Offprints from
THE ORCHIDS: SCIENTIFIC STUDIES
Edited by: Dr. Carl L. Withner
Published by: John Wiley & Sons, Inc. 1974

5

Development of the Embryo and the Young Seedling Stages of Orchids

YVONNE VEYRET

Until 1804, when Salisbury found that orchid seeds could germinate, the seeds were considered sterile. Much later, in 1889, Bernard's discovery of the special conditions necessary for their growth and development explained the lack of success in previous attempts to obtain plantules, and the success, although mediocre, when sowing of seed took place at the foot of the mother plant. Knowing the rudimentary state of minute orchid embryos, one can better understand that an exterior agent, usually a *Rhizoctonia,* can be useful in helping them through their first stages of development (Bernard, 1904).

Orchid embryos, despite their rudimentary condition, present diverse patterns of development, the most apparent of which are concerned with the character of the suspensor; there are other basic patterns that are revealed in the course of the formation of the embryonic body. These characteristics have been used differently in the classification of orchid embryos. This will be discussed in the first part of this chapter, to which will be added our knowledge of other phenomena concerning the embryo, in particular polyembryonic and apomictic seed formation. The second part of this chapter is devoted to the development of the young embryo, a study necessary for understanding the evolution of the different zones of the embryonic mass. We will also examine the characteristics of the embryo whose morphology, biology, and development are specialized when compared to other plants.

The Embryo

Embryological Classifications. The orchid embryo is still little known, since only about 60 kinds have been the object of embryological investigations, while the family numbers more than 20,000 species. In spite of that, a comprehensive view on the development of the embryo in the different groups is beginning to become clear. It is still necessary to pursue these investigations, specifically among the POLYCHONDREAE and the KEROSPHEREAE.

The first important works related to orchid embryology were due to the Dutch scientist Treub, in 1879, whose work offered a suggestive glimpse of the appearance, and sometimes the segmentation, of the embryo in diverse orchid groups. The first attempt at the classification of orchid embryos came a long time later, in 1949. At this time, Swamy distinguished two groups, A and B, following the absence or not of the suspensor. In these two groups, the first division of the egg is transverse and the proembryo after the second cellular generation shows two juxtaposed cells coming from the terminal cell; the basal cell, following a horizontal division, has yielded a middle cell and a lower cell of the suspensor. The role taken by each of these cells in the further stages of development is taken account of in the classification system. In the A group the embryo is formed, following in the order of the importance of their contribution, by the terminal cells, then by the middle cell, and finally by the initial cell of the suspensor. In the B group the early embryo is formed in large part from the cells coming from the terminal cell, and in a lesser degree by those coming from the median cell. The A group embryos correspond to "Asterad type" and those of the B group to the "Onagrad type," as Johansen (1950) understands them.

Some rare types cannot be classified in either of these groups because they do not present the same proembryonic form in the second cellular generation. The first divisions are made without definite order and end in the formation of an undifferentiated mass of six to eight cells. The majority of these cells elongate to form a suspensor complex while one of them, located near the chalazal end, becomes the mother cell of the embryo proper. This generates a proembryo armed with filamentous suspensors so that the embryo will in the end be provided with two. This way of development is defined as being the "*Cymbidium* form." In this classification, Swamy (1949) makes an attempt to give ontogenetic interpretation to these characteristics, but his study ends at only the second cellular generation, the author thinking generally that "only the first 2 or 3 cell generations in the zygote are consistent: The subsequent cell divisions

take place with no definite sequence or pattern." Swamy acknowledges, on the other hand, five kinds of suspensors that are diagramed and described on pages 174–175 of *The Orchids* and keyed on p. 179 (Wirth and Withner, 1959).

Johansen's classification (1950) is done uniquely according to the suspensor characteristics, notably characteristics relative to the presence or absence of embryonal tubes, to the number and arrangement of these tubes, and to the appearance of these cells in the case of the filamentous suspensors. Very often it is certain that the appearance of the suspensor gives a recognizable distinctiveness to the embryos of different genera (Fig. 5-1). Thirteen plans are described in his scheme and you may find that these are also keyed and described in *The Orchids* (Wirth and Withner, pp. 177–179).

If one closely follows the continuing development of the embryo proper, one ascertains that they are not without distinction and that the young forms do follow well-definable patterns. It is in this way that Veyret could determine a certain number of embryonic types among orchids that would fit into the system devised by Souèges (1936–1939). The embryonic types are characterized by the four great embryogenic laws as Souèges defines them: laws of origin, of number, of disposition or arrangement, and of destinies of the first four cellular generations. Only the law of destinies cannot be determined in the development of the orchids since the embryo at time of fruit maturity is, in general, morphologically undifferentiated. In Souèges' classification, the embryos are grouped into various megarchetypes, these being defined by the sum of the constructive potentials of the apical and basal cells, resulting from the first transverse segmentation of the zygote.

The embryos among orchids are of three kinds:

1. Fundamental types that develop following fixed rules.
2. Irregular types presenting forms which are constructed following clear rules but varying with individual species.
3. Secondary types with the early embryo differing from the fundamental types by differences in
   a. the speed of the segmentation of the homologous blastomeres; or
   b. the direction of certain segmentation walls leading to an earlier differentiation; or
   c. the very variable differentiation of the most inferior component parts of the embryo which have no constructive role to play.

The different types are classified according to Souèges' system into the first and second periods of the periodic embryogenic classification or

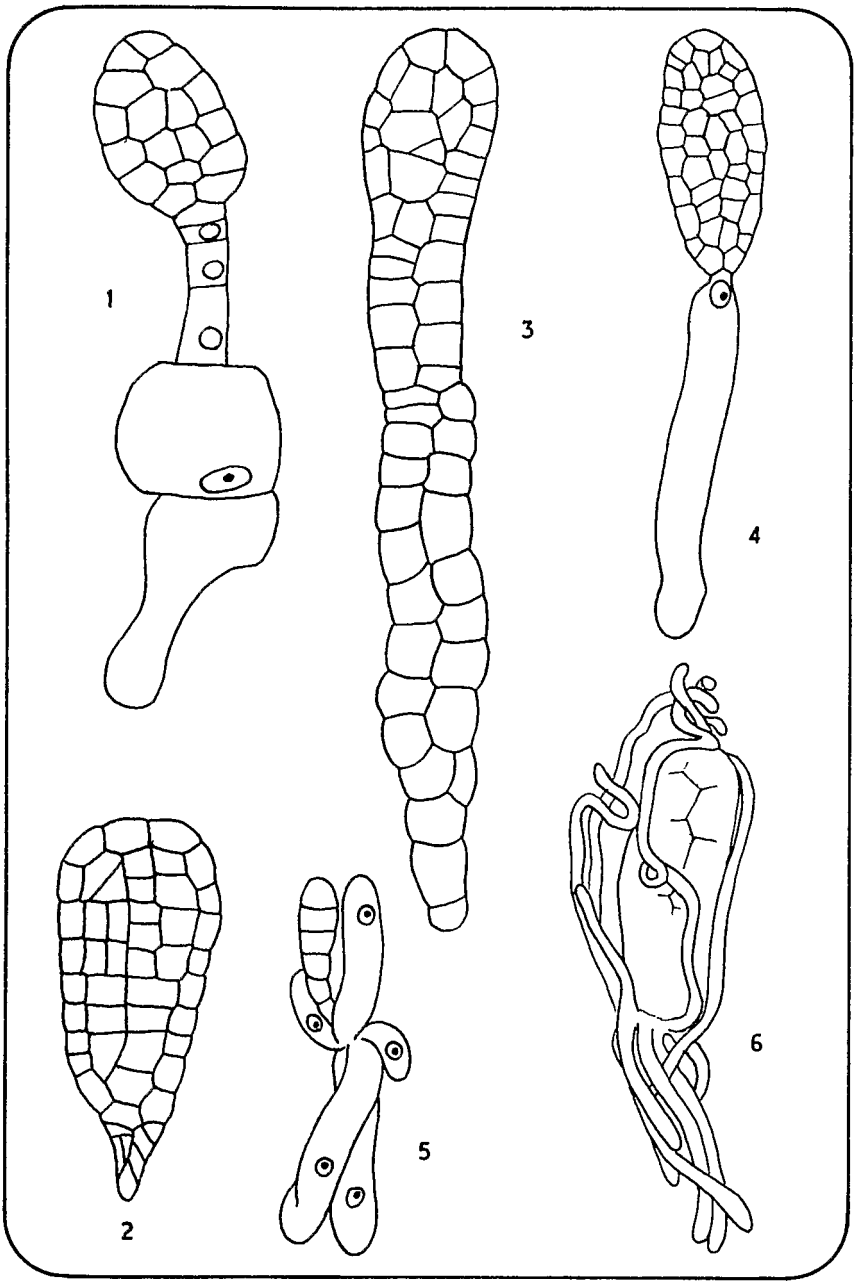


Fig. 5-1. Embryos presenting different types of suspensors. (1) ***Herminium monorchis***, according to Treub. (2) ***Vanilla fragrans***, according to Veyret. (3) ***Epidendrum ciliare***, according to Treub. (4) *Spathoglottis plicata* and (5) *Geodorum densiflorum* (proembryo), according to B. G. L. Swamy. (6) ***Phalaenopsis grandiflora***, according to Treub.

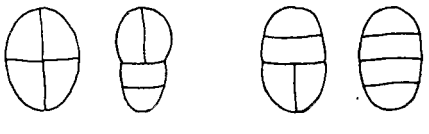


Fig. 5-2. The different forms of proembryonic tetrads among orchids.

grand divisions of the system. In the first period, the first two cells coming from the zygote, both the apical and basal, take part in the construction of the embryo, and the laws of development enter the process as soon as the first segmentation wall is established in the fertilized egg. In the second period the embryo develops only from the apical cell and the laws apply only to the apical cell. This classification and the sequence of divisions is established on presumed phylogenetic criteria, and the relative evolutionary position of the types is based mainly on the orientation of the segmentation walls and the tendency of constructive potentials to be localized in the apical cell. Thus the tetrads in A configuration are phylogenetically earlier than the tetrads in B, these being earlier than the tetrads in C; the 1 forms of these tetrads are more primitive than the 2 forms (Fig. 5-2). There are no tetrads of the B configuration in the orchids. The megarchetypes form a phylogenetic series as the role of the basal cell is reduced to only generating the suspensor.

The conventionally accepted abbreviations used in the description of the different parts of the embryo are the following:

ca: apical cell of the two-celled proembryo
cb: basal cell of the two-celled proembryo
cc: the upper daughter cell of *ca*
cd: the lower daughter cell of *ca*
m: the upper daughter cell of *cb*
ci: the lower daughter cell of *cb*
d: the upper daughter cell of *m*
f: the lower daughter cell of *m*
n: the upper daughter cell of *ci*
n′: the lower daughter cell of *ci*
h: the upper daughter cell of *n*
k: the lower daughter cell of *n*
o: the upper daughter cell of *n′*
p: the lower daughter cell of *n′*
h′: the upper daughter cell of *h*
h″: the lower daughter cell of *h*
q: the quadrant stage
l: the stage of the upper octants
l′: the stage of the lower octants

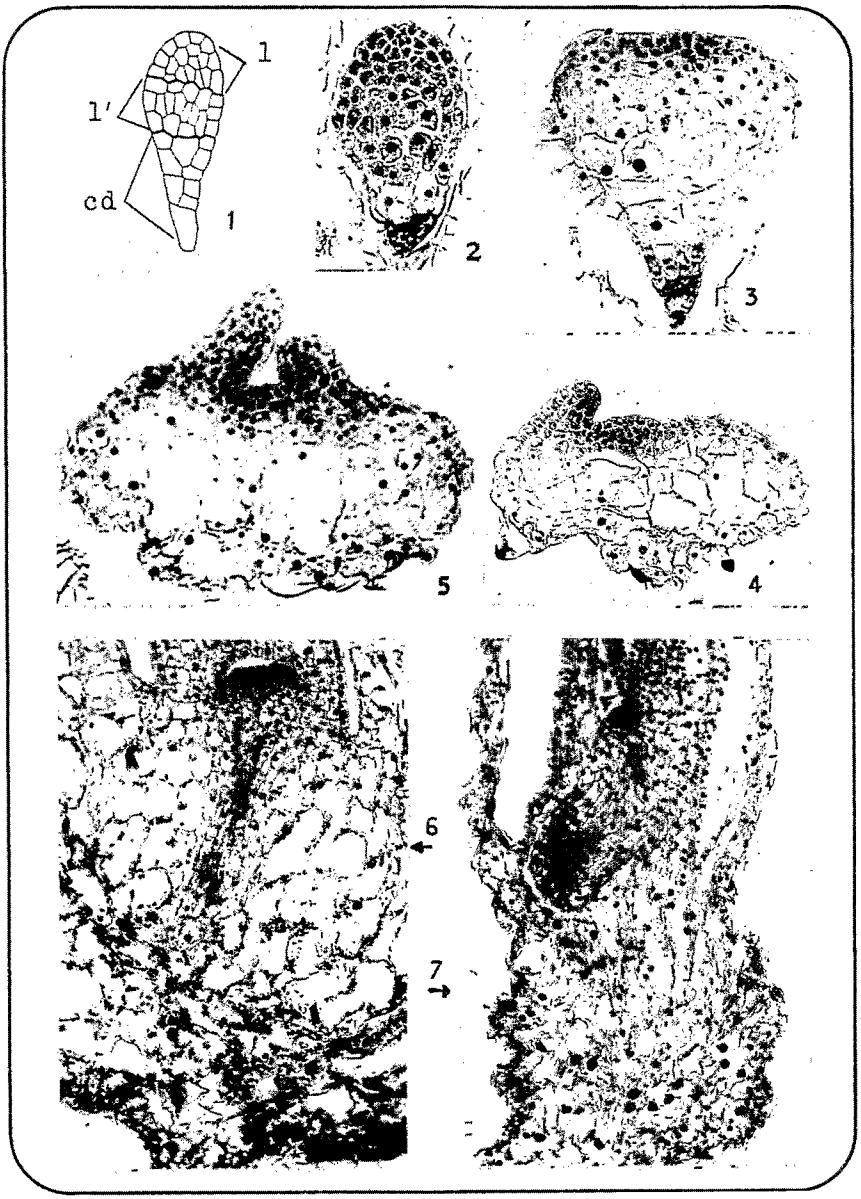


Fig. 5-3. Germination of a species without cotyledon, *Stanhopea costaricensis*. (1) Longitudinal section of a mature embryo. (2–5) Longitudinal section of a young protocorm showing the formation of the apical meristem and the first foliar member. *Bulbophyllum bufo*. (6) Differentiation of the stele in the protocorm. (7) Formation of the first root.

