

Co-occurrence of Four Types of Embryogeny in *Malaxis muscifera* (Orchidaceae)

S.K. SOOD, P. KATOCH, I.J. SINGH and D. MOGGIL

Department of Biosciences, Himachal Pradesh University, Shimla, INDIA

ヤチラン属 *Malaxis muscifera* (ラン科) の胚形成

スード S. K., カトク P., シンエ I. J., モギル D.

ヒマチャルプラデシュ大学生物科学部

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The present study on the embryogeny of *Malaxis muscifera* shows the predominant Onagrad type and its co-occurrence with three other types, viz, Asterad, Chenopodiad and Piperad types as a variation in some of the seeds; and in this respect, forms the first report of its type not only in the family Orchidaceae, but for the whole angiosperms. System of classification of orchids embryogeny is revised to accommodate the first report of the Piperad type of embryogeny.

Embryologically, the family Orchidaceae is unique in showing the ontogenetic variability in the development of embryo sac and embryo in the same species (cf. Abe 1972, Sood 1988, Swamy 1949a, Vij and Sharma 1986, Wirth and Withner 1959). However, the co-occurrence of four different types of embryogeny in the same taxon is not reported so far in the family. The present study delineates this in *Malaxis muscifera*, subtribe Liparidinae, tribe Epidendreae, family Orchidaceae.

Materials and methods

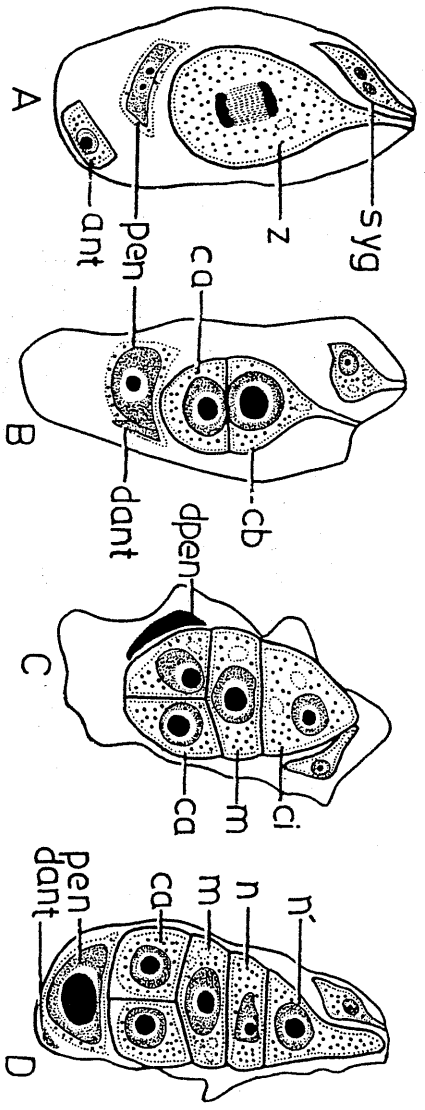
The material consisting of young and mature fruits of *Malaxis muscifera* (Lindl.) O. Ktze. were collected from Fagu, Himachal Pradesh and fixed in formalin-acetic-alcohol. Dehydration, embedding, sectioning and staining were done in the

conventional way (Berlyn and Miksche 1976). Voucher specimen has been deposited in the Herbarium of Department of Biosciences, Himachal Pradesh University.

