A CRITICAL REVIEW OF THE TYPES OF EMBRYO SACS IN ANGIOSPERMS

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(With 17 figures in the text)

THE chief features in the development of the angiosperm embryo sac were already known towards the end of the last century, but there is a good deal of confusion with regard to the terminology of the various stages, and it is therefore considered advisable to introduce this essay with a brief account of the normal course of development.

A cell in the hypodermal layer of the nucellus becomes specially prominent, and directly or after cutting off a wall cell functions as the *megaspore mother cell* or *embryo-sac mother cell*. The first division gives rise to a *dyad*; the two cells composing it may be called *dyad cells* but not megaspores, since reduction division is not yet over. The next division results in the formation of a tetrad; each of the four *tetrad cells* is a *megaspore* or *macrospore*. Only the chalazal megaspore grows further and is called the *functioning megaspore* or *primary embryo-sac cell*. The two nuclei formed after the first division soon move apart to the poles and will be referred to as *"primary micropylar"* and *"primary chalazal"* nucleus respectively. The second division gives rise to a pair of nuclei at each end and the third to two *quartets* which form the *egg apparatus*, three *antipodal cells* and two *polar nuclei*. The latter fuse to form a *secondary nucleus*.[1]

The majority of angiosperms investigated so far correspond to the type described above; many deviations have nevertheless been reported and different systems have been devised to classify them

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[1] The term "fusion nucleus" recommended by Coulter & Chamberlain (1903) has the disadvantage that it has also been used to denote the primary endosperm nucleus, which is formed only after triple fusion.

(see specially Coulter, 1908; Palm, 1915; Rutgers, 1923; Shadowsky, 1925 *b*; Chiarugi, 1927 *a* and Modilewski, 1929).[1] Without discussing the individual merits and demerits of these systems, we may say that there is a general consensus of opinion about regarding the first four nuclei formed after the reduction divisions as equivalent to megaspore nuclei; the laying down of a wall separating them is a matter of secondary importance. Consequently, an embryo sac formed from the divisions of a single megaspore nucleus should be called *monosporic*; when two take part in its development, it is *bisporic*; and when all four contribute to it, it is *tetrasporic*.

Monosporic embryo sacs may be:

(1) 16-*nucleate*, in which case the egg is removed from the mother cell by six divisions (Unknown), or

(2) 8-*nucleate*, in which case five divisions intervene between the megaspore mother cell and the egg (Normal-type), or

(3) 4-*nucleate*, when only four divisions intervene between the megaspore mother cell and the egg (*Oenothera*-type).

In the case of *bisporic* embryo sacs only the first division of the megaspore mother cell is followed by wall formation, and the two megaspore nuclei formed in each dyad remain unseparated by a wall. We have, therefore, one division less than in the monosporic types to give rise to the same number of nuclei. Thus:

(1) 16-*nucleate*, in which case the egg is removed from the megaspore mother cell by five divisions (Unknown).

(2) 8-*nucleate*, in which case the egg is removed from the megaspore mother cell by four divisions (*Allium*-type).

(3) 4-*nucleate*, when only three divisions intervene between megaspore mother cell and the egg (*Podostemon*-type).

In *tetrasporic* embryo sacs no permanent walls are laid down during the reduction divisions, and all four megaspore nuclei take part in the formation of the embryo sac:

(1) 16-*nucleate*, in which case the egg is removed from the megaspore mother cell by four divisions (*Peperomia*-type).

(2) 8-*nucleate*; the egg is still removed from the megaspore mother cell by four divisions, but due to the intervention of a secondary 4-nucleate stage, the number of nuclei is kept down to eight (*Fritillaria*-type).

(3) 8-*nucleate*; three divisions intervene between the megaspore mother cell and the egg (*Adoxa*-type).

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[1] Schnarf's recent review (1936) appeared only after this work had already been completed.

Fig. 1. Types of embryo sac development in angiosperms.

(4) 4-*nucleate*; there are only two divisions and the megaspore nuclei themselves enter into the organization of the embryo sac (*Plumbagella*-type).

In the following pages each of these types will be discussed in fair detail.

MONOSPORIC; 16-NUCLEATE

Monosporic embryo sacs with more than eight nuclei are rare. Such a condition may be due to the following reasons and the cause should in each case receive careful study:

(1) Degeneration of nucellar cells and the passing in of their nuclei into the embryo sac, as reported by Quisumbing & Juliano (1927) in *Cocos nucifera*. This is comparable to the situation in many gymnosperms where the nuclei of the jacket cells wander inside the egg, but the same appearance may also be brought about due to inadequacies of technique.

(2) Fusion of two embryo sacs lying adjacent to one another. The 16-nucleate embryo sac of *Elatine hydropiper* seen by Frisendahl (1927, Fig. 32), consisting of two egg apparatuses, two pairs of polar nuclei and two groups of three antipodals each, is clearly derived by this method. Oksijuk (1929) found some exactly similar cases in *Reseda alba*, and has very recently (1935) reported the same thing in *R. inodora*. When one of the embryo sacs is at a younger stage of development than the other, the "compound embryo sac"[1] formed by their fusion may have less than sixteen nuclei.

(3) A sixth division of some or all of the nuclei of the embryo sac. Usually such an abnormality is due to irregularities caused by a hybrid origin of the species under investigation (for literature see Chiarugi & Francini (1930) on *Ochna serrulata*; and Steinegger (1933) on apples).

Dessiatoff (1911) reported that in *Euphorbia virgata* there was a monosporic embryo sac with sixteen nuclei, but Modilewski (1911) demonstrated that this was of the *Peperomia*-type. Mauritzon (1933, p. 35) reports that in *Crassula Schmidtii* and *Umbilicus intermedius* there is a fourth division of the megaspore nucleus resulting in

[1] Juliano (1934) figures a peculiar embryo sac in a fallen flower of *Sandoricum Koetjape*. This has a normal egg apparatus and two polar nuclei. In the chalazal region there is a large cytoplasmic vesicle extending up to the middle of the sac. This was found to contain fourteen nuclei. The author believes that this could not be antipodal in origin, since the antipodals are very ephemeral in this species. It is considered probable that the embryo sac itself was formed from the third megaspore and the vesicle from free nuclear divisions in the fourth.

a 16-nucleate embryo sac with four synergids, two egg-like cells, six antipodals and four free nuclei. Cases like these are of great interest, but we need more precise information about their origin and the frequency with which they occur in the plants in question. For the present we may say that a monosporic embryo sac of the 16-nucleate type is unknown to-day except as an abnormality.

NORMAL-TYPE

Eight-nucleate embryo sacs formed from the divisions of a single megaspore are remarkably uniform in their development. The abnormalities may be grouped under three headings: *tetrad formation,*
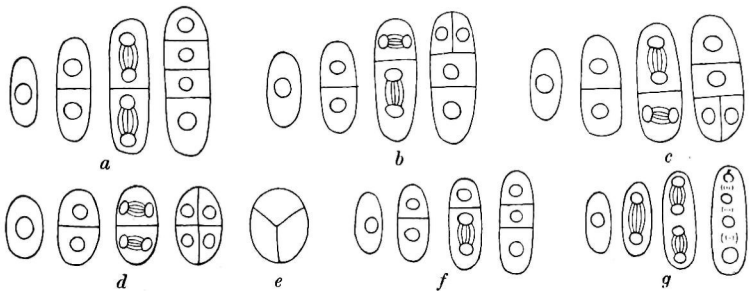

Fig. 2. Types of megaspore tetrads: (*a*) linear; (*b*) T-shaped; (*c*) ⊥-shaped; (*d*) isobilateral; (*e*) tetrahedral; (*f*) row of three cells of which the uppermost is a dyad cell; (*g*) four megaspore nuclei unseparated by walls.

divisions of the megaspore nucleus and *organization of the mature embryo sac.*

Tetrad formation.[1] In the majority of cases the megaspores are arranged in a linear row, and tetrads of this type are consequently called "linear" (Fig. 2*a*), but T-shaped tetrads[2] are also very common (Fig. 2*b*). A row of three cells is also frequently met with, but in about half the cases this is likely to be a T-shaped tetrad, one of whose megaspores is to be looked for in an adjacent section. In other cases (Fig. 2*f*) where we have really only three cells, one is not a megaspore but a dyad cell that has failed to divide again. Such an appearance has often been wrongly described in literature as a row of "three megaspores". Isobilateral tetrads (Fig. 2*d*) are known only

[1] An interesting situation has been reported in two Crassulaceae, *Rosularia pallida* and *Sedum sempervivoides* (Mauritzon, 1933, p. 25), in which the megaspores elongate and become haustorial.

[2] Salisbury (1931, p. 561; see also Pl. XVIII, fig. 3) has mistaken the upper two megaspores of a T-shaped tetrad of *Ranunculus parviflorus* as wall cells (see criticism by Singh, 1936, p. 85).

as abnormalities, as for instance in *Myrtus communis* (Greco, 1930) and *Urginea indica* (Capoor, 1937 a). A tetrahedral arrangement (Fig. 2 e) is still more rare and was noted in recent literature only in *Nymphoides peltatum* (Stover, 1932). ⌐-shaped tetrads (Fig. 2 c) occur occasionally in the Onagraceae (see under *Oenothera*-type), and may be expected only in such cases where the uppermost megaspore functions. Finally there are also such cases where the four nuclei are arranged in a linear row but without any cell plates separating them (Fig. 2 g).

Divisions of the megaspore nucleus. In the vast majority of angiosperms it is only the chalazal megaspore that grows further, while the other three are suppressed and soon degenerate. There are, however, a good many exceptions on record (see Schnarf, 1929, pp. 96–120). In the genus *Rosa* (Hurst, 1931) it is constantly the micropylar megaspore that functions, and in *Aristotelia racemosa* it is always the third from the micropylar end (Mauritzon, 1934 b). Sometimes two megaspores of a tetrad begin to grow simultaneously (Nast, 1935, in *Juglans regia*), but usually only one of the sister embryo sacs reaches maturity.

The functioning megaspore stage is characterized by a beginning of vacuolation. At first there are two vacuoles, one on each side of the nucleus in the long axis of the cell. After the first division, the two daughter nuclei migrate to the poles and a large vacuole appears in the centre. The subsequent divisions are rapid and simultaneous and result in a grouping of four nuclei at each end.[1]

Departures in the sequence of these divisions are usually in the nature of abnormalities that may occur now and then in any plant and have no special significance. Kuhn (1928, p. 420) found that in *Thalictrum Fendleri* the last division (after the 4-nucleate stage) does not always proceed at the same rate in all the four nuclei. Sabet (1931) has figured a similar abnormality in *Calotropis procera*. Millsaps (1936) reports that in *Paulownia tomentosa* it is usual for the primary chalazal nucleus to divide a little earlier than the micropylar so that a 3-nucleate embryo sac is formed for a short time. This is rather rare because delayed division commonly occurs in the lower part of the embryo sac.

Organization of the mature embryo sac. Most of the abnormalities concern the antipodal cells whose early disappearance has been recorded in many angiosperms and is a characteristic feature of

[1] Sabet (1931) figures an abnormal embryo sac of *Calotropis procera* in which these two groups are arranged like pollen tetrads.

some genera and even families. Such is the case in almost all of the Lythraceae so far investigated (Mauritzon, 1934 *a*; Joshi & Venkateswarlu, 1936 *a*), and this points the way for the derivation of the *Oenothera*-type of embryo sac, in which the antipodals are altogether absent.

Among other plants in which an early degeneration of the antipodals has been recorded, we may specially mention the following names: *Petunia violacea*, in which Cuchtmanova (1930) reports a "dégénération très prompte" of the nuclei even before the organization of the egg apparatus; *Trianthema monogyna* (Bhargava, 1935), where not only the antipodals but also the synergids degenerate very early so that the mature embryo sac has only two nuclei, i.e. the egg and secondary nucleus; and *Duabanga sonneratioides* (Venkateswarlu, 1936).

The early disappearance of the antipodals has misled some authors in the past, and it seems certain that a good many reports of 5-nucleate embryo sacs (before polar fusion) and 4-nucleate embryo sacs (after polar fusion) are due to misinterpretations caused by inadequacy of material of the right age. Puri (1934) has shown that the 5-nucleate embryo sac recorded by Rutgers (1923) in *Moringa oleifera* is really 8-nucleate. The same may be said with some confidence of *Linaria vulgaris*, *Antirrhinum majus*, *Melampyrum silvaticum*, *M. pratense* and *Tozzia alpina* (Schmid, 1906),[1] *Garcinia Kydii* and *G. Treubii*[2] (Treub, 1911), *Monophyllaea Horsfeldii* (Oehlkers, 1923), *Chamaeodorea concolor* (Suessenguth, 1921), *Sisyrinchium anceps* (Haeckel,[3] 1930, p. 73) and *Linaria genistaefolia* (Persidsky, 1934). In the last-named instance the author says that the antipodals are "apparently" not formed at all.

On the other hand, there are also cases in which a genuine reduction has occurred in the number of nuclei at the chalazal end of the embryo sac. Thus Sharp (1912) found only 6-nucleate embryo sacs in *Phajus grandifolius*, *Corallorhiza maculata* and *Broughtonia sanguinea* —a condition due to the primary chalazal nucleus dividing only once after the 2-nucleate stage.[4] In *Cinnamomum camphora* (Giuliani,

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[1] The author writes (p. 271): "Zunächst gibt es eine Anzahl von Scrophulariaceae bei denen Antipoden überhaupt nicht angelegt zu werden scheinen, wenigstens gelang es mir nie, das Vorhandensein solcher zu konstatieren."

[2] Mr V. Puri of Meerut finds that *Garcinia livingstonii* has the normal eight nuclei in the embryo sac.

[3] Since this was written, Miss Haeckel has told me, during the course of a personal talk at Halle/S., that after the publication of her work she was able to find the antipodals in her slides, although they are very small and ephemeral.

