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THE ENDOSPERM IN SCROPHULARIACEAE

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THE study of the development of endosperm in the family Scrophulariaceae dates from the year 1849 when Tulasne made his classical observations. Since then a large number of workers (Hofmeister, 1859; Balicka-Iwanowska, 1899; Schmid, 1906; Glisic, 1932, 1933; Srinath, 1934, 1940; Krishna Iyengar, 1937, 1939-42; Raghavan and his co-workers, 1940, 1941, 1946; Crété, 1948-50, 1952-54, 1958; Yamazaki, 1953, 1954, 1957) have also contributed much to our knowledge of the endosperm in Scrophulariaceae. Samuelsson's work in 1913 followed by those of Schnarf (1929, 1931), Glisic (1936-37), Krishna Iyengar (1947) and Crété (1951, 1955) have thrown much light on the nature of the endosperm and its haustorial processes and have also indicated phylogenetic relationships between the different genera of Scrophulariaceae. Recently, Yamazaki (1953, 1954, 1957) working extensively on several genera of Scrophulariaceae has established phylogenetic relationships and affinities in the different genera on the basis of morphological and embryological characters.

The present account is a review of the notable work done till 1958 particularly on the endosperm and endosperm-haustoria of Scrophulariaceae and incorporates the unpublished work carried out in the Botanical Laboratory, Calcutta University, by Dr. N. Pal. An attempt has been made on the basis of his observations and the data obtained from previous workers to show clearly the phylogenetic relationships of the different genera.

(1) *Endosperm and Endosperm-haustoria*.—The formation of a cellular type of endosperm is characteristic of the family Scrophulariaceae. The only deviation is that recorded by Evans (1919) in *Pentstemon secundiflorus* which has later been severely criticised by Dahlgren (1923). Schmid (1906), however, recorded the occurrence of free-nuclear endosperm in a single instance in *Pedicularis foliosa*.

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The first division of the endosperm in all the plants so far investigated is transverse leading to the formation of a micropylar and a chalazal chamber. The next division, which occurs in the micropylar chamber, is vertical excepting in *Pedicularis*, *Melampyrum*, *Euphrasia* and *Tozzia* (Hofmeister, 1859; Schacht, 1863; Schmid, 1906; Lundquist, 1915; Krishna Iyengar, 1942 c) and in some other members of the family such as *Alonsoa*, *Sopubia*, *Vandellia*, *Bonnaya* and *Ilysanthes* (Krishna Iyengar, 1937, 1940 a, b and c). In *Angelonia* (Srinivasan, 1940) and *Nemesia* (Crété, 1950 a and b), however, the sequence is altogether different. In the former, all the early endospermic divisions are said to be transverse and in the latter, the micropylar chamber precociously differentiates into an uninucleate haustorium instead of undergoing any further division.

The chalazal chamber formed by the first division of the primary endosperm nucleus gives rise to the chalazal endosperm-haustorium quite early in the developmental history of the endosperm tissue, with the exceptions of *Nemesia* (Crété, 1950 a and b), *Ellisiophyllum* (Yamazaki, 1957 a) and in *Pedicularis*, etc. (Schmid, 1906; Krishna Iyengar, 1942 c). Srinivasan's (1940) account on the non-occurrence of endosperm-haustorium in *Angelonia grandiflora* has been questioned by Maheshwari and Navalakha (1941). Later, Krishna Iyengar (1947) doubted the validity of such observations in *Angelonia grandiflora* and stated that the haustoria are formed at both ends of the endosperm tissue. It may be mentioned here that in *Nemesia* (Crété, 1950 a and b) and *Ellisiophyllum* (Yamazaki, 1957 a), this chalazal chamber does not differentiate directly as the haustorial cell but undergoes further divisions to give rise to the endosperm tissue, while the micropylar chamber is precociously transformed into the haustorium.