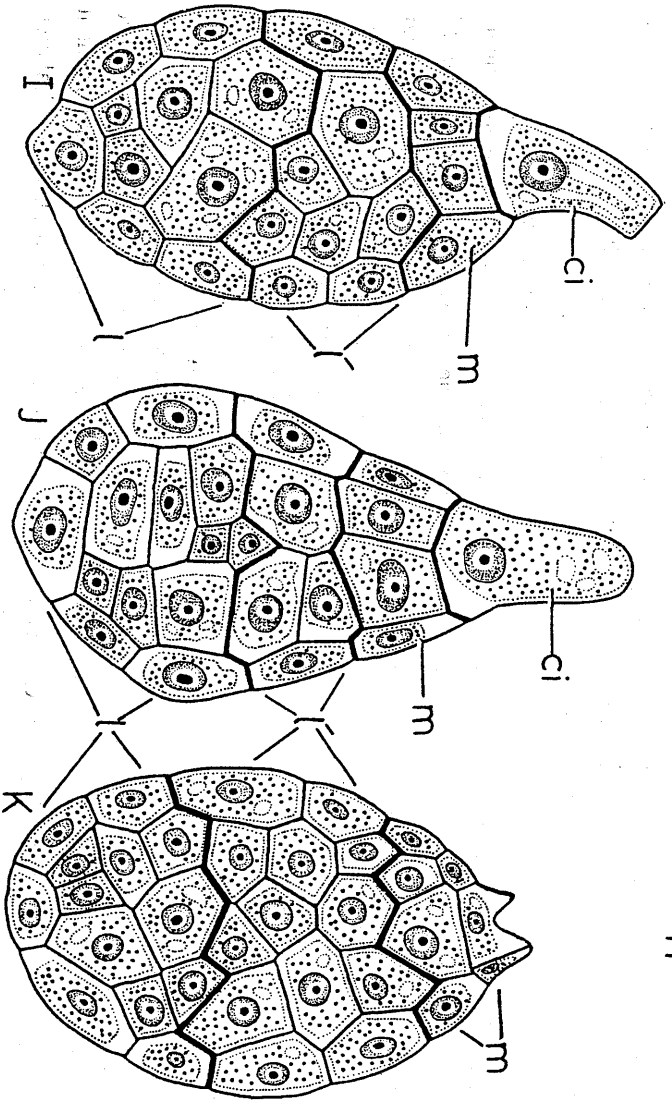
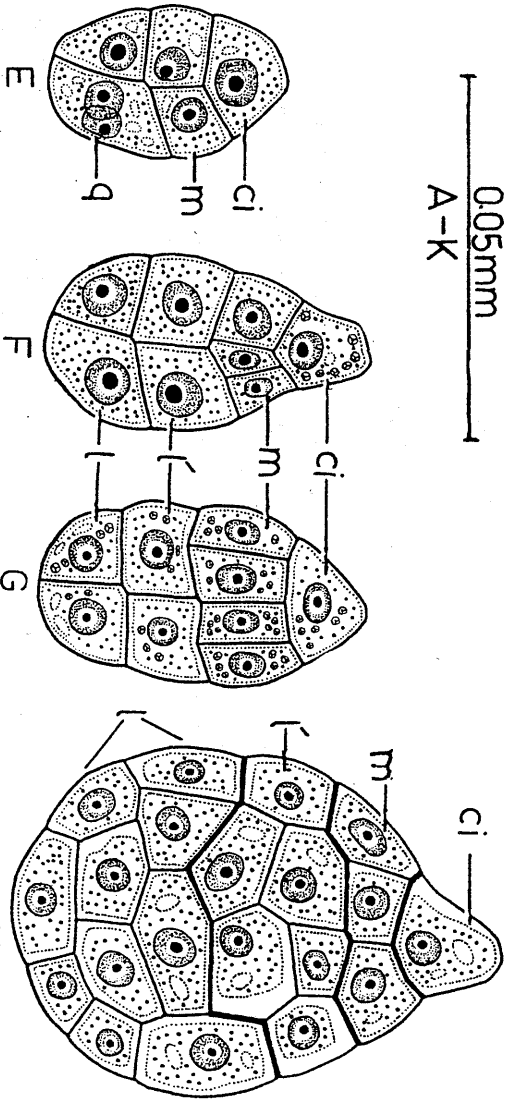
Observations

The embryogeny of *Malaxis muscifera* is unique in showing the intraspecific co-occurrence of Onagrad, Asterad, Chenopodiad and Piperad types of development. Of these four types, Onagrad mode is predominant and the occurrence of Asterad, Chenopodiad and Piperad types is a variation in the present study.

In most of the ovules, the zygote (Fig. 1A) enlarges and divides transversely, resulting in a basal cell *cb* and a terminal cell *ca* (Fig. 1B). The *cb* divides transversely, to form a suspensor initial cell *ci* and a middle cell *m* while the vertical divi-



0.05mm
A-K



sion of *ca* results in an inverted, T-shaped proembryonal tetrad (Fig. 1C). The cell *ci*, mostly, enlarges to form one-celled suspensor (Fig. 1F–J) but, very rarely, it divides into *n* and *n'* (Fig.

