

## Development of the embryo in some species of the genus *Delphinium* L.

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### Abstract

In the 10 examined species of *Delphinium* all theoretically possible types of zygote division may be found — transverse, oblique and longitudinal. With these divisions is connected the peculiar characteristic mode of differentiation of the embryo body. Embryogenesis of two species, *D. tricolor* and *D. carioptalum*, shows a number of regularities on the basis of which new types of embryo development in angiosperms may be distinguished. These types have been named Valerianad and Ranunculad.

Probably all the *Delphinium* species in which a longitudinal division of the zygote occurs are more primitive as regards embryonomic features than species in which zygote division is transverse or oblique.

### INTRODUCTION

The development of the embryo in the family *Ranunculaceae* to which the genus *Delphinium* belongs is only well known in a few species. Most extensive investigations on the embryonomy of this family were performed by Souèges (1910, 1911, 1912, 1913). This author examined and described among others the development of the embryo in *Myosurus minimus*, *Adonis autumnalis*, *A. aestivalis*, *Ficaria ranunculoides*, *Ranunculus acris*, *R. sceleratus*, *Anemone pulsatilla*, *A. japonica* and *Clematis recta*. Short incomplete descriptions of embryo development in *Ranunculaceae* may be found in the works of other authors. Up till now within the genus *Delphinium* the embryo development has been investigated in *D. consolida* (Ly Thi Ba, 1962). As indicated by the literature, the development of the embryo in the family *Ranunculaceae* is not uniform.

The present author studied to date embryo development in 10 species of *Delphinium*. Embryogenesis of the 4 most characteristic species *D. staphi-*

*sagria* L., *D. tricolor* Bernh., *D. cardiopetalum* D. C. and *D. tatsinense* Franch has been elaborated in detail, whereas in the 6 remaining species: *D. elatum* L., *D. paniculatum* Host., *D. grandiflorum* L., *D. cashmirianum* Royle. and *D. zalil* Aitch., *D. nudicaule* Terr. et Gray. the stage was investigated at which it was possible to establish the origin of the particular layers and their destination.

#### MATERIAL AND METHODS

The material of ovaries and ovules or prepared out embryos was fixed in chromium-aceto-formalin (CrAF 0.4—0.5—20.0). Sections were stained with Ehrlich's hematoxylin. In the analyses of microtome sections of essential importance was the plane along which the material was cut. Therefore a method was developed of embedding single ovules in paraffin in dependence on their plane of symmetry (Babis, 1973a).

#### RESULTS

The investigated *Delphinium* species may be classified to 4 embryonomic groups differing from one another essentially even in the earliest stages of embryonal development.