The structure of the chalazal haustorium is very variable in different species of the family which ranges from a single uninucleate, or binucleate or tetranucleate cell, to two or four uninucleate juxtaposed cells. In *Gratiola* (Glisic, 1933; Yamazaki, 1953 b), these cells, however, are superposed. The haustorium is also not equally aggressive in the different members of the family. In *Lindenbergia indica* (Pal, 1958) the haustorium is composed of a uninucleate cell while in *Mazus japonicus* (Pal, 1958) there are two such cells which are later converted into a two-nucleate cell by the dissolution of the common vertical wall between them. It may be mentioned here that in *Mazus rugosus* (Hofmeister, 1859), this haustorium is very large, and prominent at maturity while in *Mazus japonicus* it is not so. One-celled uninucleate chalazal haustorium has also been observed in *Torenia* (Balicka-Iwanowska, 1899; Krishna Iyengar, 1941; Guilford and Fisk, 1952), *Limosella* (Samuelsson, 1913; Schnarf, 1925; Svensson, 1928), *Lathraea* (Glisic, 1932), *Limnophila* (Krishna Iyengar, 1939 b); *Moniera*, *Bacopa* (Safeeulla and Govindu, 1949 and 1950); *Glossostigma* (Safeeulla, 1950), *Alonsoa* (Crété, 1950 c); *Vandellia* and *Bonnaya* (Yamazaki, 1954 b). The occurrence of a chalazal haustorium consisting of two uninucleate cells which later become a 2-nucleate cell, as in *Mazus*

japonicus, has also been found in *Alonsoa*, *Sopubia*, *Bonnaya* and *Vandellia* (Krishna Iyengar, 1937, 1940 *a, b, c*; Srinivasan, 1940).

The micropylar endosperm-haustorium also seems to be of universal occurrence in the family which differentiates by the second transverse division (occurring in the micropylar chamber) of the growing endosperm tissue, exceptions having been noted in *Pedicularis*, *Nemesia* and *Ellisiophyllum* (Schmid, 1906; Krishna Iyengar, 1942 *c*; Crété, 1950 *a* and *b*; Yamazaki, 1957 *a*) where the micropylar haustorium differentiates precociously. The micropylar endosperm-haustorium, as in the case of chalazal, differs widely in its structure as well as in the degree of aggressiveness in different species of the family. In *Lindenbergia indica* (Pal, 1958), the single vertical wall of this haustorium is developed partially, only to disappear very soon. This type of micropylar haustorium seems to have been derived from *Veronica* or *Alectrolophus* series of Glisic (1936-37). Moreover, the haustorium in *Lindenbergia* shows less activity which possibly indicates a condition of primitiveness. In *Mazus japonicus* (Pal, 1958), the micropylar endosperm-haustorium consists of two uninucleate cells which are later transformed into a binucleate one. Similar behaviour has also been recorded in *Veronica* (Glisic, 1936-37; Yamazaki, 1957 *b*) and *Rehmannia* (Krishna Iyengar, 1942 *a*). Further, in *Mazus japonicus*, one or two tubular outgrowths protrude out from this haustorium. These processes penetrate inside the integumental tissue and proceed towards the chalaza. Such lateral proliferations of this haustorium were previously reported in *Alonsoa* (Krishna Iyengar, 1937; Crété, 1950 *c*); *Vandellia* (Krishna Iyengar, 1940 *a*); *Lyperia* (Crété, 1949); *Striga* (Tiagi, 1956) and in many other species of the family. In *Mazus rugosus*, Hofmeister (1859) demonstrated several such branches coming out from the micropylar endosperm-haustorium which seem to be very different in appearance from that observed by Pal (1958).

Lindenbergia and *Mazus* (Pal, 1958) are both characterised by successive transverse divisions of the two cells of the middle tier in the three-tiered endosperm (including haustoria) leading to the formation of a long narrow biseriate endosperm tissue apart from the two terminal endosperm-haustoria (vertical walls appear later in the lower cells, *i.e.*, the cells situated towards the chalazal end producing a massive endosperm tissue). Similar development of biseriate endosperm tissue at the initial stages of growth has already been described in *Striga euphrasioides* (Srinivasan, 1946) and *Gratiola japonica* (Yamazaki, 1953 *b*). It also appears to be identical with *Angelonia grandiflora* (Srinivasan, 1940).