1D). In *m*, invariably, the first division is vertical (Fig. 1E). The cells of *ca* divide at right angles to the first division, to produce a quadrant *q* (Fig. 1E) which then divides transversely into an octant

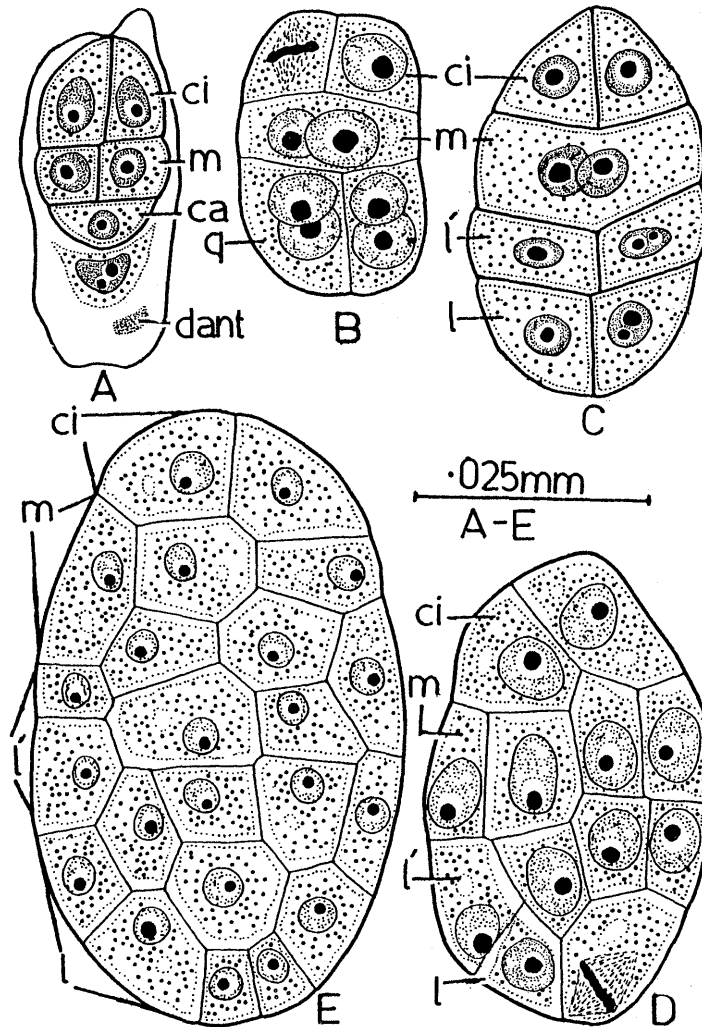


Fig. 2. *Malaxis muscifera*, Asterad embryogeny. A. Five-celled proembryo, note the vertically divided middle cell and suspensor initial cell. B–E. Stages leading to the mature, Asterad embryo. dant: degenerated antipodal cell.

Fig. 1. *Malaxis muscifera*, Onagrad embryogeny. A. Zygote in meiotic anaphase, primary endosperm nucleus, healthy antipodal cell and synergid with additional male gametes. B. Two-celled proembryo with undivided primary endosperm nucleus and degenerated antipodal cell. C. T-shaped proembryo; note persistent synergid and degenerated primary endosperm nucleus. D. Five-celled proembryo with healthy primary endosperm nucleus and persistent synergid. E. Quadrant stage. F. Octant stage. G–J. Later stages of embryogeny. K. Mature embryo. ant: antipodal cell, dpen: degenerated primary endosperm nucleus, pen: primary endosperm nucleus, syg: synergid, z: zygote.

with tiers *l* and *l'* (Fig. 1F). Further divisions in the tiers *l*, *l'* and *m* are irregular, forming first a globular and later an undifferentiated mature embryo (Fig. 1G–K). The suspensor collapses shortly before the differentiation of mature embryo

(Fig. 1K). This pattern of embryo development which is predominant, conforms to the Onagrad type.

In some developing proembryos, on the other hand, both the *ci* and *m* divide vertically while the

