdtman, 1952). Although both these families resemble in the structure of the cuticle, stomata, presence of mucilage cells in the phloem (Bailey & Nast, 1948), and the number of chromosomes (Whitaker, 1933), a careful analysis of various characters reveals important differences between them as mentioned below:

	Schisandraceae	Illiciaceae
Habit	Woody vines	Shrubs or small trees
Flower	Unisexual, torus without any sterile extension	Bisexual, receptacle ends into a conspicuous sterile extension
Stamen	Spirally arranged	Whorled
Pollen	Hexacolpate	Tricolpate
Carpel	Spirally arranged, conduplicate, stylicless	Whorled, conduplicate with a vascularized style
Ovule	1 or 2 on laminar placentation	1, borne ventrally
Seed	Reniform, testa smooth or rugulose	Ellipsoid, testa smooth or shining

daceae, or. Haloragaceae) along with *Callitriche*, *Gunnera*, *Hippuris*, *Lauremburgia*, *Loudonia*, *Myriophyllum* and *Proserpinaca*. Later, Engler & Prantl (1889-1897) removed *Hippuris* and *Callitriche* to separate families—Hippuridaceae and Callitrichaceae respectively—while the remaining genera were retained under the Halorrhagidaceae. Schindler (1905) divided the family Halorrhagaceae into two subfamilies, Halorrhagoideae and Gunneroideae, and included *Haloragis*, *Lauremburgia*, *Loudonia*, *Meziella* and *Proserpinaca* in the tribe Halorrhageae while *Myriophyllum* was assigned a position in the tribe Myriophylleae of Halorrhagoideae. The genus *Gunnera* was kept under the subfamily Gunneroideae. Wettstein (1935) as well as Rendle (1952) accepted *Haloragis* as distinct from *Hippuris*. Wettstein (1935) went a step further and segregated *Gunnera* into a separate and more advanced family Gunneraceae. Schnarf (1931) has also treated *Haloragis*, *Gunnera* and *Hippuris* under separate families. Recently Hutchinson (1959) assigned *Haloragis* along with *Hippuris* and *Gunnera* to the Haloragaceae, but removed *Callitriche* to a separate family.

The embryological data presented in the following pages are based on the material of *H. colensoi* collected by Professor P. Maheshwari from Kew Gardens in August, 1961.

The flowers are arranged in glomerules (Fig. 3 A). They are small, pedicellate, bracteate, bisexual,

It is evident that in several characters like the bisexual flower, whorled arrangement of the carpel, pollen structure, the presence of a vascularized style, and the structure of the seed and fruit the Illiciaceae deviate considerably. Similar opinions have also been expressed by Hutchinson (1959), Matsuda (1893) and McLaughlin (1933) on the basis of taxonomy, anatomy and wood structure respectively. However, a detailed embryological study of the Illiciaceae is desirable before a final opinion can be expressed about its interrelationships.

*Haloragis*: As early as 1862, Bentham & Hooker classified the genus *Haloragis* under Haloragaceae (= Halorrhagaceae, Haloragidaceae, Halorrhagi-

tetramerous and actinomorphic (Fig. 3 B, C). The ovary is tetracarpellary, tetralocular, and inferior; each locule having a single, pendulous, anatropous ovule (Fig. 3 D). The anther wall comprises the epidermis, fibrous endothecium, two middle layers, and glandular tapetum whose cells become binucleate (Fig. 3 E). The pollen grains are 4 or 5 rupidate (Fig. 3 F) and have a smooth exine.

The ovules are anatropous, bitegminal and crassinucellar (Fig. 3 J). A primary archesporial cell cuts off a parietal cell; the megaspore tetrads are linear or T-shaped; and the development of the female gametophyte is of the Polygonum type (Fig. 3 G-I). The two polar nuclei fuse in the chalazal part of the embryo sac just above the antipodal cells (Fig. 3 I, L).

Fertilization is porogamous (Fig. 3 K). The synergids degenerate soon after fertilization while the antipodal cells persist for quite some time. The first division of the primary endosperm nucleus is followed by a vertical (Fig. 3 M) or transverse wall (*H. asperima*). Subsequent divisions lead to the development of a cellular endosperm (Fig. 3 N).

