A CONTRIBUTION TO THE LIFE-HISTORIES OF *STELLARIA MEDIA*, LINN. AND *POLYCARPON LŒFLINGIÆ*, BENTH. & HOOK.

By NIRANJAN PAL, *M.Sc., Department of Botany, Calcutta University.*

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The family Caryophyllaceæ includes about 70 genera and 1,450 species, distributed mostly in the temperate regions of the Northern Hemisphere, of which only 19 genera and 104 species occur in India (Hooker, 1875). In Bengal, the genera *Stellaria* and *Polycarpon* are represented by one species each, namely *S. media*, Linn. and *P. Lœflingiæ* Benth. and Hook.

S. media is a member of the sub-family *Alsinoideæ*. It is very widely distributed and is very variable in its external characters. It occurs in waste lands around Calcutta as an annual winter herb.

P. Lœflingiæ belongs to the same sub-family, but it is placed under the tribe *Polycarpeæ*. In Bengal, it occurs as an erect or diffuse annual weed in fields and waste places. It is locally known as 'Gima sak' and is used as a green vegetable.

Investigations on the genus *Stellaria* dates from the year 1855 when Tulasne worked on the embryology of the genus. The literature up to the year 1930 has been summarised by Schnarf (1931) and so it need not be repeated here. Since then Joshi (1936) has studied the life-history of *S. media*. According to him, the previous accounts relating to the development of the female gametophyte of this plant as given by Rocén (1927) and Gibbs (1907) are contradictory. Joshi's observations also are not very clear. Maheshwari (1937) states, 'The whole thing needs careful re-investigation. It would not be surprising if in a plant like *Stellaria media* which is so variable in other respects, some difference may occur in the mode of embryo-sac development also, but Joshi's figures do not seem to prove that it is so'.

The genus *Polycarpon* has received very little attention from the embryologists. Rocén (1927) alone has studied the embryology of *P. tetraphyllum*.

MATERIALS AND METHODS.

The materials were collected from different parts of Calcutta, and fixed on bright sunny days between 9 a.m. and 12 noon, during the period January to April, 1948. Formal-acetic-alcohol and Nawaschin's fluid were used as killing and fixing reagents, both of which proved satisfactory. A suction pump was used to facilitate the penetration of the fixing fluid. The floral envelopes of the comparatively bigger buds were removed before fixation. The materials were dehydrated, cleared and embedded in paraffin in the usual way. Sections were cut 8 to 16 μ thick depending on the stage required for study. They were usually stained either with Heidenhain's Iron-alum-Haematoxylin or Newton's Gentign-violet-iodine.

OBSERVATIONS.

(i) *Organogeny of the flower.*—The development of the floral organs appears to be more or less similar in both the plants except for certain minor details. At

first a dome-shaped floral primordium makes its appearance in the axil of a leaf (Fig. 1). Generally it remains enclosed by the leaf-primordium. The different floral whorls arise in acropetal succession from the sides of this primordium. The primordia of the sepals differentiate first (Fig. 1). In *S. media*, the stamens appear next. These are followed by the primordia of the petals (Fig. 14), but in *P. Lœflingiœ*, the sequence is reversed (Fig. 2). The primordia of the carpels in both the species appear last (Fig. 3).

Rendle (1938) states that the floral formula of *S. media* varies considerably. According to him, the flower may have the formula $S_5P_5A_{5+5}G_3$ or $S_5P_5A_5G_3$ or $S_5P_5A_3G_3$. The petals may sometimes be absent. Observations made in the course of the present study based on plants fixed from different localities near about Calcutta show that the flower is typically pentamerous and pentacyclic, the carpels being generally five. It is interesting to note in this connection that Hooker (1875) and Prain (1903) both report variation of the carpels from two to five.

According to Rendle (1938), the flowers of the tribe *Polycarpeæ* are reduced. Occasionally the petals are absent and the stamens are reduced in number. In *P. Lœflingiœ*, however, the following floral formula has been observed in course of the present investigation: $S_5P_5A_5G_3$. Hooker (1875), Prain (1903) and Rocén (1927) reported the number of the carpels as three. Sometimes it has been found to be four in both the plants.

(ii) *Development and structure of microspores.*—At first the anther is composed of a homogeneous mass of meristematic cells. It is somewhat circular in outline, but as it grows, it soon becomes bilobed and later four-lobed. The archesporium is hypodermal in origin (Fig. 4). Four bands of primary archesporial cells, one in each lobe, differentiate in the anther tissue almost simulateneously. Each band is three to six cells long and two to three cells broad. The number of archesporial cells is less in *S. media*. This type of extensive archesporium in an anther has been reported in some of the related families, e.g., Amarantaceæ (Joshi & Rao, 1934; Kajale, 1940*b*), Aizoaceæ (Kajale, 1940*a*), Phytolaccaceæ (Joshi & Rao, 1936) and also in *S. media* by Joshi (1936). The archesporial cells can be easily distinguished by their larger size, greater chromaticity and larger nuclei.

The primary archesporial cells divide periclinally giving rise to a layer of primary parietal or wall cells outside and a layer of primary sporogenous cells inside (Fig. 5). All the archesporial cells, however, do not divide simultaneously. The primary wall cells increase in size and undergo periclinal divisions; the outermost cells divide again and thus three cell-layers of parietal tissue are formed in-between the epidermis and the sporogenous cells of the anthers (Fig. 6). The outermost layer of parietal cells develops into the endothecium which shows the characteristic spiral bands at maturity. The middle layer of cells is crushed in the process of development and the innermost one gives rise to a secretory tapetum. The tapetal cells become binucleate during synizesis of the pollen-mother cells. Schnarf (1931) considers this binucleate secretory type of tapetum to be a characteristic feature of the order Centrospermæ. Joshi (1936) reports the presence of more than two nuclei in a single tapetal cell.

The divisions of the primary sporogenous cells lead to the increase of the microspore-mother cells. In a cross-section of the anther of *P. Lœflingiœ*, generally five microspore-mother cells are found in each lobe, whereas in *S. media* the number is less.

The microspore-mother cells are mostly polygonal in outline and are closely packed together inside the anther loculus without any intercellular spaces. They undergo a fairly long period of rest during which the size of the cells as well as their nuclei increases. Generally one big nucleolus is present in a nucleus. Sometimes in *P. Lœflingiœ*, a small globular bud-like structure is seen associated with the nucleolus which either remains directly attached to or lies near it (Fig. 6). Due to unequal rate of growth of the pollen-mother cells and the tapetal cells, the

latter get detached from the former. In *P. Lœflingiœ*, this occurs during the first division of the pollen-mother cells. It is interesting to note that this phenomenon was also noticed by Joshi (1936). The pollen-mother cells first show signs of rounding up in the diplonema stage. In this stage, the presence of chiasmata in the separating bivalents is seen distinctly in *S. media*, whereas in *P. Lœflingiœ* it is not recognisable (Fig. 15). At diakinesis the bivalents come to lie at the periphery of the nucleus. They are mostly rod-shaped in appearance. The nucleolus disappears. A careful examination shows that the number of bivalents in the pollen-mother cells of *S. media* is 14 and in *P. Lœflingiœ* is 18 (Figs. 7 & 16). This number has also been found during the metaphase of the first division. (Figs. 8 & 17). Both the 1st & 2nd divisions appear to be normal.