[4] Svensson (1928) and Reeves (1930) report that such is also the case sometimes in *Limosella aquatica* and *Medicago sativa* respectively.

1928) it seems probable that the primary chalazal nucleus does not divide at all, so that the embryo sacs are only 5-nucleate; in later stages when this also has disappeared only four can be seen.

The opposite condition, i.e. an increase in the number of antipodal cells, is also of frequent occurrence. In the Gramineae and Compositae it seems to be almost universal. *Sasa paniculata* (Yamaura, 1933) perhaps represents the most extreme case with as many as 300 antipodal cells.

Abnormalities concerning the synergids are much rarer. Rodolico (1930) reports that they are specially prominent in *Buphthalmum salicifolium*, and Paetow (1931) writes that in *Dysoxylum ramifolium* they reach almost to the middle of the embryo sac. Joshi & Venkateswarlu (1935) reported that in *Ammania baccifera* the two synergids fuse to form a syn-synergid which becomes multi-nucleate and surrounds the embryo like a collar. Later, the same authors (1936 b) found that what they had been looking at was a mass of endosperm nuclei at the micropylar end of the sac.[1]

Cases where antipodal cells have assumed an egg-like appearance have been frequently recorded, but sometimes the whole embryo sac shows an inversed polarity, i.e. the egg apparatus lies in the chalazal part and the antipodal cells in the micropylar part. Dahlgren (1927, pp. 210–11) gave a list of such cases, and to these may be added *Saccharum officinarum* (Dutta & Subba Rao, 1933) and *Woodfordia floribunda* (Joshi & Venkateswarlu,[2] 1935 b).

More interesting than any of these are two saprophytic Gentianaceae, *Leiphaimos* sp. and *Cotylanthera tenuis*,[3] investigated by Oehler (1927). The ovules are here devoid of any integument and the embryo sac is completely inverted, i.e. the antipodal cells are on the side towards the nucellar epidermis and the egg apparatus towards the funiculus. This is of particular significance, since it shows that "die Samenanlagen von *Leiphaimos* und *Cotylanthera* sind nur äusserlich orthotrop, innerlich aber anatrop d.h., ihr Embryosack ist wie in anatropen Samenanlagen orientiert".

[1] Great care is needed in such interpretations. Rutgers (1923) reported that there is a free nuclear egg with sixteen nuclei in *Moringa oleifera*, while Puri (1934) has now shown that the first division of the zygote is followed by wall formation as in other angiosperms. It seems certain that Rutgers was looking at endosperm nuclei, while the egg itself entirely escaped his notice in earlier stages!

[2] Joshi & Venkateswarlu (1935 b, p. 843) write that theirs is the "first" clear case of reversed polarity observed in an 8-nucleate embryo sac. Actually, however, the best instances of this kind are to be seen in the Loranthaceae, Balanophoraceae, and *Leiphaimos* (Oehler, 1927).

[3] This plant is apogamous.

A brief reference may finally be made to the tubular embryo sacs of *Siparuna Eggersii* (Heilborn, 1931). The megaspore mother cell gives rise to the usual tetrad of megaspores of which the chalazal functions and the rest degenerate. This elongates considerably and penetrates downward into the nucellus but soon encounters a hypostase which checks further development. Here it becomes coiled into several turns and the end swells into a vesicle, which finally bursts and releases its contents into a nucellar cavity that has formed in the meantime just above the hypostasis. Although fertilization does not occur and the embryo sac soon degenerates, we have here an illustration of the homologies between the mega- and microspores of angiosperms; for just as pollen grains may, under certain circumstances, attain the form of embryo sacs (Stow, 1930), so embryo sacs can sometimes grow like pollen tubes.

In several instances (*Orobanche Hederae* (Glišić, 1929); *Newcastlia insignis* and *Congea villosa* (Junell, 1934); *Utricularia coerulea* (Kausik, 1935); *Putoria calabrica* (Fagerlind, 1936); and others) embryo sacs are known to protrude out of the micropyle into the loculus of the ovary, but the condition reported by Rauch (1936) in *Scurrula atropurpurea* and *Dendrophthoe pentandra* is without a parallel. Ovules and integuments are absent as in the other Loranthaceae. The embryo sac undergoes a remarkable elongation both towards the top and the bottom; at the chalazal end it is soon stopped by a layer of collenchymatous cells, but the tip grows out halfway upward into the conducting tissue of the style! Fertilization occurs here by the incoming pollen tubes, and the embryos are thrust down again by the elongating suspensors![1]

Oenothera-type

Geerts (1908) was the first to publish a clear account of the development of the embryo sac in *Oenothera lamarckiana* and Modilewski (1909 *b*) described the same features in *O. biennis*, *Epilobium angustifolium*, *E. dodonaei* and *Circaea lutetiana*. Only four divisions intervene between the megaspore mother cell and the egg, and the first two of these are the reduction divisions. Contrary to the normal condition, it is usually the micropylar megaspore that functions here (Fig. 3 *c*), but sometimes it is the chalazal (Fig. 3 *d*), and occasionally both of them may start to form embryo sacs (Fig. 3 *e*, *i*, *j*). In *Anogra pallida* (Johansen, 1931 *c*), *Zauschneria*

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[1] Such a condition recalls that in *Welwitschia*, but of course the two plants are too far apart to permit further comparisons.

latifolia (Johansen, 1931 b) and *Ludwigia parviflora* (Maheshwari & Gupta, 1934), ⊥-shaped tetrads (Fig. 2c) have sometimes been observed. In every case the megaspore nucleus undergoes only two more divisions, and all the four nuclei so formed lie in the micropylar end of the embryo sac. Three of these organize into the egg apparatus and the fourth functions as the single polar nucleus. The third mitosis is entirely omitted, and consequently there are no antipodals nor a lower polar nucleus. It happens, however, that the three degenerating megaspores persist for a long time at the base of the embryo sac and may give the deceptive appearance of antipodal cells (Fig. 3h).
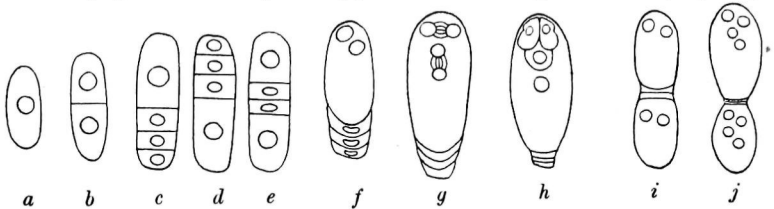

Fig. 3. Stages in development of *Oenothera*-type of embryo sac: (a) megaspore mother cell; (b) dyad; (c, d, e) tetrads of megaspores; (f, g) 2- and 4-nucleate stages; (h) mature embryo sac; (i, j) both micropylar and chalazal megaspores growing into embryo sacs.

This type of development has been reported in all the members of the Oenotheraceae so far investigated, and may indeed be regarded as a valuable diagnostic character for the family. The only exception is *Trapa*, which has an 8-nucleate embryo sac, but even here the antipodal nuclei acquire no walls and promptly degenerate. Ishikawa (1918), who gave a brief account of the development in *T. natans*, thinks that the difference is important enough to justify the separation of this genus from the family.[1]

The following list attempts to bring together all the species of this family that have been investigated and found to have tetra-nucleate embryo sacs:

Name of plant	Author
Anogra pallida	Johansen (1931 c)
Boisduvalia densiflora	Täckholm (1915)
Circaea lutetiana	Modilewski (1909 b), Werner (1915)
C. *pacifica*	Johansen (1934)
C. *quadrisulcata*	Ishikawa (1918)
Clarkia sp.	Werner (1915)
C. *elegans*	Täckholm (1915), Johansen (1930 a)
C. *pulchella*	Täckholm (1915)
Epilobium angustifolium[2]	Modilewski (1909 b), Werner (1915), Täckholm (1915), Ishikawa (1918)

[1] In the latest edition of the *Syllabus der Pflanzenfamilien* the genus *Trapa* has been placed in the family Hydrocaryaceae (see Engler, 1936, p. 306).

[2] Michaelis (1925) has also investigated some species of *Epilobium*, but his account deals chiefly with the development of the embryo and chromosome numbers.

Name of plant	Author
Epilobium Dodonaei	Modilewski (1909 b)
E. hirsutum	Täckholm (1915)
E. hirsutum × E. montanum	Håkansson (1924)
E. parviflorum	Schwemmle (1924)
E. roseum	,,
Fuchsia sp.	Werner (1915)
F. coccinea	Täckholm (1915)
F. "Emile de Wildeman"	,,
F. fulgens	,,
F. "Marinka" and other cultivated varieties	,,
F. procumbens	,,
F. pumila	,,
Gaura Lindheimeri	Ishikawa (1918)
G. parviflora	,,
Gayophytum ramoisissimum	Johansen (1932)
Godetia sp.	Ishikawa (1918)
G. amoena	Täckholm (1915)
G. "gloriosa"	,,
G. Whitneyi	,,
Hartmannia tetraptera	Johansen (1929)
Jussieua repens	Ishikawa (1918), Maheshwari & Gupta (1934)
J. suffruticosa	Täckholm (1915)
J. villosa	,,
Lopezia coronata	Täckholm (1914)
L. parviflora	Maheshwari & Gupta (1934)
L. prostrata	Ishikawa (1918)
Oenothera albata	Hoeppener & Renner (1929)
O. biennis	Modilewski (1909 b), Davis (1910), Renner (1914), Werner (1915)
O. coccinea	Werner (1915)
O. cruciata	Rudloff & Schmidt (1932)
O. fallax	Langendorf (1930)
O. grandiflora	Gerhard (1929)
O. Hookeri	Rudloff & Schmidt (1932)
O. Hookeri albata	Langendorf (1930)
O. Lamarckiana	Geerts (1908), Werner (1915), Haberlandt (1927)
O. "Lamarckiana-gigas"	Hoeppener & Renner (1929)
O. "R.-Lamarckiana"	Rudloff & Schmidt (1932)
O. lutescens	Hoeppener & Renner (1929)
O. muricata	Haberlandt (1927)
O. "R. muricata"	Rudloff & Schmidt (1932)
O. nutans	Ishikawa (1918)
O. pachycarpa	Rudloff (1930)
O. pycnocarpa	Ishikawa (1918)
O. rhizocarpa	Werner (1915)
O. rubiflava	Hoeppener & Renner (1929)
O. rubrinervis	O'Neal (1923), Rudloff & Schmidt (1932)
O. rubririgida	Langendorf (1930)
O. suaveolens	Hoeppener & Renner (1929)
O. tetraptera	Werner (1915)
Stenosiphon linifolium	Johansen (1931 c)
Taraxia ovata	Johansen (1931 a)
Zauschneria latifolia	Johansen (1931 b)

Abnormalities with regard to the number of nuclei are relatively rare. When less than four occur, this is mostly due to a failure of division of the primary synergid nucleus resulting in a 3-nucleate embryo sac with only one synergid, an egg and a polar nucleus (as in *Hartmannia tetraptera*, Johansen, 1929). A multinucleate

condition often results due to a fusion of two gametophytes. As mentioned before, there is a tendency in several members of this family for a concurrent development of both the terminal megaspores, thus resulting in twin embryo sacs (Fig. 3*j*). The two megaspores lying in the middle are soon crushed, and if the separating wall dissolves, eight (four from each gametophyte) or six (four from one and two from the other) nuclei may be seen in a common chamber.

Täckholm (1915, p. 352) figures an embryo sac of *Fuchsia procumbens* which must have originated from a 7-nucleate condition; the three cells of the egg apparatus are all binucleate and there is a single polar nucleus. The same author also described some embryo sacs with five nuclei in *Jussieua*, *Godetia* and *Fuchsia*, and believes that the extra nucleus probably arose by a division of the polar nucleus.

Haberlandt (1927) records several interesting abnormalities in *Oenothera lamarckiana* and *O. muricata*, and cites cases where the number of nuclei may ascend up to fifteen, a condition resulting in his opinion from a "Rückbildung" or "Vegetativwerden des Embryosackes". A still more striking and perhaps unparalleled situation exists in *Anogra pallida* (Johansen, 1931*c*), in which the number of nuclei in some well-nourished embryo sacs may be as high as 140. This is due to a repeated amitotic division of the polar nucleus which seems to possess an unusual vitality in this plant.[1]

We may now turn to some other cases where an *Oenothera*-type of embryo sac has been reported. Arnoldi (1912) stated that *Ceramanthus*, *Glochidion* and *Codiaeum* also belong here. For *Codiaeum* (p. 143) he writes: "Die Urmutterzelle des Embryosackes von *Codiaeum* wird durch eine gewöhnliche Reduktionsteilung in eine in Fig. 8 abgebildete Tetrade zerlegt. Die unterste Zelle wird zum Embryosack, in dem durch zweimalige Kernteilung vier Kerne entstehen (Figs. 9–11). Damit werden die Teilungen eingestellt. Der Embryosack führt also ausser der Eizelle und den zwei Synergiden nur noch einen Kern (Fig. 12). Weder der andere Polkern, noch die antipodalen Kerne lassen sich auf der durch den Embryosack geführten Schnittserie entdecken."

The term "*Codiaeum*-type" thus came to be regarded as synonymous with "*Oenothera*-type", and some authors have actually preferred the former (Palm, 1915; Wettstein, 1935). A recent investigation of *Codiaeum variegatum* (Lundberg, 1931) has, however, shown that the embryo sac is really 8-nucleate and arises in the normal way. Arnoldi's error is explained by an early fusion of the polar

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[1] This may also be regarded as the formation of a haploid parthenogenetic endosperm.

nuclei and a degeneration of the antipodals. Maheshwari & Chowdry (1937) have shown the same thing in *Phyllanthus* (=*Ceramanthus*) *niruri*, and it seems certain that *Glochidion* will yield similar results. Thus the occurrence of the *Oenothera*-type of embryo sac in the Euphorbiaceae remains unproved and the name "*Codiaeum*-type" has no meaning.