The first division of the zygote is transverse resulting in a small apical (*ca*) and a large basal (*cb*) cell (Fig. 3 O). The former divides transversely (Fig. 3 Q) to form *cc* and *cd* while the latter undergoes a single vertical division (Fig. 3 P, Q) to give rise to a 2-celled haustorium containing large nuclei and highly vacuolated cytoplasm. The cells of the

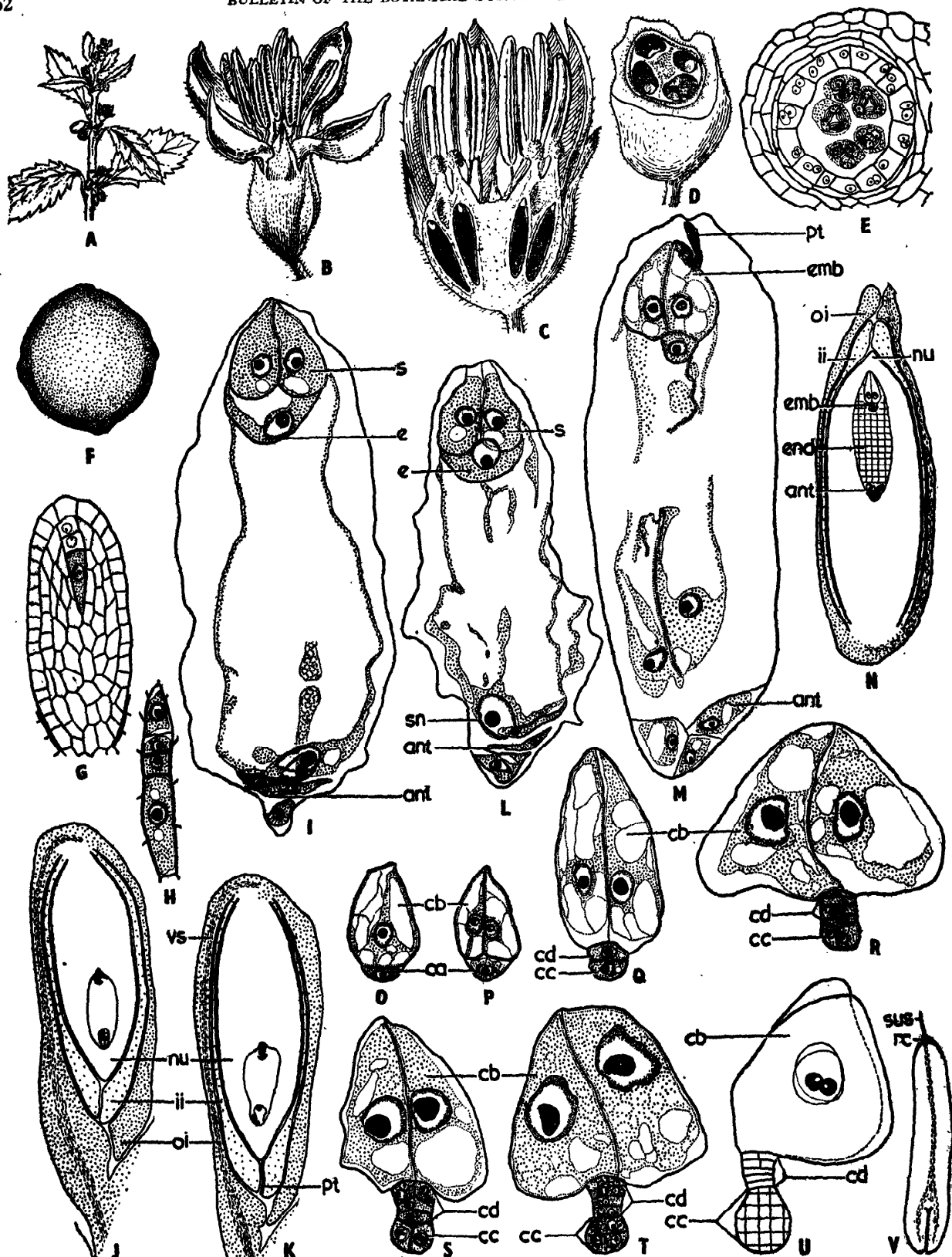


FIG. 3A-V—*Halbragis colensoi* (ant, antipodal cell; e, egg; emb, embryo; end, endosperm; ii, inner integument; nu, nucellus; oi, outer integument; pt, pollen tube; rc, root cap; s, synergid; sn, secondary nucleus; sus, suspensor; vs, vascular supply). A. Portion of a branch bearing inflorescences in the axils of leaves. x 1. B. Flower. x 10. C. Flower spread open. x 17. D. T. s. ovary showing tetralocular condition. x 10. E. Transverse section of an anther lobe showing binucleate tapetal cells. x 435. F. Palynogram. x 782. G. Megaspore mother cell. x 435. H. Linear megaspore tetrad. x 782. I. Organized embryo sac; polar nuclei have migrated to the chalazal end. x 782. J. L. s. anatropous ovule at the mature embryo sac stage. x 122. K. Same showing porogamous fertilization. x 122. L. Mature embryo sac; the polar nuclei have fused just above the antipodal cells. x 782. M. Two-celled endosperm. x 435. N. L. s. ovule showing cellular endosperm and persistent antipodal cells. x 782. O-V. Embryogeny (explanation in text); O. x 478; P-T. x 435; U. x 274; V. x 43.

haustorium become massive (Fig. 3 R-U). Their degenerating remnants may be seen above the suspensor of the dicotyledonous embryo (Fig. 3 V). The tier *cc* divides by a vertical wall; subsequent divisions lead to the formation of the embryo proper. Divisions in *cd* contribute to the organization of the root cap and suspensor which is connected with the haustorium.