Cytokinesis takes place by furrowing. The arrangement of the pollen tetrads is mostly tetrahedral, but in a few cases isobilateral arrangement has also been observed (Fig. 18).

Both in *S. media* and *P. Lœflingiœ*, when first formed, the pollen grains are smooth and more or less triangular in shape. Very soon they increase in size and assume a spherical form. The intine and exine become differentiated. The latter is smooth and thick and shows no markings on its outer surface. In *P. Lœflingiœ*, the pollen grains show a peculiar intermediate structure. They become long and narrow and possess three alternate longitudinal ridges and furrows (Figs. 9 & 10). As they grow, they become gradually spherical in outline and at maturity they are almost spherical. Erdtman (1943) reports two types of pollen grains in this family:—(*a*) *Cribellate* (which is the predominating type) and (*b*) *Colpate* (*tricolpate*). It is interesting to note that in *P. Lœflingiœ*, the pollen grains become *tricolpate* in an intermediate stage of their development.

The germ-pores are somewhat circular in outline and provided with a special marginal area as mentioned by Erdtman (1943). The number of pores in the pollen grains of *P. Lœflingiœ* is only three, but in *S. media* it is six or more. In *S. aquatica*, the number has been reported to be 12. The mature pollen grains are 20–35 μ in diameter in *S. media* and 15–30 μ in *P. Lœflingiœ*. It is interesting to recall that the diameter of the pollen grains has been recorded to be 35 μ in *S. aquatica* and 29 μ in *S. uliginosa*. According to Joshi (1936) the pollen grains of *S. media* vary from 18 to 30 μ in diameter.

In both the plants, degeneration of the microspores while inside the microsporangium is a common phenomenon. They may degenerate in the tetrad stage or at a later stage, and the number of such degenerating microspores was found to be few or many inside a microsporangium. This phenomenon was also noted by Joshi (1936) in *S. media*.

The nucleus of the pollen grains moves towards the periphery before division; a small generative nucleus is cut off which becomes delimited by a cytoplasmic membrane as is commonly seen in other plants (Fig. 11). Later on, the generative and the vegetative nuclei lie side by side in the cytoplasm (Fig. 12). The generative nucleus next divides to form two minute lens-shaped male nuclei (Figs. 13 & 19).

The mature pollen grains are rich in starch grains. They attain maturity when the embryo-sacs of the same flowers are in 1- or 2-nucleate stages. They are shed in the 3-nucleate stage which is considered by Schnarf (1931) to be a characteristic feature of the order Centrospermæ.

(iii) *Development and structure of the ovule.*—The placenta is very massive and is composed of large cells surrounding the central vascular strand. In later stages of development it shows many lysigenous cavities in the peripheral region.

The placentation is axile in both the species in the beginning, with two rows of ovules in each cell (Fig. 30). In *P. Lœflingiœ*, the number of the septa in the ovary is three and each of them is composed of about five layers of cells. These partition walls persist in the ovary even in the post-fertilisation stages. Later, when the embryo is fairly developed, these partition walls become crushed and

FIGS. 1–13. *Polycarpon Læflingiæ*. Figs. 1–3. Developmental stages of the floral parts. × 120. Figs. 4–6. Development of microspore-mother cell. × 700. Figs. 7 & 8. Diakinesis and Metaphase I (polar view). × 1500. Figs. 9–13. Development of pollen grains, Fig. 9, being T.S. of a ridged pollen grain. × 700.

FIGS. 14–24. *Stellaria media*. Fig. 14. Development of floral organs. × 120. Figs. 15–17. Diplotene, Diakinesis and Metaphase I of pollen-mother cell. × 1500. Fig. 18. Isobilateral pollen tetrad. × 1500. Fig. 19. Mature pollen grain. × 700. Fig. 20. T. S. of ovary showing the development of free central placentation from the axile condition. × 90. Fig. 21. Multiple archesporium in an ovule. × 700. Fig. 22. One-celled archesporium in divisional stage. × 700. Figs. 23–24. Stages of reduction division in the megaspore-mother cell. × 700.

obliterated, and then only the placentation becomes free central. But in *S. media*, the septa which in the early developmental stages are five in number and are absent at the top of the ovary, degenerate very soon. As a result of this, the axile placentation becomes free central at an early stage of development of the gynœcium. The signs of degeneration of the septa appear with the differentiation of the megaspore-mother cell in the ovules and by the time the chalazal megaspore begins to enlarge into embryo-sac, the ovary is completely one-chambered (Fig. 20). It may be pointed out here that Rocén (1927) describes a three chambered ovary in *S. media*.

The ovules arise as minute protuberances of the placenta. At first the tissue is uniform in structure with a tapering apex but soon the apical part of the tissue enlarges and differentiates as the massive nucellus. The integuments which are two in number, arise from the base of the thick nucellus one after another in basipetal succession. They are first noted as annular outgrowths after the differentiation of the primary archesporial cells. Each integument is composed of two layers of cells which seems to be a characteristic feature of the order. The inner integument soon covers the entire nucellus. Its apical region continues to grow further and forms a cap-like structure over the nucellus resulting in an elongated micropyle. It is four cells thick in *S. media* and three in *P. Lœflingiœ*. The outer integument does not overgrow the inner, and so takes no part in the formation of the micropyle (Figs. 23 & 40). In *S. media*, during the later stages of the development of the ovule some yellow granules become deposited in the cells of the outer layer of the outer integument and in the inner layer of the inner integument. In *P. Lœflingiœ*, no such deposition is, however, noted in the latter layer. The nucellar cap is composed of four layers of cells in *S. media*. In *P. Lœflingiœ*, the sub-epidermal cells of the cap degenerate and the embryosac lies next to the epidermis, the cells being elongated radially, which was also found in *Sisuvium portulacastrum* by Kajale (1940*a*) and in *Trianthema monogyna* by Bhargava (1935).

In *P. Lœflingiœ*, a peculiar structure is seen associated with the funicle. After the differentiation of the integuments, the ovule assumes an anatropous form. At this stage the funicle is seen to branch at the point of attachment of the ovule on the outer side. This branch increases in size, becomes tapering and extends up to the chalazal end of the ovule (Fig. 31).