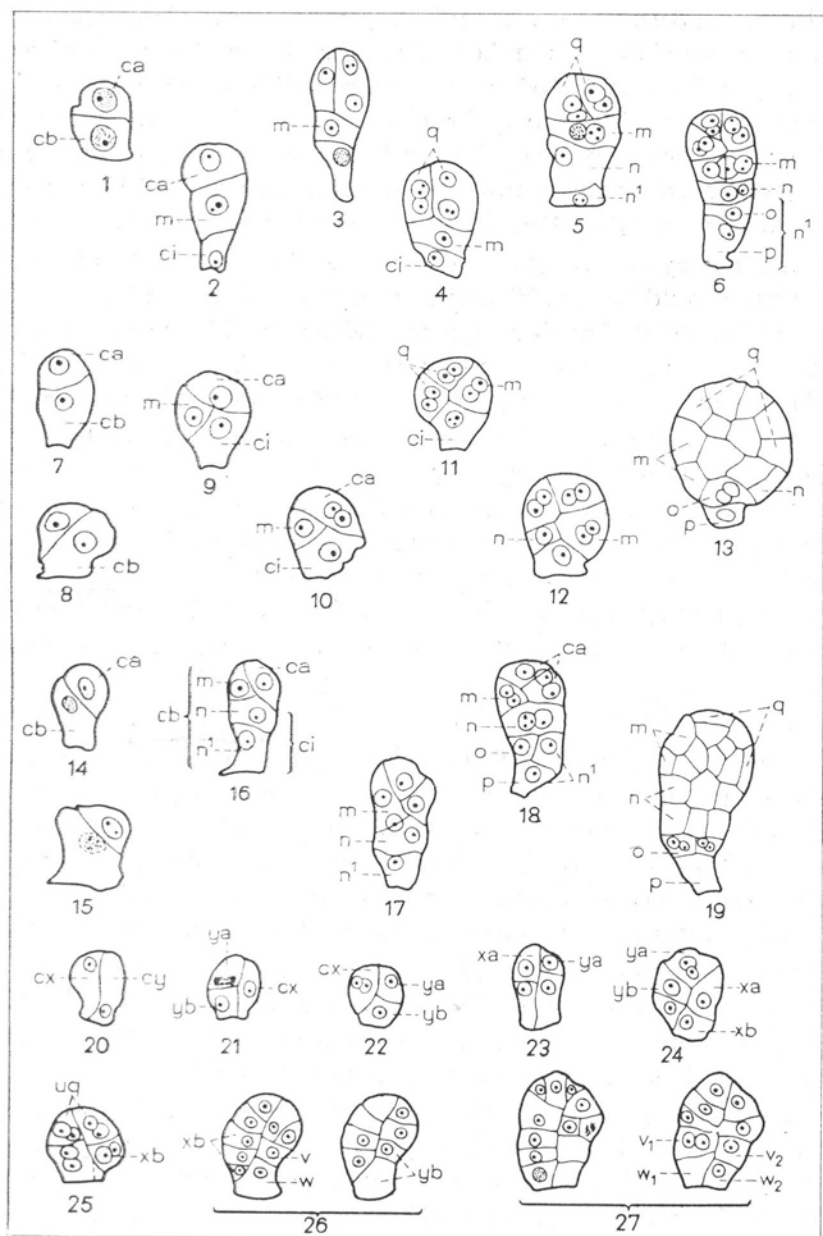
To the first embryonomic group belongs: *D. staphisagria*, *D. elatum* and *D. paniculatum*. In *D. staphisagria* (Plate Fig. 1—6) the zygote divides as a rule transversely and so does the basal cell. The tetrad is 3-layered. In the 8-celled proembryo 4 homogeneous layers can be distinguished. From layer *q* arise *pco* + *pvt* +  $\frac{1}{2}$  *phy* (cotyledones + growth tip of the embryo shoot +  $\frac{1}{2}$  hypocotyl), from layer *m* —  $\frac{1}{2}$  *phy* ( $\frac{1}{2}$  of hypocotyl) arises, from layer *n* — *icc* + *iec* + *co* (initial cells of the central cylinder of the embryonal root + embryonal root cap) are formed and from layer *n*<sup>1</sup> — *s* (the suspensor). The embryo development in *D. elatum* and *D. paniculatum* is similar as in *D. staphisagria*. In these three species the proembryos are characterized by a radial symmetry on account of both the general habitus and the position of the first walls in early stages of development.

Development of the embryo in *D. staphisagria*, *D. elatum* and *D. paniculatum* may be classified to the Asterad type in Johansen's classification (1950) or to period I of series A of the megaarchaetype III in the classification of Souèges (1948).

To the embryonomic group II belong *D. tricolor*, *D. grandiflorum*, *D. cashmirianum*, *D. zalil* and *D. nudicaule*.

In *D. tricolor* (Plate, figs 7—13) the zygote divides as a rule more or less obliquely and so does the basal cell. The tetrad consists of two and one

half layers. In the 8-cellular proembryo 3 layers can be distinguished: the homogeneous layer  $q$  from arise which  $pco + pvt + 1/2 phy$ , the nonhomogeneous layer  $m + n$  forming  $1/2 phy$  and the homogeneous layer  $n^1$



Initial stages of the development of the embryo in *Delphinium*  
 Figs 1—6. *D. staphisagria*, Figs 7—13. *D. tricolor*, Figs 14—19. *D. cardiopetalum*,  
 Figs 20—27. *D. tatsinense* (Magn. ca  $\times 250$ )  
 Abbreviations in the text

giving rise to  $icc + iec + co + s$ . In these species the proembryo exhibits in early stages of development a dorso-ventral symmetry, both as regards general habitus and spatial position of first walls. The development of the embryo in *D. tricolor* is similar to that in *D. grandiflorum*, *D. cashimiri-num*, *D. zalil* and *D. nudicaule*. Embryo genesis of the above named 5 *Delphinium* species shows a number of regularities on the basis of which a new type can be established in angiosperms. This type has been termed Valerianad. To the latter may be classified the forms described up till now in the literature as irregular and occurring in *Lycopsis arvensis* (Souèges, 1938), *Symphytum officinale* (Souèges, 1941a) and *Tilia platyphyllos* (Souèges 1941b) and in several other species.