We may now pass on to *Gastrodia elata* (Kusano, 1915), in which the megaspore mother cell forms a row of three cells of which the chalazal functions. The 2- and 4-nucleate stages follow. According to the author there are no further divisions, and an egg apparatus and a single polar nucleus are now organized. As in *Cypripedium* (Pace, 1907), a synergid nucleus is said to leave its place and take part in triple fusion. It will be shown later than Pace's account of *Cypripedium* was incorrect and the same may be said of *Gastrodia*.

Recently Miss Parks (1935) has reported a 4-nucleate embryo sac in *Commelinantia Pringlei* and *C. anomala*, said to arise from the lowest cell of a row of three (as in *Gastrodia*). *Commelina benghalensis* (Maheshwari & Singh, 1934), a closely allied plant, is perfectly normal. It seems certain that the antipodal nuclei *are* formed in Miss Parks' plants also, but were overlooked by her due to their ephemeral nature.

BISPORIC; 16-NUCLEATE

Bisporic embryo sacs with sixteen nuclei are not known with certainty in any plant. Campbell (1910, 1911) investigated *Pandanus artocarpus*, *P. odoratissimus* and *P. coronatus* and reports many-nucleate embryo sacs in each case. Schnarf (1929, p. 197) has provisionally included *Pandanus* under bisporic embryo sacs, but Campbell's account is very old and lacks clearness. It is very desirable that this genus be reinvestigated in detail.

Modilewski (1929, p. 38) writes: "Ich habe einmal statt eines achtkernigen einen sechzehnkernigen Embryosack, wo die Kerne, ohne Zellen auszubilden, parallel der Längsaxe des Embryosackes lagerten, beobachtet. Falls die Art, in welcher dieser Embryosack entstanden war, zu dem *Scilla*-Typus gehörte, wie es bei normalen Embryosäcken von *Allium odorum* geschieht, so haben wir hier ein Beispiel eines bisporischen sechzehnkernigen Embryosackes."

Allium-type[1]

A bisporic embryo sac with eight nuclei was first reported by Strasburger (1879) in *Allium fistulosum*, and has been described since then in many angiosperms belonging to different families.

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[1] Most authors have used the name "*Scilla*-type", but this seems to be less appropriate since *Allium* has the claim of priority.

The megaspore mother cell divides into two cells of which the upper usually degenerates quickly while the lower undergoes three divisions to form an 8-nucleate embryo sac. There is thus a total of four divisions—one less than in the Normal-type.

In some cases the nucleus of the upper dyad cell also divides, but degeneration may start before the division is completed (*Lycopsis arvensis*, Svensson, 1925); in other cases the nuclear division is followed by an anticlinal or periclinal wall. In a few plants the
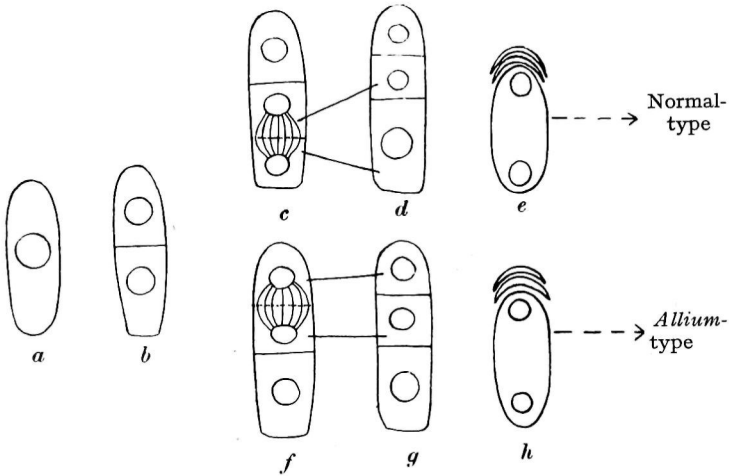

Fig. 4. Explanation of origin of "row of three cells": (*a*) megaspore mother cell; (*b*) dyad; (*c, d, e*) only the lower dyad cell has divided. Of the three cells in (*d*) the chalazal cell develops into an embryo sac (Normal-type); (*f, g, h*) only the upper dyad cell has divided. Of the three cells in (*g*), the chalazal develops into an embryo sac (*Allium*-type).

nucleus may undergo more than one division, and finally there are some cases where it is the upper dyad that functions and the lower degenerates. In *Scilla nonscripta* (Hoare, 1934) the micropylar functions, but the nucleus of the chalazal cell also divides and forms an "antigone" consisting of four nuclei.

Finally, it is necessary to call attention to the "row of three cells", which has led to some confused interpretations. This may arise in two ways: either the uppermost cell is an undivided dyad in which case the development is to be regarded as of the normal monosporic type (Fig. 4 *c, d, e*), or the lower cell is an undivided dyad, in which case the development is to be regarded as of the bisporic type (Fig. 4 *f, g, h*). Shadowsky fails to make this point clear in his papers on *Pancratium maritimum* (1925 *a*) and *Pistia stratioites* (1931), and

his figures admit both interpretations. The occurrence of the *Allium*-type remains unproved in such cases.

As described under the Normal-type, we have here also the occurrence of egg-like antipodal cells in some plants. Modilewski (1931) reports that in *Allium nigrum* one antipodal cell frequently resembles an egg cell, while the other two closely resemble the synergids even in the possession of a filiform apparatus. Messeri (1931) has reported the occurrence of such "antipodal egg cells" in *A. subhirsutum* and *A. schoenoprasum*. Rutishauser (1935) has recently reported in *Korthalsella Dacrydii* a condition somewhat similar to that already described in *Leiphaimos* (Oehler, 1927). Of the two cells formed from the megaspore mother cell, the lower degenerates and the upper functions. After the 4-nucleate stage the embryo sac begins to curve round at the base and soon attains a U-shaped form. The two nuclei at each end now undergo the last division resulting in the 8-nucleate stage. The peculiar thing is that the egg apparatus differentiates at the morphologically lower end of the sac and the antipodals at the upper end. "Der Embryosack verhält sich so, *als ob er einer anatropen Samenanlage angehören würde*. Da wir kein Organ entdecken können, das einer anatropen Samenanlage entspricht, wollen wir den Embryosack von *K. Dacrydii* als in sich anatrop bezeichnen" (Rutishauser, p. 407). Such embryo sacs, anatropous in themselves, seem to be characteristic of other Loranthaceae as well, although their earlier development does not always seem to agree with that described for *Korthalsella*.

There are a number of plants under the *Allium*-type, in which the embryo sacs have less than eight nuclei (see Fig. 5). Reduction always occurs at the chalazal end. The Alismaceae, investigated by Johri (1935 *a*, *b*, *c*, 1936 *b*), are specially interesting in this connexion. In *Limnophyton obtusifolium* (Johri, 1935 *a*) the embryo sacs have sometimes all eight nuclei formed in the usual way, more often there are only seven (this is due to a failure of division of the lowest nucleus of the 4-nucleate stage) but the commonest of all is the 6-nucleate condition. The development proceeds normally up to the 4-nucleate stage, but after this only the micropylar pair divides while the chalazal remains undivided.

Further reduction has been seen in *Nipa fruticans* (Radermacher, 1925), *Echinodorus ranunculoides* (Dahlgren, 1928), *E. macrophyllus* (Dahlgren, 1934), *Butomopsis lanceolata* (Johri, 1936 *a*) and several genera of the Podostemonaceae, viz. *Apinagia, Cladopus, Lophogyne, Mourera, Oenone, Rhyncolacis, Tristicha* (Went, 1910, 1912, 1926)

and *Lawia* (Magnus, 1913). In these plants the primary chalazal nucleus does not divide at all, and the embryo sacs are only 5-nucleate with a normally organized egg apparatus, a single polar nucleus and one degenerated nucleus at the chalazal end. In *Lawia* this sometimes remains healthy for a longer time and may even fuse with the upper polar nucleus (Magnus, 1913).
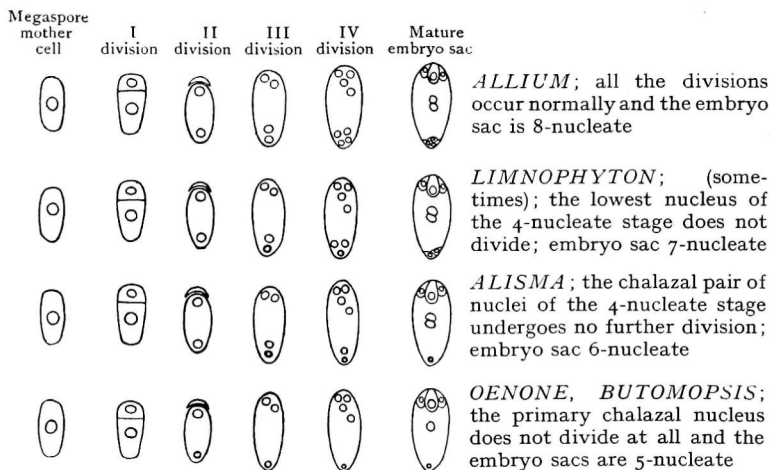

Fig. 5. Diagrams to show reduction of number of nuclei in chalazal part of embryo sac of *Allium*-type.

Pace (1907) had described a peculiar type of embryo sac in *Cypripedium spectabile*, *C. pariflorus*, *C. pubescens* and *C. candidum*, in which the lower dyad cell was reported to divide twice, resulting in a pair of nuclei at each end of the embryo sac. The upper pair formed the two synergids and the lower contributed to the egg and single-polar nucleus. At the time of fertilization one of the synergid nuclei was observed to descend and take part in triple fusion. This type of development, so far known as the *Cypripedium*-type (Palm, 1915), was subjected to many criticisms, and a recent investigation of *C. guttatum* (Prosina, 1930) and some other species of this genus (Francini, 1931) shows that the development is essentially the same as in *Allium* with some reduction at the chalazal end, so that frequently there are only six or five nuclei in the embryo sac. A 4-nucleate condition may arise only in very exceptional cases, but even here its origin is quite different from that described by Pace (see Francini, 1931).

The following is a list of such angiosperms in which the *Allium*-type has been reported so far. When any name is preceded by an asterisk, this indicates doubt about the reliability of the observations.

When there are two such marks, this either means that such an interpretation was later found to be wholly incorrect or that there are very strong reasons to think that this is so. "s" indicates that the development is usually of the normal type, but *Allium*-type was observed in isolated cases.

SAURURACEAE

Saururus cernuus	Johnson (1900a)	—

SALICACEAE

Salix petiolaris *S. glaucophylla* *S. discolor* *S. tristis* *S. cordata*	Chamberlain (1897)	Sometimes *Adoxa*-type is also reported to have been found, and the author states that such variations are common in the genus. Jönsson (1879–80), however, found Normal-type in *S. fragilis* and *S. aurita*, and Håkansson (1929) has done the same in *S. viminalis* and *S. caprea*
Populus canadensis *P. tremula*	Graf (1921)	The author is himself somewhat doubtful

PODOSTEMONACEAE

Apinagia divertens	Went (1910)	In all these cases the embryo sacs
A. perpusilla	Went (1910, 1926)	are only 5-nucleate, due to a reduc-
Cladopus Nymani	Went (1926)	tion in the number of divisions at
Lawia zeylanica	Magnus (1913)	the chalazal end
Lophogyne capillacea	Went (1910)	
Mourera fluviatilis	Went (1910, 1926)	
Oenone Imthurni	Went (1910)	
O. Richardiana	Went (1926)	
O. versteegiana	Went (1910, 1926)	
Rhyncolacis macrocarpa	Went (1912)	—
Tristicha hypnoides	Went (1926)	—

LORANTHACEAE

Arceuthobium americanum (= *A. oxycedri*)	Dowding (1931)	The account is very brief and without any figures to illustrate the development of the embryo sac
Dendrophthora gracile[1]	York (1913)	—
Korthalsella Dacrydii	Rutishauser (1935)	Stevenson (1934) has, however, figured a tetrad of four megaspores in *K. Lindsayi*[2]
Viscum album	Steindl (1935)	—
V. articulatum (= *Korthalsella opuntia*)	Steindl (1935)	—

[1] *D. opuntioides* (York, 1913) also shows the same type of development, but according to the author no reduction seems to occur here and the development is apomictic. For the same reason *Balanophora elongata* and *B. globosa* (Ernst, 1914) have not been included in this list.

[2] The Loranthaceae, Balanophoraceae and Santalaceae are among the most difficult angiosperms for embryological investigation, and the variations of development reported in them are to be attributed chiefly to: (1) environmental differences caused by their parasitic or semi-parasitic habit, (2) difficulties of technique (fixing as well as staining), and (3) inadequacy of material. Botanists from Europe and America have usually collected the material from the tropics and then studied it at home only to find that some of the most important stages are still missing. It seems certain that if the same plants were to be carefully reinvestigated by botanists resident in the country where they grow, many new facts would be discovered.