The seeds are albuminous. The seed coat comprises one or two layers of flattened cells at maturity and is formed by the outer integument while the inner integument disorganizes almost completely excepting a few cells at the tip. The fruit is a nut and the pericarp becomes very hard due to the presence of sclerenchymatous cells.

The morphological and embryological features of *Haloragis*, *Hippuris* and *Gunnera* are summarized in the following table (for literature see Juell, 1911; Schnarf, 1931; Lawrence, 1951):

	<i>Haloragis</i>	<i>Hippuris</i>	<i>Gunnera</i>
Flower	Bracteate, bisexual, 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+4, obdiplostemonous	Single stamen placed medianly	2, antipetalous
Pollen	4 or 5 rupoidate	4-6 colpate	3-5 colpate
Gynoecium	Tetracarpellary, tetralocular; single, pendulous ovule in each locule	Monocarpellary, unilocular; single pendulous ovule	Bicarpellary, unilocular; solitary ovule
Ovule	Anatropous, bitegminal, crassinucellar with a feeble funicular obturator	Anatropous, naked or unitegminal; tenuinucellar, nucellar cap and a feeble funicular obturator present	Anatropous, bitegminal, crassinucellar; obturator absent
Parietal cells	Present	Absent	Present
Embryo sac	Polygonum type	Polygonum type	Peperomia type
Fertilization	Porogamous	Pollen tube penetrates the embryo sac laterally	Porogamous
Embryo	Large, cylindrical, suspensor haustorium present	Large, cylindrical, suspensor haustorium absent	Minute, obcordate, without suspensor haustorium

there is nothing in its anatomy "which is inconsistent with the suggestion that the plant may belong to the Begoniaceae." However, Metcalfe & Chalk (1950) themselves include it as an anomalous genus in the Campanulaceae.