To the embryonic III group distinguished by the present author in *Delphinium* should be classified the embryo development in *D. carioptetalum* (Babis, 1966). The first zygote division in this species (Plate, Figs 14—19) is as a rule notably slanting, the basal cell also divides obliquely. Tetrads probably occur only sporadically. The 8-celled proembryo comprises 4 layers. The proximal layer is nonhomogeneous and consists of  $m + ca$  cells from which  $pco + pvt + 1/2 phy$  arise, the central layer  $n$  is homogeneous and gives rise to  $1/2 phy$ , layer  $o$  is also homogeneous and from it forms  $icc + iec + co$  and from the basal layer  $p$  which also is homogeneous  $s$  arises. A characteristic feature of this species in embryonal development is the fact that one cotyledone forms from derivatives of the apical cell  $ca$ , and the second one from derivatives of the basal cell  $cb$ .

In *D. carioptetalum* the development of the apical cell is inhibited in relation to the basal one. The proembryos, in view of their shape, show a radial or dorso-ventral symmetry, whereas as regards the position of the first internal walls their symmetry is dorsoventral. The type of embryo development found in *D. carioptetalum* has not so far been described in the literature. It is a new type in angiosperms, not included in embryonomic classifications and has been termed by the author *Ranunculad* type.

To the embryonomic group IV should be classified the embryo development in *D. tatsinense* (Plate, Figs 20—27). The zygote divides as a rule almost longitudinally or vertically. The sister cells of the 2-celled proembryo usually divide transversally. The tetrad is generally two-layered, or sometimes the layers are not completely delineated. The 8-celled proembryo is usually two-layered. It is only in proembryos composed of a dozen cells or so that 3 layers can be distinguished: the proximal nonhomogeneous layer  $xa + ya$  from which  $pco + pvt + 1/2 phy$  arise, the nonhomogeneous layer  $xb + v$  from which  $1/2 phy$  forms and the homogeneous layer  $w$  giving rise to  $icc + iec + co + s$ . If the zygote divides longitudinally, the basal layer is also nonhomogeneous. The proembryos on account of their shape exhibit as a rule radial symmetry, whereas in

relation to the spatial arrangement of the first walls their symmetry is dorso-ventral and radial.

The type of embryo development in *D. tatsinense* is similar to that in *Scabiosa succisa* and *S. columbaria* described by Souèges (1937, 1957) and to that in *Euphorbia rothiana* described by Srivastava (1952). It may be classified to the type *Piperad* of Johansen (1950).

The particular members of the embryo in *D. tatsinense* are denoted by new symbols (Plate, Figs. 20—27) on account of a number of inconsistencies in the so far used notations. After vertical or almost longitudinal division of the zygote, sister cells arise which have been denoted by the symbols *cx* and *cy*. The symbol *cy* marks the largest cell or the one dividing earlier and giving more derivatives. The smaller cell *cx* after transverse division forms the upper cell *xa* and the bottom one *xb*, the larger cell correspondingly forms *ya* and *yb*. From the sister derivatives of the cells, *xa* and *ya*, a 4-celled apical layer *uq* is formed corresponding to the quadrants *q*. If the zygote divides almost longitudinally, then from the cell *yb*, two derivatives form — an upper *v* and a lower *w* one. However, if the zygote divides longitudinally, the *xb* and *yb* cells form after transverse division 2 derivatives. From cell *xb* *v*<sub>1</sub> and *w*<sub>1</sub> and from cell *yb* — *v*<sub>2</sub> and *w*<sub>2</sub> differentiate.