(iv) *Megasporogenesis*.—The primary archesporium differentiates in the ovule even before the appearance of the integuments. Generally it consists of a group of hypodermal and sub-hypodermal cells varying in number from 1 to 7, but in *S. media* the number varies from 1 to 4 (Figs. 21, 22, 32 & 33). Rocén (1927) found only one archesporial cell in *P. tetraphyllum*. On the other hand, Joshi (1936) records 4–6 archesporial cells in *S. media*. Dahlgren (1916) and Rocén (1927) also described multicellular archesporium in different species of *Stellaria*.

All the archesporial cells do not behave in the same manner. In *S. media*, one of the median hypodermal cells cuts off a parietal cell outside and then functions as the megaspore-mother cell. With the increasing size of this mother cell, the other archesporial cells become indistinguishable. In no case, more than one functional archesporial cell has been found. But in *P. Lœflingiœ*, their behaviour is different. All those in the hypodermal position cut off parietal cells and thus several megaspore-mother cells are formed. However, further growth of most of them is arrested. Generally only the median one grows further and as a result of this the other megaspore-mother cells and the remaining archesporial cells become indistinguishable. As has been observed by Rocén (1927) in *P. tetraphyllum*, not more than one functioning megaspore-mother cell is met with. The cells underlying the megaspore-mother cell are somewhat larger than the surrounding nucellar cells. These appear to be archesporial in origin, having been displaced by the developing megaspore-mother cell. Their number and arrangement are variable (Figs. 34–38).

In *S. media*, a normal linear tetrad of megaspores is formed by the reduction division of the megaspore-mother cell of which only the chalazal one functions to give rise to a normal type of embryo-sac. Different stages of this division have been observed during the present investigation (Figs. 23–25). But in *P. Lœflingiœ*, the behaviour of the megaspore-mother cell during the reduction division is variable. After the heterotypic division, only the lower dyad cell divides again homotypically to give rise to two megaspores. Thus a row of three cells, i.e., one micropylar dyad and two chalazal megaspores is formed (Fig. 40). In this case only the lowermost megaspore functions to give rise to a normal type of embryo-sac (Fig. 41). But in other cases, a normal row of four megaspores is seen of which the micropylar megaspore is functional (Fig. 42). The presence of a row of two megaspores and one micropylar dyad (which may be 2-nucleate) and a normal linear tetrad of megaspores in the same plant has also been noted in the related families, e.g., Amarantaceæ (Joshi & Rao, 1934), Aizoaceæ (Kajale, 1940*a*) and Nyctaginaceæ (Rocén, 1927).

(v) *Development and organisation of the embryo-sac.*—The development of the embryo-sac is of the 'Normal type'. The nucleus of the functioning megaspore lies in the centre of the cell and enlarges. Small vacuoles develop at the two poles of the cell. The nucleus divides; the daughter nuclei migrate to the two opposite poles of the embryo-sac. The embryo-sac continues to increase in size and later only a single vacuole is seen in the centre. An abnormal case has been observed in *P. Lœflingiœ* where the two nuclei migrated towards the two lateral sides of the embryo-sac and consequently two big vacuoles appeared at the two poles. Some of the four-nucleate embryo-sacs of *P. Lœflingiœ* contain conspicuous bigger nuclei than others (Figs. 43 & 44). On reaching the two poles, each of the daughter nuclei of the 2-nucleate embryo-sacs divide twice to form an eight-nucleate embryo-sac (Figs. 28 & 45).

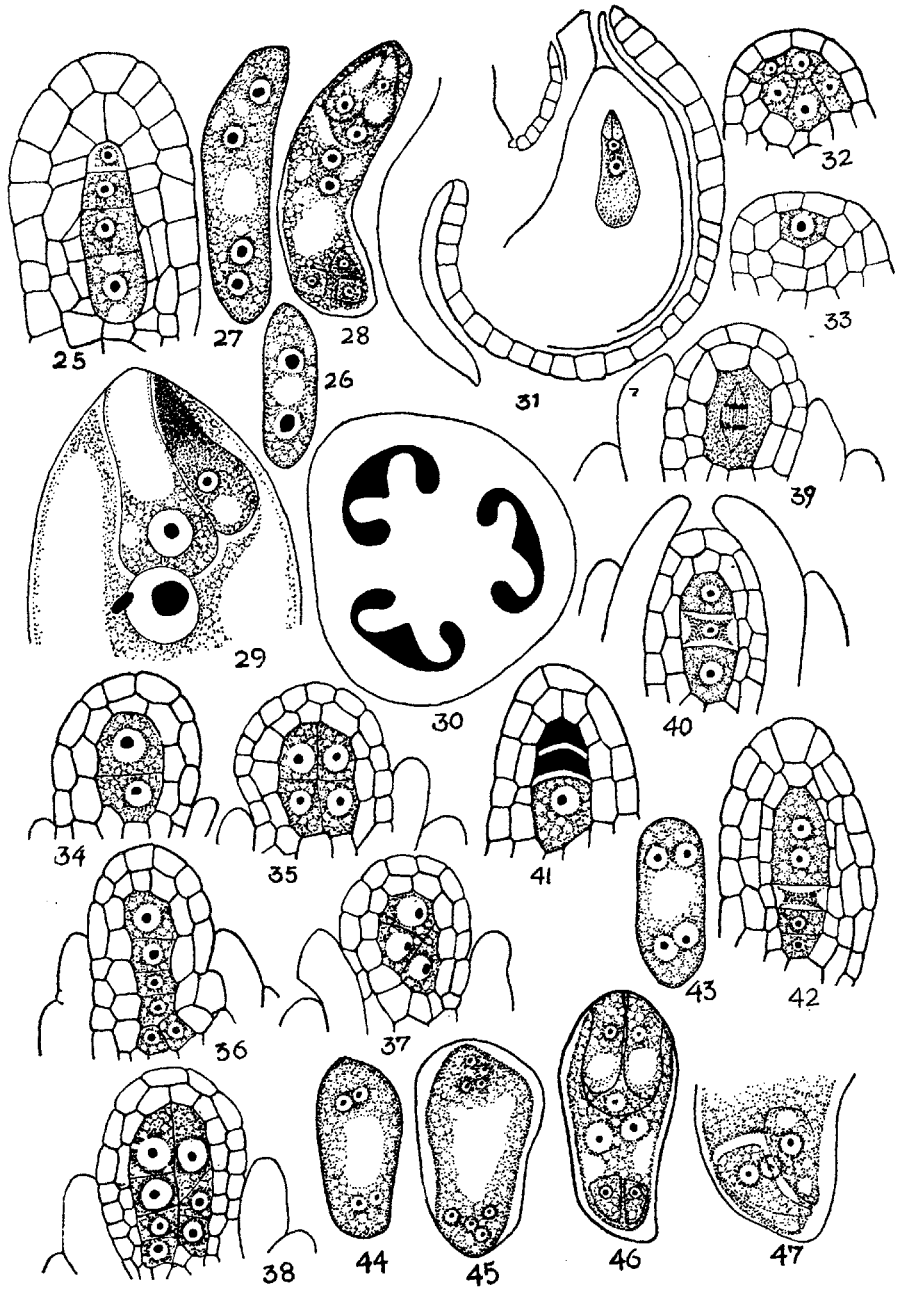
The organisation of the embryo-sac is of the normal angiospermous type. The synergids are pear-shaped with vacuoles at their chalazal ends. Egg-like synergids with vacuoles at the micropylar end have also been noted in *S. media*. In other cases, vacuoles are found at both ends (Fig. 28). In form the egg appears somewhat similar to that of the synergids, the position of the vacuole is, however, different (Fig. 29). The egg is mostly covered by synergids, only the rounded distal end being visible (Figs. 28 & 46). The secondary nucleus is comparatively big and lies very near the egg apparatus (Fig. 29). The antipodal cells are somewhat triangular in shape and lie together at the chalazal end. Their shape and arrangement are variable (Figs. 28, 46 & 47). They are ephemeral in nature and at the time of fertilisation no trace of them is found. It is interesting to note that in *P. tetraphyllum* Rocén (1927) observed three free antipodal nuclei.