Recently Airy Shaw (1941, 1954) sought to exclude *Pentaphragma* from the Campanulaceae and raised it to the status of a new family Pentaphragmataceae. According to him the habit and foliage of the plant suggest certain Begoniaceae, Rubiaceae (*Argostemma*), and Gesneriaceae (*Epi-thema*); the succulence of the stem and leaves recalls the Cucurbitaceae; the scorpioidally cymose inflorescence is similar to that of some Hydrophyllaceae and Boraginaceae; while the indumentum of branched, multicellular hairs resembles the Solanaceae. He also emphasized that "almost every

These differences justify the recognition of *Haloragis* as distinct from *Hippuris* and *Gunnera*. The separation of *Haloragis* from *Hippuris* is also supported on anatomical (Metcalfe & Chalk, 1950) and palynological (Erdtman, 1952) grounds. Similarly, characters like the presence of four wall layers in the anther, Peperomia type of embryo sac, absence of suspensor haustorium, and floral morphology, all support the segregation of *Gunnera* from *Haloragis*. Hence the inclusion of these genera in different families is amply justified.

*Pentaphragma*: Bentham & Hooker (1876) and Engler & Prantl (1889) assigned *Pentaphragma* to the Campanulaceae. Hallier (quoted in Airy Shaw, 1941) retained this genus in the Campanulaceae, but admitted that it showed certain resemblances in its inflorescence with the Boraginaceae, Convolvulaceae (*Jacquemontia*) and Loasaceae (*Kissenia*). According to Metcalfe (cited in Airy Shaw, 1941)

author who has dealt with *Pentaphragma* has admitted its highly anomalous position in the Campanulaceae, and it is, therefore, surprising that it has not been removed earlier."

In view of the divergent opinion of taxonomists an embryological study of *P. horsfieldii* was undertaken by Kapil & Vijayaraghavan (1962) on the basis of materials very kindly provided by Mr K. Jong and Dr A. N. Rao of the Universities of Malaya and Singapore respectively.

The flowers are borne in acropetal succession on a scorpioid cymose inflorescence (Fig. 4 A). They are bisexual and actinomorphic (excepting the calyx; Fig. 4 B) and possess a bicarpellary, bilocular and inferior ovary containing several anatropous ovules on an axile placenta. The wall of the anther consists of five layers—the epidermis, the fibrous