In spite of the rather wide differences in embryo development in various *Delphinium* species, there exist between them certain similarities. Embryos in ripe seeds have in all species straight lobe-like cotyledons between which lies in the form of a small apex the primordium of the shoot meristem. In the proembryos the complex of epiphyseal cells differentiates at almost the same time as does dermatogen. At the moment when dermatogen begins to differentiate, a body of cells forming the plerome can be distinguished. The apical root meristem shows an open structure.

The notions of homogeneous and nonhomogeneous layer and of proximal layer have been introduced in the present paper. As homogeneous layer is denoted in the embryo such a layer which arose from one cell of the proembryo as the result of transverse division, e.g. layer *m* in *D. staphisagria* (Plate Fig. 2). The nonhomogeneous layer is a layer arising owing to two or more divisions e.g. the layer *m* + *n* in *D. tricolor* (Plate Fig. 12), composed of cells which are not sisters or of their derivatives. The apical nonhomogeneous layer of the embryo formed of cells which are not sisters or of their differentiated derivatives resulting from several divisions is termed the proximal layer, e.g. the layer *m* + *ca* in *D. carioptalum* (Plate, Fig. 16) and layer *xa* + *ya* in *D. tatsinense* (Plate, Fig. 23).

In the examined *Delphinium* species all theoretically possible types of zygote division can be found. Between the 4 embryonomic groups distinguished by the author in *Delphinium* essential differences occur associated with the direction of zygote division. After transverse division, already in the primary stages of development of the embryo, a close relation is

noted between division and the early differentiation of certain areas. In oblique division and, particularly, almost longitudinal or vertical division these areas appear later. The delay in differentiation of the proembryo along the axis is noticeable in an early period of development. In *D. staphisagria* (group I) — transverse division of the zygote — the tetrad is 2-layered. The hypophysis forms from layer n differentiated in the 3rd cell generation. In *D. tricolor* (group II) — oblique division of zygote — the tetrad is composed of two and one half layers. The hypophysis arises from layer o in the 4th cell generation. In *D. tatsinense* (group IV) — almost longitudinal or vertical zygote division — the tetrad is usually 2-layered. The hypophysis differentiates as late as in the more than 10-cell old proembryo.

#### DISCUSSION

Le b è q u e (1952) suggests that evolutionally most progressive is the type of embryo development in which the hypophysis and particular tissues and organs are earlier differentiated. If we accept this suggestion, it would seem that all the *Delphinium* species in which a longitudinal division of the zygote occurs are more primitive as regards embryonomic features than the species in which the zygote divides obliquely or transversely. Species in which the latter type of division occurs would be most progressive.

To date the embryonomy of only some few species of the genus *Delphinium* is known (B a b i s, 1973b, 1974, 1976)). H u t h (1895) distinguishes within the genus *Delphinium* the subgenera *Consolida* and *Eudelphinium*. In the subgenus *Consolida* up till now only transverse zygote division has been found, and according to this, it would seem that this subgenus comprises species which as regards embryonomic features are evolutionally more progressive than the species of the subgenus *Eudelphinium*. The same is indicated by the morphology of the flowers and the annual life span of plants belonging to the subgenus *Consolida*.

None of the so far known genera exhibits such a far going differentiation as regards embryonomic features as does the genus *Delphinium*.

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## Rozwój zarodka u niektórych gatunków rodzaju *Delphinium* L.

### Streszczenie

U przebadanych 10 gatunków *Delphinium* stwierdzono wszystkie możliwe teoretycznie typy podziału zygoty — poprzeczny, skośny mocno skośny i podłużny. Z podziałami tymi związany jest szczególny, charakterystyczny sposób różnicowania się

ciała zarodka. Embriogeneza dwóch gatunków, tj. *D. tricolor* i *D. cardiopetalum* wykazuje szereg prawidłowości, na podstawie których można wyodrębnić nowe typy rozwoju zarodka wśród okrytonasiennych. Typy te zostały nazwane: Valerianad i Ranunculad.

Prawdopodobnie wszystkie te gatunki *Delphinium*, u których występuje podłużny podział zygoty, są bardziej prymitywne pod względem cech embrionomicznych od gatunków, u których podział zygoty jest skośny lub poprzeczny.