Embryonic Types

Before going further with the embryogenic classification of the orchids, it is necessary to anticipate and examine what is going to happen at the moment of germination when the embryo differentiates. Two situations are presented, embryos with and those without cotyledons. In the case of acotyledonous species, which are in the majority, the vegetative point of the stalk is formed by the upper part of the embryo represented by the layer *l* (Figs. 5-3 and 5-4), in the case of the rare species with cotyledons, it is the cotyledon that is formed by the terminal layers while the vege-

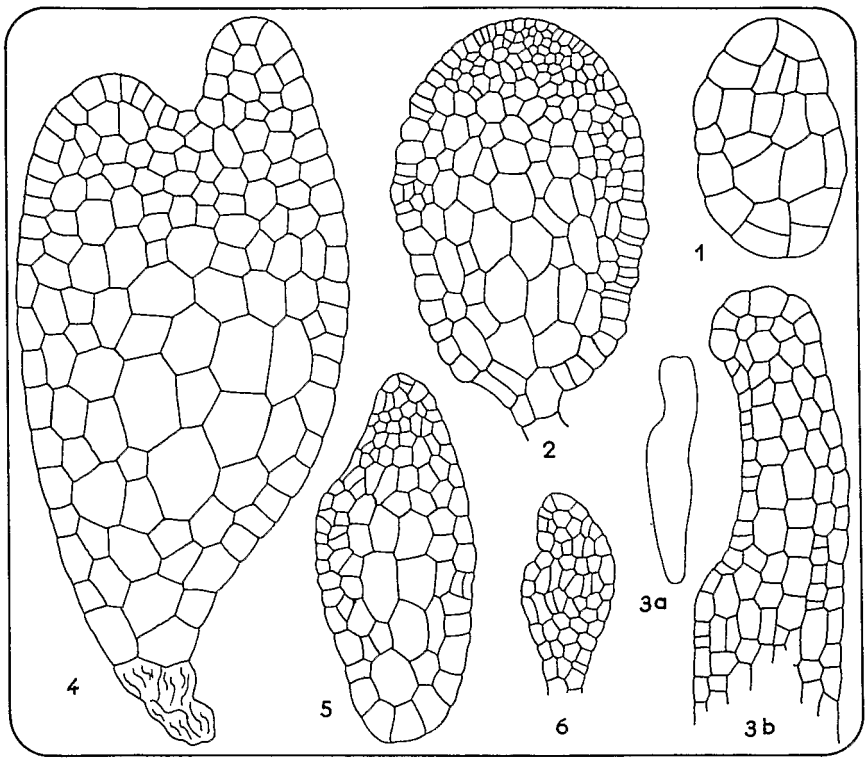


Fig. 5-4. Longitudinal sections of diverse embryos. Embryos without cotyledons: (1) *Listera ovata,* one of the most rudimentary; and (2) *Epidendrum radicans,* one of the most differentated histologically, according to Veyret. Embryos with cotyledons: (3) *Sobralia macrantha:* (3a) mature embryo, (3b) cotyledon at tip, according to Treub; (4) *Bletilla hyacinthina,* according to Bernard; (5) *Polystachya microbambusa* and (6) *Epidendrum vitellinum,* according to Veyret. All these embroys are mature except for *E. vitellinum.* All 136X except for Fig. 3a, which is 41X.

tative point of the stalk is derived from the layer of more centrally located cells, *l'*, located directly under the terminal cells (Figs. 5-4 and 5-5). The degeneration of the lowermost cell layers of the embryo has been ascertained among some species where it is possible to follow rigorously the pattern of development and to observe the definable boundary in the seed between the suspensor and the embryo proper. With such develop-

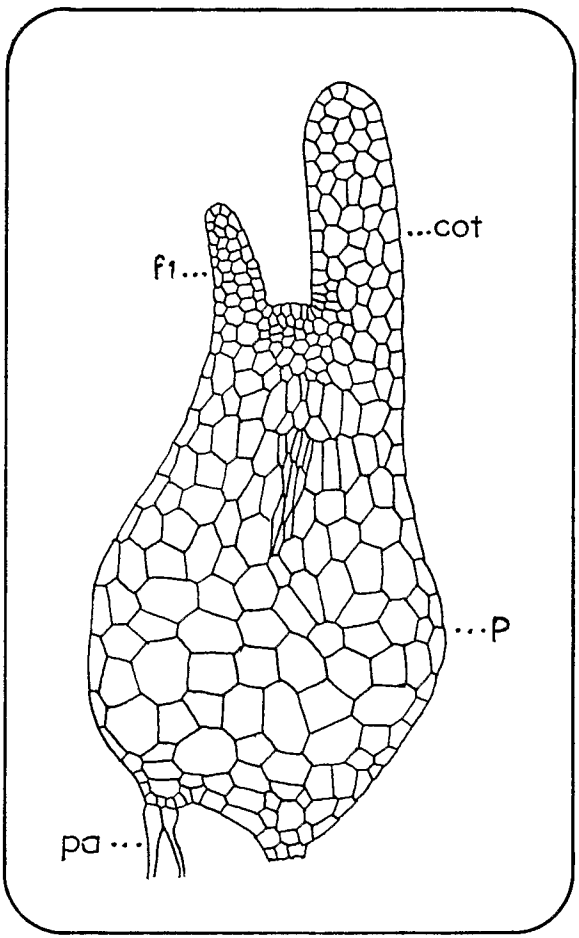


Fig. 5-5. Germination of a cotyledoned species, *Bletilla hyacinthina*, after Bernard. Longitudinal section of a young plantlet, 100X. cot = cotyledon; pvt = apex of stem; p = protocorm; pa = absorbing hairs.

mental information one can establish only a general formula relating to two patterns of the megarchetypes:

1. Among the cotyledonous species, the terminal cells may form the cotyledon.
2. Among the acotyledonous species, the terminal cell may form the vegetative apex of the stalk.

Within these two principal divisions—depending on presence or absence of cotyledon—the types can be grouped according to the form of the tetrad (second cellular generation), and then the subsequent formation of the embryo proper. One can emphasize here the difficulty that exists at times in determining the boundary between the so-called embryo and the suspensor. Classification of any orchid may be temporary—to be revised at the time when additional data relating to the destiny of all the blastomeres are obtained. The further study of orchid embryonic differentiation will thus enable us to establish the megarchetypes more precisely (Figs. 5-6–5-8).

The following is a key for the determination of the different groups of orchidaceous embryonic types:

A. Species without cotyledon
  B. Species of the first period
    C. Tetrad in A1
      Embryo = $ca + cb$ — *Neottia nidus-avis* group
    CC. Tetrad in A2
      Embryo = $ca + cb$ — *Manniella gustavi* group
      Embryo = $ca + m + n + o$ — *Limodorum abortivum* group
      Embryo = $ca + m + n$ — *Lecanorchis japonica* group
      Embryo = $ca + m + h'$ — *Orchis maculata* group
      Embryo = $ca + m$ — *Liparis pulverulenta* group
    CCC. Tetrad in C2
      Embryo = $ca + m + n + o$ — *Eulophia oedoplectron* group
  BB. Species of the second period
    D. Second tetrad in A1
      Embryo = $cc + cd$ — SARCANTHEAE group

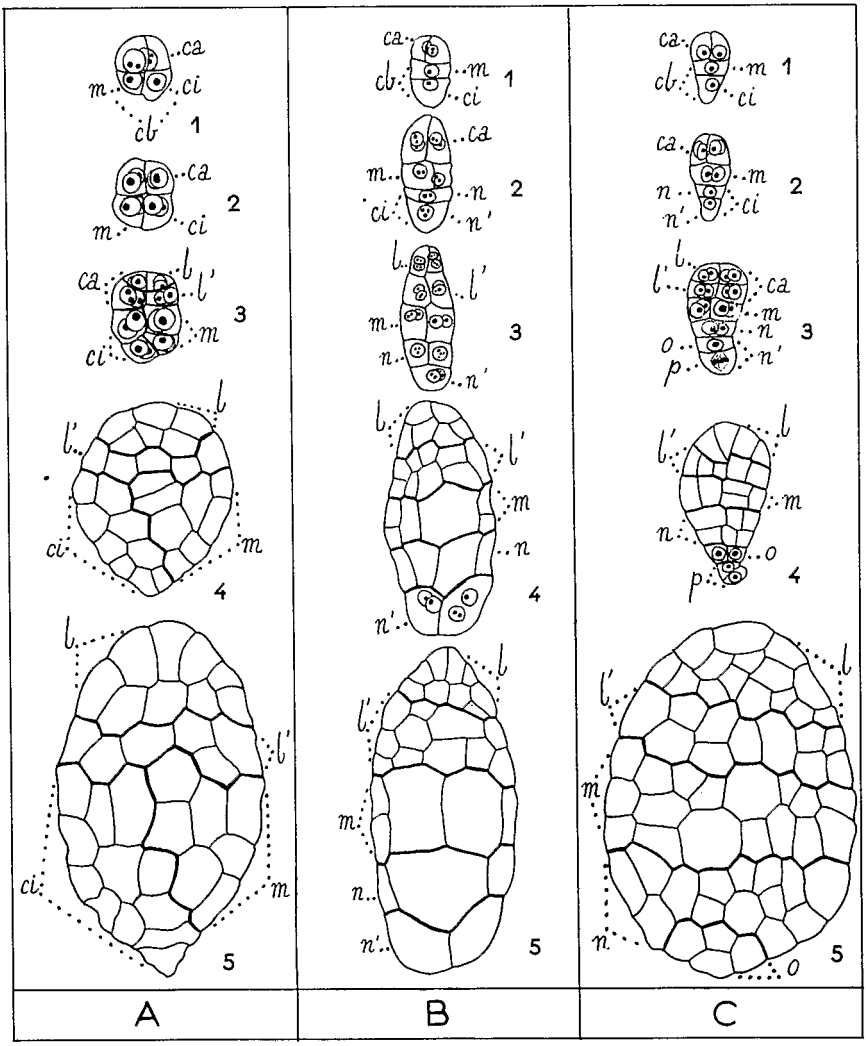


Fig. 5-6. Stages of embryogenesis among regular species. (A) *Epipactis atrorubens,* (B) *Manniella gustavi,* and (C) *Limodorum abortivum,* all according to Veyret. 1 = second cellular generation (tetrad); 2 = third cellular generation (quadrant stage); 3 = fourth cellular generation (octant stage); 4 = intermediary stage; 5 = adult embryo. 136X.

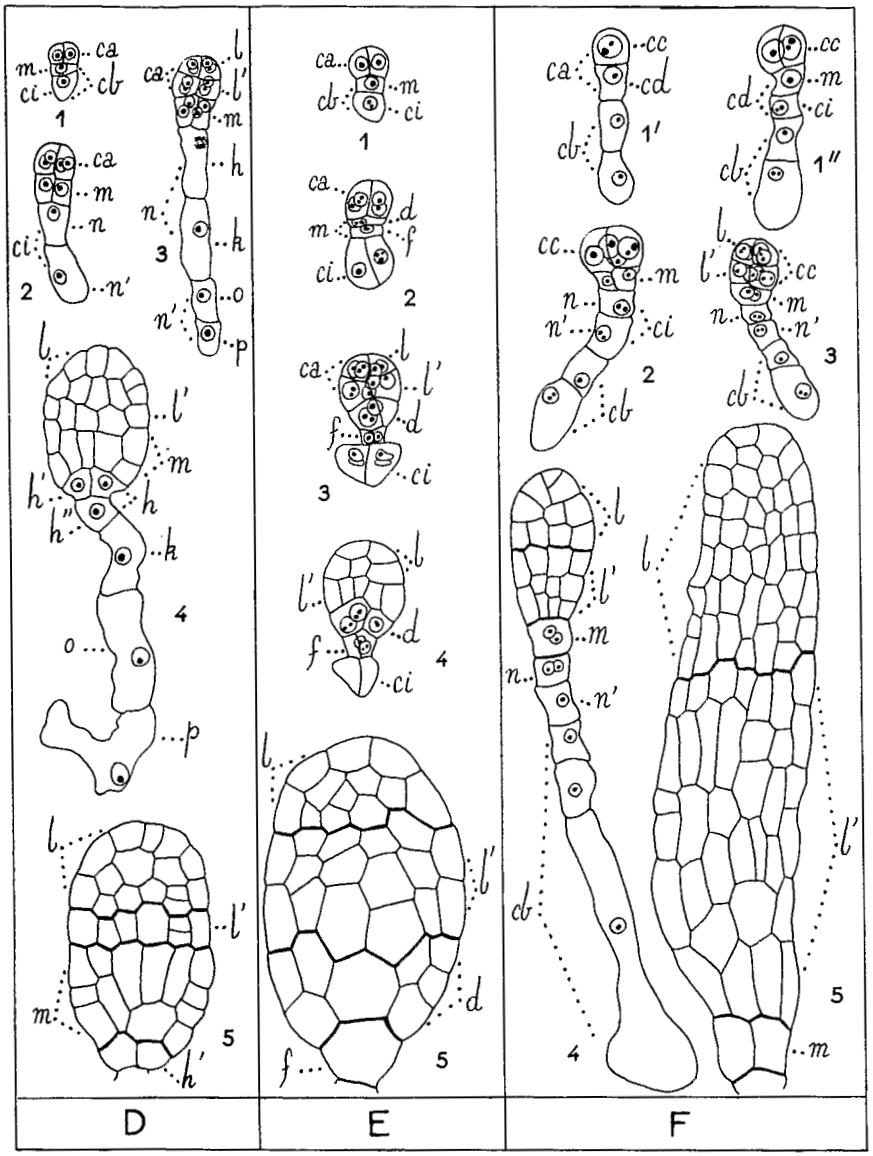


Fig. 5-7. Stages of embryogenesis among regular species. (D) *Serapias longipetala*, (E) *Liparis pulverulenta*, and (F) *Coelogyne parishii*, all according to Veyret. 1′ = first tetrad; 1″ = second tetrad (second period); for the other stages see caption of Fig. 5-6. 136X for Fig. 5-7D; 225X for the others.