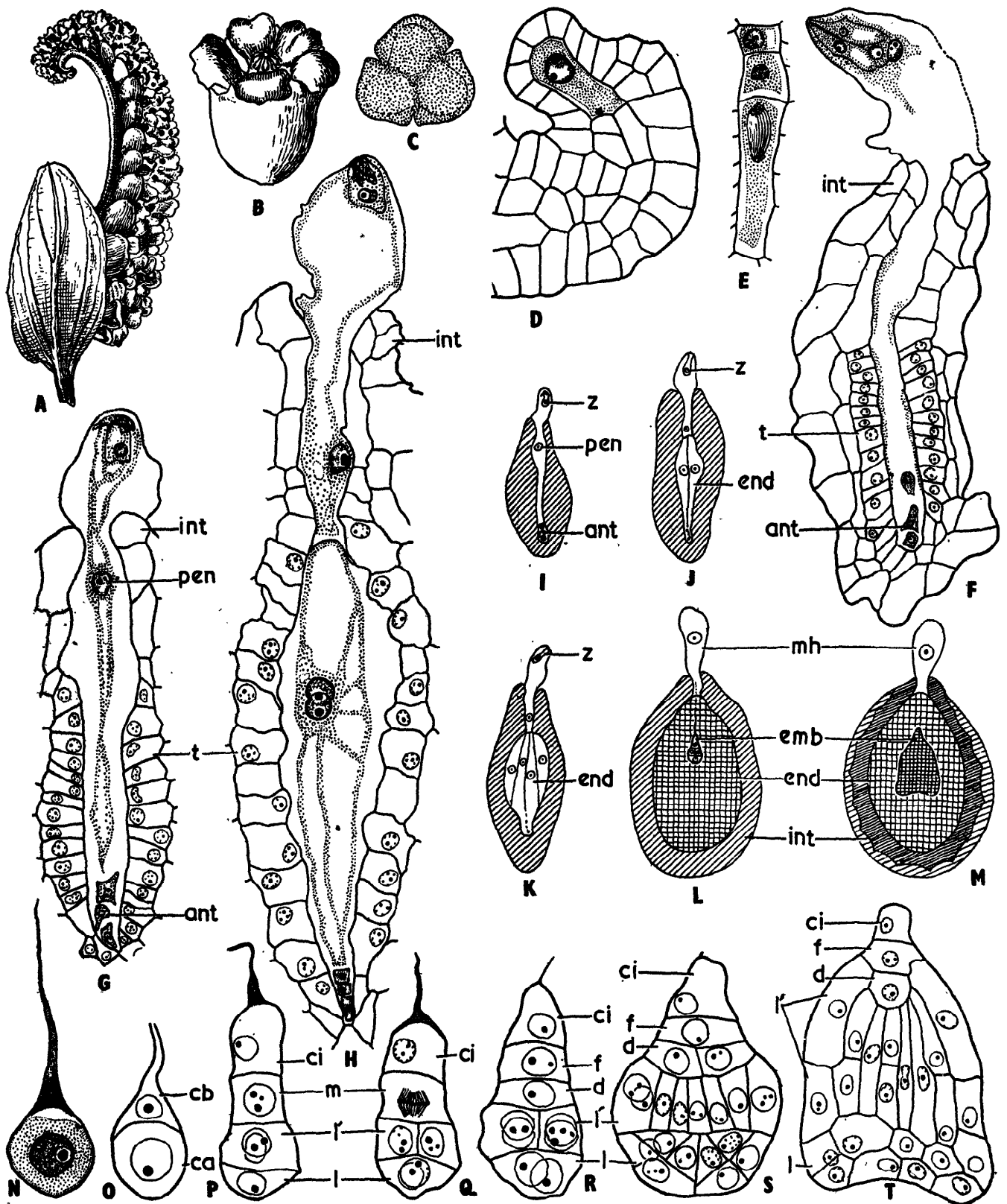


FIG. 4A-T—*Pentaphragma horsfieldii* (ant, antipodal cells; emb, embryo; end, endosperm; int, integument; mh, micropylar haustorium; pen, primary endosperm nucleus; t, endothelium; z, zygote). A. Scorpioid cymose inflorescence. x 1.5. B. single flower x 7. C. Palynogram. x 885. D. Megaspore mother cell. x 885. E. Formation of linear megaspore tetrad. x 885. F. Mature embryo sac with extramicrophyllar egg apparatus. x 475. G. Embryo sac showing zygote and primary endosperm nucleus; the antipodal cells are still healthy. x 475. H. Three-celled endosperm. x 475. I-M. Stages in the development of endosperm (diagrammatic). N-T. Embryogeny (see text), N-S. x 885; T. x 548.



endothecium, two middle layers and the glandular tapetum with binucleate cells. The pollen grains are tricolporate (Fig. 4 C) and have a thick exine.

The ovules are anatropous, unitegminal and tenuinucellar. A single hypodermal archesporial cell differentiates and functions as the megaspore mother cell (Fig. 4 D) without cutting off any parietal cell. A linear tetrad is formed (Fig. 4 E) and the chalazal megaspore gives rise to an 8-nucleate gametophyte of the Polygonum type. At the 4-nucleate stage the micropylar portion of the embryo sac (Fig. 4 F) invariably comes out of the integument due to the degeneration of the nucellus. However, its lower portion is in direct contact with the inner layer of the integument which differentiates into an endothelium.

The first division of the primary endosperm nucleus is followed by a transverse wall resulting in a small micropylar and a large chalazal chamber (Fig. 4 G, H). The remnants of the antipodal cells may be seen up to the first few divisions of the endosperm. The micropylar chamber remains undivided and forms a haustorium with a hypertrophied nucleus. Vertical divisions in the chalazal chamber result in a 4-celled endosperm followed by further divisions to give rise to the endosperm proper (Fig. 4 I-M). The development of the endosperm is, therefore, *ab initio* Cellular.

The zygote elongates considerably (Fig. 4 N) and pushes its way into the endosperm. The first two divisions are transverse resulting in a 4-celled, linear proembryo designated as *l*, *l'*, *m* and *ci*. The tiers *l* and *l'* divide by vertical walls to form an octant while *m* divides transversely to produce *d* and *f*. The tier *l* gives rise to the cotyledons and shoot

apex; *l'* to the hypocotyl and root cortex; and *d* to the root tip. The remaining cells *f* and *ci* produce the suspensor. The development of the embryo (Fig. 4 N-T) thus conforms to the Solanad type.