The formation of a group of small cells, rich in cytoplasm, by the endosperm tissue at one or both ends (*i.e.*, chalazal and micropylar) just below the haustoria has been recorded in many members of the family (Michell, 1915; Glisic, 1933; Souéges, 1935; Krishna Iyengar, 1937, 1939 *a* and *b*, 1940 *a-c*, 1941, 1942 *a-c*; Srinath, 1940; Guilford and Fisk, 1952; Crété, 1953; Yamazaki, 1953 *b*, 1954 *b*, 1957 *b* and Tiagi, 1956). Balicka-Iwanowska's (1899) 'Secondary haustorium'

in *Linaria cymbalaria* and Berg's (1954) 'Cutis forming cells' in *Pedicularis silvatica* are also possibly identical in nature. In *Lindenbergia indica* (Pal, 1958), these cells are absent at the chalazal end. At the micropylar end of this plant, as well as in *Mazus japonicus*, the endosperm cells become specialised.

In *Mazus japonicus* (Pal, 1958), two uninucleate cells (which later become a single binucleate cell) of the chalazal haustorium degenerate very early and seem to be replaced by a second one, having originated secondarily from the lowermost tier of the endosperm tissue. Further, this structure becomes complicated by the addition of many new and small cell elements from the endosperm tissue. The ultimate amoeboid structure seems to form a modified type of chalazal conductive tissue of the endosperm which lasts for a considerable length of time in the developmental history of the seed. It may be mentioned here that Srinivasan (1946) considered the densely staining group of cells at the chalazal end in *Striga* as the secondary chalazal haustorium. Tiagi (1956), working with the same genus, differed from him and suggested that the function of these cells are only conductive in nature. It should be noted that the origin and structure of this tissue in *M. japonicus* are more or less different from any other species so far investigated in the family.

It may thus be said that in *M. japonicus* and *L. indica* (Pal, 1958), though the sequence of cell divisions in the endosperm is more or less identical, yet the behaviour of the tiers of cells is very different, which may be apparent from Figure 1.

(2) *Evolutionary tendencies in the development of endosperm-haustoria in the family Scrophulariaceae.*—Samuelsson (1913) and Schnarf (1929, 1931) have classified the different types of endosperm development in the members of this family. Later, Srinath (1940) discussed the origin and interrelationships in them. Glisic (1936–37), however, for the first time, produced an elaborate account on the trends of evolution of endosperm-haustoria in this family, which has later been enriched by the work of Krishna Iyengar (1947). Still later, Crété (1951, 1955) and Pal (1958) modified the diagrammatic chart of Glisic and also attempted to find out the interrelationships of the family with the allied ones. On the other hand, Yamazaki (1953, 1954, 1957) tried to correlate the morphological and embryological data in several genera of the family. It may be useful here to discuss some of the available evidences regarding the evolutionary trends in the development of endosperm-haustoria in the family Scrophulariaceæ.

The lines of evolution (as indicated here) are based mainly on the characteristic features of endosperm formation which have been followed by the previous authors. The multicellular (uninucleate cells) nature of the endosperm-haustoria has been considered as a primitive character, other characteristics being (1) sequence of early divisions in endosperm, (2) occurrence and behaviour of the partition walls (if any) in the haustoria, (3) number of cell or cells and/or nuclei in the