The mature embryo-sac is curved like the ovule which is hemianatropous in form. The curvature is initiated at the four-nucleate stage and after fertilisation it becomes very prominent.

(vi) *Fertilisation.*—Fertilisation is porogamous and normal. The pollen tube passes through one of the synergids. Double fertilisation has been observed in *S. media* (Fig. 29).

(vii) *Development of the endosperm.*—The endosperm is of the nuclear type. The division of the primary endosperm nucleus takes place before the first division of the fertilised egg. Numerous free nuclei are formed which are mostly aggregated at the chalazal and micropylar ends of the embryo-sac. All the endosperm nuclei in an embryo-sac divide almost simultaneously.

Wall-formation around the endosperm nuclei is first noted when the cotyledonary initials are well-differentiated in the embryonal mass. The process starts at the micropylar region and extends towards the other end. In *S. media*, wall-formation does not take place at the chalazal region which is absorbed in the free-nuclear condition by the growing embryo. The endosperm cells are very



FIGS. 25–29. *Stellaria media*. Fig. 25. Linear tetrad of megaspores. ×700. Figs. 26–28. Development of the embryo-sac. ×700. Fig. 29. Double fertilisation. ×700.

FIGS. 30–47. *Polycarpon Læflingiæ*. Fig. 30. T.S. of ovary showing axile placentation. ×90. Fig. 31. Section of an ovule showing the outgrowth (aril) from the funicle. ×260. Fig. 32. Multiple archesporium in the ovule. ×700. Fig. 33. One-celled archesporium in the ovule. ×700. Figs. 34–38. Different arrangements of the megaspore-mother cells and the primary archesporial cells. ×700. Fig. 39. Reduction division of megaspore-mother cell. ×700. Fig. 40. A row of the micropylar dyad cell and two chalazal megaspores. ×700. Fig. 41. Functional chalazal megaspore with degenerating dyad cell and other megaspore. ×700. Fig. 42. Development of the embryo-sac from the micropylar megaspore of a complete linear tetrad. ×700. Figs. 43–44. Size variation of the nuclei in 4-nucleate embryo-sacs. ×700. Fig. 45. 8-nucleate embryo-sac. ×700. Fig. 46. Mature embryo-sac. ×700. Fig. 47. Structure and arrangement of antipodals. ×1500.

rich in cytoplasm and starch grains. The embryo during its development destroys the endosperm tissue. Only a thin layer of endosperm cells is, however, found to be capping the radicle of the mature embryo in *S. media*. The embryo-sac ultimately assumes a horse-shoe-shaped form.

(viii) *Development of the embryo.*—The fertilised egg rests for some time before commencing activity. It elongates rapidly and has a broadened apex. No trace of synergids is noted at this stage. The first division in the oospore takes place when the primary endosperm nucleus has divided twice in succession (Fig. 48). This division is always followed by the formation of a transverse wall giving rise to a primary embryonal cell *ca* and a primary suspensor cell *cb* (Figs. 49 & 72). The two cells behave differently during further development in the two plants.

In *S. media*, the basal cell does not divide further, but elongates and becomes hypertrophied. The apical cell alone divides in a transverse plane to give rise to *cc* and *cd* (Figs. 49 & 50). These cells next divide by transverse walls either simultaneously or one after the other and a five-celled pro-embryo is formed which remains as such until the longitudinal divisions take place (Figs. 50–53). In a solitary instance, however, the apical cell *cc* was found to divide longitudinally (Fig. 54).

For the sake of convenience the specific cells of the pro-embryo are designated by symbols used by Souèges (1924) for *Sagina procumbens* and are as follows (from apex to base in the five-celled condition): *l*, *l'*, *m*, *ci* and *cb*.

The first two longitudinal walls appear in *l'* and *m* at right angles to each other (Fig. 55). In a few cases the apical cell is found to have divided longitudinally prior to either of *l'* or *m* (Fig. 56). Almost simultaneously with the longitudinal divisions in *l'* and *m*, the cell *ci* also divides transversely to give rise to *n* and *n'*. This cell *n* is the new fourth cell from apex which forms the hypophysis (Fig. 55). The other cell *n'* may or may not undergo any more transverse division. If it divides, it does so either simultaneously with or after the longitudinal division of *n* (Figs. 59 & 60). These daughter cells of *n'* which may be called *o* and *p* (Fig. 61), may or may not divide further. When they divide, they do so always in a transverse direction and the divisions may take place once either in *o* or in both the cells (Figs. 63 & 65). Thus the suspensor may be 2–5 cells long. Rocén (1927) also describes a considerably long suspensor in *S. media*.

The next longitudinal division takes place in the apical cell (Fig. 55). In one isolated case, however, the hypophysial cell *n* was observed to have divided longitudinally prior to the apical cell (Fig. 57).

Quadrant formation in *l'* and *m* takes place in close succession which takes place first mostly in *m* (Figs. 58 & 59). These vertical walls are at right angles to the first longitudinal walls in the corresponding cells. Longitudinal division is next observed in the hypophysial cell *n*. This division occurs almost simultaneously with or before the quadrant formation in the penultimate cell *l'* (Fig. 59). The third quadrant appears in *n* (Fig. 61), which may be considered as premature and differing from the sequence observed in *Sagina procumbens* by Souèges (1924). In the meantime, the cells of the third tier *m* divide periclinally to give rise to an octant tier (Fig. 61). Soon the penultimate tier *l'* attains the same condition (Fig. 62). Meanwhile the apical tier *l* becomes four-celled (Fig. 62). Afterwards these four cells divide again obliquely with the production of four inner and four outer cells. Thus the dermatogen differentiation proceeds in an acropetal order, which is a characteristic feature of the order.