HYDNORACEAE

*Prosopanche bertoniensis	Chodat (1916)	—

NYCTAGINACEAE

s Oxybaphus nyctagineus ⎫ s Mirabilis jalapa ⎭	Rocén (1927, p. 23)	Usually Normal-type; *Allium*-type and *Adoxa*-type both occur rarely *as abnormalities*

CARYOPHYLLACEAE

**Sabulina longifolia	Fischer (1880)	But see Rocén (1927, p. 113), who considers this to belong to the Normal-type

CRUCIFERAE

s Ionopsidium acaule	Corti (1930)	Usually Normal-type; *Allium*-type occurs *only in exceptional cases*

DROSERACEAE

s Dionaea muscipula	Smith (1929)	Usually Normal-type; but Fig. 42 of the author indicates that *sometimes* *Allium*-type may also occur

CRASSULACEAE

Sedum fabaria ⎫ S. populifolium ⎪ S. populifolium ⎬ var. Notarjanni ⎭	Mauritzon (1933, p. 27)	—

SAXIFRAGACEAE

**Ribes pallidum	Himmelbaur (1911)	Mauritzon (1933) thinks it to be normal

MIMOSACEAE

**Acacia rostellifera	Jönsson (1879–80)	This is almost certainly incorrect, for Guignard (1881) reported Normal-type in three species of *Acacia* and recently Newman (1934) has done the same in *A. baileyana*

PAPILIONACEAE

**Lupinus luteus ⎫ **L. polyphyllus ⎭	Guignard (1881)	This is very doubtful. Both species need to be reinvestigated
**Lathyrus odoratus	Jönsson (1879–80)	This is certainly incorrect, for Roy (1933) finds Normal-type

RUTACEAE

s Xanthoxylum alatum ⎫ s X. Bungei ⎭	Mauritzon (1935)	In both cases usually Normal-type occurs. *Allium*-type *only as an abnormality*

MALPIGHIACEAE

Galphimia gracilis	Stenar (1937)	—

EUPHORBIACEAE

Euphorbia mauritanica	Ventura (1934 a)	—

CELASTRACEAE

**Evonymus latifolius	Jönsson (1879–80)	As pointed out by Andersson (1931), this is incorrect

BALSAMINACEAE

*Impatiens sultani	Ottley (1918)	Schürhoff (1931, p. 328) thinks this to be a mistake and regards the development as normal

RHAMNACEAE

Zizyphus sativa	Chiarugi (1930)	—

DATISCACEAE

Datisca cannabina	Himmelbaur (1909), Mauritzon (1936*a*)	—

MYRTACEAE

s *Myrtus communis*	Greco (1930)	*Only occasionally*; usual course of development is perfectly normal

UMBELLIFERAE

Bupleurum aureum	Håkansson (1923)	In *B. junceum* and most other plants of the family Normal-type occurs

OLEACEAE

Olea chrysophylla *O. europaea* }	Andersson (1931, p. 56)	—
s *Syringa vulgaris*	Andersson (1931, p. 53)	*Only sometimes*

ASCLEPIADACEAE

*Cynanchum vincetoxicum	Seefeldner (1912, p. 275)	Needs confirmation

CONVOLVULACEAE

*Cuscuta reflexa	Johri & Nand (1934)	Fedortschuk (1931) and Smith (1934) report Normal-type in the species investigated by them

POLEMONIACEAE

*Polemonium coeruleum	Jönsson (1879–80, p. 17)	An old account that needs confirmation

BORAGINACEAE

Anchusa officinalis	Svensson (1925)	—
Lycopsis arvensis	Svensson (1925)	—

VERBENACEAE

*Avicennia officinalis	Karsten (1891)	Needs reinvestigation
*A. marina var. *alba*	Junell (1934)	Needs confirmation

SOLANACEAE

Datura	Satina & Blakeslee (1935)	—
Nicotiana rustica	Persidsky & Modilewski (1934)	Sometimes more than eight nuclei are reported to occur
N. glauca	Modilewsky (1936)	—

GESNERIACEAE

s **Rhytidophyllum crenulatum*	Cook (1907)	The author saw only one instance of *Allium*-type and states that mostly the development is of the *Adoxa*-type

RUBIACEAE

*Scyphiphora hydrophyllacea	Karsten (1891)	An old account that needs confirmation, specially since the more recently investigated plants of this family are normal

CAPRIFOLIACEAE

Viburnum acerifolium *V. lantana* }	Suneson (1933)	—

COMPOSITAE

Erigeron glabellus	Carano (1921)	
E. alpinus	Chiarugi (1927b)	*Peperomia*-type also occurs
E. Coulteri	Holmgren (1919)	
E. unalaschkensis	Holmgren (1919)	
Vittadinia triloba	Palm (1922)	Earlier stages in development show some interesting features which deserve further study

POTAMOGETONACEAE

*Potamogeton foliosus	Wiegand (1900)	Seems incorrect; all other plants of this family are normal

NAJADACEAE

*Najas flexilis	Campbell (1897)	Needs confirmation

ALISMACEAE

Alisma plantago	Dahlgren (1928), Johri (1936b)	All of these plants show a reduction in the chalazal part of the embryo sac, which is commonly 6-nucleate. Narasimha-Murthy (1933) reports only 8-nucleate embryo sacs in *L. obtusifolium*, but this is regarded as incorrect by Johri (1935 a)
A. plantago-aquatica	Johri (1936b)	
Damasonium alisma	Dahlgren (1928)	
Echinodorus macrophyllus	Dahlgren (1934)	
E. ranunculoides	Dahlgren (1928)	
Limnophyton obtusifolium	Johri (1935 a)	
Sagittaria sagittifolia	Dahlgren (1934), Johri (1935b)	
S. guayanensis	Johri (1935c)	
S. latifolia	Johri (1935c)	
S. graminea	Johri (1936b)	

BUTOMACEAE

Butomopsis lanceolata	Johri (1936a)	—
Limnocharis emarginata (=*L. flava*)	Johri's (1936a) interpretation of the figures of Hall (1902)	—
Hydrocleis nymphoides	Johri (in the press)	—

HYDROCHARITACEAE

*Hydromystris stolonifera	Tassi (1900)	Needs reinvestigation

GRAMINEAE

**Cornucopiae nocturnum	Guignard (1882)	From Hérail's (1889) statement Normal-type seems more likely
**Melica nutans **M. altissima	Fischer (1880)	The account is old and seems to be incorrect; all later investigated Gramineae have turned out to be normal

COMMELINACEAE

**Commelina stricta	Guignard (1882)	Maheshwari & Singh (1934) report Normal-type in *C. benghalensis* and it is almost certain that *C. stricta* will also be found to be so on reinvestigation

PALMACEAE

Nipa fruticans	Radermacher (1925)	—
Chamaedorea latifolia	Jönsson (1879–80)	—

ARACEAE

*Antherurus attenuatus	Jönsson (1879–80)	—
*Arisaema triphyllum	Gow (1908a)	Pickett (1915) has, however, figured a tetrad of megaspores
*Arum maculatum	Jönsson (1879–80)	But see remarks by Schnarf (1931, p. 282)
*Dieffenbachia seguine	Campbell (1900)	—
*Homalonema argentea	Gow (1913)	—
H. alba H. rubra	Jüssen (1928)	—
*Nephthytis Gravenreuthii	Gow (1908b)	The author's statements are not quite clear
*Pistia stratioites	Shadowsky (1931); sometimes	See p. 372 of this paper

LEMNACEAE

Lemna trisulca	Jönsson (1879–80)	—
Wolffia arrhiza	Gupta (1935)	—

LILIACEAE

Allium fistulosum	Strasburger (1879)	—
A. odorum	Schürhoff (1922), Modilewski (1925)	—
A. oleraceum	Stenar (1932)	—
A. roseum var. bulbilliferum A. nigrum A. subhirsutum A. neapolitanum A. schoenoprasum A. triquetrum	Messeri (1931)	—
A. rotundum, etc.	Weber (1929)	The author has investigated several species, but all the stages were not seen by her
A. ursinum	Schniewind-Thies (1901)	—
**Convallaria majalis	Wiegand (1900)	See, however, Schniewind-Thies (1901, p. 5)
s Galtonia candicans	Schniewind-Thies (1901); sometimes	Usually Normal-type
Nothoscordum fragrans	Messeri (1931), Stenar (1932)	—
Ornithogalum pyrenaicum	Guignard (1882)	—
Paris quadrifolia	Ernst (1902)	—
Ruscus aculeatus	De Philippis (1936)	—
Scilla campanulata S. hyacinthoides var. coerulea	McKenney (1904)	—
S. nonscripta	Hoare (1934)	—
S. sibirica	Schniewind-Thies (1901)	—
S. nutans S. patula	Guignard (1882)	—
S. hispanica	Treub & Mellink (1880)	—
Trillium grandiflorum	Ernst (1902)	—
T. cernuum	Heatley (1916)	—
T. recurvatum	Heatley (1916)	Coulter & Chamberlain (1903) report this as normal, but this is incorrect
T. sessile	Spangler (1925)	—
Tulbaghia violacea	Stenar (1933)	

AMARYLLIDACEAE

Crinum latifolium	Stenar (1925b), also Tomita (1931)	—
C. longifolium	Stenar (1925)	—
s *Hypoxis decumbens*	Stenar (1925)	—
Furcraea andina	Nevins (1927)	—
Narcissus micranthus	Guignard (1882)	—
N. Tazetta	Treub & Mellink (1880), Guignard (1882)	—
*Pancratium maritimum	Shadowsky (1925a)	See p. 372 of this paper

BURMANNIACEAE

Burmannia candida	Ernst & Bernard (1912)	—

ORCHIDACEAE

Cypripedium guttatum	Prosina (1930)	—
C. calceolus	E. Oberhammer (unpubl.)	—
C. spectabile *C. parviflorum* *C. pubescens* *C. candidum*	Pace (1907)	See remarks on p. 374 of this paper
Epidendrium variegatum	Sharp (1912)	—
s *Epipactis latifolia*	Vermoesen (1911); *only sometimes*	—
s *E. pubescens*	Brown & Sharp (1911); *only sometimes*	—
s *Gyrostachis cernua* s *G. gracilis*	Pace (1914); *sometimes*	—
Neottia nidus avis	Modilewski (1918)	—
s *Orchis sambucina*	Afzelius (1916); *only rarely*	—
O. praetextum	Afzelius (1916)	—
Paphiopedilum insigne	Afzelius (1916)	—
P. Leeanum *P. spicerianum* *P. barbatum* *P. villosum* *P. venustum*	Francini (1931)	—

Podostemon-type

Among bisporic embryo sacs, *Podostemon subulatus*,[1] *Hydrobium* (=*Zeylandium*) *olivaceum*, *Farmeria metzgerioides* (Magnus, 1913) and *Weddelina squamulosa* (Chiarugi, 1933) show the greatest reduction. In these cases the nucleus of the lower dyad cell divides only twice, resulting in four nuclei that organize into the egg apparatus and a single polar nucleus. There is no nucleus at the chalazal end. We have a total of only three nuclear divisions between the megaspore mother cell and the egg and therefore these embryo sacs cannot be classified under the *Allium*-type. It is clear, however, that this is the result of only a continued tendency towards reduction and the family Podostemonaceae itself shows a reduced *Allium*-type in some plants and the *Podostemon*-type in others.

[1] Since this was written, Hammond (1937) has described the occurrence of a 5-nucleate embryo sac in *Podostemon ceratophyllum*, similar in origin to the type found by Went in the Podostomaceae investigated by him.

The problematical embryo sac of *Dicraea elongata* (Magnus, 1913) may also be considered here. All stages have not been found in this case, but according to the statements of Magnus the nucleus of the upper dyad cell divides to form one synergid and the egg, while the lower cell divides anticlinally to form two cells that may be called antipodals. A polar nucleus does not exist and consequently double fertilization is not possible. As pointed out by Schnarf (1936) the occurrence of such an embryo sac does not seem to be very probable and a thorough reinvestigation is necessary before these conclusions can be accepted.

Trisporic embryo sacs

Till recently there was no case known where three megaspore nuclei took part in the formation of an embryo sac. Mauritzon (1933, p. 29) has found that this happens in *Aeonium* (= *Aldasorea*) *guttatum* in a sufficient number of cases to justify its being classified under a new type.

This plant was found to be rather variable in its behaviour and three different types of development may occur:

(1) There is no wall formed after the heterotypic division. After the homotypic division walls are laid down in such a fashion that the middle cell is binucleate. It is, however, the chalazal megaspore that functions and in this instance the development corresponds to the Normal-type.

(2) Wall formation was not seen to occur at all after the reduction divisions. The further history of such cases was not followed, but it may lead to the formation of an 8-nucleate (*Adoxa*-type) or 16-nucleate (*Peperomia*-type) embryo sac.

(3) In still other cases only one wall is laid down after the reduction divisions and that in such a way as to form a 3-nucleate cell at the top and one uni-nucleate cell at the bottom. Usually the chalazal cell develops further and gives rise to an 8-nucleate embryo sac of the normal type.

In a few cases, however (and it is these with which we are concerned here), it is the micropylar cell that functions and each of the three nuclei divides twice so as to form a total of twelve nuclei, which give rise to a normal egg apparatus of three cells, a group of three antipodal cells and *six* polar nuclei.

Mauritzon thinks that this mode of development must be referred to a new type by itself.

Peperomia-type[1]

Campbell (1899) was the first to call attention to certain peculiarities in the embryo sac of *Peperomia pellucida*, but Johnson

[1] See Fig. 6 for a diagrammatic representation of the variations under this type.

(1900 b) gave a fuller account of the development. The four nuclei formed after the first two divisions of the megaspore mother cell are arranged like the spores of a tetrad and are connected in the beginning by strands of granular cytoplasm. These divide to form eight nuclei imbedded in the peripheral cytoplasm, each of which now divides again resulting in sixteen free nuclei, of which one forms the egg, another gives rise to a synergid, eight fuse to form a secondary nucleus, and the remaining five are cut off as antipodal cells.

A few years later the same author (Johnson, 1914) described the embryo sac of *P. hispidula* and found that the egg and synergid are formed as in *P. pellucida* but the remaining fourteen nuclei all fuse together in the centre to form a larger secondary nucleus.

Four other investigators, viz. Brown (1908), Fisher (1914), Häuser (1916) and Abele (1923, 1924), have examined several other species of this genus with results essentially similar to those in one or the other of the above two cases. Evanescent cell plates, often formed between the nuclei in the first two divisions, indicate that they should be regarded as equivalent to the nuclei of the once-walled spores. It is to be noted that in spite of the larger number of nuclei in the sac, the egg is removed from the megaspore mother cell by only four divisions as against the normal five.