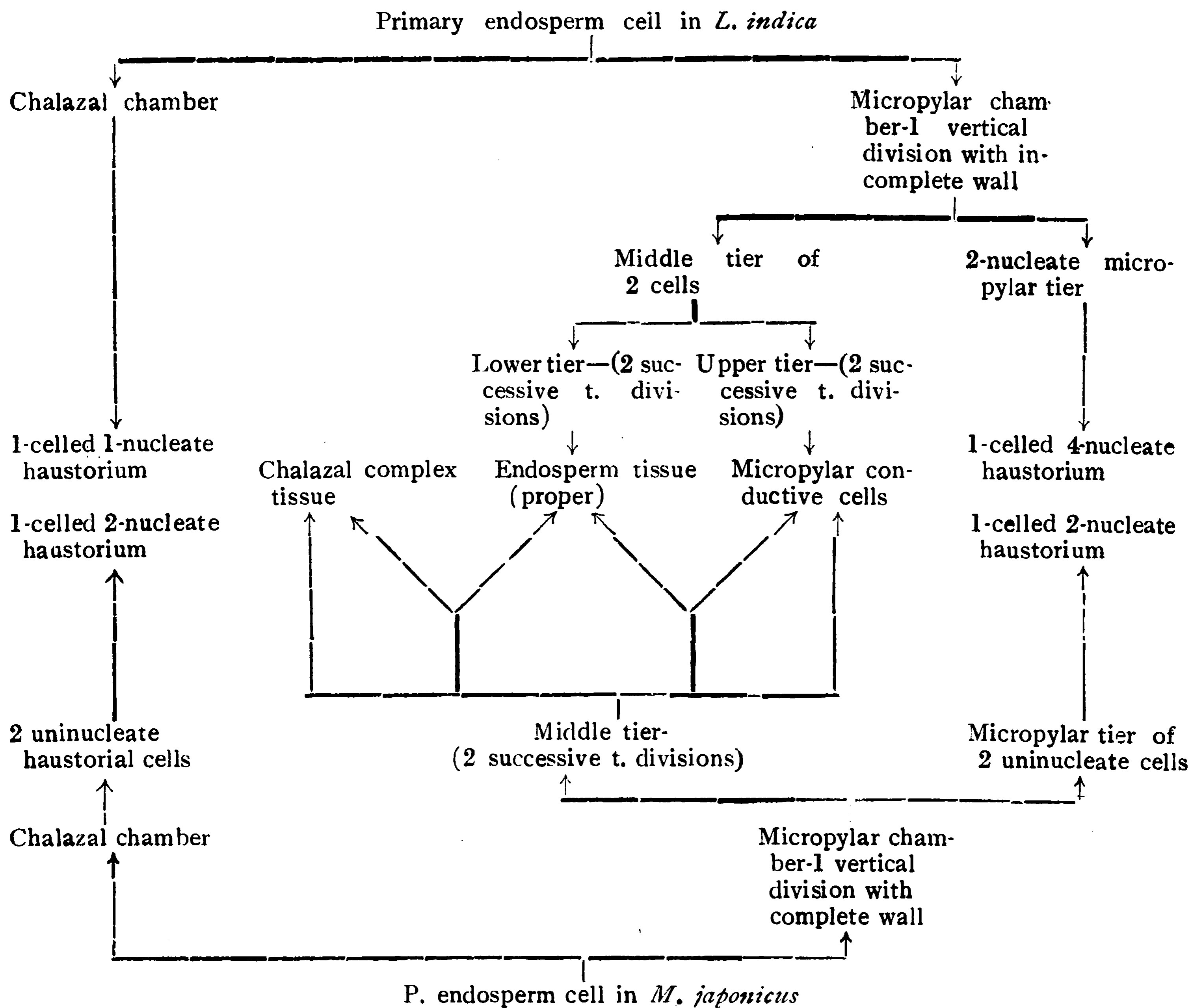


FIG. 1

haustoria and (4) plane of wall formation (if multicellular) in the haustoria.

Glisic's (1936-37) chart indicates three major lines of evolution of endosperm formation in the family. However, difficulties are encountered in accepting his proposal. First, he had to assume some hypothetical types like 'Pro-Veronica', 'Pro-Limosella' (this was probably unavoidable due to the lack of sufficient information available at his time) in his system. Secondly, the type, where the chalazal chamber (haustorium) of the endosperm undergoes a division with the formation of a vertical wall, and the type where the said division is not associated with wall formation, was considered by him to represent parallel lines of evolution and not as a derivative of the former type. Moreover, he could not assign a proper place for 'Pedicularis type' in his chart. It should be mentioned here that though in all the three lines of evolution in Glisic's chart, the division in the micropylar chamber of the endosperm (*i.e.*, the second division of the endosperm) is vertical but in *Pedicularis*, *Melampyrum*, *Euphrasia* and *Tozzia* (Schmid, 1906;