In the meantime the differentiation of the other two histogenic layers begins. The dermatogen cells divide only by anticlinal walls and so do not contribute to the inner tissues of the embryo. The inner two layers of cells divide again in a periclinal direction to give rise to an outer layer of cells or periblem and two inner layers of cells or plerome (Fig. 63). Afterwards, this outer layer divides again

periclinally to give rise to a two-layered periblem (Fig. 65). The cells constituting the plerome divide in all directions (Figs. 63 & 64).

The octant derived from the apical cell *l* divides at a slow rate and gives rise only to the stem-apex of the embryo at a very late stage of development. The activity of the tier *l'* is not rapid in the early stages. Later it gives rise to the cotyledonary initials which grow very vigorously and develop into two large cotyledons. The third tier *m* divides actively in both directions and differentiates into the hypocotyl and radicle, except the dermatogen layer of the root-apex. The hypophysial cell *n* gives rise to a quadrant in an early stage of the development of the embryo as mentioned previously. Then the activity of this tier is arrested for sometime, the cells dividing again tangentially, only when the cotyledonary initials are about to differentiate. The inner cells contribute to the dermatogen of the root-apex and the outer ones give rise to the median portion of the root cap (Fig. 66). The other cells taking part in the formation of the root cap are the lowermost two tiers of dermatogen cells derived from *m*. These cells, too, in their turn, undergo tangential divisions and differentiate in the same manner as *n* (Fig. 67).

The primary basal cell *cb* does not divide at all, but enlarges immensely. It has a very large nucleus situated near the centre surrounded by dense cytoplasm (Figs. 49–65). The nucleus becomes granular at maturity, takes deep stain and appears like a bunch of small beads. After the initiation of the cotyledonary initials, the activity of *cb* diminishes gradually and ultimately the growing embryo gets free due to the breaking down of the latter. Otherwise the suspensor cells gradually degenerate and in the mature seed their remnants are unrecognisable.

The form of the mature embryo is somewhat semi-circular (Fig. 68). The inner cotyledon is seen to be smaller than the outer. Starch grains are deposited in the embryo chiefly in the cells of dermatogen and cotyledons. The embryo completely absorbs the endosperm tissue except a small portion which forms a cap-like structure over the root-apex.

In *P. Lœflingiæ*, both the primary suspensor cell and the primary embryonal cell divide transversely again. The basal cell usually divides first though simultaneous divisions and even the reverse sequence are not uncommon (Figs. 72–74). The four cells of the pro-embryo may be disignated as *l*, *l'*, *m* and *ci* from apex to base, as used by Souèges (1920) for *Chenopodium Bonus-Henricus*. The penultimate cell *l'* divides transversely to give rise to l_1' and l_2' and thus a five-celled pro-embryo is formed (Figs. 75 & 76). The first longitudinal wall in the apical cell *l* appears in this five-celled pro-embryo (Fig. 76) but in a few cases the latter may increase in length due to the transverse divisions of *ci* or of both *ci* and *m* before the commencement of any longitudinal division (Figs. 77 & 78). The second longitudinal division occurs in the penultimate cell l_1' (Fig. 79). In a solitary instance, however, the penultimate cell was seen to divide longitudinally prior to the apical one (Fig. 93). Meanwhile the two basal cells *m* and *ci* divide transversely (Figs. 79 & 80). Soon the two cells of the apical tier *l* divide again vertically and an apical quadrant is formed (Fig. 80). The next transverse division occurs in l_2' giving rise to l_3' and l_4', l_3' being adjacent to the penultimate cell l_1' and the other being the hypophysial cell (Figs. 80 & 81).

After this the cells of the penultimate tier l_1' divide again vertically and thus a second quadrant is formed (Fig. 82). Soon l_3' undergoes a longitudinal division followed by a similar division in the hypophysial cell l_4' (Figs. 82–84). The latter, however, may remain undivided in a few cases until the apical octants are formed (Fig. 85). Thus the longitudinal divisions in the four cells take place in a basipetal succession as found in *Boerhaavia* by Kajale (1938). In most of the other investigated plants of the order, however, the order of these divisions is somewhat acropetalous (Souèges, 1920 and 1924; Joshi and Rao, 1934 and 1936; Kajale, 1935 and 1940*b*).

Next, the apical quadrant gives rise to an octant by the formation of transverse walls. Thus two tiers of quadrants arise from the apical cell *l* (Fig. 85). Almost simultaneously with it the cells of the penultimate tier l_1' divide by periclinal walls to give rise to another octant (Fig. 85). All the cells, however, do not divide simultaneously. Soon the lower four cells of *l* divide periclinally to give rise to another penultimate octant tier (Fig. 86). Further divisions in the tier l_1' take place by transverse walls and thus two tiers of cells are also derived from the penultimate cell of the five-celled pro-embryo (Fig. 87). Later, the four apical cells of *l* divide by oblique walls (Fig. 88). Thus the dermatogen differentiation proceeds in an acropetal succession as seen in *S. media* and other plants of the order. It is interesting to note, however, that the initiation of periclinal divisions occurs simultaneously with the formation of transverse walls in the apical and penultimate tiers, i.e., *l* and l_1'. Moreover, though the appearance of vertical walls is in basipetal succession, the periclinal walls appear in an acropetal order.

After the differentiation of the dermatogen layer, the other histogenic layers differentiate in the same sequence as found in *S. media*. The two tiers of cells of *l* divide chiefly in vertical directions and later differentiate into the stem-tip and the cotyledons of the embryo. The former is very small even when the latter are fairly large. The stem-tip arises from the central part of the apical tissue and the cotyledonary initials from the peripheral region of the latter. The next two tiers of cells are derived from the penultimate cell l_1' which gives rise to the hypocotyl. The third cell l_3' shows less activity after the quadrant formation. It gives rise to an octant tier only in later stages of embryo-development and develops into a semi-circular body which ultimately gives rise to the radicle.