DD. Second tetrad in A2
Embryo = *cc* + *m* + *ci* — *Polystachya geraensis* group
Embryo = *cc* + *m* — *Coelogyne parishii* group

AA. Species with cotyledon
E. Species of the first period
Tetrad in A2
Embryo = *ca* + *m* — *Epidendrum vitellinum* group

EE. Species of the second period
Second tetrad in A2
Embryo = *cc* + *m* + *ci* — *Polystachya microbambusa* group

Another group may be represented by *Eulophia epidendraea;* this would be placed in this classification after the *Coelogyne parishii,* but the observations of Swamy do not provide the developmental details, only the final structure.

The different embryonic types are defined by the developmental laws in the first four cellular generations. Since the first division of the egg is always transverse and the types of each group exhibit the same tetrad formation, these common characteristics will not be repeated in the descriptions of the various types within the groups (Figs. 5-6–5-8).

Neottia nidus-avis Group

Neottia nidus-avis Type. In the third cellular generation, the quadrants present a circumaxial arrangement, the division of the *m* and *ci* cells occurring following a longitudinal division. In the fourth cellular generation the octants are distributed in two layers:

l = layer of the upper octants
l′ = layer of the lower octants

The *m* and *ci* cells are transversally divided.

Listera ovata Type. This differs from the preceding by the transverse division of the *ci* cell in the third cellular generation.

Spiranthes autumnalis Type. This type is irregular: in addition to some forms identical to those of the *Neottia,* the quadrant cells can arrange themselves in two superimposed layers or in a tetrahedron.

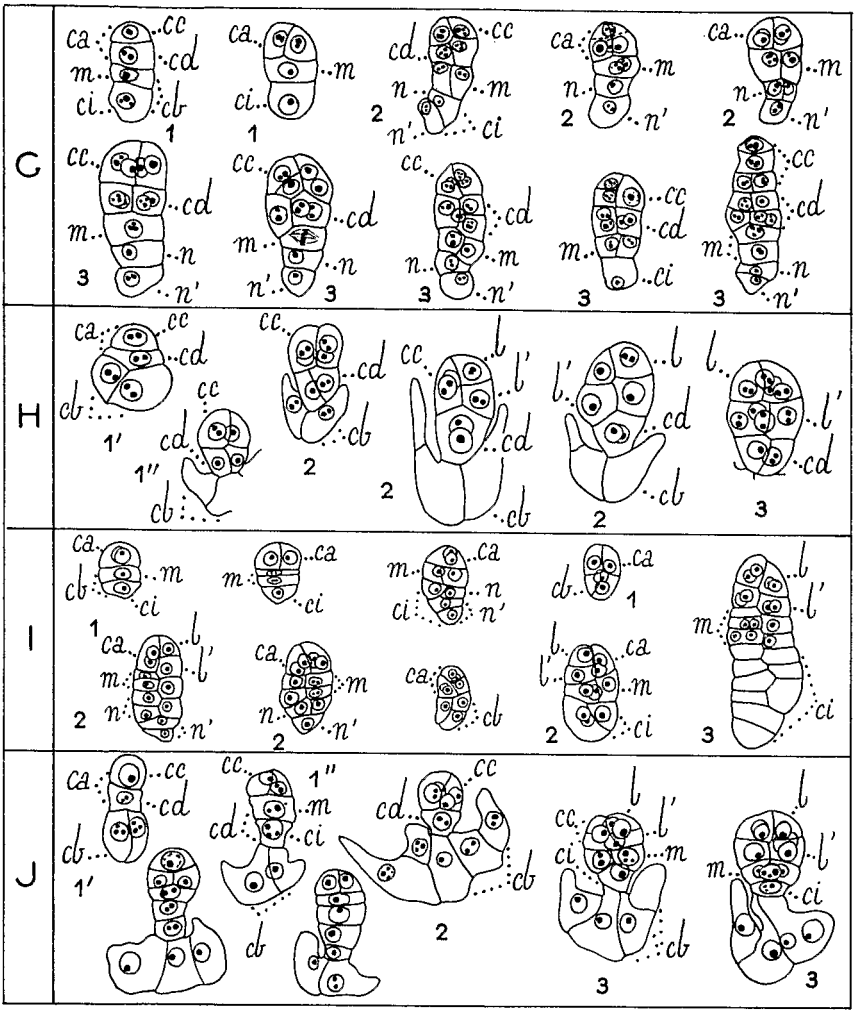


Fig. 5-8. Stages of embryogenesis among irregular species. (G) *Eulophia oedoplectron*, (H) *Angraecum distichum*. (I) *Epidendrum radicans*, (J) *Polystachya microbambusa*, all according to Veyret. Same stages as for Figs. 5-6 and 5-7. 320X for Fig. 5-8H; 225X for the others. In some figures the quadrant stage may be found slightly ahead, or the octants not all formed as yet, but these figures clearly indicate the mode of segmentation of the blastomers issued from *ca*.

Manniella gustavi Group

Manniella gustavi Type. In the third cellular generation the quadrants are arranged on an even plane, the *m* state is formed from two juxtaposed blastomeres, and the *ci* cell has engendered two superimposed components *n* and *n'*. In the fourth cellular generation the octants are distributed in two layers, the *m* stage is formed from four juxtaposed cells, and each of the *n* and *n'* cells is divided longitudinally.

Limodorum abortivum Group

Limodorum abortivum Type. This type is identical to that of *Manniella gustavi* type in the third cellular generation only. In the octant stage, this type differs from it by the transverse division of *n'*.

Lecanorchis japonica Group

Lecanorchis japonica Type. The quadrants are in circumaxial arrangement; at the same stage tier *m* is represented by two juxtaposed cells, and the cell *ci* has produced the two superimposed blastomeres *n* and *n'*. By the fourth cell generation, the octants are distributed in two layers of four cells, the row *m* is composed of four juxtaposed blastomeres, the cell *n* is divided longitudinally, and the cell *n'*, which forms a short suspensor, already shows signs of degeneration.

Orchis maculata Group

Orchis maculata Type. In the third cellular generation the *ca* layer is formed from quadrants arranged on the same plane, the cell *m* is divided longitudinally and the cell *ci* transversely. In the fourth cellular generation the octants are distributed in two layers, the *m* layer is formed from four circumaxial cells; the components coming from *ci* form an elongated four-celled suspensor.

Platycoryne paludosa Type. This type presents some forms constructed like those of the *Orchis,* but also some irregular forms, in the third cellular generation, by an arrangement of the quadrants in two superimposed dyads, or in a tetrahedron, and by a superimposed arrangement of the two blastomeres of *m;* and in the fourth cellular generation by a tetrahedral arrangement or in two superimposed dyads of the four components of *m.*

Liparis pulverulenta Group

Liparis pulverulenta Type. The embryo of the third cellular generation presents some quadrants in circumaxial arrangement, two superimposed cells *d* and *f* issued from *m,* two juxtaposed blastomeres in *ci.* The

octants are normally distributed in two layers and at this stage the cells *d* and *f* are divided vertically and the layer *ci* is formed from four circumaxial cells.

Bulbophyllum oreonastes Type. This differs from the preceding one by the lengthwise division of *m* and the transverse division of *ci* in the octant stage, by a new longitudinal division of the two cells of *m*, and by the joint possession of *ci* in the octant stage.

Masdevallia veitchiana Type. This differs from that of the *Liparis* by the arrangements of the quadrants in two superimposed dyads and the joint possession of the cells *m* and *ci* in the course of the third and fourth cellular generations.

Eulophia oedoplectron Group

Eulophia oedoplectron Type. This type is especially irregular. Some forms, uncommon ones, originate from a tetrad in A2, but the majority of the forms are constructed from a tetrad in C2. The quadrants are represented by the circumaxial cells or arranged in two superimposed dyads or in a tetrahedron. The octants can distribute themselves normally in two superimposed layers, or they can present a normal lower layer while the upper layer will be provided with homologous octant cells; they can still arrange themselves in two superimposed tetrahedrons or else the *l'* layer only will have its blastomeres arranged in tetrahedron, while the *l* layer will be made of two juxtaposed lower cells and of two other superimposed cells. In the third generation the *m* cell segments vertically, and the *ci* cell segments horizontally in *n* and *n'*. These new blastomeres remain undivided in the fourth generation.

Sarcantheae Group. The types in this group differ little among themselves; they are all irregular.

Angraecum distichum Type. The quadrants are arranged either in two superimposed dyads, or in a tetrahedron, or following a circumaxial arrangement. The octants distribute themselves normally in two layers. The two lower cells of the tetrad, which constitute the *cd* layers, remain undivided in the third cellular generation, sometimes still undivided in the octant stage; their division is generally transverse, more rarely periclinal.

Acampe renschiana Type. One finds again the same kinds of quadrants as those in the *Angraecum distichum* except for those whose arrangement is circumaxial; in the third cellular generation the two cells of the *cd* layer can divide and arrange themselves in a tetrahedron.

Cyrtorchis sedeni Type. In this species there has only been observed an arrangement of the quadrants, that of two superimposed dyads; the two cells of the *cd* layer divide in a periclinal manner.

Polystachya geraensis Group

Polystachya geraensis Type. This type is especially irregular since some forms originating from a tetrad in A1 add themselves to those derived from the tetrad in A2. The quadrants can arrange themselves in a tetrahedron or in two superimposed dyads; in this stage the cell *m* has engendered two juxtaposed blastomeres, and the cell *ci* has remained undivided. In the fourth generation the octants constitute the two layers *l* and *l'*; the two cells of the *m* layer and the *ci* cell are not segmented.

Coelogyne parishii Group

Coelogyne parishii Type. The third generation is represented by a layer of quadrants, two juxtaposed cells in *m*, and two superimposed blastomeres *n* and *n'* issued from the transverse division of *ci*. In the fourth generation there is the formation of two layers of octants, the cells of the *m* layer. The blastomeres *n* and *n'* remain undivided.

Epidendrum vitellinum Group

Epidendrum vitellinum Type. Epidendrum vitellinum embryos present two sorts of irregularities: the first comes from the presence of a supplementary tetrad in A1, and the second from a variable distribution of the blastomeres; in the forms derived from the tetrad in A2, the second are the most numerous. It is thus that in the third cellular generation the quadrants are found grouped on one layer only, or they are distributed in a tetrahedron with the two cells of *m* separated by a longitudinal transverse division, and that in the fourth cellular generation. The four blastomeres from *m* form a tetrahedron, or two superimposed dyads, while the octants are normally distributed in two layers.

Polystachya microbambusa Group

Polystachya microbambusa Type. This type is irregular because some proembryonic stages proceed from a tetrad in A2, while others, less numerous, derive from a tetrad in C2. The quadrants present two arrangements, either circumaxial or in a tetrahedron. At this same stage the cell *m* is found vertically divided, and the blastomere *ci* remains undivided. It will still be so in the fourth cellular generation while the *m* layer will be formed from four circumaxial cells and the quadrants will have engendered two layers of octants.

In Table 5-1 we classify all the species whose embryology is known, although often in a very imperfect manner so that it is necessary to distribute some of them in several columns. The species that are irregular are noted with an asterisk. They are destined to be replaced by species of regular type as they are discovered and described. In the third column the species with secondary differences are listed for each type.

Each species is followed by a letter in parentheses which indicates the tribe or one of its divisions according to Schlechter (1926):

C: CYPRIPEDILOIDEAE
O: OPHRYDOIDEAE
P: POLYCHONDREAE
A: KEROSPHAEREAE-ACRANTHAE
S: KEROSPHAEREAE-PLEURANTHAE-SYMPODIALES
M: KEROSPHAEREAE-PLEURANTHAE-MONOPODIALES

The number in brackets corresponds to a reference in the bibliography.

The Embryo in the Seed

Embryogenesis is a relatively short stage, in comparison to other concurrent phenomena, in the formation of the fruit. It starts toward the middle of the period, occurring between the pollination and the dehiscence of the ovary, and lasts an average of about two weeks. When the pod is ready to dehisce, the internal integument of the ovule as well as the deepest layers of the external integument are generally found to be degenerated. In the majority of the POLYCHONDREAE, however, and in many European OPHRYDOIDEAE, the cuticle of the epidermis of the inner integument of the ovule persists, and this seems to have the effect of impeding the hydration of seeds and thus hindering their germination *in vitro* (Veyret, 1969). The outer cell layer of the external integument constitutes by itself the cover of the seed. The embryo in the absence of *Rhizoctonia* may be in limited contact with the seedcoat or may be more or less isolated in the center according to the importance of the development of the external integument in the course of the embryogenesis. The cells of the coat are dead, empty, and generally transparent. Their walls can be simple or diversely ornamented, rarely very thick as among seeds of some species of *Apostasia, Neuwiedia, Selenipedium,* and the VANILLEAE—*Vanilla, Galeola, Epistephium.* In the VANILLEAE, the seed of the latter two is also winged.

By the time the fruit has matured, the suspensor of the embryo has degenerated, and the cotyledon is not at all or scarcely developed. There is only slight cotyledonary formation in embryos of *Platyclinis glumacea*

TABLE 5-1

Classification of orchids by embryological type†

Embryological Group	Embryological Type
Neottia nidus-avis	*Neottia nidus-avis* (P)(1)
	**Spiranthes autumnalis* (P)(1)
	Listera ovata (P)(1)
Maniella gustavi	*Maniella gustavi* (P)(1)
Limodorum abortivum	*Limodorum abortivum* (P)(1)
Lecanorchis japonica	*Lecanorchis japonica* (P)(2)
Orchis maculata	*Orchis maculata* (O)(3)
	**Platycoryne paludosa* (O)(1)
Liparis pulverulenta	*Liparis pulverulenta* (A)(1)
	Bulbophyllum oreonastes (S)(1)
	Masdevallia veitchiana (A)(1)
Eulophia oedoplectron	**Eulophia oedoplectron* (S)(1)
SARCANTHEAE	*Angraecum distichum* (M)(1)
	Acampe renschiana (M)(1)
	Cyrtorchis sedeni (M)(1)
Polystachya geraensis	**Polystachya geraensis* (A)(5)
Coelogyne parishii	*Coelogyne parishii* (A)(1)
Epidendrum vitellinum	**Epidendrum vitellinum* (A)(1)
Polystachya microbambusa	**Polystachya microbambusa* (A)(1)

†See text, page 239, for details.