The following table summarizes our knowledge of the nuclear arrangement and embryo sac organization in the species of *Peperomia*

Name of species	Author	Egg	Syner-gids	Polar nuclei	Antipodal nuclei
P. arifolia	Brown (1908)	I	I	8	6
P. blanda	Fisher (1914)	I	I	±6	±8
*P. Fraseri var. residiflora	Fisher (1914)	I	I	8–6	6–8
*P. galioides	Fisher (1914)	I	I	8–6	6–8
P. hispidula	Johnson (1914)	I	I	14	Nil
P. incana	Abele (1924)	I	I		?14?[1]
P. Magnoliifolia	Häuser (1916)	I	I	8	6
P. metallica	Abele (1923)	I	I	6	8
P. Ottoniana	Brown (1908)	I	I	8	6
P. pellucida	Johnson (1900b)	I	I	8	6
P. reflexa	Fisher (1914)	I	I	8–6	6–8
*P. residiflora	Häuser (1916)	I	I	8	6
P. scandens	Fisher (1914)	I	I	8–5	6–9
P. sintensii	Brown (1908)	I	I	8	6
P. verschaffeltii	Abele (1923)	I	I		?14?
P. verticillata	Fisher (1914)	I	I	8–6	6–8

* Denotes species that have not been very fully investigated.

[1] Authors (Fisher, 1914; Abele, 1924) have called attention to the difficulty in determining the exact number of nuclei that fuse to form the secondary nucleus and others that remain as antipodals. This is due to the fact that the nuclei do not always fuse at one and the same time and the number of lobes on the secondary nucleus or the nucleoli within it are not sufficiently accurate indicators of the number of nuclei that entered into the fusion.

so far studied. It is rather remarkable that in all cases only a single synergid is present. Some authors have expressed the view that the egg and synergid are sister cells in *Peperomia*, but this has been taken for granted merely because of their relative position and this point still remains to be proved one way or the other.

At present tetrasporic embryo sacs with sixteen nuclei are known in seven other families besides the Piperaceae: Euphorbiaceae,
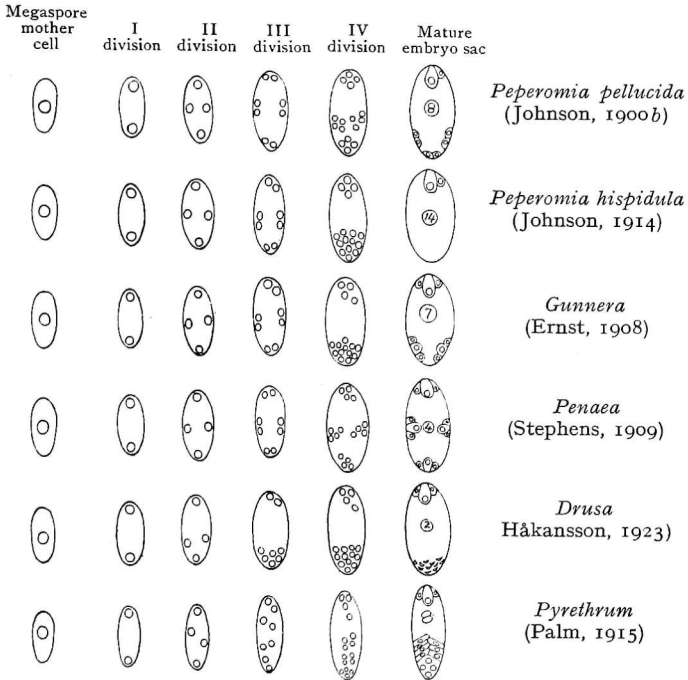

Fig. 6. Diagrams to show more important types of variations found under the *Peperomia*-type of embryo sac.

Penaeaceae, Gunneraceae, Malpighiaceae, Umbelliferae, Compositae and Liliaceae. We shall group the abnormalities in such a way as to call attention to their similarities.

Penaea-form. Miss Stephens (1909) found that in three genera of the Penaeaceae (*Penaea ovata, P. mucronata, Brachysiphon imbricatus, Sarcocolla squamosa, S. formosa* and *S. furcata*), the first two divisions form a tetrad of nuclei just as in *Peperomia*. These separate and each divides twice to form a group of four nuclei. Cell walls are now organized around three nuclei of each quartet;

the remaining four move to the centre and fuse to form a secondary nucleus.

This type of development has since been reported in some other plants also, viz. *Acalypha* sp. (Arnoldi, 1912); *A. australis* (Tateishi, 1927); *A. indica* (Maheshwari & Johri, 1937; see also Maheshwari, 1935); *Euphorbia palustris* (Modilewski, 1911); *E. procera* (Modilewski, 1909*a*, 1910; Schürhoff, 1924); *E. virgata* (Modilewski, 1911); *Malpighia coccifera*, *M. urens*, and *Brunchosia nitida* (Schürhoff, 1924); *Azorella trifurcata* (Håkansson, 1927).

Tateishi (1927) and some others have expressed the opinion that such an embryo sac corresponds to four monosporic tetranucleate embryo sacs arranged at right angles to one another. The important point to determine is whether the "egg" in the other three triads besides the one at the micropylar end can function and give rise to an embryo. The figures of most of the authors cited above do not always show an appreciable differentiation into egg and synergids in these triads.

Gunnera-form. The embryo sac of *Gunnera* was first studied by Schnegg (1902), but the full details were available only after the work of Modilewski (1908) on *G. chilensis* and Ernst (1908) and Samuels (1912) on *G. macrophylla*. Of the sixteen nuclei formed after the fourth division, three at the micropylar end form a normal egg apparatus, the fourth descends and fuses with six of the chalazal nuclei to form a large secondary nucleus and the remaining six are cut off to form antipodal cells. Ernst thinks that they may be said to represent two egg apparatuses, but this would hardly be acceptable till we know more about their function.

Drusa-form. The embryo sacs of *Drusa oppositifolia* (Håkansson, 1923), *Bowlesia tenera* (Håkansson, 1927), *Majanthemum bifolium* (Stenar, 1934) and *Mollatus japonicus* (Ventura, 1934*b*) are somewhat different. After the reduction divisions are over, three of the megaspore nuclei pass down to the chalazal end and only one remains at the micropylar. At the 8-nucleate stage we have, therefore, a 2+6 arrangement and after the last division four nuclei are seen at the micropylar end and twelve at the chalazal. The former group gives rise to the egg apparatus and leaves one nucleus free to move down and fuse with another from the lower end; the remaining eleven nuclei are cut off as antipodals.

Stenar (1934) has seen that in *Smilacina stellata* also the development proceeds in an exactly similar fashion up to the 8-nucleate stage and shows a 2+6 arrangement of the nuclei. Further development could not be traced but he thinks it highly probable that here

also there is one more division resulting in a 16-nucleate embryo sac of the same kind as in *Majanthemum bifolium*.

Pyrethrum-form. Palm (1915) gave a full account of the development in *Pyrethrum parthenifolium* var. *aureum* (=*Chrysanthemum parthenium* var. *aureum*). After the reduction divisions are over, the four nuclei become arranged in a single row and each of them divides to form a group of four. The mature embryo sac contains a normal egg apparatus, two polar nuclei, seven uninucleate antipodal cells and one large antipodal cell with four nuclei. The embryo sacs of *Erigeron dubius* (Tahara, 1921), *E. alpinus* (Chiarugi, 1927 *b*), *E. eriocephalus*, *E. politus* (Holmgren, 1919) seem to be similar, although they have not been so thoroughly studied.

Embryo sacs of the *Peperomia*-type, with a greater or smaller number of nuclei than the usual sixteen, may occur occasionally as abnormalities, but *Tanacetum vulgare* (=*Chrysanthemum vulgare*) studied by Palm (1915) seems to be the only case where 12- and 14-nucleate embryo sacs are of common occurrence. The development differs from *Pyrethrum* in the fact that one or both of the megaspore nuclei at the chalazal end of the embryo sac fail to undergo one division. *Erigeron karwinskianus* (Carano, 1921) shows the opposite condition, for here the number may go up to twenty, which is due to a fifth division of some of the chalazal nuclei.

Fritillaria-type

Until recently it used to be thought that in *Lilium* the development of the embryo sac is of a very simple type. Treub & Mellink (1880) reported that in *L. bulbiferum* the megaspore mother cell does not form the usual tetrad of megaspores, but undergoes only three divisions (against the usual five) to give rise to an octo-nucleate embryo sac. After Treub & Mellink's work, this method of development was reported in many other plants, and for the sake of convenience it began to be known as the "*Lilium*-type".

A thorough investigation of the embryo sac of *Fritillaria persica* and *Lilium candidum* (Bambacioni, 1928 *a*, *b*) showed that instead of the egg being removed from the megaspore mother cell by three divisions, four actually intervene. After the hetero- and homotypic divisions, the four megaspore nuclei arrange themselves in such a fashion that only one remains at the micropylar end while the other three migrate to the chalazal end of the sac. All of these now divide simultaneously, but the spindles of the three chalazal nuclei fuse to form a large common spindle, which is multipolar in the beginning but soon becomes bipolar. As a result of this division, the embryo

sac is *again 4-nucleate*, the two micropylar nuclei being haploid and also smaller than the chalazal nuclei which are triploid. One further division occurs and the eight nuclei now formed are arranged in two groups: a micropylar quartet of four haploid ones and a chalazal quartet of four triploid ones. All the cells of the egg apparatus and the upper polar nucleus are consequently haploid; the lower polar nucleus and the antipodals are triploid, but two of the latter, formed by the division of the lowest chalazal nucleus of the secondary 4-nucleate stage, are usually very ephemeral from the very beginning of their formation.

A couple of years later, Bambacioni & Giombini (1930) described the same phenomenon in *Tulipa gesneriana* and Bambacioni (1931) herself added *T. praecox* and *Lilium bulbiferum* to the list. Recently Cooper (1935) has investigated a number of species of *Lilium* and finds the same type of development in all of them. It is interesting to note that Guignard (1891), Sargant (1896), Coulter (1897) and Mottier (1898) saw abnormal appearances pointing towards the same conclusion in the species of *Lilium* investigated by them, but they thought these to be caused by some physiological or pathological conditions and failed to pursue the point further.

In a still more recent paper, Romanov (1936) reports the same type of development in *Gagea ova* and *G. graminifolia* and considers its occurrence to be very probable in *G. tenera* also, which was however not so fully studied. By comparing Stenar's (1927) figures of *G. lutea* with his own preparations of these three species, he comes to the conclusion that the same type occurs in Stenar's plant also.[1]

As Dr Cooper (1935) has remarked, there is now very strong reason to think that this type of development is characteristic of the genus *Lilium* as a whole, and it has been suggested (Maheshwari, 1936, and others) that the name "*Lilium*-type" be discarded altogether. What we so far understood by this term should now be called the "*Adoxa*-type", since *A. moschatellina* (Jönsson, 1879–80) was the first plant in which all the four megaspore nuclei were to divide once to give rise to an 8-nucleate embryo sac.

The new cases, described above, have tetrasporic embryo sacs, in which four divisions intervene between the megaspore mother cell and the egg. The result is, however, not a 16-nucleate embryo sac as in *Peperomia*, but a normal-looking one whose 8-nucleate condition is brought about by special conditions, i.e. the interposition

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[1] Since this was written, Westergård (1936) has added *Gagea minima* also to the list and Oikawa (1937) has demonstrated the occurrence of the *Fritillaria*-type in *Cardiocrinum cordatum*.

of a secondary 4-nucleate stage. We think that this type is distinctive enough to earn a new name—the "*Fritillaria*-type".

Although typically the number of nuclei is eight, cases of a reduction in their number are not infrequent (see Fig. 7). Of the two chalazal nuclei of the secondary 4-nucleate stage, the innermost is usually in a degenerating condition right from the time of its formation. In *Fritillaria*, it succeeds in going through a normal division, but in *Lilium* (Cooper, 1935) the division is more or less abortive. In *Gagea*

Megaspore mother cell	I division	II division	III division	IV division	Mature embryo sac	

FRITILLARIA; all the divisions occur normally; embryo sac 8-nucleate

GAGEA; the lowest nucleus of the secondary 4-nucleate stage does not divide; embryo sac 7-nucleate.

GAGEA OVA (sometimes); the chalazal pair of nuclei of the secondary 4-nucleate stage undergoes no further division; embryo sac 6-nucleate

Fig. 7. Diagrams to show reduction of number of nuclei in chalazal part of embryo sac of *Fritillaria*-type.

this division commonly does not take place at all and the embryo sacs are 7-nucleate; finally there are some cases in *G. ova* where both of the chalazal nuclei fail to divide and the mature embryo sac is therefore only 6-nucleate. All three conditions may also occur in the same plant, viz. *Myricaria germanica* (Frisendahl, 1912).[1]

The following appearances are thus quite characteristic of the *Fritillaria*-type:

(1) A 1 + 3 arrangement of the megaspore nuclei.

(2) A fusion of three spindles in the chalazal region resulting in a larger number of chromosomes on the equatorial plate.

(3) A secondary 4-nucleate stage, easily recognized by the greater size of the chalazal nuclei which are triploid.

[1] A further reduction may occur if the 3 chalazal nuclei of the primary 4-nucleate stage fuse to form a triploid nucleus, which does not undergo any further division. Such 5-nucleate embryo-sacs have been seen by Mauritzon (1936 c) in *Caulophyllum robustum*.

Now we may call attention to certain doubtful cases, which have been reported to belong to the *Adoxa*-type, but (judging from the figures and descriptions of the authors themselves) may really come under the *Fritillaria*-type.