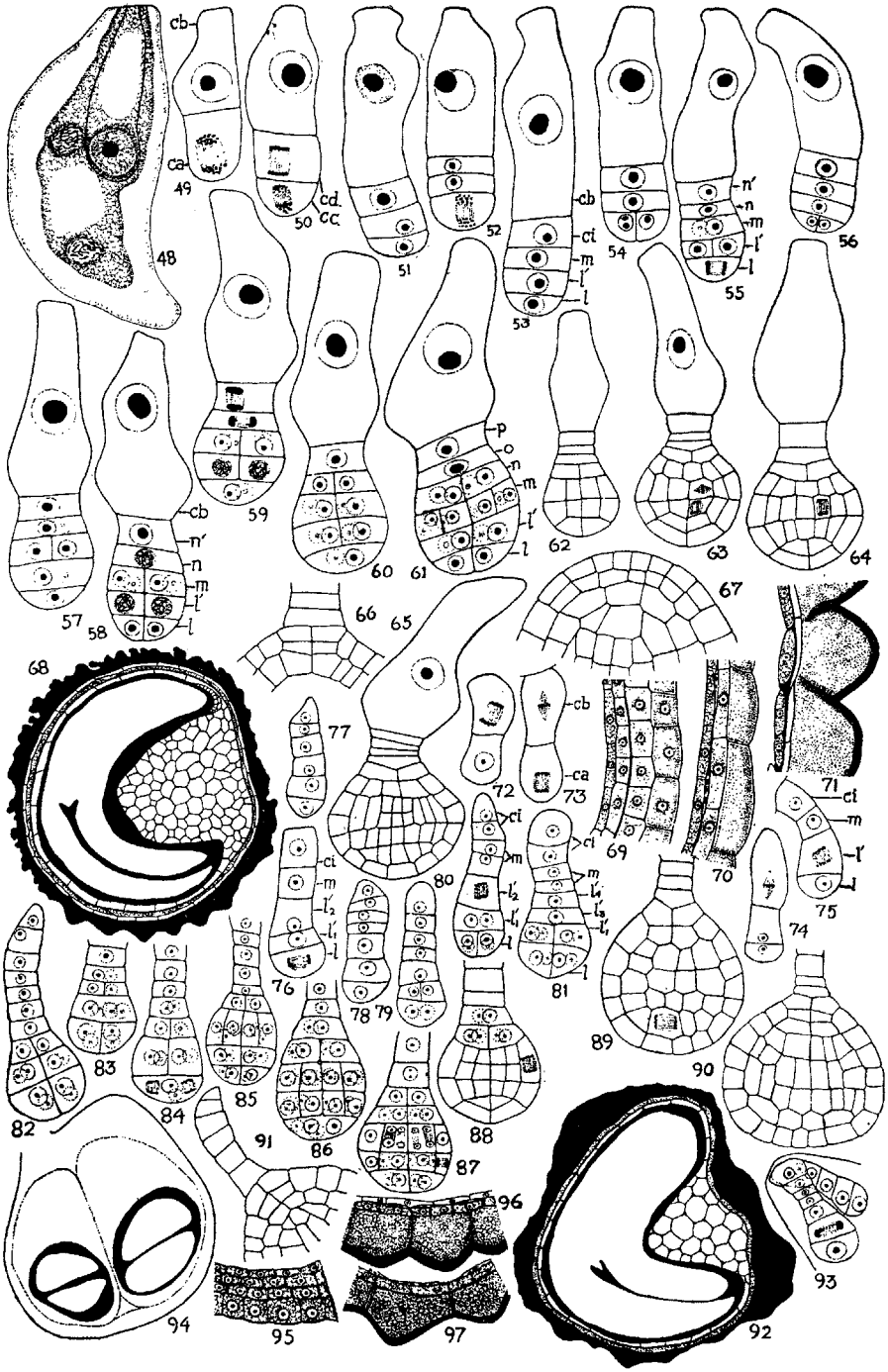
The first longitudinal division in the hypophysial cell l_4' takes place only after the formation of two quadrants in the apical cells. The next longitudinal divisions commence only after the differentiation of the histogenic layers in the embryo (Fig. 89). Afterwards these cells divide tangentially. The inner cells give rise to the dermatogen of the root-apex and the outer ones to the rootcap (Figs. 90 & 91).

As mentioned previously, the divisions of the basal cells of the five-celled pro-embryo are initiated simultaneously with those of the apical cells. These cells divide always transversely and ultimately a row of 5–10 suspensor cells is derived as found in *P. tetraphyllum* by Rocén (1927). In a very few cases any one of the suspensor cells may divide once in a longitudinal direction but the suspensor never becomes biseriate or massive. Unlike *S. media*, the primary suspensor or basal cell divides transversely in this plant to give rise to all of the suspensor cells. Rocén (1927) describes a weak haustorial basal cell in *P. tertraphyllum*, which was not found in the present material. The mature embryo is not exactly semi-circular, but it is bent prominently in the hypocotylar region (Fig. 92). In *P. tertraphyllum*, Rocén (1927) described a slightly curved embryo. The structure of the cotyledons is similar to that of *S. media*. Starch grains are found in the cells of dermatogen, plerome and the cotyledons. The endosperm tissue is completely absorbed by the growing embryo and nothing is left even in the root-apex area. The size of the embryo is much smaller than that of *S. media*.

(ix) *Polyembryony.*—A case of polyembryony has been observed in *P. Lœflingiæ*. Two pro-embryos have been observed side by side in the same embryo-sac (Fig. 93). One is 7 cells long with the penultimate cell undergoing the first longitudinal division and the other consists of only 5 cells in a row. The bigger pro-embryo appears to have developed in the usual way from a normal fertilized egg. The origin of the other is perhaps from one of the synergids.

Double nucelli in one ovule have also been found in both the plants, each containing an embryo-sac in advanced stage of development (Fig. 94).

(x) *Development and structure of the seed.*—The mature seed contains a large quantity of perisperm which extends from the base to the centre and is enclosed by the mature embryo from three sides. The embryo is somewhat cylindrical



Figs. 48–71. *Stellaria media*. Fig. 48. Elongation of the oospore in a curved embryo-sac. Two endosperm nuclei in the dividing stage. ×200. Figs. 49–68. Various stages in the development of the embryo. Figs. 49–61. ×200. Figs. 62–65. ×125. Figs. 66–67. ×200. Fig. 68. ×25. Figs. 69–71. Development of the seed coat. Figs. 69 and 70. ×125. Fig. 71. ×70.

Figs. 72–97. *Polycarpon Læflingiæ*. Figs. 72–92. Various developmental stages of the embryo. Figs. 72–91. ×200. Fig. 92. ×30. Fig. 93. A case of polyembryony showing two pro-embryos in a single embryo-sac. ×200. Fig. 94. Double nucelli with two embryos. ×30. Figs. 95–97. Development of the seed coat. Fig. 95. ×200. Fig. 96. ×125. Fig. 97. ×70.

and narrow, and lies at the peripheral region of the seed encircled by a single layer of perisperm cells (Figs. 68 & 92).