TABLE 5-1 (continued)

Species Identical to or Differing by Secondary Characteristics from the Type	Species Definitely Belonging to Group
Epipactis atrorubens (P)(1)	*Epipogium aphyllum* (P)(10,11)
Goodyera repens (P)(1)	*Epipactis palustris* (P) (12) *E. latifolia* (12) *Spiranthes australis* (P)(13, 14) *S. cernua* (27)(15)
Cephalanthera ensifolia (P)(1)	*Hetaeria shikokiana* (P)(16)
Gymnadenia conopsea (O)(6) *Habenaria platyphylla* (O)(7) *Loroglossum hircinum* (O)(8) *Ophrys lutea* (O)(1) *Orchis aristata* (O)(9) *O. laxiflora* (1) *O. longibracteata* (1) *Phyllomphax helleborine* (O)(1) *Platanthera bifolia* (O)(1) *Serapias longipetala* (O)(1)	*Habenaria decipiens* (O)(7) *H. heyenecina* (7) *H. longicalcarata* (7) *H. longicornu* (7) *H. marginata* (7) *H. plantagenea* (7) *H. rariflora* (7) *H. viridiflora* (7)
	Dendrobium microbulbon (A)(7) *Epidendrum ciliare* (A)(12)
Vanilla fragrans (P)(1) *Corallorhiza innata* (S)(1)	*E. lacerum* (17) *E. prismatocarpum* (18) *E. radicans* (1)
Maxillaria variabilis (S)(1)	*Laelia brysiana* (A)(12)
Rangaeris muscicola (M)(1)	

*See text, pages 234-238, for details.

TABLE 5-1 (continued)

Classification of orchids by embryological type†

Species Appearing to Belong to the Group	Species Little Known Embryologically or Known Only from General Characteristics	
	Cypripedium parviflorum (C)(25) *C. reginae* (26) *C. spectabile* (12) *Goodyera tesselata* (P)(27) *Prescottia micrantha* (P)(1) *Spiranthes annua* (P)(28) *Zeuxine sulcata* (P)(29, 30)	No Suspensor
Epipactis pubescens (P)(19) *Galeola septentrionalis* (P)(20)		
Hetaeria nitida (P)(21)		
Anacamptis pyramidalis (O)(12) *Herminium monorchis* (O)(12) *Orchis latifolia* (O)(12) *Peristylus grandis* (O)(4) *P. spiralis* (17) *Serapias pseudocordigera* (O)(23)	*Cypripedium barbatum* (C)(12) *C. venustum* (12) *Gastrodia elata* (P)(31) *Haemaria discolor* (P)(12) *Chamaeorchis alpina* (O)(32) *Cynorkis ampullacea* (O)(33) *C. lilacina* (34) *C. ridleyi* (33) *Habenaria blephariglottis* (O)(27) *H. ciliaris* (35) *H. integra* (35) *H. rariflora* (36) *H. tridentata* (27) *Nigritella angustifolia* (O)(32) *N. nigra* (37) *Ophrys myodes* (O)(38) *Platanthera montana* (O)(32) *Pterygodium newdigatae* (O)(39) *Satyrium nepalense* (O)(40) *Serapias lingua* (O)(12) *Coelogyne breviscapa* (A) (17) *Dendrobium anosum* (A) (41) *D. barbatulum* (17) *D. graminifolium* (17) *D. nobile* (42, 43) *Epidendrum cochleatum* (A)(44) *E. variegatum* (44) *E. verrucosum* (44) *Cattleya* sp. (45) *Arundina bambusifolia* (A)(46) *Pleurothallis clausa* (A)(47) *P. racemiflora* (47) *P. procumbens* (A)(48) *Restrepia vittata* (A)(47) *Trichosma suavis* (A) (49) *Aplectrum hiemale* (S)(27) *Bletia shepherdii* (S)(44) *Bulbophyllum mysorense* (S)(17) *Calanthe madagascariensis* (S)(1) *C. veitchii* (50) *Catasetum* sp. (S)(43) *Corallorhiza multiflora* (S)(27) *Maxillaria crassifolia* (S)(51) *M. punctulata* (S)(47) *Odontoglossum crispum* × *O. adrianae* (S)(52) *Peristeria elata* (S)(17) *Phajus grandiflorus* (S)(44) *P. wallichii* (12) *Zygopetalum mackayi* (S)(24) *Cymbidium bicolor* (S)(24, 53) *C.* sp. (52) *Eulophia epidendraea* (S)(54) *E. cucculata* (1) *Geodorum densiflorum* (S)(17) *Stanhopea costaricensis* (S)(1) *S. oculata* (12)	Suspensor Present No Cotyledon Present
Spathoglottis plicata (S)(17)		
Aerides sp. (M)(17) *Cottonia* sp. (M)(17) *Diplocentrum conjestrum* (M)(17) *Luisia* sp. (M)(17) *Phalaenopsis schillerana* (M)(12) *P. grandiflora* (12) *Rhyncostylis* sp. (M)(17) *Saccolabium* sp. (M)(17) *Vanda parviflora* (M)(24) *V. roxburgii* (24) *V. spathulata* (24) *V. tricolor* (12)		
	Bletilla hyacinthina (P)(52) *B. striata* (55) *Sobralia macrantha* (P)(12)	Cotyledon Present

References:

1. Veyret, 1965.
2. Tohda, 1971b.
3. Montéverdé, 1880.
4. Treub, 1883.
5. Chaiyasut, unpublished.
6. Ward, 1880.
7. Swamy, 1946c.
8. Heusser, 1915.
9. Tohda, 1971a.
10. Afzélius, 1954.
11. Geitler, 1956.
12. Treub, 1879.
13. Maheswari and Narayanaswami, 1950.
14. Maheswari and Narayanaswami, 1952.
15. Swamy, 1948a.
16. Tohda, 1967.
17. Swamy, 1949.
18. Swamy, 1948b.
19. Brown and Sharp, 1911.
20. Kimura, 1971.
21. Olsson, 1967.
22. Baranov, 1924.
23. Baranov, 1915.
24. Swamy, 1942a.
25. Carlson, 1940.
26. Schnarf, 1931.
27. Leavitt, 1901.
28. Leavitt, 1900.
29. Seshagiriah, 1941.
30. Swamy, 1946b.
31. Kusano, 1915.
32. Dumée, 1910.
33. Veyret, 1972.
34. Veyret, 1967.
35. Brown, 1909.
36. Swamy, 1943a.
37. Afzélius, 1928.
38. Senianinova, 1924.
39. Duthie, 1915.
40. Swamy, 1944.
41. Pastrana and Santos, 1931.
42. Poddubnaja-Arnoldi, 1959.
43. Poddubnaja-Arnoldi, 1960a.
44. Sharp, 1912.
45. Knudson, 1935.
46. Mitra, 1971.
47. Prillieux, 1860.
48. Afzélius, 1966.
49. Baranov, 1917.
50. Poddubnaja-Arnoldi, 1960b.
51. Fleischer, 1874.
52. Bernard, 1909.
53. Swamy, 1946a.
54. Swamy, 1943b.
55. Tohda, 1968.

(Beer, 1863), *Sobralia macrantha* (Treub, 1879), *Bletilla hyacinthina* (Bernard, 1909), B. *striata* (Tohda, 1968), *Epidendrum vitellinum,* and *Polystachya microbambusa* (Veyret, 1965). In a rather larger number of species, it is only possible to distinguish an apical zone of small cells, the rest of the embryo being formed from bulky cells, stuffed with reserve substances, which are all similar morphologically. There is, however, histological and physiological differentiation along the axis.

The orchid embryo has developed in a sac without benefit of an endosperm, and this has generally been interpreted as the cause of the rudimentary state of the embryo. The endosperm does not ordinarily form in the orchids, either from a lack of fusion of the second sperm nucleus with the endosperm nuclei, or from an immediate degeneracy of the nucleus of the endosperm if the double fertilization does take place. Among a few species, however, the segmentation of the nucleus of the endosperm does take place, but it never leads to the production of a normal endosperm. In ovules of *Chamaeorchis alpina* and *Paphiopedilum insigne* (Afzelius, 1916), and in *Limodorum abortivum* (Veyret, 1965) and *Pogonia japonica* (Abe, 1968), there form only two nuclei; *Cephalanthera damasonium* and *C. longifolia* (Hagerup, 1947) form a few; *Cypripedium guttatum* (Prosina, 1930), *C. parviflorum, C. spectabile,* (Pace, 1907), *Polystachya geraensis,* (Chaiyasut, unpublished), and *Lecanorchis japonica* (Tohda, 1971b) form four; *Bletilla striata* (Abe, 1971) forms eight; and *Vanilla planifolia* (Swamy, 1947), forms twelve. There are sixteen in *Galeola septentrionalis* (Kimura, 1971). This endosperm is entirely reabsorbed before the end of embryogenesis. The embryo in certain species may be more developed than among species which have endosperm. One cannot therefore attribute a cause and effect relationship to this phenomenon.

In the absence of the endosperm, Treub (1879) attributed the role of nourishment to the suspensor; or, in the absence of the suspensor, to the slight contact of the embryonic sac with the embryo. But the influence of such assimilatory structures, nuclei of the sac, or the suspensor, or relations of proximity between the embryo and the walls of the embryonic cavity, do not seem related to a better development of morphological differentiation of the embryo. In addition, in the cases of polyembryony, the embryos of the same sac reach an equal or nearly equal size in development, and, particularly, a histological differentiation comparable to that of single embryos. These facts all favor the unique qualities of orchid embryos.

Polyembryony and Apomixis

Usually the embryo in the seed is single, but in numerous species, the phenomenon of polyembryony occurs, true or false, facultative or predominant. Multiple embryos in many instances are related to apomixis (Fig. 5-9), rather than to true polyembryony.

Cases of pseudopolyembryony are rare in orchids. There are double embryo sacs in the same nucellus in *Orchis morio* (Schacht, 1850; Braun, 1859), *Gymnadenia conopsea* (Strasburger, 1878), *Lecanorchis japonica* (Tohda, 1971b), and *Listera nipponica* (Abe, 1972), and both are functional. In *Pterygodium newdigatae* (Duthie, 1915) there may also be the formation of two archesporial cells in a single ovule that would be partly responsible for the polyembryony in the seed. Often there are ovules enclosing two separate nucelli in *Bletilla striata* (Abe, 1971). One embryo sac seems to develop normally in each of these.

True polyembryony is more frequent, and has been reviewed by Wirth and Withner (1959) with illustrations from the literature. In addition to the examples cited there, Duthie (1915) has also shown that some of the embryos of *Pterygodium newdigatae* are the result of segmentation of the embryo proper.

When they have been formed, the development of a synergid into an embryo, in addition to a normal embryo, is found in a facultative manner in *Orchis maculata* and *Listera ovata* (Hagerup, 1944, 1947). The synergids begin segmentation without there being any fusion with a sperm nucleus, so that, in this case, we are dealing with haploid apogamy. The same process can be responsible for the twin embryos in *Vanilla planifolia* (Swamy, 1947) and *Platanthera sachalinensis* (Abe, 1972).

Other forms of apomixis involve haploid parthenogenesis, somatic apospory, megasporic embryony, omnisaccate diploid embryony, and probably diplospory. Haploid parthenogenetic development has been discovered in a certain number of orchids, particularly those where fertilization is late in occurring (Hagerup, 1945, 1947; Maheswari and Narayanaswamy, 1950), and has been described for *Gastrodia elata* by Kusano (1915). In the F_1 generation of a cross between *Bletilla striata* var. *gebina* and *Eleorchis japonica*, Miduno (1940) ascertained that a certain number of the plants are haploid; he thinks that they must have a parthenogenetic origin. Somatic apospory (Swamy, 1948) and related examples are cited by Wirth and Withner (1959).

Megasporic embryony has been recognized by Seshagiriah (1941) in *Zeuxine sulcata*. Gametogenesis does not occur, and the four meiotically

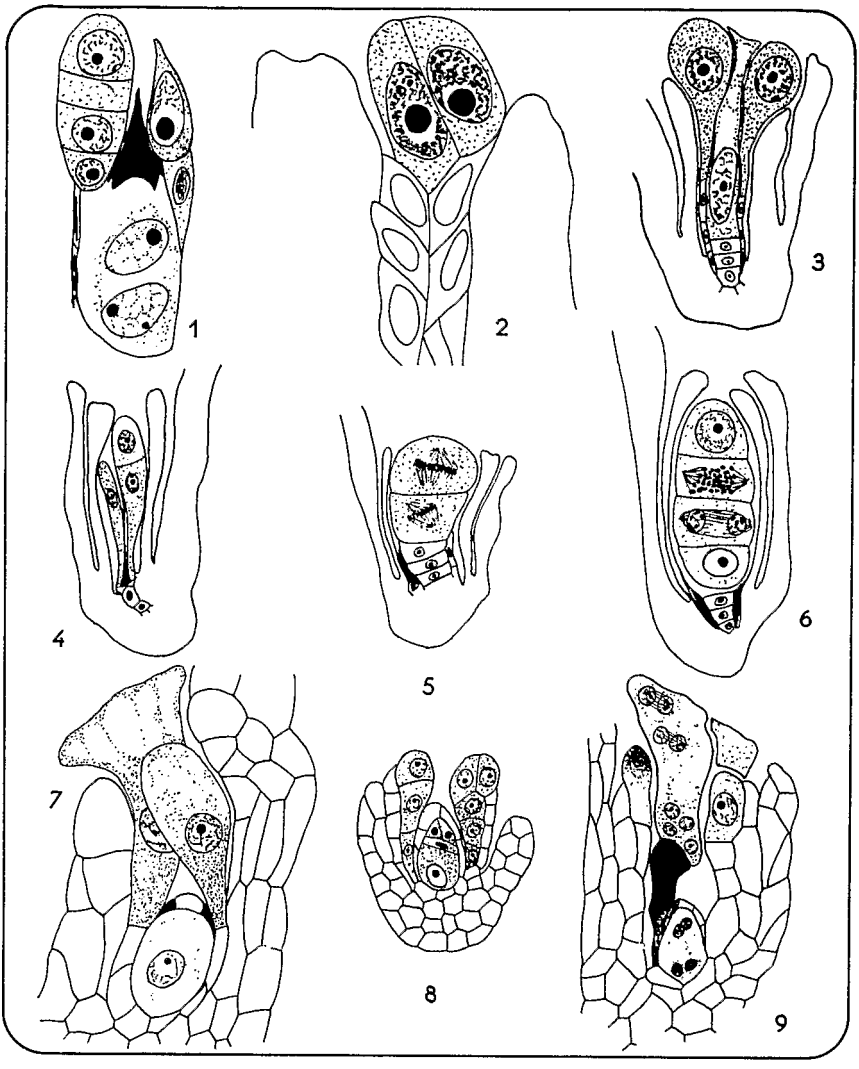


Fig. 5-9. Different forms of apomixis. Parts 1 through 4 show nucellar embryony. (1, 2) *Nigritella nigra,* according to Afzelius. (3, 4) *Zeuxine sulcata,* according to Seshagiriah. (5, 6) Formation of the embryo from the tetrads of macrospores in *Zeuxine sulcata,* according to Seshagiriah. (7, 8) Integumentary embryony in *Spiranthes cernua,* according to Swamy. (9) Somatic apospory in *Spiranthes cernua,* according to Swamy.