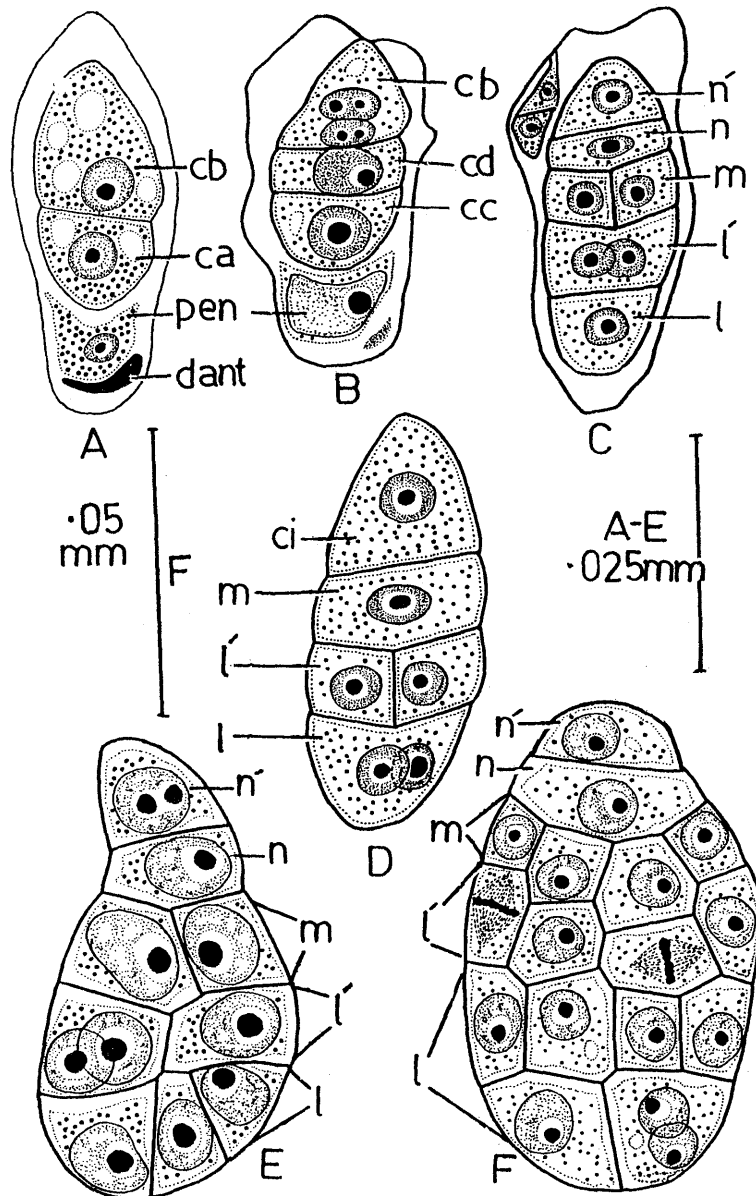


Fig. 3. *Malaxis muscifera*, Chenopodiad embryogeny. A. Two-celled proembryo, primary endosperm nucleus and degenerated antipodal cell. B. Three-celled proembryo showing the tiers *cc*, *cd* and the occurrence of a transverse division in *cb*. C–F. Later stages of embryogeny conforming to the Chenopodiad type. *dant*: degenerated antipodal cell, *pen*: primary endosperm nucleus.

cell *ca*, by three vertical divisions, forms an octant with tiers *l* and *l'* (Fig. 2A–C). Further divisions in *l*, *l'*, *m* and *ci* are irregular and result in the formation of undifferentiated mature embryo of the Asterad type (Fig. 2D, E).

Rarely some embryos follow the Chenopodiad type of development. Here, the filamentous proembryo of three to five cells is formed due to the transverse divisions in the tiers *ca* and *cb* (Fig. 3A, B). During the course of further development, the

tiers *cc*, *cd* and *m* become segmented due to the occurrence of two longitudinal divisions oriented at right angles to each other (Fig. 3C, D). Subsequently, irregular divisions in the tiers *l*, *l'* and *m* result first in a globular (Fig. 3E, F) and then a mature embryo. Derivatives of the suspensor initial cell do not persist in the mature embryo.

Very rarely the first division of zygote is vertical (Fig. 4A). Next division is transverse in both the juxtaposed cells, resulting in an isobilateral pro-