Two cell layers constitute the testa in both the plants. The cells of the outer layer become very big in size at maturity. Some yellow granular substance begins to be deposited in these cells from a very early stage. The deposition begins at the chalazal end and extends towards the micropyle. In the meantime marked changes occur in the cell walls. The outer walls of these rectangular cells begin to bulge out along with the deposition of the granules. At this time the nucleus lies near the outer wall of the cell (Figs. 69 & 95). Later, the convex walls of the cells become greatly thickened; the cells become completely filled up with the yellow particles and the nuclei become invisible. The cells fuse laterally with each other to form a homogeneous mass of thick brown testa (Figs. 70, 71, 96 & 97). The inner layer of cells of the outer integument remains unthickened.

The tegmen is altogether absent from the seeds of *P. Læflingiæ*. In course of development both the cell layers of the inner integument of the ovule are compressed and finally crushed. In *S. media*, a single layered tegmen is present. The outer layer is destroyed during the developmental stages of the seed by the compression of inner and outer tissues. The inner layer of cells of this integument becomes hardened by the deposition of some yellow particles probably of the same nature as seen in the outermost cell layer of testa (Figs. 69–71). The structure of the seeds of *S. media* is similar to that of *S. holosia* studied by Rocén (1927).

Discussion.

According to Rendle (1938), the placentation of the order Centrospermæ is at first axile and later the free-central placentation is derived by the dissolution of the septa of the ovary. This condition has been substantiated by the present study. It is notable, however, that the axile placentation is retained in *P. Læflingiæ* till the end. In *P. tetraphyllum*, Rocén (1927) observed the other type.

Rocén (1927) first determined the chromosome number of *S. media* as $2n = 40$. This was confirmed by Joshi (1936). Based on Paterson's (1936) account, Darlington and Janaki-Ammal (1945) report the $2n$ number to be 40 and 44. Study of meiosis during this investigation clearly showed the presence of 14 bivalents in diakinesis and in the metaphase of first division. Darlington and Janaki-Ammal (1945) also report the chromosome number $n = 10$, 11, 12 and 13 in the genus *Stellaria*: the number $n = 14$ as determined in the present investigation, therefore, tends to show that there is considerable aneuploidy within the genus. It can, therefore, be suggested that *S. media*, as occurs in lower Bengal, belongs to a different ecological species. The chromosome number in *P. Læflingiæ* in the present study has been found to be $n = 18$. This apparently has not been recorded before. The number $n = 18$ has also not been previously recorded in this family, though the monoploid numbers 10, 12, 13, 14, 15 & 17 appear to be common.

The number of integuments of the ovule has been found to be two only. In *P. Læflingiæ*, however, an additional structure is found developing from the funicle near the base of the ovule and growing to some extent parallel to the chalazal surface of the latter. It, however, never grows long enough to function as an aril, but soon becomes arrested in its development. Kajale (1940*a*) also found a similar structure in *Sisuvium portulacastrum* where it covers only $\frac{1}{3}$ of the ovule. He regards this as an aril. The presence of a third integument or aril was reported in *Trianthema monogyna* by Bhargava (1935).

In *Silene*, *Melandrium*, *Agrostemma*, *Dianthus*, *Lychnis* and *Scleranthus* (Schnarf, 1931) more than one archesporial cells were found by several investigators. According to Gibbs (1907), there is only one primary archesporial cell in the ovule of *S. media*. In the present study the number is found to be one or more, frequently 2 to 4. Joshi (1936) also records the number to be 4 to 6. Dahlgren (1916) and

Rocén (1927) have found several archesporial cells in *S. graminea*, *S. media* and in some other plants of the family. Perotti (1913) holds the same view. It is interesting to note that in *P. Lœflingiœ* this number is still greater. Rocén (1927), however, records the presence of single archesporial cell in *P. tetraphyllum*. All the archesporial cells do not develop in the same manner. In *S. media* only one hypodermal archesporial cell functions as a megaspore-mother cell after cutting a parietal cell as has been previously observed by Joshi (1936). This agrees with the observations of Gibbs (1907) on *S. media* and Souèges (1924) on *Sagina procum bens*. Rocén (1927) who has worked on a number of species of the family did not, however, find this condition except in *Gypsophila*. Schnarf (1931) believes the non-occurrence of the parietal cell in Caryophyllaceæ as uncertain or a false record. The number of megaspore-mother cells in *P. Lœflingiœ* may be more than one as stated before. The presence of more than one megaspore-mother cells in Caryophyllaceæ has also been mentioned by Schnarf (1931).

Gibbs (1907) described the development of embryo-sac in *S. media* as of the 'Adoxa type' (then called 'Lilium type'). Later Rocén (1927) contradicted her and described the embryo-sac development of the same and many other members of the family as of the 'Normal type'. Joshi (1936), however, gave an altogether different account. According to him, the development of the embryo-sac of the plant is either of the 'Adoxa type' as described by Gibbs or less frequently of the 'Allium type', but it never follows a 'Normal type' of development as described by Rocén. He could not get a row of three or four megaspores. Yet he mentions about the possibility of a 'Normal type' of development of the embryo-sac in this species on account of its great morphological variability. The present investigation conclusively proves a 'Normal type' of development of female gametophyte in *S. media*. Rocén's observations are, therefore, correct. It is interesting to note that in *P. Lœflingiœ* generally a complete megaspore tetrad is lacking, as the micropylar dyad cell generally does not divide, but degenerates as such. In the few cases, where a complete megaspore tetrad has been noted, it is the micropylar megaspore and not the chalazal one, which functions to give rise to the 'Normal type' of embryo-sac. Rocén (1927), however, states that the micropylar dyad cell in *P. tetraphyllum* always divides without wall formation and the chalazal megaspore functions.

Gibbs (1907) opined that the primary endosperm nucleus in *S. media* divides later than that of the oospore. Joshi (1936) contradicted her. The present investigation supports Joshi's view. Based upon the nature of cell formation in the endosperm tissue Rocén (1927) has placed the genus *Stellaria* and the tribe *Polycarpeæ* under the 'Heliosperma type', but the present investigation shows that the cell-formation in the endosperm tissue of *P. Lœflingiœ* takes place throughout the embryo-sac and so following Rocén's system of classification this plant should be placed under the 'Silene type' and not under the 'Heliosperma type'. The formation of a diverticulum of the embryo-sac which has been recorded in several plants of the family has not been observed in the present material.