At the time of fertilization the single integument comprises the epidermis, a middle layer and an endothelium. However, only the outer epidermis persists in the mature seed and its cells become thickened in the lower portion (Fig. 4 M).

Although *Pentaphragma* shows some resemblances with the Begoniaceae in its anatomy (see Airy Shaw, 1941; 1954), members of the latter differ radically in other respects. They are characterized by monoecious and unisexual flowers with two or five valvate sepals; 2-5 imbricate petals (sometimes absent); a bi- or tricarpellary inferior ovary which is usually two or three (rarely four or six) chambered; 2-5 connate styles with twisted stigma; winged fruits and seeds with scanty endosperm. The ovule is bitegminal and crassinucellar; the antipodal cells are ephemeral and degenerate before the organization of the embryo sac; the endosperm is Nuclear; and the embryogeny follows the Onagrad type (see also Swamy & Parameswaran, 1960). Hence any close relationship with this family is out of question.

The embryological features of *Pentaphragma*, Boraginaceae and Campanulaceae are compared below (for literature see Souèges, 1936; Subramanyam, 1951; Crété, 1956; Johri & Vasil, 1956):

These data suggest that *Pentaphragma* is very close to the Campanulaceae in its embryological characters and is correctly assigned to this family. However, it has a few distinctive features

	<i>Pentaphragma</i>	Boraginaceae	Campanulaceae
Flower	Bisexual, actinomorphic (except calyx), epigynous	Bisexual rarely zygomorphic, hypogynous	Bisexual, actinomorphic or zygomorphic, epigynous
Anther tapetum	Secretory, cells binucleate	Secretory, cells multinucleate	Secretory, cells binucleate
Pollen	Tricolporate	Usually tricolporate	Variable
Gynoecium	Inferior, bicarpellary, bilocular	Superior, bicarpellary uni- or bilocular with a tendency to tetra to decalocular condition	Inferior, bicarpellary, bilocular
Ovule	Many, anatropous, unitegminal and tenuinucellar	1-4, anatropous or hemianatropous, unitegminal and crassinucellar	Many, anatropous, unitegminal and tenuinucellar
Endothelium	Restricted to the chalazal portion of the embryo sac	Covers the entire embryo sac	Restricted to the chalazal portion of the embryo sac
Embryo sac	Polygonum type, the micropylar portion of the embryo sac comes out of the integumentary level, the antipodal cells degenerate after fertilization	Polygonum or Allium type, micropylar part of the embryo sac remains within the integuments, antipodal cells degenerate before fertilization	Polygonum type, micropylar portion remains within the integumentary level; antipodal cells degenerate after fertilization
Endosperm	Cellular; micropylar haustorium single-celled; no chalazal haustorium	Nuclear, Cellular or Helobial; when Cellular it shows 4-celled micropylar and chalazal haustoria	Cellular; micropylar haustorium 2-celled; chalazal haustorium two or 1-celled
Embryogeny	Solanad type	Chenopodiad type	Solanad type

like the extramicropylar embryo sac, uninucleate, single-celled endosperm haustorium and short embryonal suspensor which justify its inclusion in the Campanulaceae as a separate subfamily, Pentaphragmoideae.

#### ACKNOWLEDGEMENTS

I am grateful to Professor P. Maheshwari for advice and criticism; to Messrs S. Jalan, M. R. Vijayaraghavan, N. N. Bhandari and Miss S. Bala Sethi, research scholars in the department for their active cooperation and help in the preparation of this manuscript. Thanks are also due to Mr D. M. Sonak for making some illustrations and to the National Institute of Sciences of India for the award of Senior Fellowship.