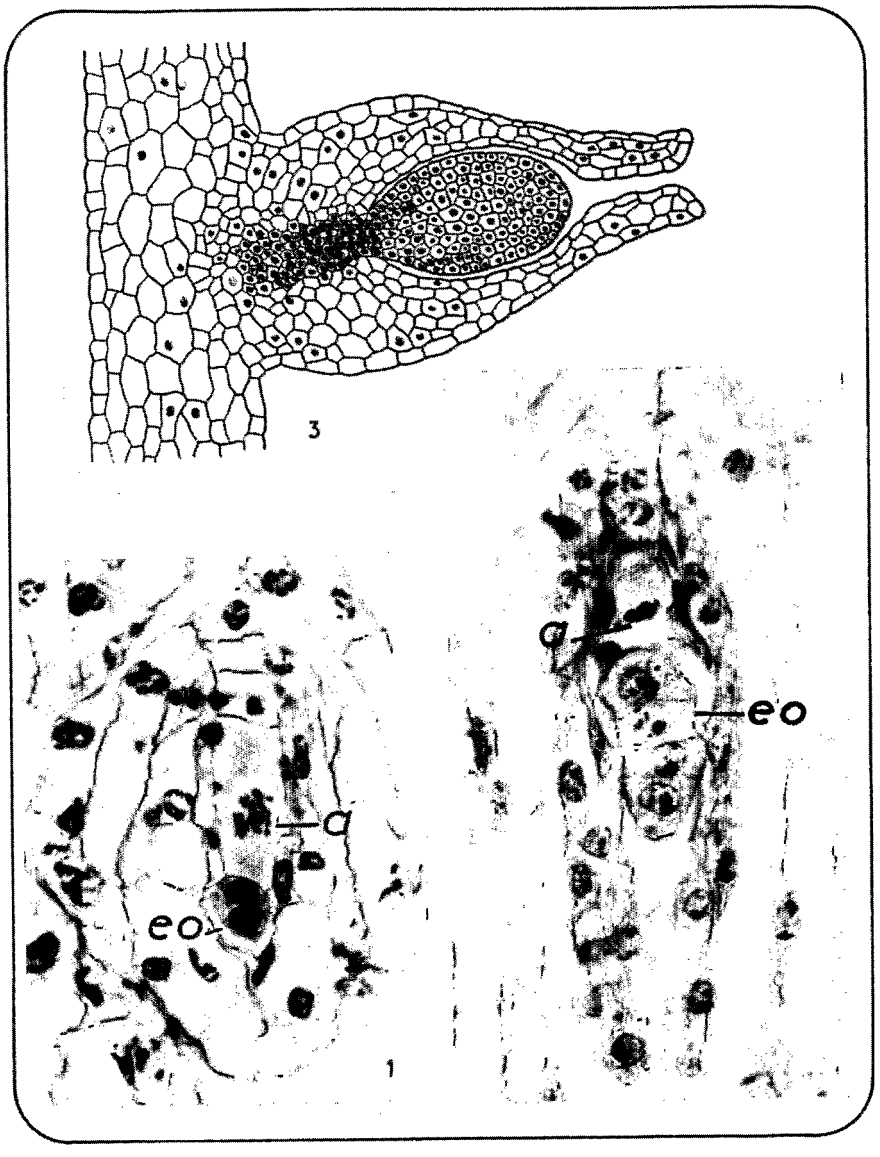


Fig. 5-10. Parts 1 and 2 present omnisaccate diploid embryony. (1) In the presumed hybrid of *Cynorkis lilacina* × *C. ridleyi.* (2) In *C. ridleyi, a* = archesporial cell; *eo* = omnisaccate diploid embryo, after Veyret. 565X. (3) Foliar embryo of *Malaxis paludosa,* after Taylor. 100X.

produced spores all join in the formation of the embryo. In *Cynorkis lilacina* only one or two of the spores participate (Veyret, 1965).

Omnisaccate diploid embryony (Fig. 5-10) is known in *Cynorkis ridleyi* and *C. ampullacea,* and the hybrid presumed to be *C. lilacina* × *C. ridleyi.* Diplospory is supposed to occur among triploid hybrids such as *Dactylorchis fuchsii* × *D. purpurella* and *D. fuchsii* × *D. praetermissa* (Heslop-Harrison, 1959).

In some cases, although apomictic formation of seed has been recognized, it has not been determined by which process. This is the case for the probable triploid population of *Listera borealis* studied by Simon (1968). Apomixis occurs in *Zygopetalum mackayi* when pollinated with foreign pollen. In addition to the earlier paper of Suessenguth (1923), Afzélius (1959) has confirmed this process.

Cases of adventitious embryo formation from the nucellus or integuments have been described for the orchids, generally after problems in gametogenesis. Earlier cases are detailed by Wirth and Withner (1959).

A new example of nucellar origin has been described by Veyret (1967, 1972) for *Cynorkis lilacina, C. ridleyi, C. ampullacea,* and the presumed hybrid *C. lilacina* × *C. ridleyi.* It is also noted in *Zeuxine sulcata* (Seshagiriah, 1932), though in a different manner of apomixis. The adventive embryony is integumentary in *Spiranthes cernua* (Leavitt, 1900; Swamy, 1948). In these cases the embryos form from cells of the inner integument (Fig. 5-9). In *Nigritella nigra* it is only the races of high chromosome number ($2n = ca\ 64$) known in the mountains of Scandinavia that are adventive (Afzélius, 1932). They are apparently survivors from ancient glacial periods.

The anomalies in the development of the gametes, male or female, are abnormal meiosis in the pollen mother cells in *Zeuxine* (Seshagiriah, 1934); degeneration of the pollen *in situ* in *Spiranthes*; frequent formation of abberrant tetrads with more than four nuclei in *Cynorkis ampullacea*; abortion of the pollen in the presumed hybrid of *C. lilacina* × *C. ridleyi* and also certain races of *C. ridleyi.* The pollen forms normally in *Nigritella* and *Spiranthes,* but its germination has never been observed. On the female side, tetrads form in *Nigritella, Zeuxine,* and *Spiranthes,* but the embryo sac mother cell produces an incomplete and nonfunctional gametophyte. In *Cynorkis* the archesporial cell is the embryo sac mother cell, and it degenerates after an abnormal meiosis and gives rise to a gametophyte consisting generally of two cells. The gametophyte is nonfunctional, with certain exceptions in *C. lilacina.*

Finally, some species are known that produce polyembryonic seeds without the process being known. They are *Orchis latifolia* (Schleiden,

cited by Strasburger, 1878), *Orchis morio* (Müller, 1847) *Goodyera tesselata, G. pubescens, Aplectrum hiemale, Habenaria tridentata, H. blephariglottis* (Leavitt, 1901), *Satyrium nepalense* (Swamy, 1944), and *Cypripedium calceolus* (Strasburger, 1877).

Vegetative Apomixis

An unusual means of apomixis was confirmed for the first time by Dickie in 1875. In *Malaxis paludosa* small protuberances or bulbils form at the apical margins of adult leaves. Taylor (1967) showed that these structures simulate an ovule provided with an embryo, and they may properly be called foliar embryos. These embryos are capable of giving rise to secondary foliar embryos by division of their integuments (Fig. 5-10).

The Different Types of Young Seedling

Bernard (1889) found that the seeds of orchids germinate in nature through the symbiosis established between them and the mycelium of the fungal genus *Rhizoctonia.* In the laboratory the simplest way to obtain germination is to use an appropriate culture medium. The germination *in vitro* or under natural conditions is accompanied by a general development pattern common to all species: formation of a tubercle, called the protocorm, which is covered with rhizoids on about two-thirds of its basal part, a lack of formation of the radicle, generally late development of a first root, while several leaves begin developing from the apex.

The form of the young protocorm can be characteristic of certain groups, although there are several exceptions. Among the POLYCHONDREAE the young protocorm is generally elongated and much less thick than in the other taxa and its tip is often curved (Fig. 5-11). Among the KEROSPHAERAE-PLEURANTHAE-MONOPODIALES the protocorm is clearly dorsiventral. It is even provided with a dorsal crest in *Phalenopsis* and *Vanda* (Bernard, 1909) and *Taeniophyllum* (Goebel, 1889) (Fig. 5-12). *Aerides minimum* (Raciborski, 1898) has an appearance resembling *Taeniophyllum.* In asymbiotic germination *in vitro* the dorsiventrality is often less clear. In contrast among the KEROSPHAEREAE-ACRANTHAE and the KEROSPHAEREAE-PLEURANTHAE-SYMPODIALES (Fig. 5-13) the protocorm is a "cattleya" type generally in the form of a top. The protocorm may in a certain species even become discoid. Among several species of these taxa, the protocorm is narrow, as Fuchs and Ziegenspeck (1927a) showed for *Microstylis* (*Acroanthus*), *Corallorhiza innata,* and *Liparis loeselii.* It swells afterward into a club-shaped mass in this last species. The protocorm of a species of *Phymatidium* seems to resemble that of *Taenio-*

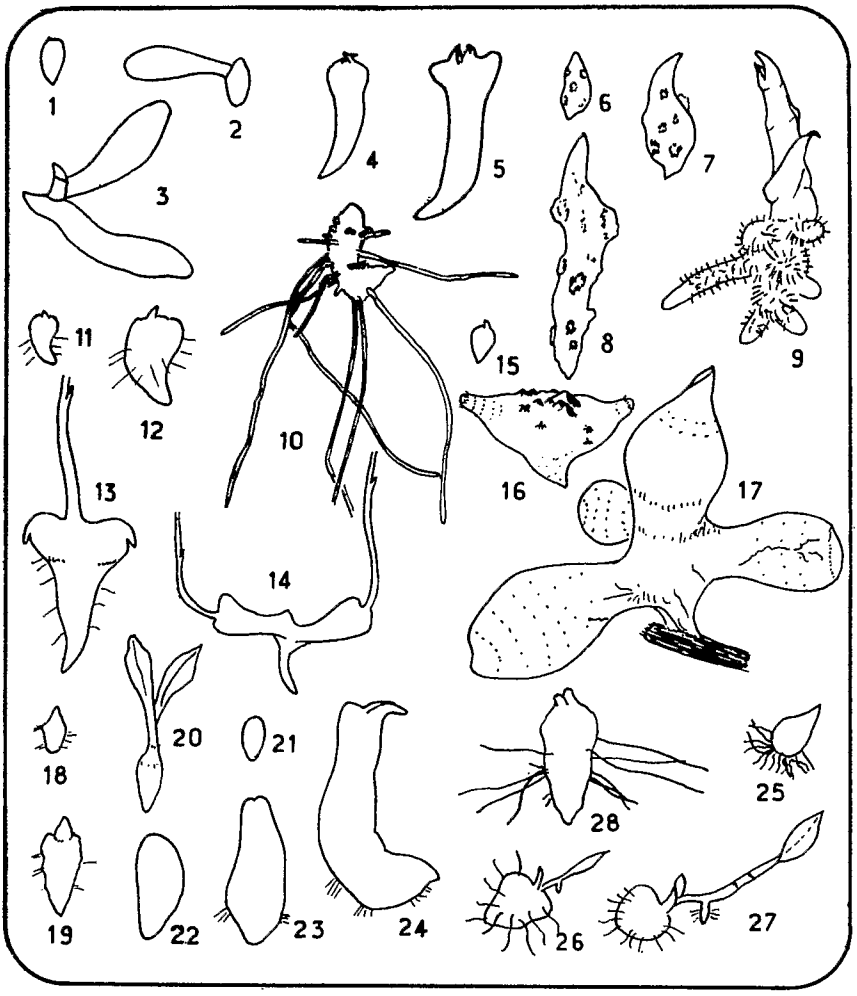


Fig. 5-11. Germination of the POLYCHONDREAE. (1-3) *Listera ovata,* according to Fuchs and Ziegenspeck. (4, 5) *Neottia nidus-avis;* according to Bernard, 5X. (6-8) *Vanilla madagascariensis,* according to Tonnier. (9) *Vanilla fragrans,* according to Bouriquet. (10) *Nervilla crispata,* according to Burgeff, 20X. (11-14) *Epipogium aphyllum,* according to Irmisch. (16, 17) *Didymoplexis minor,* according to Burgeff. (18-20) *Spiranthes spiralis,* according to Fuchs and Ziegenspeck. (21-24) *Manniella gustavi,* according to Veyret 15X. (25-27) *Goodyera repens,* according to Beer. (28) *Goodyera pubescens,* according to Knudson, 10X.