The two plants studied differ widely in their embryogeny. The sequence of transverse divisions in the oospore to form a filamentous pro-embryo is altogether different. In this respect and in the later development of the embryo *S. media* somewhat resembles *Lychnis alba* (Devine, 1950) and *Sagina procumbens* (Souèges, 1924). But the sequence of cell-divisions in *P. Lœflingiœ* follows *Portulaca sp.* (Kajale, 1942) and *Chenopodium Bonus-Henricus* (Souèges, 1920) in some respects. The number of apical cells taking part in the formation of the embryo proper is found to be more or less constant for certain members of the order, varying from three to five. In both the plants investigated this number was found to be four. Of course, the nature and differentiation of these cells varies widely in different members. In *Sagina procumbens* (Souèges, 1924), *Lychnis alba* (Devine, 1950) and *Stellaria media* the primary embryonal cell gives rise to all the four apical cells as

well as the suspensor cells except the basal one. In the latter, the number of the suspensor cell may be in some cases three or four or even one. But in *P. Læflingiæ* all the suspensor cells are derived from the primary suspensor or basal cell and the four apical cells taking part in the formation of the embryo proper are derived from the primary embryonal cell.

According to Johansen's (1945) classification, the sequence of embryo-development of *S. media* follows the 'Caryophyllad type' as found in other plants of the family, but in *P. Læflingiæ* it is after the 'Solanad type'. Following his (1950) 'Law of Destination' the embryonomic formulæ of *Stellaria media* and *Polycarpon Læflingiæ* may be recapitulated in the following table to show the relationship of the different organs of the embryo to that of the cells of the pro-embryo, which is, however, very different in the two plants.

I. First Cell Generation: Pro-embryo of two cells disposed in two tiers. (The basal cell is omitted in *S. media*.)

S. media	*P. Læflingiæ*
cc—*pvt*+*pco*	*ca*—*pvt*+*pco*+*phy*+*icc*+*iec*+*co*
cd—*phy*+*icc*+*iec*+*co*+*s*	*cb*—*s*

II. Second Cell Generation: Pro-embryo of four cells disposed in four tiers.

S. media	*P. Læflingiæ*
l—*pvt*	*l*—*pvt*+*pco*
l'—*pco*	*l'*—*phy*+*icc*+*iec*+*co*
m—*phy*+*icc*+*iec*	*m*— } *s*
ci—*co*+*s*	*ci*— }

III. Third Cell Generation.

S. media (Embryo of 7-8 cells disposed in 5 tiers).	*P. Læflingiæ* (Embryo of 5-6 cells disposed in 5 tiers).
l—*pvt*	*l*—*pvt*+*pco*
l'—*pco*	l_1' —½ *phy*+*icc*
m—*phy*+*icc*+*iec*	l_2' —½ *phy*+*iec*+*co*
n—*co*	*m*— } *s*
n'—*s*	*ci*— }

IV. Fourth Cell Generation.

S. media (Embryo of 20 cells disposed in 6 tiers).	*P. Læflingiæ* (Embryo of 11 cells disposed in 7 tiers).
l—*pvt*	*l*—*pvt*+*pco*
l'—*pco*	l_1' — ½ *phy*+*icc*
m—*phy*+*icc*+*iec*	l_2' —½ *phy*+*iec*+*co*
n—*co*	*m*—(2-tiered)— } *s*
o— } *s*	*ci*—(2-tiered)— }
p— }	

V. Fifth Cell Generation: (In *P. Læflingiæ* only). Embryo of 14 cells disposed in 8 tiers.

l—*pvt*+*pco*
l_1' —½ *phy*+*icc*
l_3' —½ *phy*+*iec*
l_4' —*co*
m—(2-tiered)— } *s*
ci—(2-tiered)— }

In some members of Caryophyllaceæ the suspensor is massive or biseriate. In *P. Lœflingiæ*, however, it is uniseriate (though in some cases a cell is found to have divided longitudinally) and derived entirely from the primary basal cell. An intermediate type as mentioned by Schnarf (1931) is found in *Sagina procumbens* (Souèges, 1924), *Lychnis alba* (Devine, 1950), *Stellaria media* and in the genera *Melandrium, Cerastium, Silene, Agrostemma*, etc. Here the basal cell is bladder-like and prominently haustorial in nature. The other suspensor cells in *S. media* which vary from one to four are derived from the primary embryonal cell and are found to be normal in structure. A weakly developed haustorial basal cell has been found also in *P. tetraphyllum* by Rocén (1927).

SUMMARY.

The present paper deals with the development of the flower, pollen, embryo-sac, embryo and seed in *Stellaria media* and *Polycarpon Lœflingiæ*.

1. The organogeny of the flowers is normal, except in *S. media* where the stamens arise prior to the petals. In *P. Lœflingiæ*, the condition of the axile placentation is retained even in the young fruits.

2. The tapetal cells in the anthers are binucleate and are of the secretary type.

3. The haploid number of chromosomes is 14 in *S. media* and 18 in *P. Lœflingiæ*. Cytokinesis takes place by furrowing. The pollen grains are spherical at maturity. In *P. Lœflingiæ*, they are deeply furrowed in the intermediate stages of development. The pollen grains are rich in starch and are shed in the 3-nucleate condition.

4. The ovules are hemianatropous and bitegmic. The micropyle is formed only by the inner integument. The presence of a nucellar cap over the embryo-sac is a characteristic feature. The nucellus is massive and the integuments are two cells thick.

5. The primary archesporium of the ovule is generally multicellular and hypodermal in origin, but in *S. media* a single archesporial cell functions as the megaspore-mother cell after cutting a parietal cell. In *P. Lœflingiæ*, however, several mother cells may be formed but only the median one functions.

6. In *S. media*, a linear tetrad of megaspores is formed and the chalazal megaspore functions to give rise to a 'Normal type' of embryo-sac. In *P. Lœflingiæ*, however, generally a linear row of two chalazal megaspores and one micropylar dyad cell is formed of which the chalazal megaspore functions. In a few cases normal linear tetrads of megaspores have also been observed of which the micropylar one functions.

7. Fertilization is normal and porogamous.

8. The division of the primary endosperm nucleus takes place before that of the oospore. The endosperm is of the 'Nuclear type' and the nature of cell-formation of the endosperm tissue conforms to the 'Heliosperma type' in *S. media* and 'Silene type' in *P. Lœflingiæ*.

9. The nature of development of the embryo is different in the two plants investigated. The development of the embryo in *S. media* is after 'Caryophyllad type', but in *P. Lœflingiæ* it is after 'Solanad type'. In *S. media* the primary suspensor cell becomes bladder-like and haustorial, while it is not so in *P. Lœflingiæ*. In the latter, polyembryony has been noted in one instance.

10. The seed contains a large amount of perisperm, and a trace of endosperm at the micropylar end of *S. media* only. The testa is two-layered of which the outer one is characteristically thickened and modified. In *P. Lœflingiæ* the tegmen is absent, while in *S. media* it is one-layered.

In conclusion, I desire to express my sincerest thanks and gratitude to Dr. I. Banerji under whose guidance and care this work was carried out. I am also very much indebted to Principal J. C. Sen Gupta and Prof. P. Maheshwari who helped me with literature.

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