Krishna Iyengar, 1942 *c*), the second division in the endosperm was found to be transverse in the chalazal chamber. Krishna Iyengar (1947) has, however, attempted to fill this gap by introducing a 'fourth line' in the evolutionary sequence where in the second cell generation, all the three cells of the endosperm lie in one row, the said division in the micropylar chamber (?) being transverse. The position of the 'Pedicularis type' has also been indicated by some of his observations on several species of the family, viz., species of *Alonsoa*, *Ilysanthes*, *Bonnaya*, *Sopubia*, *Vandellia* (Krishna Iyengar, 1937, 1940 *a-c*) where the said transverse division occurs in the 'micropylar chamber'. Similar sequence has also been noted in species of *Striga* (Michell, 1915) as well as in *Pedicularis* (Lundquist, 1915). Later, Cr  t   (1951) cited two examples of the occurrence of both longitudinal or transverse divisions in the micropylar chamber in the same species and expressed his doubt on the systematic value of such variations. Further, he referred to the observations on some species of *Euphrasia* (Wurdinger, 1910) and *Veronica* (Weiss, 1932) where the sequence is similar to *Pedicularis*.

But in spite of all these evidences, the position of 'Pedicularis type' is yet open to question. The following points need consideration in this connection: (1) the most important contribution on this type (Schmid, 1906) lacks illustrations representing the successive stages; (2) most of the observations (Hofmeister, 1859; Schacht, 1863; Schmid, 1906; Lundquist, 1915; Michell, 1915) on this type (except those of Krishna Iyengar, 1937, 1940 *a-c* and 1942 *c*) are records of earlier investigations on the family; (3) in the majority of cases the division of the micropylar chamber in the members of this family is vertical and not transverse; and (4) a number of genera and species in which such observations have been made (*i.e.*, occurrence of transverse division in the micropylar or chalazal chamber), also present examples of the types where this division is longitudinal such as *Veronica* (Gscheidle, 1924; Wiess, 1932; Yamazaki, 1957 *b* and as classified by Glisic, 1936-37), *Alonsoa* (Cr  t  , 1950 *c*), *Ilysanthes* (Raghavan and Srinivasan, 1941 *a*; Yamazaki, 1954 *b*), *Vandellia* (Srinivasan, 1940; Yamazaki, 1954 *b*) and *Striga* (Srinivasan, 1946; Tiagi, 1956). Moreover, Schmid's (1906) and Krishna Iyengar's (1942 *c*) descriptions on *Pedicularis* do not tally with other observations on the genus (Lundquist, 1915), as they state that the micropylar haustorium, instead of the chalazal one, is differentiated by the first division of the primary endosperm cell and further wall formation takes place only in the chalazal chamber, and thus the chalazal haustorium originates at a later stage of development. This sequence seems to be unnatural in this family though, the same has been substantiated later by the observations of Cr  t   (1950 *a* and *b*) in *Nemesia* where the chalazal haustorium does not develop at all.

Recent observations of Berg (1954) on *Pedicularis silvatica* seems to invalidate the conception of 'Pedicularis type' of endosperm formation. He clearly demonstrated the formation of a vertical wall in the micropylar chamber of this species and suggested that Schmid's