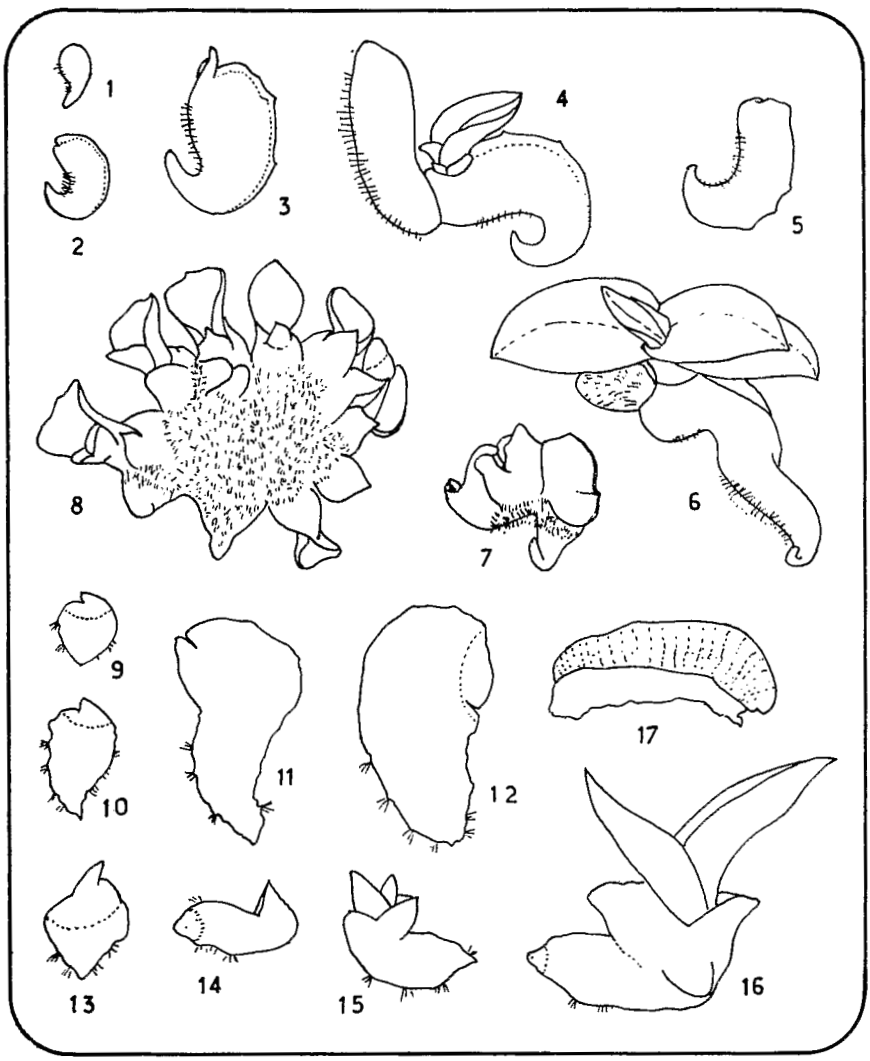
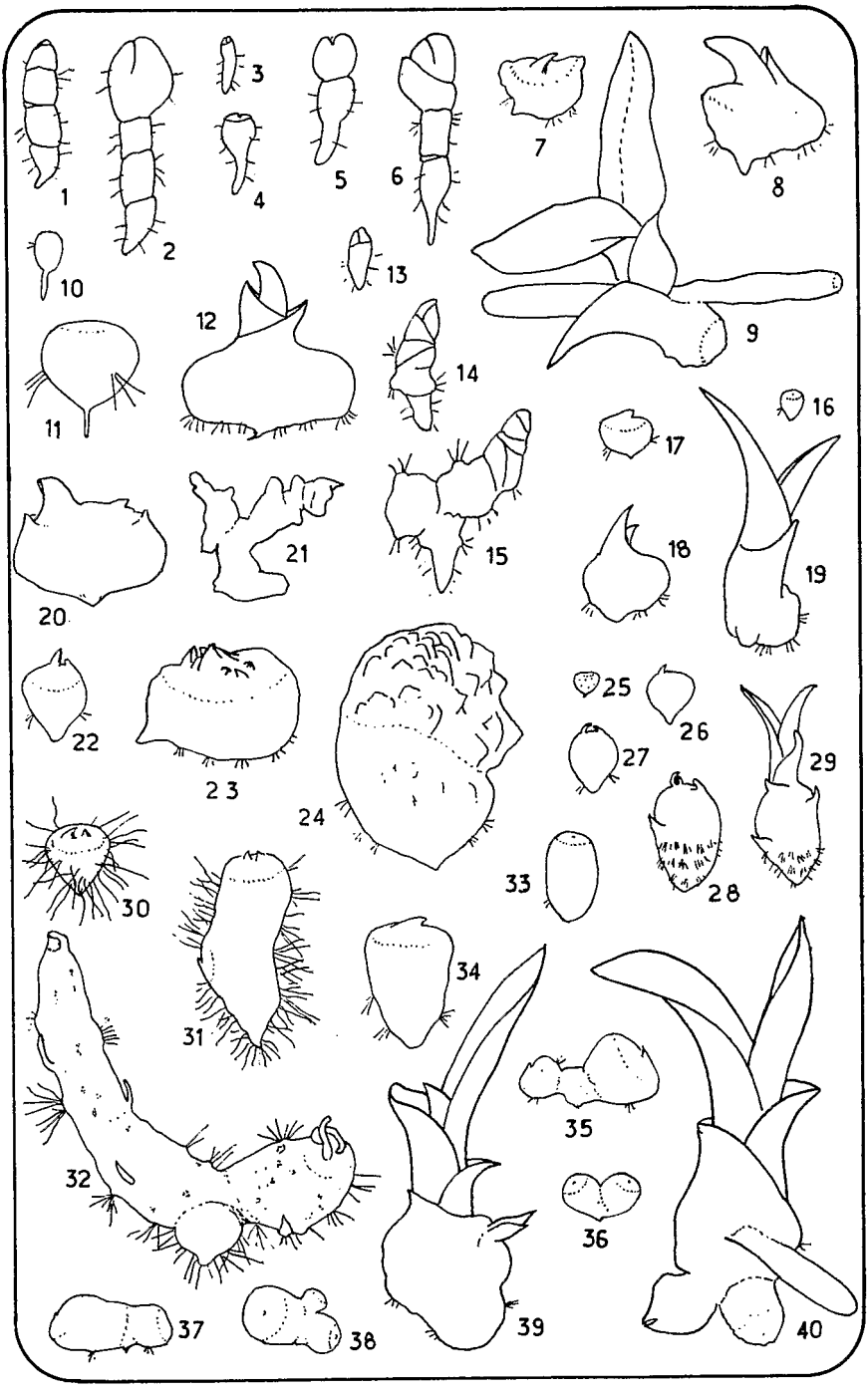


Fig. 12. Germination of the PLEURANTHAE-MONOPODIALES. (1-4) *Phalaenopsis amabilis* × *P. rosea*. 5X. (5-8) *Vanda tricolor*, after Bernard. 5X. (9-12) *Angraecum distichum*, after Veyret. 15X. (13-16) *Acampe renschiana*, after Veyret. 15X. (17) *Taeniophyllum tjibodasanum*, after Burgeff, 5X.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40

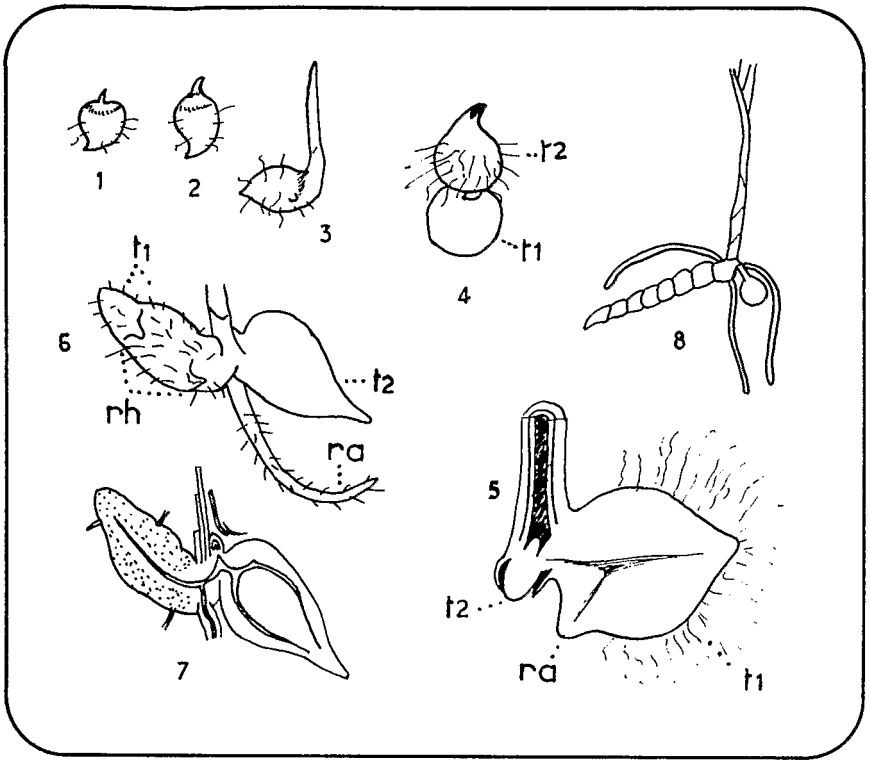


Fig. 5-14. Germination of the OPHRYDOIDEAE. (1–3) *Orchis militaris,* according to Irmisch. (4, 5) *Ophrys apifera,* according to Fabre. (4) One of the first forms under which the plantule of the second year is shown. The diameter of the lower tubercule is from 1 to 3 mm. (5) Longitudinal section showing the formation of the tubercule of the second year. (6, 7) *Platanthera montana,* according to Bernard. (6) Plantule of the second year. (7) Section of the same plantule (the infected zone is indicated by the dotted area). 2X. t1 = tubercule of the first year; t2 = tubercule of the second year; ra =root; rh = rhizome.

Fig. 5-13. Germination of the ACRANTHAE (1-12) and the PLEURANTHAE-SYMPODIALES. (1, 2) *Microstylis* (*Acroanthus*), and (3-6) *Liparis loeselii,* after Fuchs and Ziegenspeck. (7-9) *Epidendrum nocturnum,* after Veyret. 15X. (10-12) *Cattleya,* after Bernard. 20X. (13-15) *Corallorhiza innata,* after Fuchs and Ziegenspeck. (16-19) *Bulbophyllum bufo,* after Veyret. 10X. (20, 21) *Eulophia maculata* (*Angraecum maculatum*), according to Prillieux and Rivière, after Bernard, and (22–24) after Veyret. (25–29) *Cymbidium giganteum,* after Bernard, 10X. (30–32) *Cymbidium,* after Burgeff. 10X. (33–38) *Odontoglossum pulchellum,* 15X, and (39–40) 10X, after Veyret.

phyllum zollingeri, but it is less elongated (Müller, 1895). Among the OPHRYDOIDEAE (Fig. 5-14) and the CYPRIPEDIOIDEAE (Irmisch, 1853; Curtis, 1943; Stoutamire, 1964a) the young protocorm is of the general "cattleya" type, and the tuberization is much less important.

In the sequence of development other differences appear which are the first manifestations of the establishment of a more adult appearance. Among the POLYCHONDREAE, the protocorm evolves in several ways: it continues to elongate while forming a slightly thickened rhizome and is rapidly provided with roots. This is the case for *Neottia nidus-avis* (Bernard, 1889), *Epipactis atropurpurea, Listera ovata,* and *Limodorum abortivum* (Fuchs and Ziegenspeck, 1962a, 1962b) and *Goodyera pubescens* (Knudson, 1941). Among the vanillas (Bouriquet, 1947; Knudson, 1950; Tonnier, 1952) one can verify a similar evolution but the formation of the roots is much later; and among some plants with tuberous roots, like *Spiranthes,* the protocorm rapidly takes the form of a tubercle (Fuchs and Ziegenspeck, 1927b). *Sobralia macrantha* seems to resemble it (Hofmeister, 1861). As for the protocorm of *Goodyera repens,* it is strongly tuberized (Beer, 1863), which is surprising for this species with slender, branching roots. Finally, among some kinds of *Epipogium,* the summit of the protocorm enlarges and several primordia appear which produce the characteristic coralloid roots and aphyllous stems (Irmisch, 1853). The recent work of Stoutamire (1963, 1964b) shows that the protocorm and young seedlings of plants in the genera *Caladenia, Microtis, Stenostylis, Thelymitra,* and *Diuris* show the classic development of the POLYCHONDREAE. In the ACRANTHAE and the PLEURANTHAE-SYMPODIALES a cluster of three to five leaves generally forms before the appearance of the first root, which is thick-set and generally similar to that of the adult. Such young seedlings are found in the following genera: *Cattleya* (Bernard, 1903; Knudson, 1935), *Epidendrum* (Pfitzer, 1877; Veyret, 1965); *Laelia* (Bernard, 1903); *Polystachya, Bulbophyllum, Stanhopea,* and *Maxillaria* (Veyret, 1965); *Odontoglossum,* (Bernard, 1909; Burgeff, 1936; Veyret 1965); *Miltonia* (Prillieux, 1860); and *Arundina* (Mitra, 1971).

In contrast, Bernard (1909) showed in seedlings of a *Cymbidium* hybrid that after a normal differentiation of the terminal bud at the tip of the protocorm, tuberization is initiated so that the greatly reduced first leaves are spread apart. The protocorm thus appears to have several internodes like the pseudobulb of an adult plant. The protocorm of *Corallorhiza innata* (Irmisch, 1853) rapidly evolves into a coralloid root. The protocorm of *Eulophia maculata* (known then by Prillieux and Riviere, 1856, as *Angraecum maculatum* or *Eulophidium maculatum*;

Veyret, 1956) also takes on a branched appearance after a conventional germination. The protocorms of *Liparis loeselii* and of one species of *Microstylis* (Fuchs and Ziegenspeck, 1927b) offer a succession of several internodes, somewhat tuberized, before the terminal bud grows, and pseudobulbs in these species are generally scanty.

Among the species of the PLEURANTHAE-MONOPODIALES the elongation of the protocorm in natural conditions is important. The protocorm seems to behave as an aerial root adhering intimately to its support, as do the mature roots of these epiphytes. In an asymbiotic milieu the protocorm is generally shorter and thicker. If in these different groups the habit of the adult is acquired directly at the onset, in several rare exceptions is it different. Among the OPHRYDOIDEAE the sympodial form is slow in establishing itself. This is what Irmisch (1853) showed in *Orchis militaris,* Fabre (1856) in *Ophrys apifera,* Bernard (1900) in *Platanthera montana,* and Fuchs and Ziegenspeck (1927b) among various species of OPHRYDOIDEAE (Fig. 14). In effect the terminal bud develops at most a single small green leaf. The first tubercle of the plant then forms from this bud. It is isolated by the end of the year but is still joined to the original protocorm by a short rhizome that bears a few roots. In the course of the second year the terminal bud with a new tubercle is found drawn away. It is only from this time on that the new growth will be formed from an axillary bud. In *Orchis ustulata,* according to Fuchs and Ziegenspeck (1927a), the young plantule thus produces a succession of tubercles, up to eight, of which the ensemble may reach 20–30 mm. Bernard (1902) thought that this mode of development was closely tied to the mode of infection of the plantule.