Piper subpeltatum. Some of Palm's (1915) figures of this plant show a clear 1 + 3 arrangement of the megaspore nuclei and also an appreciable difference in the relative sizes of the micropylar and chalazal nuclei of the 4-nucleate stage. Schnarf (1931, p. 11) stated that the development here is not of the *Adoxa*-type as described by Palm, but of the *Fritillaria*-type. Others (Maheshwari, 1936; Romanov, 1936) have expressed an agreement with this view.

Piper betel var. *monoicum.* A glance at Johnson's (1910) Figs. 56, 7 and 58 (reproduced here as Fig. 8 *c*, *a*, *b*) shows that they were drawn in an incorrect sequence. Prof. Johnson (1910, p. 725) writes: "The four nuclei resulting from this second division of the embryo sac may sometimes remain near the ends of the sac, where they are formed, or there may be a single nucleus at one end and three at the other (Figs. 56, 58). Often, however, perhaps in half the cases seen, these nuclei may be closely grouped near the middle of the embryo sac (Fig. 57)." What remained a puzzle to Prof. Johnson 25 years ago, may now be explained as follows without even taking the trouble of reinvestigating the plant:

Fig. 57 (here Fig. 8 *a*). Primary 4-nucleate stage; megaspore nuclei as seen just after the homotypic division is over.

Fig. 58 (here Fig. 8 *b*). Later stage, megaspore nuclei showing 1 + 3 arrangement.

Fig. 56 (here Fig. 8 *c*). End of mitosis leading to the formation of the secondary 4-nucleate stage; the chalazal nuclei are distinctly larger in size, which is obviously due to their triploid origin.

Piper medium. Johnson's (1902) Figs. 7 and 8 have again been drawn in an inverted sequence and Fig. 8 called by the author as a later stage, is actually the earlier one, as is also borne out by the size of the nucellus and the embryo sac itself. Fig. 7 shows the telophase of the mitosis leading to the formation of the secondary 4-nucleate stage.

Heckeria umbellata. In this case also Johnson (1902) made a similar mistake. His Fig. 21 (reproduced here as Fig. 9 *b*) shows the megaspore nuclei passing into the 1 + 3 arrangement, while Fig. 20 (reproduced here as Fig. 9 *a*) must be regarded as representing the telophase of the third division leading to the secondary 4-nucleate stage.

In all the three cases cited above Prof. Johnson must be given the credit of having accurately drawn what he saw, although he failed to give the correct interpretation due to the lack of certain important stages. It seems probable that the other species of *Heckeria* and *Piper* will yield similar results on a reinvestigation.

Euphorbia dulcis. Since Carano (1925, 1926) had actually seen

a fusion of the three spindles in the chalazal end of the sac, there seems to be no doubt that the *Fritillaria*-type occurs here (see also Schnarf, 1931, p. 11).

Myricaria germanica. Frisendahl's (1912) figures show the 1 + 3 arrangement as well as a difference in the relative size of the micropylar and chalazal pairs of nuclei of the 4-nucleate stage. There is,
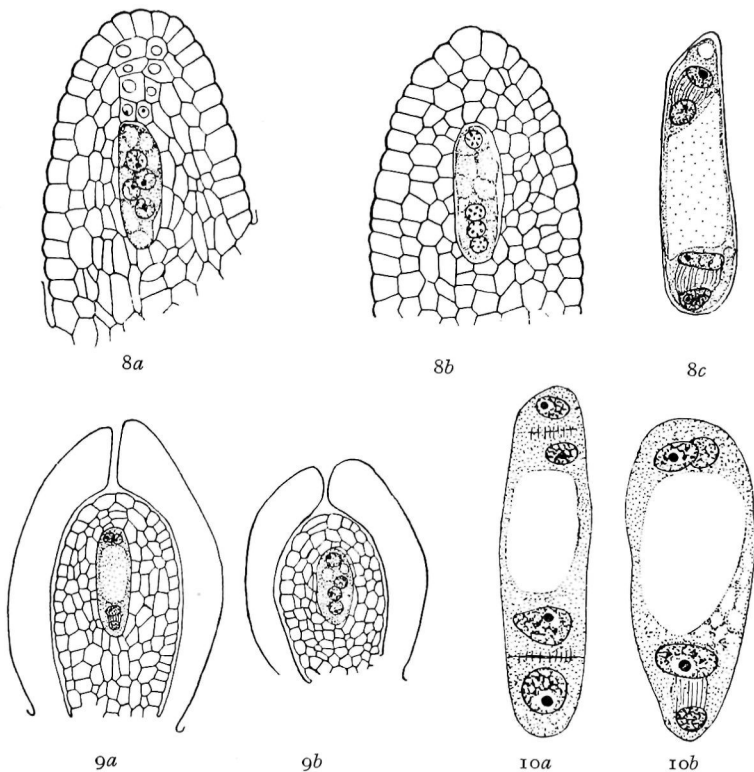
Figs. 8–10. Fig. 8 *a, b, c.* Some stages in development of embryo sac of *Piper betel* var. *monoicum* (after Johnson, 1910). Fig. 9 *a, b. Heckeria umbellata* (after Johnson, 1902). Fig. 10 *a, b. Medeola virginica* (after MacAllister, 1914).

therefore, no doubt that the *Fritillaria*-type occurs here, but this plant seems to be rather variable in its behaviour and therefore a reinvestigation is likely to give interesting results.

Tamarix. Mauritzon (1936a), who investigated *T. tetrandra* and five other species of the same genus, reports the *Adoxa*-type in every case. Joshi & Kajale (1936) have, however, been able to demonstrate that in *Tamarix dioica* the development is of the *Fritillaria*-type.

Since Mauritzon's figures do not give any indication of a 1+3 arrangement nor a difference in size of the nuclei at the two ends of the embryo sac, it is not possible to go further into the question and a fuller investigation of the genus *Tamarix* seems to be desirable.[1]

Rudbeckia hirta. In a preliminary note entitled "Ein neuer Embryosacktypus (bei *Rudbeckia hirta* L.)", Palm (1934) has recently reported a type of development in this Composite, which does not come under any of the existing types. No walls are laid down during the reduction divisions (Fig. 11 *a–d*). The micropylar nucleus remains in its original position, but the two lateral nuclei move down to the
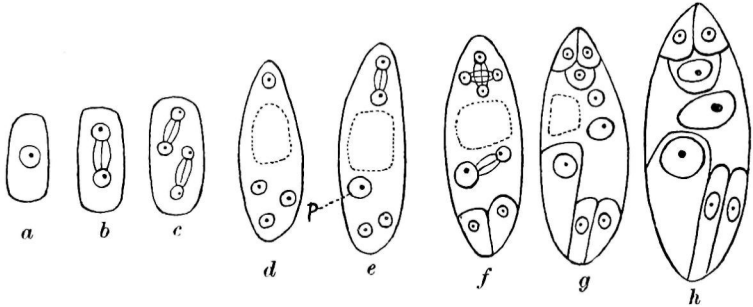
Fig. 11 *a–h*. Development of embryo sac of
Rudbeckia hirta (after Palm, 1934).

bottom of the embryo sac giving the characteristic 1+3 arrangement (Fig. 11*d*). Two of these nuclei, according to Palm, become cut off by membranes to give rise directly to antipodal cells, while the third (*p*) enlarges and takes up a more central position. The micropylar megaspore nucleus quickly undergoes two divisions to form the egg apparatus and the upper polar nucleus and at the time of its second division, "*p*" divides to give rise to the lower polar nucleus and one large antipodal cell (Fig. 11 *e–h*).

Palm's fuller paper will doubtless be awaited with interest. Meanwhile it may be said that this embryo sac shows some significant similarities to that of *Fritillaria* and *Lilium*, i.e. (1) a 1+3 arrangement of the megaspore nuclei, (2) lower polar nucleus much larger than the upper, and (3) one antipodal cell larger than the other two.

Clintonia borealis. Several embryologists (Schnarf, 1931, 1936; Stenar, 1934) have expressed doubts about the reliability of Smith's (1911) observations on this plant. According to the original account, three of the megaspore nuclei formed after reduction degenerate, while the fourth, situated at the micropylar end, undergoes two divisions to form four nuclei, which give rise to the egg apparatus and a single polar nucleus.

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[1] My pupil, Prof. V. Puri of Meerut, has made a detailed study of *Tamarix chinensis* and finds his observations to be in accordance with those of Joshi & Kajale. His full paper is now in the press.

This satisfies the requirements of the *Oenothera*-type, and if Smith's observations are correct *Clintonia* should be regarded as an interesting example of a monosporic tetranucleate embryo sac. Some of Smith's own figures are, however, capable of being interpreted differently. Thus:

Fig. 12 *a*. Megaspore mother cell.

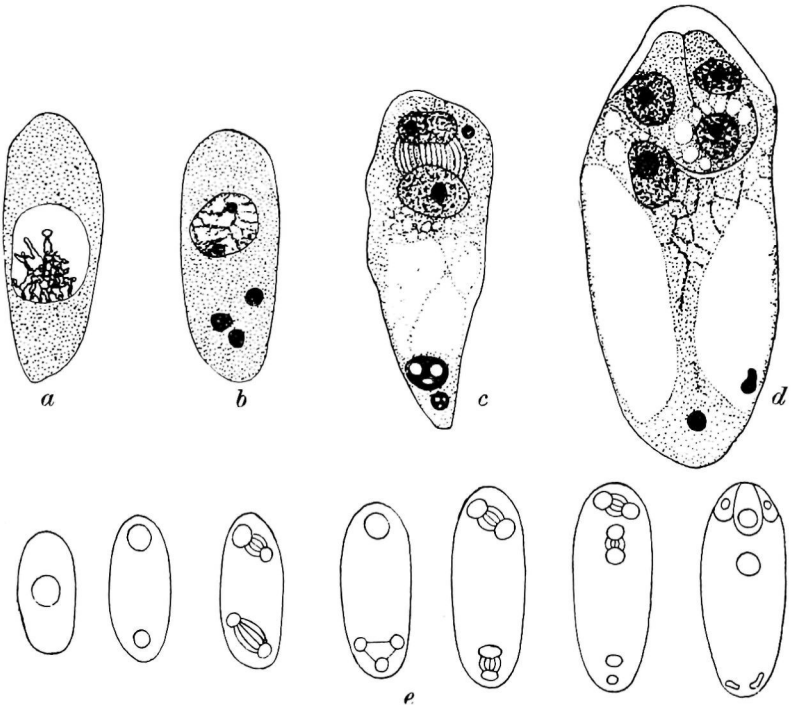Fig. 12 *b*. 1 + 3 arrangement of megaspore nuclei.

Fig. 12 *a–e*. *a–d*, some stages in development of embryo sac of *Clintonia borealis* (after Smith, 1911); *e*, series of diagrams from megaspore mother cell to mature embryo sac stage drawn to illustrate the interpretation of Smith's figures proposed in the text.

Fig. 12 *c*. Perhaps a secondary 4-nucleate stage. The chalazal nuclei are not so large here as in *Lilium* and *Fritillaria* but this may be regarded as a natural consequence of the degenerating and feeble character of the three megaspore nuclei which have contributed to their formation. The three clear spaces in each nucleus may perhaps be taken to provide a strong evidence of their triploid nature.

Fig. 12 *d*. Here we see the last remains of the chalazal pair of nuclei.

If the view put forth above is correct, we have in *Clintonia* an instance of a reduced embryo sac of the *Fritillaria*-type with six

nuclei instead of the normal eight (see Fig. 12 *e* for an explanation of the interpretation proposed here). Such embryo sacs are known to occur in *Gagea* (Romanov, 1936) and *Myricaria* (Frisendahl, 1912) and their occurrence in *Clintonia* should be specially common in view of the degenerating nature of the megaspore nuclei from the very first.

Erythronium dens canis. Hrubý (1934), who investigated some stages in the development of the embryo sac, seems to have been ignorant of Bambacioni's work. The four reduction nuclei are arranged in the same manner as in *Fritillaria* ($1+3$). The mature embryo sacs are 8-nucleate. Intervening stages were not seen, but the author gives an ingenious explanation of the origin of the 8-nucleate stage by supposing that the micropylar nucleus divided twice to form a quartet, while at the chalazal end only one nucleus divided so that the number does not exceed four at this end also![1] Romanov (1936) thinks that the development, as far as it has been traced by Hrubý, indicates a close similarity with *Fritillaria* and we are in complete agreement with this view.

Fritillaria imperialis. Heinricher (1928) gave a figure of the primary 4-nucleate stage showing the $1+3$ arrangement. Lenoir (1934) has demonstrated by chromosome counts that the development is similar to that in *F. persica*.

Fritillaria pudica. Sax's (1916) figures of triple fusion show that the lower polar nucleus is much larger than the upper.

Medeola virginica. McAllister (1914) reported *Adoxa*-type, but two of his figures (reproduced here as Fig. 10 *a*, *b*) seem to indicate that the *Fritillaria*-type occurs here also. A reinvestigation is of course necessary to clear up the point.

Adoxa-type

This type of development is characterized by all four megaspore nuclei undergoing one more division to form an 8-nucleate embryo sac with a normal mature organization. It was described almost simultaneously by Jönsson (1879–80) in *Adoxa moschatellina* and Treub & Mellink (1880) in *Lilium bulbiferum* and *Tulipa gesneriana*. Recent work, already outlined in the preceding pages, leaves no doubt that its occurrence in *Lilium* and *Tulipa* was mistaken, but the findings of Jönsson were confirmed by Lagerberg (1909). The old name "*Lilium*-type" has, therefore, to be replaced by "*Adoxa*-type".

Several other plants, in which older authors reported an *Adoxa*-type of development, have either turned out to be perfectly normal or found to pass through a secondary 4-nucleate stage (*Fritillaria*-type) before attaining the 8-nucleate condition. A few instances cited here will show the necessity for great caution in this respect.

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[1] Note the similarity with Palm's interpretation of *Rudbeckia hirta*.