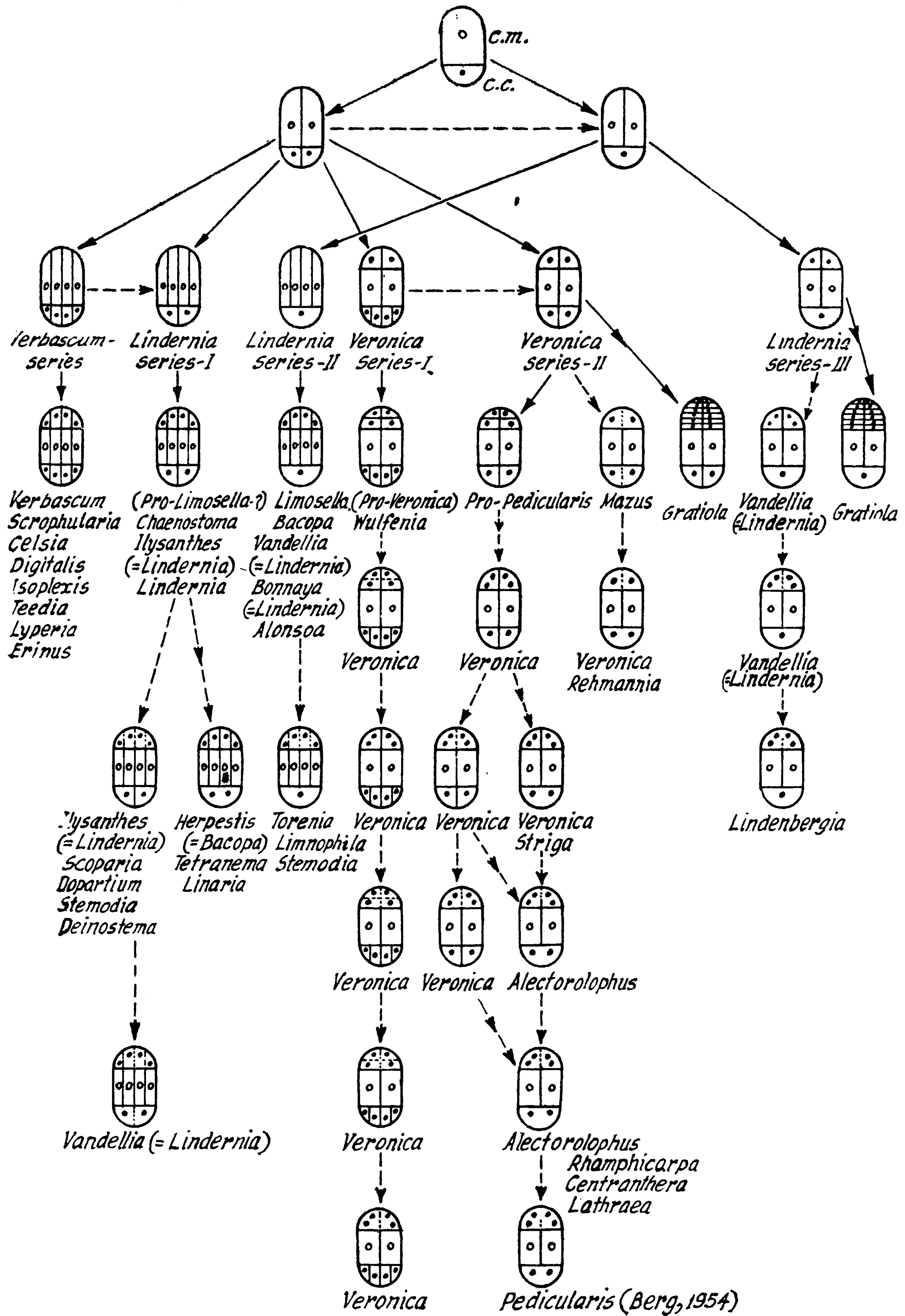


FIG. 2

interpretations were possibly erroneous due to several reasons as has already been admitted by himself (Schmid, 1906). It should be mentioned here that Glisic (1936-37) also expressed his doubts on the validity of such a type of development of endosperm as described previously in *Pedicularis*.

Glisic's (1936-37) 'Pro-Limosella type' has, however, been substantiated later by the observations of Crété (1948) and Yamazaki (1954 *b*) on *Chaenostoma*, *Ilysanthes* and *Lindernia*. 'Pro-Veronica type,' on the other hand, has been demonstrated in *Wulfenia carinthiaca* (Yamazaki, 1957 *a*).

Figure 2 gives a diagrammatic representation of the probable evolutionary sequence of the endosperm types in the family. It should, however, be mentioned that the diagram is a modified representation based on the works of Glisic, Krishna Iyenger and Crété. Further, in plants where the sequence has not been definitely established or where the division of the micropylar chamber has been found to be transverse or where the organisation of the embryo-sac does not follow the general scheme, have not been considered.

The chart is self-explanatory and no elaboration is necessary. The arrows indicate the sequence of development. The broken lines with arrows denote the probable lines of evolution of the different derivative types. The hypothetical "Pro-Pedicularis type" introduced here is the intermediate stage of *Gratiola* I type in Glisic's system and is yet to be demonstrated in the family. The dotted lines in the diagrams indicate the position of walls which in course of time have become obliterated.

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