In certain cases, as we just noted, the budding of the protocorm is normal and characteristic; it contributes to the building of the plantule. The budding of the protocorm is a general phenomenon among orchids and is able to end in the formation of multiple plantules. They are produced with variable frequency according to the species and the medium used for multiplication.

One or several protocorms can differentiate from the epidermal cells of the initial protocorm. Sometimes, however, the adventitious buds can be directly fixed on the initial protocorm, as has been seen in some plantules of *Bulbophyllum bufo* and *Odontoglossum pulchellum* (Veyret, 1965). This phenomenon can be provoked, augmented, or intensified by provoking a growth factor disorder by the action of a nonspecific species of *Rhizoctonia,* as in experiments by Bernard (1909) on *Vanda tricolor* and *Cymbidium*; or this can be accomplished artificially, as in experiments on *Cattleya* by Mariat (1952), who added some derivatives of barbituric

acid to the culture medium. Curtis and Nichol (1948) obtained masses of tissues resembling callus on *Vanda, Cymbidium,* and *Cattleya,* but the exact causes of these proliferations are not yet clearly known.

The Differentiation of the Protocorms

The embryo in mature seeds can be in two different forms, the most frequent by far being the acotyledonous forms. We know of the germination of the cotyledonous species by Bernard's figures (1909) of *Bletilla hyacinthina.* The cotyledon represents the terminal or upper part of the embryo (Figs. 5-4 and 5-5) when its origin can be determined with precision. From the start of germination (Fig. 5-5) what would be the second foliaceous member appears opposite the cotyledon. In the continuation of development, the cotyledon and the first leaf take the form of small, enfolded leaves.

When the embryo presents no morphological differentiation, as in *Stanhopea costaricensis* (Fig. 5-3), germination is accompanied by a general cellular growth except in the upper cells of the embryo. This zone is distinguished increasingly clearly by its meristematic activity, while the greater growth of the cells of the central regions, accompanied by some longitudinal division, ends in the formation of a conical protocorm. The upper part of the protocorm then forms the vegetative apex of the stem. A leaf primordium is not slow in forming from this zone, and the protocorm continues to enlarge. A second foliaceous primordium appears afterward, opposite and a certain distance from the first, thus delimiting the vegetative point of the stem.

The differentiation of the radicle is still incomplete. In the central part of the protocorm axial files of cells organize themselves into conductive elements and form a stele. It is difficult to assign an exact lower limit to this stele because it never entirely differentiates. The stele does not extend to the base of the protocorm even following the degeneracy of some of the lowest cells of the embryo in the course of the germination as is the case with *Polystachya geraensis* or of *Stanhopea costaricensis.* The first root is produced well after the first leaves among the KEROSPHAEREAE and the CYPRIPEDILOIDEAE. Among these taxa, the endogenous origin of the root has been noted in *Bulbophyllum bufo* (Veyret, 1965), *Polystachya geraensis* (Chaiyasut), *Arundina bambusifolia* (Mitra, 1971), *Paphiopedilum* (Bernard, 1909), and *Cypripedium calceolus* (Irmisch, 1853). Among the POLYCHONDREAE, the first root forms while the bud is still little developed. It has an exogenous origin in *Neottia nidus-avis* (Bernard, 1889), and probably in *Vanilla fragrans* (Bouriquet, 1947),

also for *C. calceolus* in the CYPRIPEDILOIDEAE (Fuchs and Ziegenspeck, 1926a).

The phenomenon of terminality of the vegetative point seems characteristic for most orchids as compared to most other monocotyledons. Some years ago Souèges (1954) showed in a definitive manner that the vegetative tip of the stem of certain monocots such as *Potomageton natans* or various members of the COMMELINACEAE was also lateral, even though other investigators had thought the origin was terminal. Souèges thought that there might nevertheless be transitional types between the two major groups of angiosperms, as is the case for *Zannichelia palustris* of the NAIADACEAE (Campbell, 1897) where the cotyledon and the vegetative point of the stem are juxtaposed in a terminal position. Among the majority of the orchids this stage is surpassed since the tip of the stem is strictly terminal. One cannot therefore generalize on the opinion of Pfitzer (1877), who, according to his research on the germination of *Dendrochilum glumaceum,* considered the apical part of the embryo as being a cotyledon.

Concluding Remarks

Strongly homogeneous taxa from the morphological point of view are equally so from an embryological viewpoint. The embryos in a broad sense are essentially similar, and the embryogenesis is essentially the same. This applies particularly among the OPHRYDOIDEAE and the KEROSPHAEREAE-PLEURANTHAE-MONOPODIALES. When the various groups are heterogeneous, as among the POLYCHONDREAE or the KEROSPHAEREAE-ACRANTHAE and the PLEURANTHAE-SYMPODIALES, the heterogeneity is manifest in the embryo as well. The POLYCHONDREAE, nevertheless, apart from *Vanilla,* are older than other MONANDRAE (Pfitzer, 1906) and one finds generally among the nonmonopodial KEROSPHAEREAE an embryo belonging to the *Liparis* group, although the species of that group possess different suspensors according to their species or type.

Embryonic characteristics determined by the great laws of embryogeny appear to constitute more certain criteria for classification and for understanding family interrelationships than those relative to the appearance of the suspensor. Resemblances are revealed in the course of embryogenesis that permit one to grasp some of the real affinities by the sequence of the appearance of characteristics in common even before the separation into various taxa. In addition, even in the same genus the suspensor can vary according to the species. For instance, Swamy indicated that the suspensor of *Dendrobium barbatulum* consisted of an enormous

haustorial vesicle, while that of *D. microbulbon* was represented by a single short cell.

One could argue that certain principles of an embryological classification are in default when a single genus, such as *Epidendrum* or *Polystachya,* includes both cotyledonous and noncotyledonous species. This phenomenon is explainable since these are distinctly irregular species and possess different types of tetrads as well, revealing probably an old hybrid origin among different species or genera. It is interesting to note that these two taxa are reunited by Dressler and Dodson (1960) in the subtribe EPIDENDRINAE, and that they represent an important crossroad as suggested in their diagram of relationships within the subtribe.

Johansen's classification loses much of its interest because of too detailed emphasis on the character of the suspensor. In Swamy's classification of the plants in the A group, the proembryo of the second cellular generation does not always offer a similar arrangement of blastomeres in a T formation, the wall of the division being vertical in the terminal cell as well as in the basal cell of the two-celled proembryo of *Listera* and *Neottia.* This is important since among certain POLYCHONDREAE where the proembryo is formed by the whole egg cell, the species having a proembryonic tetrad of A1 type (Fig. 5-2) are embryologically less involved than others in the A2 category.

The DIANDRAE are little known embryologically and the APOSTASIEAE are hardly known at all. In the MONANDRAE one passes from the POLYCHONDREAE, the oldest of the MONANDRAE, to the OPHRYDOIDEAE, then to the KEROSPHAEREAE, sympodial and, finally, monopodial. This means that the evolution of the orchid is from a terrestrial habit to an epiphytic one, from the granular to a solid state for the pollinia, and from having only a caudicle to having a stipe. Among the plants that disturb this scheme embryologically are those in the genus *Vanilla,* in the POLYCHONDREAE, placed embryologically in the *Liparis* group closer to the KEROSPHAEREAE. This may be explained since the vanillas are different from other POLYCHONDREAE by their vining growth and by their pollinia with simple grains united by viscous material and not by elastic threads. There are genera as well, *Eulophia* in part, *Cymbidium, Geodorum, Stanhopea,* and *Polystachya,* that by their belonging to a category of embryological classification other than the first period, show even higher level than that occupied by the PLEURANTHAE-MONOPODIALES. But these genera may be considered vandaceous in the first sense of the term as introduced by Lindley (1830–1840)—"with a distinct caudicula united to a deciduous stigmatic gland." The caudicle of these plants is actually properly called a stipe, since the origin of the structure is different from the caudicle of the BASITONAE. These plants are therefore among the most evolved.

Among the plants where the pollen apparatus presents these characters, one also finds some genera, such as *Maxillaria,* belonging to the first period. This would coordinate better with Garay's (1972) recent discussion of evolution in the orchids where he suggests two major tribes in the previously known KEROSPHAEREAE or ACRANTHAE-PLEURANTHAE, the EPIDENDREAE and VANDEAE, based on anther and column structure, rather than the older systems based on the inflorescence and sympodial or monopodial growth habits. It is certain that much research must still be done to explain the heterogeneous mixtures of embryological types in those taxa.

It is interesting to note that among some species of *Eulophia,* such as *E. oedoplectron,* the tetrad is in C2 form apart from the characteristics that bring about the passage from the first to the second period of embryological classification. This species is in addition irregular and does not follow the general mode of embryological development of other *Eulophia.* It is necessary here to underline that the species of *Eulophia* constitute a strongly variable genus with some species terrestrial, others epiphytic, although more rarely so. The stems may be leafed to the base, or twining, or more or less thickened into rhizomes, or into aerial pseudobulbs. As for the species of *Coelogyne,* their place in the second period cannot yet be explained. We have few data on the embryo of the CYPRIPEDILOIDEAE, and it is a little surprising to find such heterogeneity within the single genus *Cypripedium* where the embryo may or not be provided with a suspensor, and the root has a different origin.

The relative morphological characteristics of the young embryos are very general, but they confirm the reality of the large taxonomic groups and allow one to separate more clearly the MONOPODIALES (or VANDEAE following Garay's usage) in the midst of the KEROSPHAEREAE, and to bring closer the ensemble of the ACRANTHAE with the sympodial PLEURANTHAE. These last two taxa could then be subdivided, first taking into consideration the characteristics of the pollinarium and no longer emphasizing the terminal or lateral position of the inflorescence. Garay, in effect, has done this. The characteristics of the embryo relative to the origin of the vegetative apex of the stem, and the corresponding precocious histological differentiation of the proembryo, as well as those characteristics of subsequent development, confirm the highly evolved state of the orchids.

Bibliography

ABE, K. 1968. Contributions to the embryology of the family Orchidaceae, II. Development of the embryo sac in *Pogonia japonica* Reich. f. *Sci. Rep. Tôhoku Univ. ser. 4, Biol.* 34:59–65.

——. 1971. Contributions to the embryology of the family Orchidaceae, IV. De-

velopment of the embryo sac in *Bletilla striata*. *Sci. Rep. Tôhoku Univ. ser. 4, Biol.* 35:213–218.

———. 1972. Contributions to the embryology of the family Orchidaceae, VI. Development of the embryo sac in 15 species of orchids. *Sci. Rep. Tôhoku Univ. ser. 4, Biol.* 36:135–178.

AFZÉLIUS, K. 1916. Zur Embryosackentwicklung der Orchideen. *Svensk. Bot. Tidskr.* 10:183–227.

———. 1928. Die Embryobildung bei *Nigritella nigra*. *Svensk Bot. Tidskr.* 22:82–91.

———. 1932. Zur Kenntnis der Fortpflanzungsverhältnisse und chromosomenzahlen bei *Nigritella nigra*. *Svensk Bot. Tidskr.* 26:365–369.

———. 1954. Embryo sac development in *Epipogium aphyllum*. *Svensk Bot. Tidskr.* 48:513–520.

———. 1959. Apomixis and polyembryony in *Zygopetalum mackayi* Hook. *Acta Horti Bergiami* 19:2.

———. 1966. Cleistogamy in *Pleurothallis procumbens* Lindl. *Acta Horti Bergiami* 20:313–317.

BARANOV, P. 1915. Recherches sur le développement du sac embryonnaire chez les *Spiranthes australis* Lindl. et *Serapias pseudocordigera* Moric. *Bull. Soc. Imp. Nat. Moscou. N.S.* 29:74–92.

———. 1917. Contributions à l'étude de l'embryologie des Orchidées. (French summ.) *J. Soc. Bot. Russ.* 2:20–29.

———. 1924. Contributions à l'étude de l'embryologie des Orchidées, II. *Herminium monorchis* R. Br. *J. Soc. Bot. Russ.* 9:5–9.

BEER, J. B. 1863. *Beiträge zur Morphologie und Biologie der Familie der Orchideen.* Wien.

BERNARD, N. 1889. Sur la germination du *Neottia nidus-avis*. *Compt. Rend. Acad. Sci. Fr.* 128:1253–1255.

———. 1900. Sur quelques germinations difficiles. *Rev. Gén. Bot.* 12:108–120.

———. 1902. Études sur la tubérisation. *Rev. Gén. Bot.* 14:5–101.

———. 1903. La germination des Orchidées. *Compt. Rend. Acad. Sci. Fr.* 137:483–485.

———. 1904. Recherches expérimentales sur les Orchidées. *Rev. Gén. Bot.* 16:405–451; 458–476.

———. 1909. L'evolution dans la symbiose. Les Orchidées et leurs champignons commensaux. *Ann. Sci. Nat. Bot. 9e sér.* 9:1–196.

BOURIQUET, G. 1947. Sur la germination des graines de Vanillier (*Vanilla planifolia* And.) *Agron. Trop.* 2:150–164.

BRAUN, A. 1859. Über Polyembryonie und Keimung von *Coelebogyne*, ein Nachtrag zur der Abhandlung über Parthenogenesis bei Pflanzen. *Abhand. Königl. Akad. Wiss. Berlin* 1859:109–263.

BROWN, W. H. 1909 The embryo sac of *Habenaria*. *Bot. Gaz.* 48:241–250.

BROWN, W. H., and SHARP, L. W. 1911. The embryo sac of *Epipactis*. *Bot. Gaz.* 52: 439–452. Pl. X.

BURGEFF, H. 1936. *Samenkeimung der Orchideen und Entwicklung ihre Keimpflazen.* Gustave Fisher, Jena.

CAMPBELL, D. H. 1897. A morphological study of *Naias* and *Zannichelia*. *Proc. Cal. Acad. Sci. 3rd ser. Bot.* **1**:1–67.

CARLSON, M. C. 1940. Formation of the seed of *Cypripedium parviflorum*. *Bot. Gaz.* **102**:295–301.

CHAIYASUT, K. (Unpublished.) Embryologie et blastologie du *Polystachya geraensis* Rodrig.

CURTIS, J. T. 1943. Germination and seedling development in five species of *Cypripedium* L. *Am. J. Bot.* **30**:199–206.

CURTIS, J. T., and NICHOL, M. A. 1948. Culture of proliferating orchid embryos *in vitro*. *Bull. Torrey Bot. Club* **75**:358–373.