Schaffner (1897b) in his work on *Typha latifolia* writes: "In the rear of the primary sporogenous cell, or the macrospore mother cell, a long axial row of cells is developed (Figs. 38–41). Often, if the section is not quite longitudinal, so that only three or four of the cells of the axial row are left back of the macrospore mother cell, there is an appearance as though there were a row of four or five megaspores. It is evident that extreme care must be taken not to mistake the large cells of the axial row for potential macrospores. It is possible that misinterpretations may sometimes have been made in this way. In *Typha* I was only able to determine conclusively the real fate of the macrospore mother cell by tracing out its development step by step, so closely did the cells of the axial row agree in size, structure, and staining reaction with the macrospore mother cells. The macrospore mother cell develops directly into the fertile macrospore without any division...." Dahlgren (1918) showed 20 years later that in spite of the "extreme care", which Schaffner claims to have exercised in formulating his conclusions, he made a mistake; *a tetrad of megaspore is formed* in *Typha* and the development is perfectly normal. Sporogenous cells may occasionally be arranged in a linear row (see Johri, 1935d, on *Berberis nepalensis*) and get mistaken for megaspores, as Joshi & Rao (1934) did in the case of *Digera arvensis*.[1] However, if the nucleus can be observed in synizesis or some other stage of reduction division, the recognition of the megaspore mother cell stage is not difficult.

In recent years Heilborn (1921, 1928) has reported that in *Carica papaya* and some other species of this genus no tetrad of megaspores is formed but that all the four nuclei lie free and only one at the micropylar end divides again to form a 5-nucleate embryo sac! Agharkar & Banerji (1930) have nevertheless shown that tetrad formation does occur and Kratzer (1918) did the same.

An interesting situation has developed around the embryo sac of *Stellaria media*. Miss Gibbs (1907) reported that the development was of *Adoxa*-type, while Rocén (1927) who investigated this plant and many other members of the family Caryophyllaceae contended

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[1] The need for accurate and detailed figures is particularly imperative in embryological work. Numerous instances can be cited in which the incorrect interpretations of certain authors have been corrected later by other investigators only if the figures were sufficiently accurate. The case of *Digera* itself has been fully dealt with by Puri & Singh (1935). It may be emphasized that the vast majority of angiosperms have a monosporic 8-nucleate embryo sac and deviations from this will be found only rarely if the material is well-fixed and the technique is adequate. When a different type of development *does* occur, statements must be fully supported by drawings of all important stages.

that it was perfectly normal. In a more recent work P. C. Joshi (1936) writes: "The further development of the megaspore mother cell is variable, and the results of the present investigation are at variance with those of Gibbs and Rocén. A row of three or four megaspores, formed as a result of the usual two successive divisions of the mother cell, was never seen. Only in a few cases the mother cell had divided to form two superposed daughter cells with a transverse or oblique wall in between (Figs. 35, 36)." One would conclude from this that according to Joshi the development is usually of the *Adoxa*-type and sometimes of the *Allium*-type. He does not however appear to be quite sure about it and states later that this "does not preclude the possibility that the two megaspores[1] may give rise to three or four megaspores". The whole thing needs careful reinvestigation. It would not be surprising if in a plant like *Stellaria media*, which is so variable in other respects, some differences may occur in the mode of embryo sac development also, but Joshi's figures do not seem to prove that it is so. On the other hand, the row of three cells shown in Fig. 35 and the four cells arranged in the form of a T in Fig. 36 would perhaps seem to speak for a normal type of development.

Among the plants belonging to the *Adoxa*-type, *Plumbago capensis* is of special interest. Dahlgren (1916), who was the first to investigate it, reported that the four megaspore nuclei formed after the reduction divisions directly entered into the organization of the mature embryo sac (*Plumbagella*-type). Haupt (1934), who has made a thorough study of this plant, finds that there is one more division, but of the eight nuclei so formed three degenerate and four fuse in the centre to form the secondary nucleus; the single nucleus remaining at the micropylar end is cut off to form the egg (Fig. 13 *a–f*). The mature embryo sac is therefore only 2-nucleate (Fig. 13*g*), and without a complete series of stages such as Haupt found it would be easy to be led away to other interpretations of their origin.

The genus *Thesium* provides a good illustration of a reduction of the number of nuclei forming the mature embryo sac. Modilewski (1928, p. 67) called attention to the difficulty in finding the antipodals in *T. intermedium* and concluded that they were extremely ephemeral. In some cases he saw only two nuclei at the chalazal end, of which one functioned as the lower polar nucleus and the other disorganized. Schulle (1933) has confirmed these observations on *T. montanum*

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[1] As explained before, the two cells formed after the first division of the megaspore mother cell must be called dyad cells and not megaspores.

and finds that the 7- and 6-nucleate embryo sacs are due to a failure of division of one or both of the chalazal nuclei of the 4-nucleate stage. The conditions existing here offer a parallel to those in *Limnophyton obtusifolium* (Johri, 1935 a), which has already been discussed under the *Allium*-type.
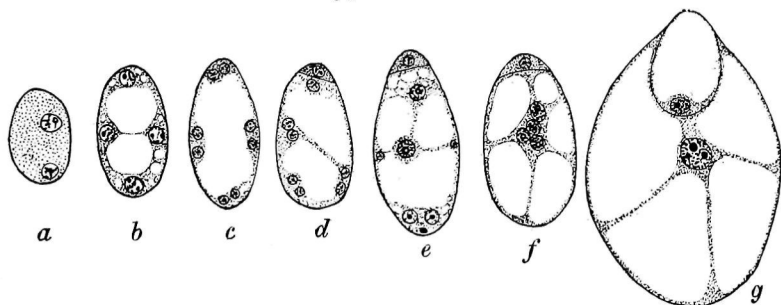

Fig. 13 *a–g*. Stages in development of embryo sac
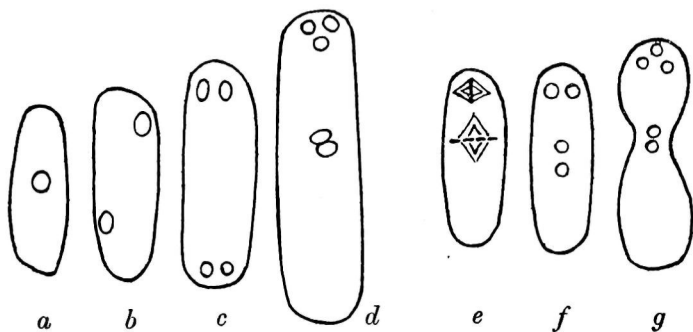of *Plumbago capensis* (after Haupt, 1934).

Fig. 14 *a–g*. *a–d*, stages in development of embryo sac of *Eugenia jambos*;
e–g, *E. bancana* (after Pijl, 1934).

The observations of Pijl (1934) recording a 5-nucleate embryo sac in *Eugenia jambos* and *E. bancana* cannot be regarded as conclusive. The author states that after the four megaspore nuclei have been formed, only one at the micropylar end divides again to give rise to the egg and one synergid, the second micropylar nucleus functions directly as a synergid and the two chalazal nuclei as polars. Pijl's figures, reproduced here on a slightly smaller scale (Fig. 14), are too diagrammatic and entirely inadequate to substantiate this conclusion. The fact that some other species of *Eugenia* investigated by the same author have a normal tetrad of megaspores, leads to the

unavoidable conclusion that the embryology of this interesting genus needs to be investigated more fully.

Tetrasporic embryo sacs of the *Adoxa*-type with more than eight nuclei occur only as abnormalities. *Ulmus americana* (Shattuck, 1905) is a well-known instance in which as many as twelve nuclei were seen in some cases. Some of the extra nuclei fused together with the polar nuclei and others organized as antipodal cells. Recently Billings (1933) has also noted some such cases in *Phoradendron villosum* and *P. flavescens*.

The following is a list of such plants in which the *Adoxa*-type of embryo sac has been reported. As will be seen from the preceding asterisks and "remarks", only a very few of these can now be regarded as correct:

Name of plant	Author	Remarks
PIPERACEAE		
**Heckeria umbellata* *H. peltata*	Johnson (1902)	In almost all of these the occurrence of a *Fritillaria*-type of embryo sac seems certain. See pp. 388 of this paper
***Piper betel* var. monoicum	Johnson (1910)	
P. medium	Johnson (1902)	
***P. subpeltatum*	Palm (1915)	
P. tuberculatum	Fisher (1914)	
JUGLANDACEAE		
***Carya amara* ***C. tomentosa*	Karsten (1902)	The author himself confesses that he had insufficient material. Langdon (1934), Woodroof (1928) and Shuhart (1932) have reported Normal-type in this genus
***Juglans cordiformis* nigra ***J. regia*	Karsten (1902)	Nawaschin & Finn (1913), Langdon (1934) and Nast (1935) report Normal-type in this genus
Pterocarya fraxinifolia	Karsten (1902)	This is also very uncertain
ULMACEAE		
Ulmus americana	Shattuck (1905), Capoor (1937*b*)	—
U. hollandica belgica	Leliveld (1935)	—
U. Wilsoniana	Leliveld (1935)	These two species were not so fully studied
U. pumila pinnato-ramosa	Leliveld (1935)	
SANTALACEAE		
Thesium intermedium *T. montanum*	Modilewski (1928) Schulle (1933)	Guignard (1885) had, however, reported Normal-type in *T. divaricatum*
LORANTHACEAE		
Phoradendron villosum	—	—
P. flavescens var. *macrophyllum*	Billings (1933)	—
HYDNORACEAE		
Hydnora africana	Dastur (1922)	The stages figured in the paper are insufficient to justify *Adoxa*-type

BALANOPHORACEAE[1]

s *Balanophora dioica*	Ekambaram & Panje (1935)	The authors state that usually the development is of Normal-type, but there is sometimes a "tendency" towards *Adoxa*-type

NYCTAGINACEAE

s *Mirabilis jalapa* s *Oxybaphus nyctagineus* }	Rocén (1927); only as abnormality	—

AIZOACEAE

***Mesembryanthemum pseudotruncatellum*	W. Schmid (1925)	Neumann (1935) calls this "eine aus verschiedenen Gründen recht zweifelhafte Angabe". See also Bhargava (1936)

CARYOPHYLLACEAE

*Stellaria media	Gibbs (1907), P. C. Joshi (1936)	Rocén (1927) reported Normal-type. See pp. 393–4 of this paper for further information

CRASSULACEAE

**Sedum sp.	D'Hubert (1896)	Mauritzon (1933, p. 21) calls this "fehlerhaft"

SAXIFRAGACEAE

***Philadelphus coronarius*	Van der Elst (1909)	Gäumann (1919) and Mauritzon (1933, p. 109) find Normal-type

LEGUMINOSAE

**Lupinus polyphyllus*	Guignard (1881)	Needs reinvestigation
**Medicago arborea	Guignard (1881)	Reeves (1930) and Cooper (1936) find Normal-type
**Melilotus alba	Young (1905)	Cooper (1933) finds Normal-type

RUTACEAE

s *Xanthoxylum alatum* s *X. Bungei* }	Mauritzon (1935); only rarely	Usually Normal-type occurs

LIMNANTHACEAE

Limnanthes Douglasii	Stenar (1925 a)	—

TAMARICACEAE

**Myricaria germanica*	Frisendahl (1912)	Needs reinvestigation; see remarks on p. 389 of this paper
**Tamarix tetrandra* **T. aestivalis* **T. africana* **T. gallica* **T. odessana* **T. pentandra* }	Mauritzon (1936 a)	Joshi & Kajale (1936) have reported *Fritillaria*-type in *T. dioica*. A reinvestigation is necessary

CARICACEAE

***Carica candamarcensis* ***C. chrysopetala* ***C. papaya* ***C. pentagona* }	Heilborn (1921, 1928)	Kratzer (1918), and Agharkar & Banerji (1930) have found Normal-type in *C. papaya*

CACTACEAE

**Phyllocactus sp.	d'Hubert (1896)	On the basis of their experience of some other Cactaceae, both Mauritzon (1934 c) and Neumann (1935) regard this as quite incorrect

[1] The parthenogenetic species are not listed here.

Myrtaceae

*Eugenia jambos *E. bancana	Pijl (1934)	See remarks on p. 395 of this paper

Oenotheraceae

**Trapa natans	Gibelli & Ferrero (1891)	Ishikawa (1918) saw megaspore tetrads and Maheshwari (unpubl.) in *T. bispinosa*

Araliaceae

*Aralia spinosa	Ducamp (1902)	Needs reinvestigation

Plumbaginaceae

Armeria alpina A. plantaginea A. vulgaria	Dahlgren (1916) — —	In view of Haupt's (1934) work, a reinvestigation of the other Plumbaginaceae is very desirable
s Ceratostigma plumbagi- noides[1]	Dahlgren (1916)	—
Plumbago capensis	Haupt (1934)	—
Statice bahusiensis	—	—
S. Gmelini	Dahlgren (1916)	—
S. macroptera	—	—

Oleaceae

**Forsythia suspensa	Billings (1901)	Andersson (1931, p. 52) has shown that Normal-type occurs

Solanaceae

**Solanum muricatum	Nanetti (1912)	See remarks by Rees-Leonard (1935)
**S. tuberosum	Young (1923)	Corrected by Rees-Leonard (1935), who finds Normal-type

Gesneriaceae

*Rhytidophyllum crenu- latum	Cook (1907)	Needs reinvestigation

Acanthaceae

*Acanthus ilicifolius	Karsten (1891)	Needs reinvestigation, since the author is himself uncertain

Caprifoliaceae

*Sambucus racemosa	Lagerberg (1909)	Jönsson (1879–80) reported Normal-type

Adoxaceae

Adoxa moschatellina	Jönsson (1879–80), Lagerberg (1909)	—

Compositae

s Leontodon hispidus	Bergman (1935)	Usual development is normal, but in some cases the walls separating the megaspore nuclei dissolved and there was only one more division

Typhaceae

**Typha latifolia	Schaffner (1897b)	Dahlgren (1918) showed this to be incorrect and found Normal-type

Alismataceae

**Alisma plantago	Schaffner (1896)	Dahlgren (1916) & Johri (1936b) have shown that the development is of the *Allium*-type

[1] An 8-nucleate condition was seen in only one case.