#### LITERATURE CITED

- AIRY SHAW, H. K. Additions to the Flora of Borneo and other Malay Islands: The Pentaphragmataceae of the Oxford University expedition to Sarawak, 1932. *Kew Bull.* : 233-236, 1941.
- Pentaphragmataceae. *Flora Malesiana* : 517-528, 1954.
- BAILEY, I. W. AND C. G. NAST. Morphology and relationships of *Illicium*, *Schisandra* and *Kadsura*. I. Stem and leaf. *J. Arnold Arbor.* 29 : 77-89, 1948.
- BENTHAM, G. AND J. D. HOOKER. *Genera Plantarum*. London. 1862-1876.
- CRETE, P. Contribution à l'étude de l'albumen et de l'embryon chez les Campanulacées, les Lobeliacées. *Bull. Soc. bot. France* 103 : 447-454, 1956.
- EARLE, T. T. Embryology of certain Ranales. *Bot. Gaz.* 100 : 257-275, 1938.
- ENGELER, A. AND K. PRANTL. *Die Natürlichen Pflanzenfamilien*. Leipzig. 1889-1897.
- ERDTMAN, G. *Pollen Morphology and Plant Taxonomy*. Waltham. 1952.
- HAYASHI, Y. On the microsporogenesis and pollen morphology in the Magnoliaceae. *Sci. Rep. Tôhoku Univ. (Biol.)* 27 : 45-52, 1960.
- HUTCHINSON, J. *The Families of Flowering Plants. I. Dicotyledons*. London. 1926.
- HUTCHINSON, J. *The Families of Flowering Plants. I. Dicotyledons*. Oxford 1959.
- JOHRI, B. M. AND I. K. VASIL. The embryology of *Ehretia laevis* Roxb. *Phytomorphology* 6 : 134-143, 1956.
- JUEL, H. O. Studien über die Entwicklungsgeschichte von *Hippuris vulgaris*. *Nova Acta Soc. Upsal.* 2 : 1-26, 1911.
- KAPIL, R. N. AND M. R. VIJAYARAGHAVAN. Embryology and systematic position of *Pentaphragma horsfieldii* (Miq.) Airy Shaw. *Curr. Sci.* 31 : 270-272, 1962.
- LAWRENCE, G. H. M. *Taxonomy of Vascular Plants*. New York. 1951.
- MCLAUGHLIN, R. P. Systematic anatomy of the woods of the Magnoliales. *Trop. Woods* 34 : 3-39, 1933.
- MAHESHWARI, P. *An Introduction to the Embryology of Angiosperms*. New York. 1950.
- Embryology in relation to taxonomy. (In Press), 1962.
- MATSUDA, S. On the anatomy of the Magnoliaceae. *J. Coll. Sci., Imp. Univ., Tokyo* 4 : 115-149, 1893.
- METCALFE, C. R. AND L. CHALK. *Anatomy of the Dicotyledons*. Oxford. 1950.
- OZENDA, P. Sur l'anatomie liberoligneuse de Schizandracées. *C. R. Acad. Sci. Paris* 223(4) : 207-209, 1946.
- PADMANABHAN, D. A contribution to the embryology of *Michelia champaca*. *J. Madras Univ.*, B. 30 : 155-165, 1960.
- RENDLE, A. B. *The Classification of Flowering Plants. II*. Cambridge. 1952.
- SCHINDLER, A. K. Halorrhagaceae. In Engler's *Das Pflanzenreich*. Leipzig. 1905.
- SCHNARF, K. *Vergleichende Embryologie der Angiospermen*. Berlin. 1931.
- SMITH, A. C. The families Illiciaceae and Schisandraceae. *Sargentia* 7 : 1-224, 1947.
- SOUE'GES, R. Embryogénie des Campanulacées. Développement de l'embryon chez le *Campanula patula* L. *C. R. Acad. Sci. Paris* 202 : 2009-2011, 1936.
- SUBRAMANYAM, K. Interrelationships of Campanulatae. *J. Mysore Univ.* 12 : 5-13, 1951.
- SWAMY, B. G. L. AND N. PARAMESWARAN. A contribution to the embryology of *Begonia crenata*. *J. Indian bot. Soc.* 39 : 140-148, 1960.
- WETTSTEIN, R. *Handbuch der Systematischen Botanik*. Leipzig & Wien. 1935.
- WHITAKER, T. W. Chromosome number and relationships in the Magnoliales. *J. Arnold Arbor.* 14 : 376-385, 1933.