DICKIE, G. 1875. Note on the bud development of *Malaxis*. *J. Linn. Soc. London, Botany* **14**:1–3.

DRESSLER, R. L., and DODSON, C. H. 1960. Classification and phylogeny in the Orchidaceae. *Ann. Mo. Bot. Gard.* **47**:25–68.

DUMÉE, P. 1910. Quelques observations sur l'embryon des Orchidées. *Bull. Soc. Bot. Fr.* **47**:83–87.

DUTHIE, A. V. 1915. Note on apparent apogamy in *Pterigodium newdigatae*. *Trans. Royal Soc. S. Africa* **5**:593–598.

FABRE, J. H. 1856. De la germination des Ophrydées et de la nature de leurs tubercules. *Ann. Sci. Nat. Bot. 4e sér.* **5**:163–186.

FLEISCHER, E. 1874. Beiträge zur Embryologie der Monokotylen und Dikotylen. *Flora* **57**:419–423. Pl. VIII.

FUCHS, A., and ZIEGENSPECK, H. 1926a. Die Entwicklungsgeschichte der Axen der einheimischen Orchideen und ihre Physiologie und Biologie, I. *Cypripedium, Helleborine, Limodorum, Cephalanthera*. *Bot. Arch.* **14**:165–260.

———. 1926b. II. *Listera, Neottia, Goodyera*. *Bot. Arch.* **16**:360–413.

———. 1927a. Die Entwicklungsgeschichte der einheimischen Orchideen und der Bau ihre Axen, II. *Bot. Arch.* **18**:378–475.

———. 1927b. Entwicklung, Axen und Blätter einheimischen Orchideen, IV. *Bot. Arch.* **20**:275–422.

GARAY, L. A. 1972. On the origin of the Orchidaceae, II. *J. Arnold Arboretum* **53**: 202–215.

GEITLER, L. 1956. Zur Fortpflanzungsbiologie, Embryologie und mechanistichen Deutung der Embryogenese von *Epipogium aphyllum*. *Oester. Bot. Zeit.* **103**: 312–325.

GOEBEL, K. 1889. Pflanzen biologische Schilderungen. I.

HAGERUP, O. 1944. On fertilization, polyploidy and haploidy in *Orchis maculatus* L. *sensu lato*. *Dansk. Bot. Arkiv.* **2**:1–25.

———. 1945. Facultative parthenogenesis and haploidy in *Epipactis latifolia*. *Det. Kgl. Danske Vidensk. Selsk. Biol. Medd.* **19**:1–14.

———. 1947. The spontaneous formation of haploid, polyploid and aneuploid embryos in some orchids. *Det. Kgl. Danske Vidensk. Selsk. Biol. Medd.* **20**:1–22.

HESLOP-HARRISON, J. 1959. Apomictic potentialities in *Dactylorchis*. *Proc. Linn. Soc. London.* **170**:174–178.

HEUSSER, K. 1915. Die Entwicklung der generativen Organe von *Himantoglossum hircinum* Spr. (= *Loroglossum hircinum* Rich.) *Beih. Bot. Centralbl. Abt.* **12:** 218–277.

HOFMEISTER, W. 1861. Neue Beiträge zur Kenntnis der Embryobildung der Phanerogamen, II. Monocotyledonen. *Abh. Sächs. Ges. Wiss.* **7:**629–760.

IRMISCH, T. 1853. *Beiträge zur Morphologie und Biologie der Orchideen.* Leipzig.

JOHANSEN, D. A. 1950. *Plant embryology. Embryology of the Spermatophyta. Chron. Bot.* Waltham, Mass.

KIMURA, C. 1971. Embryological studies of *Galeola septentrionalis* Reich. f. (Orchidaceae). *Sci. Rep. Tôhoku Univ. ser. 4* **35:**253–258.

KNUDSON, L. 1935. Germination of orchid seed. *Am. Orchid Soc. Bull.* **3:**65–66.

——. 1941. Germination of seed of *Goodyera pubescens. Am. Orchid Soc. Bull.* **10:** 199–201.

——. 1950. Germination of seeds of *Vanilla. Am. J. Bot.* **37:**341–347.

KUSANO, S. 1915. Experimental studies on the embryological development in an angiosperm. *J. Coll. Agric. Univ. Tokyo* **6:**7–120.

LEAVITT, R. G. 1900. Polyembryony in *Spiranthes cernua. Rhodora* **2:**227–228.

——. 1901. Notes on the embryology of some New England orchids. *Rhodora* **3:**61–63; 202–205.

LINDLEY, J. 1830–1840. *The Genera and Species of Orchidaceous Plants.* London.

MAHESWARI, P., and NARAYANASWAMI, S. 1950. Parthenogenetic development of the egg in *Spiranthes australis. Curr. Sci. India* **19:**249–250.

——. 1952. Embryological studies on *Spiranthes australis* Lindl. *Trans. Linn. Soc. London* **53:**474–486.

MARIAT, P. 1952. Recherches sur la physiologie des embryons d'Orchidées. *Rev. Gén. Bot.* **59:**324–377.

MIDUNO, T. 1940. Chromosomen Studien an Orchidaceen, III. Über das Vorkommen von haploiden Pflanzen bei *Bletilla striata* Reichb. f. var. *gebina* Reichb. f. *Cytologia* **2:**156–177.

MITRA, G. C. 1971. Studies on seeds, shoot-tips and stem-discs of an orchid grown in aseptic cultures. *Indian J. Exp. Biol.* **9:**79–85.

MONTEVÉRDÉ, M. 1880. Recherches embryologiques sur l'*Orchis maculata. Bull. Acad. Sci. St-Pétersbourg* **26:**326–335.

MÜLLER, F. 1895. Orchideen von unsicherer Stellung. *Ber. Dtsch. Bot. Gesell.* **13:** 199–210.

MÜLLER, K. 1847. Beiträge zur Entwicklungsgeschichte des Pflanzen Embryos. *Bot. Z.* **5:**73–78.

OLSSON, O. 1967. Embryological studies in the Orchidaceae. The genus *Hetaeria. Svensk. Bot. Tidskr.* **61:**33–42.

PACE, L. 1907. Fertilization in *Cypripedium. Bot. Gaz.* **44:**353–374.

PASTRANA, M. D., and SANTOS, J. K. 1931. A contribution to the life history of *Dendrobium anosmum* Lindl. *Nat. Appl. Sci. Bull. Philippines Univ.* **1:**133–134.

PFITZER, E. 1877. Beobachtungen über Bau und Entwicklung der Orchideen. *Nat. Med. Verhandl. Heidelberg* **2:**23–30.

——. 1906. On the phylogeny of orchids. Report of the third international conference on genetics. *Royal Hort. Soc. London* **1906**:476–481.

PODDUBNAJA-ARNOLDI, V. A. 1959. (In Russ.) Ovule culture of some orchids on synthetical media. *Dokl. Akad. Nauk. SSSR* **1959**:223–226.

——. 1960a. Study on fertilization in the living material of some Angiosperms. *Phytomorphology* **10**:185–198.

——. 1960b. (In Russ.) Polyembryony in orchids. *Bjull. Glavn. Bot. Sada.* **36**: 56–61.

PRILLIEUX, E. 1860. Observations sur la germination du *Miltonia spectabilis* et de diverses autres orchidées. *Ann. Sci. Nat. Bot. 4e sér.* **13**:288–296. Pl. 14.

PRILLIEUX, E., and RIVIÈRE, A. 1856. Observations sur la germination et le développement d'une orchidée (*Angraecum maculatum*). *Ann. Sci. Nat. Bot. 4e sér.* **5**: 119–136. Pl. 5 to 7.

PROSINA, M. N. 1930. Über die von *Cypripedium*-typus abweichende Embryosackentwicklung von *Cypripedium guttatum*. *Sw. Z. Wiss. Biol. Planta* **12**:532–544.

RACIBORSKI, M. 1898. Biologische Mittheilungen aus Java. *Flora* **75**:325–361.

SALISBURY, R. A. 1804. On the germination of the seeds of Orchideae. *Trans. Linn. Soc.* **7**:29–32.

SCHACHT, H. 1850. *Entwicklungsgeschichte der Pflanzen embryon.* Verhand. Eerste Klasse Koninkl. Nederland Inst., Amsterdam.

SCHLECHTER, R. 1926. Das System der Orchidaceen. *Nat. Bot. Gart. Mus. Berlin-Dahleim* **9**:563–591.

SCHNARF, R. 1931. *Vergleichende Embryologie der Angiospermen.* Berlin.

SENIANINOVA, M. 1924. (In Russ. with French summ.) Étude embryologique de l'*Ophrys myodes*. *J. Soc. Bot. Russ.* **9**:10–13.

SESHAGIRIAH, K. N. 1932. Development of the female gametophyte and embryo in *Spiranthes australis* Lindl. *Curr. Sci.* **1**:102.

——. 1934. Pollen sterility in *Zeuxine sulcata*. *Curr. Sci.* **3**:205–206.

——. 1941. Morphological studies in Orchidaceae, I. *Zeuxine sulcata* Lindl. *J. Indian Bot.* **20**:357–365.

SHARP, L. 1912. The orchid embryo sac. *Bot. Gaz.* 54:372–384.

SIMON, W. 1968. Chromosome numbers and B chromosomes in *Listera*. *Caryologia* **21**:181–189.

SOUÈGES, R. 1936–1939. *Exposés d'embryologie et de morphologie végétale,* Vol. IV. *La segmentation. Les blastomères;* Vol. VIII. *Les lois du développement;* Vol. IX. *Embryogénie et classification. Essai d'un système embryogénique.* Hermann et Cie., Paris.

——. 1954. L'origine du cône végétatif de la tige et la question de la "terminalité" du cotylédon des Monocotylédones. *Ann. Sci. Nat. Bot. IIe sér.* **72**:1–20.

STOUTAMIRE, W. P. 1963. Terrestrial orchid seedlings. *Australian Plants, Orchidaceae* **2**:119–122.

——. 1964a. Seeds and seedlings of native orchids. *Mich. Bot.* **3**:107–119.

——. 1964b. Terrestrial orchid seedlings, II. *Australian Plants, Orchidaceae* **2**:264–266.

STRASBURGER, E. 1877. Über Befruchtung und Zelltheilung. *Jenaische Z.* 2:435–536.

———. 1878. Über Polyembryonie. *Jenaische Z.* 12:647–669.

SUESSENGUTH, K. 1923. Über Pseudogamie bei *Zygopetalum mackayi* Hook. *Ber. Dtsch. Bot. Gesell.* 41:16–23.

SWAMY, B. G. L. 1942a. Female gametophyte and embryogeny in *Cymbidium bicolor* Lindl. *Proc. Indian Acad. Sci. B.* 15:194–201.

———. 1942b. Morphological studies in three species of *Vanda. Curr. Sci.* 2:285.

———. 1943a. Embryology of Orchidaceae. *Curr. Sci.* 12:13–17.

———. 1943b. Gametogenesis and embryogeny of *Eulophia epidendracea* Fisher. *Proc. Nat. Inst. Sci. India* 9:59–65.

———. 1944. The embryo sac and the embryo of *Satyrium nepalense* Don. *J. Indian Bot. Soc.* 23:56–70.

———. 1946a. Some notes on the embryo of *Cymbidium bicolor* Lindl. *Curr. Sci.* 15:139–140.

———. 1946b. The embryology of *Zeuxine sulcata* Lindl. *J. Indian Bot. Soc.* 20:357–365.

———. 1946c. Embryology of *Habenaria. Proc. Nat. Inst. Sci. India* 12:413–426.

———. 1947. On the life history of *Vanilla planifolia. Bot. Gaz.* 108:449–456.

———. 1948a. Agamospermy in *Spiranthes cernua. Lloydia* 2:149–162.

———. 1948b. The embryology of *Epidendrum prismatocarpum. Bull. Torrey Bot. Club* 75:245–249.

———. 1949. Embryological studies in the Orchidaceae, II. Embryogeny. *Am. Midl. Nat.* 41:202–232.

TAYLOR, R. L. 1967. The foliar embryos of *Malaxis paludosa. Can. J. Bot.* 45:1553–1556.

TOHDA, H. 1967. An embryological study of *Hetaeria shikokiana,* a saprophytic orchid in Japan. *Sci. Rep. Tôhoku Univ. ser. 4, Biol.* 33:83–95.

———. 1968. Development of the embryo of *Bletilla striata. Sci. Rep. Tôhoku Univ. ser. 4, Biol.* 34:125–131.

———. 1971a. Development of the embryo of *Orchis aristata. Sci. Rep. Tôhoku Univ. ser. 4, Biol.* 36:239–243.

———. 1971b. Development of the embryo of *Lecanorchis japonica. Sci. Rep. Tôhoku Univ. ser. 4,* 35:245–251.

TONNIER, J. P. 1952. Le Vanillier. *Bull. Rech. Agron. Madagascar* 1952:55–59.

TREUB, M. 1879. Notes sur l'embryogénie de quelques orchidées. *Naturk. Verh. Koninkl. Akad. Amsterdam* 19:1–50. Pl. I to VIII.

———. 1883. Notes sur l'embryon, le sac embryonnaire et l'ovule. *Ann. Jard. Bot. Buitenzorg* 3:76–87. Pl. XII.

VEYRET, Y. 1965. Embryogénie comparée et blastogénie chez les Orchidaceae-Monandrae. *Mémoires ORSTOM* 12.

———. 1967. L'apomixie chez le *Cynosorchis lilacina* Ridley (Orchidaceae). *Compt. Rend. Acad. Sci. Fr. sér. D,* 265:1713–1716.

———. 1969. La structure des semences des Orchidaceae et leur aptitude a la germi-

nation *in vitro* en cultures pures. *Mus. Hist. Nat. Paris, Trav. Lab. "La Jaysinia"* 3e fasc. 89–98. Pl. III and IV.

———. 1972. Études embryologiques dans le genre *Cynorkis* (Orchidaceae). *Adansonia, sér. 2* **12**:389–402.

WARD, H. M. 1880. On the embryo sac and development of *Gymnadenia conopsea*. *Q. J. Microsc. Soc.* **10**:1–18.

WIRTH, M. W., and WITHNER, C. L. 1959. Embryology and development in the Orchidaceae, in *The Orchids: A Scientific Survey*. Ronald Press, New York, pp. 155–188.