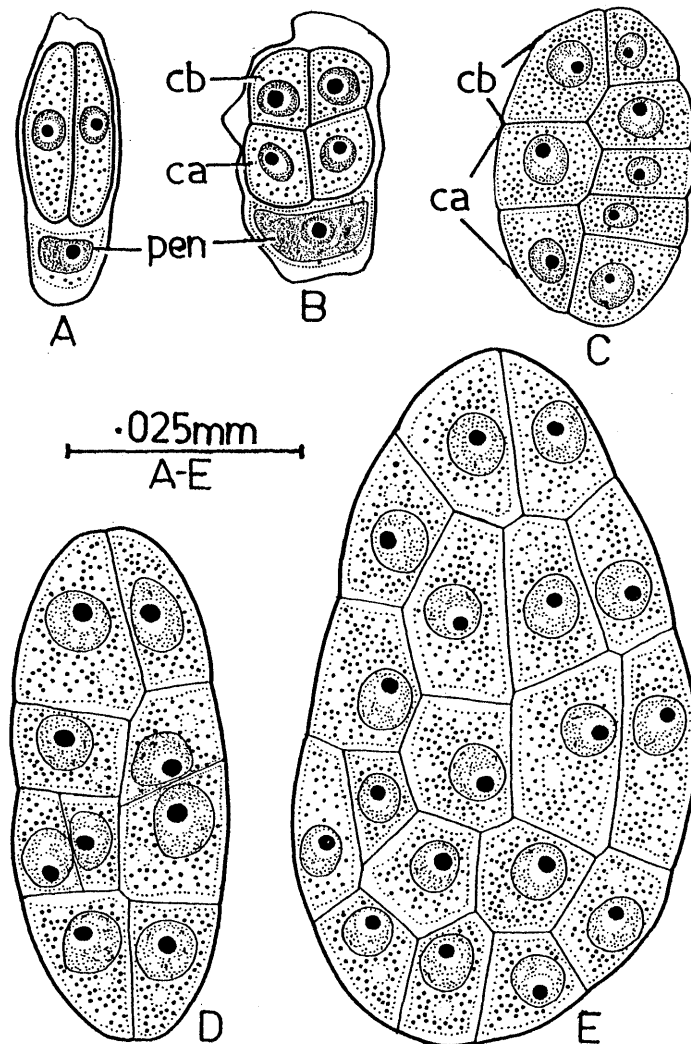


Fig. 4. *Malaxis muscifera*, Piperad embryogeny. A. Vertically divided zygote. B. Isobilateral proembryonal tetrad. C, D. Stages showing the irregular divisions of the tiers *ca* and *cb*. E. Mature embryo. pen: primary endosperm nucleus.

embryonal tetrad (Fig. 4B). Further divisions in the tiers *cb* and *ca* result in suspensorless, mature embryo (Fig. 4C–E). The embryogeny is of the Piperad type.

Irrespective of the mode of development, the mature embryo is ovoid and undifferentiated (Figs. 1K, 2E, 4E), and is surrounded by reticulate seed coat. Occasionally, the seeds are polyembryonate due to the additional embryos arising either from the fertilized or unfertilized synergid (Fig. 3C).

Discussion and conclusions

Based upon the plane of division in the basal cell and the terminal cell and their contribution in the organisation of mature embryo, Swamy (1949b) classified orchids embryogeny into Group 'A' (Asterad type: All the derivatives of basal cell and terminal cell take part in the organisation of mature embryo), Group 'B' (Onagrad type: basal cell contributes little to the organisation of mature embryo which otherwise is formed mostly from the derivatives of terminal cell) and Cymbidium type, in which, irregular divisions occur both in the terminal and basal cells. However, due to the occurrence of Chenopodiad embryogeny and its

co-occurrence with the Onagrad type in *Satyrium nepalense*, Sood (1988) revised the classification of orchids embryogeny, so as to accommodate the first report of this type in the family. The embryogeny in the present study is unique in showing the predominant Onagrad type and its co-occurrence with three other types viz, Asterad, Chenopodiad and Piperad as a variation in some of the seeds; and forms the first report of its type not only in the family Orchidaceae, but for the whole angiosperms. In view of the fact that the classification of Sood (1988) did not recognise the Piperad type of embryogeny for the family, hence, it is revised so as to incorporate it (Table 1).

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Table 1. Classification of Orchids Embryogeny

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| I. <i>First division in zygote is transverse</i> | |
| Type 1: | The terminal cell of the two-celled proembryo divides by a vertical wall. Group 'A' (Asterad type): The terminal cell and basal cell contribute equally in the organisation of mature embryo; suspensor absent. Group 'B' (Onagrad type): The basal cell plays a minor part in the organisation of mature embryo, suspensor present. |
| Type 2: | The terminal cell of the two-celled proembryo divides by a transverse wall. Group 'C' (Chenopodiad type): The basal cell and terminal cell take part in the organisation of mature embryo; suspensor present. |
| Type 3: | Group 'D' (Cymbidium type): Both the terminal and basal cells divide by irregular divisions; suspensor present. |
| II. <i>First division in zygote is vertical</i> | |
| Type 4: | Group 'E' (Piperad type): Both the juxtaposed derivatives take part in the organisation of mature embryo; suspensor absent. |

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要 旨

ラン科ヤチラン属の *Malaxis muscifera* の胚形成を研究した。基本的には Onagrada type の発生を行うが、例外的に Chenopodiad type, Asterad type, Piperad type のものが見られた。同一種類で4型が見られた例は初めてである。Swamy (1949) はラン科に Asterad type, Onagrada type, Cymbidium type を認めた。Sood (1988) はこれに Chenopodiad type を追加した。今回 Piperad type を加えることになる。ラン科における Type の分類様式を総括した。