BUTOMACEAE

Limnocharis emarginata Hall (1902) Johri (1936b) has given a different interpretation of Hall's figures and believes that *Allium*-type occurs here

PALMACEAE[1]

Cocos nucifera Quisumbing & Juliano (1927) } Earlier stages have not been fully investigated
Chamaerops humilis Gioelli (1930b)

ARACEAE

**Acorus calamus* Mücke (1908) Jüssen (1928) reports Normal-type
Anthurium violaceum var. *leucocarpum* Campbell (1905) Needs reinvestigation
**Richardia africana* Gow (1913) Michell (1916) finds Normal-type
**Zantedeschia aethiopica* Gow (1913) Michell (1916) finds Normal-type

LEMNACEAE

Lemna minor Caldwell (1899) Jönsson (1879–80) reported *Allium*-type in *L. trisulca*

BROMELIACEAE

s *Tillandsia usneoides* Billings (1904) In a very few abnormal cases no walls were seen after reduction division

CYNASTRACEAE

**Cynastrum Johnstoni* Th. C. E. Fries (1919) Stenar (unpubl.) has found Normal-type in *C. Goetzeanum*, and Nietsch (unpubl.) in some other species of the same genus

LILIACEAE

Aloe arborescens } Gioelli (1930a) Schnarf & Wunderlich (unpubl.) find Normal-type in the species of *Aloe* they have investigated. Gioelli's Fig. 9 of *A. caesia* probably shows a T-shaped tetrad of megaspores that has been misinterpreted as a 4-nucleate embryo sac due to bad fixation
A. caesia
A. ciliaris
A. Todari var. *praecox*
A. Varvari

Camassia Quamash Leffingwell (1930) Only a few stages have been figured by the author

**Convallaria majalis* Wiegand (1900) Schniewind-Thies (1901) found Normal-type

Erythronium albidum } Schaffner (1901) A reinvestigation may reveal that the *Fritillaria*-type occurs here
E. americanum

Gagea lutea Stenar (1927) Romanov (1936) has demonstrated *Fritillaria*-type in three species of this genus and thinks that its occurrence is almost certain in *G. lutea* also

Medeola virginica McAllister (1909) Figs. 40 and 41 of the author admit interpretation of *Fritillaria*-type

**Majanthemum canadense* McAllister (1914) Stenar (1934) has found *Peperomia*-type in *M. bifolium*

[1] As pointed out by Schnarf (1931, p. 280) a reinvestigation of the Palmaceae is very desirable. The lack of agreement among the various authors who have worked on this family seems to be due to the earlier development taking place while the inflorescence is still inside the spathe—a fact often realized by the investigator only *after* he has finished his collections and sectioned the material he had.

*Smilacina sessilifolia	McAllister (1914)	See remarks by Stenar (1934) who suspects that a 16-nucleate embryo sac of the *Peperomia*-type is present here also, as in *Majanthemum*
*S. stellata	McAllister (1909, 1914)	
**Tulipa gesneriana	Ernst (1901)	Figs. 13 and 14 of Ernst show a 'secondary 4-nucleate stage"; later Bambacioni & Giombini (1930) demonstrated that *Fritillaria*-type does occur
*T. celsiana	Guignard (1900)	In the light of Bambacioni's work a detailed reinvestigation of all these species seems to be imperative
*T. humilis	Newton (1926)	
*T. kalpakowskiana	Newton (1926)	
*T. silvestris	Guignard (1900)	

<div align="center">AMARYLLIDACEAE</div>

*Amaryllis belladonna	Schlimbach (1924)	The account is very meagre and there are absolutely no illustrations in this paper
*Buphane disticha	Schlimbach (1924)	
*Cooperia Drummondii	Church (1916)	Needs reinvestigation
**Crinum asiaticum	Schlimbach (1924)	Stenar (1925b) & Tomita (1931) report *Allium*-type in other species of this genus
*Cyrtanthus sanguineus	Farrel (1914)	The author says it " seems" to follow the *Adoxa*-type. Stiffler (1925) has shown that Normal-type occurs in *C. parviflorus*
*Nerine curvifolia	Schlimbach (1924)	Needs reinvestigation

<div align="center">ZINGIBERACEAE</div>

**Costus sp.	Humphrey (1896)	Both of these reports seem to be incorrect. Banerji & Venkateswarlu (1936) have demonstrated a normal tetrad of megaspores in *C. speciosus*
**C. igneus	Mauritzon (1936b); "very probable"	

<div align="center">

Plumbagella-type

</div>

Dahlgren, in 1916, reported that in *Plumbagella micrantha*, *Plumbago capensis*, *P. pulchella*, *P. zeylanica* and *Ceratostigma plumbaginoides*,[1] only two divisions intervene between the megaspore mother cell and the egg and these are the obviously necessary reduction divisions. Of the four free nuclei thus formed after reduction, the micropylar pair gives rise to the egg and upper polar nucleus and the chalazal pair forms the single ephemeral antipodal and the lower polar nucleus.

As mentioned before, Haupt (1934) has reinvestigated *Plumbago capensis* very fully and the radical differences between his account and that of Dahlgren (1916) raise some doubts about the reliability of the earlier observations.[2] Dr Dahlgren (as mentioned in a private communication to the writer) is investigating some species himself

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[1] In this case Dahlgren observed one 8-nucleate embryo sac also.

[2] See also the remarks by Schnarf (1936, p. 577).

and further opinion may therefore be deferred till his latest observations have been published.

The embryo sacs of *Aglaonema simplex* and *A. modestum*, usually included under the *Adoxa*-type, may with greater propriety be considered here. According to Campbell's (1912) statement, the four megaspore nuclei are arranged in the usual manner, but only one of

Name of species	Megaspore mother cell	I division	II division	III division	Mature embryo sac	Remarks
F. splendens (less than 50% cases)						Embryo sac 8-nucl. (*ADOXA*-type)
F. splendens (commonest condition)						Embryo sacs 6-nucl. (reduced *ADOXA*-type). 2 syn. and 2 antipodals always present, but sometimes only 1 polar nucleus and an egg; sometimes 2 "presumable" polars and *no egg*
F. splendens (only rarely); *F. burragei*; *F. peninsularis* ("always")						Embryo sac 5-nucl. After 4-nucl. stage, only one micropylar nucl. divides, forming the 2 synergids. (*AGLAONEMA*-type.)

Fig. 15. Diagrams prepared to illustrate the range of variation reported to occur in *Fouquiera* by Johansen (1936).

the micropylar nuclei divides again and this division gives rise to the two synergids; the second *undivided* nucleus functions as the egg and the two chalazal nuclei as polars. If these observations are correct, one of the megaspore nuclei itself functions as the egg, which is therefore removed from the mother cell *by only two divisions*. The third division concerns only the production of the two synergids and therefore this type of embryo sac may be considered as a modification of the *Plumbagella*-scheme. As Michell (1916, p. 333) remarked, however, "the obstacle in the way of accepting Campbell's view is that he has never been able to demonstrate the supposed nuclear division".

Very recently Johansen (1936) has reported the same type of development in three species of *Fouquiera*: *F. splendens*, *F. peninsularis* and *F. burragei* (see Fig. 15). In some cases (only in *F. splendens*)

it was found that both the micropylar nuclei divided instead of only one, resulting in 6-nucleate embryo sacs with two different types of organization, and in still others all four has divided to form 8-nucleate embryo sacs (*Adoxa*-type). On the other hand Mauritzon (1936*a*, p. 95) who has also studied *F. splendens* (independently and without knowledge of Johansen's work) says that the development follows the Normal-type. The differences between these two observers point to the need of a reinvestigation.

In conclusion it may be said that the *Plumbagella*-type, which remained unquestioned for about 20 years (largely because no other embryologist besides Dahlgren studied this family), must now be regarded as uncertain. The range of variation reported in *Aglaonema* and *Fouquiera* is possible but not probable and both demand a fresh study.

HOMOLOGIES OF THE ANGIOSPERM EMBRYO SAC

This is a question whose solution does not seem to be possible, at least at present. There are three main views in the field:

(1) That the embryo sac of angiosperms is derived by reduction from that of some hypothetical conifer and now consists of only two archegonia without any prothallial tissue (Porsch, 1907). The synergids (=neck cells), egg, and upper polar nucleus (=ventral canal nucleus) are supposed to constitute the first archegonium, while the three antipodal cells and lower polar nucleus form the second but now functionless archegonium (for explanation see Fig. 16).

(2) That one synergid (=a ventral canal nucleus) and the egg, both of which are sister cells, constitute one archegonium, while the second synergid and the upper polar nucleus constitute a second archegonium. The remaining nuclei are to be regarded as prothallial. Prof. Schürhoff (1928), who put forward this view, thinks that this also gives a rational explanation of "double fertilization", for both the archegonia are fertilized, although only one happens to give rise to the embryo.

(3) That all the nuclei of the embryo sac are potential eggs, although only one of them produces an embryo. This idea was inspired by the discovery of certain features in the ovule and embryo sac of *Gnetum*, which seemed to show a strong resemblance to angiosperms (see literature cited in Thompson, 1916).

The first and the second view both depend on certain assumptions which are contrary to one another. While Porsch thinks that the synergids are sister cells, Schürhoff contends that one synergid

nucleus is sister to the egg and the second to the upper polar nucleus. Leaving alone certain abnormal cases (like *Peperomia* spp., which do not yet seem to have been fully investigated from this point of view) there is an overwhelming evidence in favour of Porsch's view. Several recent workers have reported that the synergids are formed
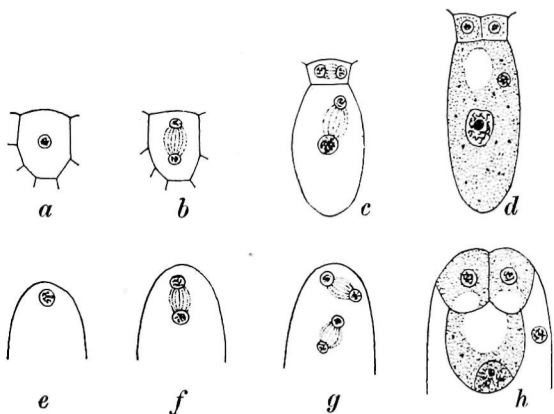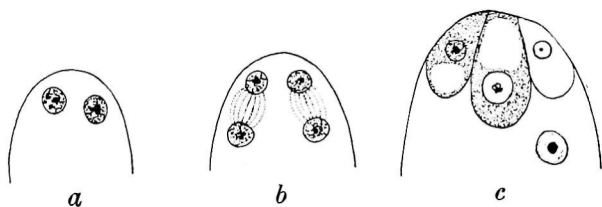

Fig. 16

Fig. 17

Figs. 16, 17. Fig. 16 *a–d*, stages in development of an archegonium of a gymnosperm; *e–h*, stages in development of upper half of angiosperm embryo sac (after Porsch, 1907). Fig. 17 *a–c*. Diagrams of upper half of angiosperm embryo sac, prepared to illustrate Schürhoff's view. In (*c*) the egg and one synergid (shaded) represent "one archegonium", while the other synergid and polar nucleus (unshaded) represent the "second archegonium".

from the division of one nucleus, and the egg and upper polar nucleus from another nucleus of the 4-nucleate stage.[1]

There are, however, other difficulties in accepting Porsch's view. What reason is there for the ventral canal nucleus (upper polar

[1] Only a few instances may be cited here: *Hartmannia tetraptera* (Johansen, 1929), *Boerhaavia diffusa* (Maheshwari, 1929), *Ionopsidium acaule* (Corti, 1930), *Dysoxylum ramiflorum* (Paetow, 1931), *Urginea indica* (Capoor, 1937 *a*). See also Langlet (1927).

nucleus) to leave its position above the egg and come down into the centre of the embryo sac to fuse with another nucleus from the chalazal end which is also the ventral canal nucleus of a second archegonium? We have absolutely no records of such plants which may be visualized as providing a real series of intermediate stages between Porsch's hypothetical gymnospermic ancestor and the modern type of angiosperm.

A detailed discussion of the third view does not seem to be possible. While formerly it was thought that the many-nucleate embryo sacs of *Pandanus*, *Peperomia*, etc. represented a transition from the condition in *Gnetum* to that in the typical angiosperm, no one seriously holds the view at present. The number of abnormal embryo sacs discovered in angiosperms is very small indeed and those, that have been found, occur in the most primitive as well as the most advanced families.

The angiosperms which we see to-day cannot be compared with any other living group. It is true that the Gnetales show certain significant resemblances in the organization of the ovule and in the development of the anther and female gametophyte, but modern trend of thought is in favour of regarding this only as an instance of parallel development. Fossil plants are seldom so well preserved as to give an insight into the structure of the gametophytes, but results of considerable value will be obtained when such material *is* found (Florin's recent work on Cordaitales is an instance of this kind). The question continues to be as baffling as before, but we believe that detailed investigations on the morphology of the Gnetales on the one hand and the more primitive angiosperms on the other will yield results that will eventually help in the solution of the problem.[1] Dr Johri's (1936a) recent discovery of the occurrence of pollen grains in the stylar canal and ovary of *Butomopsis* is an instance of the surprises that lie in wait for us.

[1] Prof. W. P. Thompson, who made a very thorough investigation of the embryology of several species of *Gnetum*, writes (1916, p. 176): "the sum of the evidence from all sides seems to lead to the conclusion that Angiosperms are phylogenetically related to Gnetales. This does not mean that any modern member of the Gnetales represents the type from which Angiosperms were derived but that the ancestors of Angiosperms were not far removed from the genus *Gnetum*."

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