

Cvetana D. Daskalova

## Evolutionary patterns in seed formation of the Bulgarian taxa of *Thalictrum* (*Ranunculaceae*)

### Abstract

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A detailed cytoembryological study of seed development in the eight Bulgarian *Thalictrum* taxa showed that embryogeny conforms to the primitive Onograd type and the endosperm is nuclear. Some advanced features were found in mature seeds, in which respect *T. simplex* subsp. *rhodopaeum*, by the formation of a primordial plumule and procambial vessels, appears to represent the highest evolutionary level known for the whole family. These and other data demonstrate that the evolution of cytoembryological features within the genus *Thalictrum* shows both parallelism and heterobathmy.

### Introduction

The family *Ranunculaceae* is well known for showing a remarkable combination of primitive and advanced characteristics. *Thalictrum* species are of particular interest because of scantiness of relevant information. A comparative embryological study of the Bulgarian *Thalictrum* taxa (Daskalova 1984) has shown that they have retained some primitive features while at the same time developing new, progressive ones. Against this background, the results of a comparative cytoembryological study of their seed development are presented here.

### Material and methods

Seed from the eight Bulgarian species and subspecies of *Thalictrum* (Panov 1970, but with *T. minus* not subdivided) was collected between 1976 and 1980 in the wild, from native populations (Table 1). The plants from which seeds were taken have been deposited in SOM as voucher specimens, and are indicated in the text and table by their respective collecting numbers (prefixed with *T.*).

Table 1. A list of cytoembryologically studied populations and voucher specimens.

<i>Thalictrum</i>	Locality (voucher No.)
<i>aquilegifolium</i> L. subsp. <i>aquilegifolium</i>	Mt Vitoša, grassy places by the river Drenovicka in the Botanic Garden (T-11237) Mt Slavjanka, in <i>Pinus sylvestris</i> wood mixed with <i>Fagus sylvatica</i> and <i>Picea abies</i> above the village Paril (T-12504) Mt Pirin, grassy places in <i>Pinus heldreichii</i> wood by the hut "Javorov", 1800 m (T-12519)
<i>aquilegifolium</i> subsp. <i>storgosiacum</i> Panov	Danube plain, grassy and rocky places at "Kajlaka" near Pleven (T-14500)
<i>foetidum</i> L.	Krajste, grassy and stony places by the river Erma near Tran (T-1406)
<i>minus</i> L.	Stara planina, Kotelnska part, grassy and rocky places at "Barmukbair" (T-11203)
<i>simplex</i> L. subsp. <i>simplex</i>	Krajste, Cepan subregion, grassy places by Belidjehan (T-13504)
<i>simplex</i> subsp. <i>rhodopaeum</i> (Rech. f.) Panov	Western boundary mts, Vlahina planina, grassy places by the frontier (T-1199) Mt Slavjanka, grassy places above the village Paril (T-12500) Western Rodope Mts, grassy places in mixed <i>Pinus sylvestris</i> and <i>Picea abies</i> forest at Beglika, 1600 m (T-11273)
<i>lucidum</i> L.	Sofija region, wet meadows by the village Gorubljanе (T-12505)
<i>flavum</i> L.	Danube plain, distr. Lom, wet places and meadows by the village Orsoja (T-13507)

The material was fixed in Navashin's mixture, embedded in paraffin using the classical methods, and sectioned with a rotary microtome. The microtome sections were stained in Heidenhain's haematoxylin.

### Results and discussion

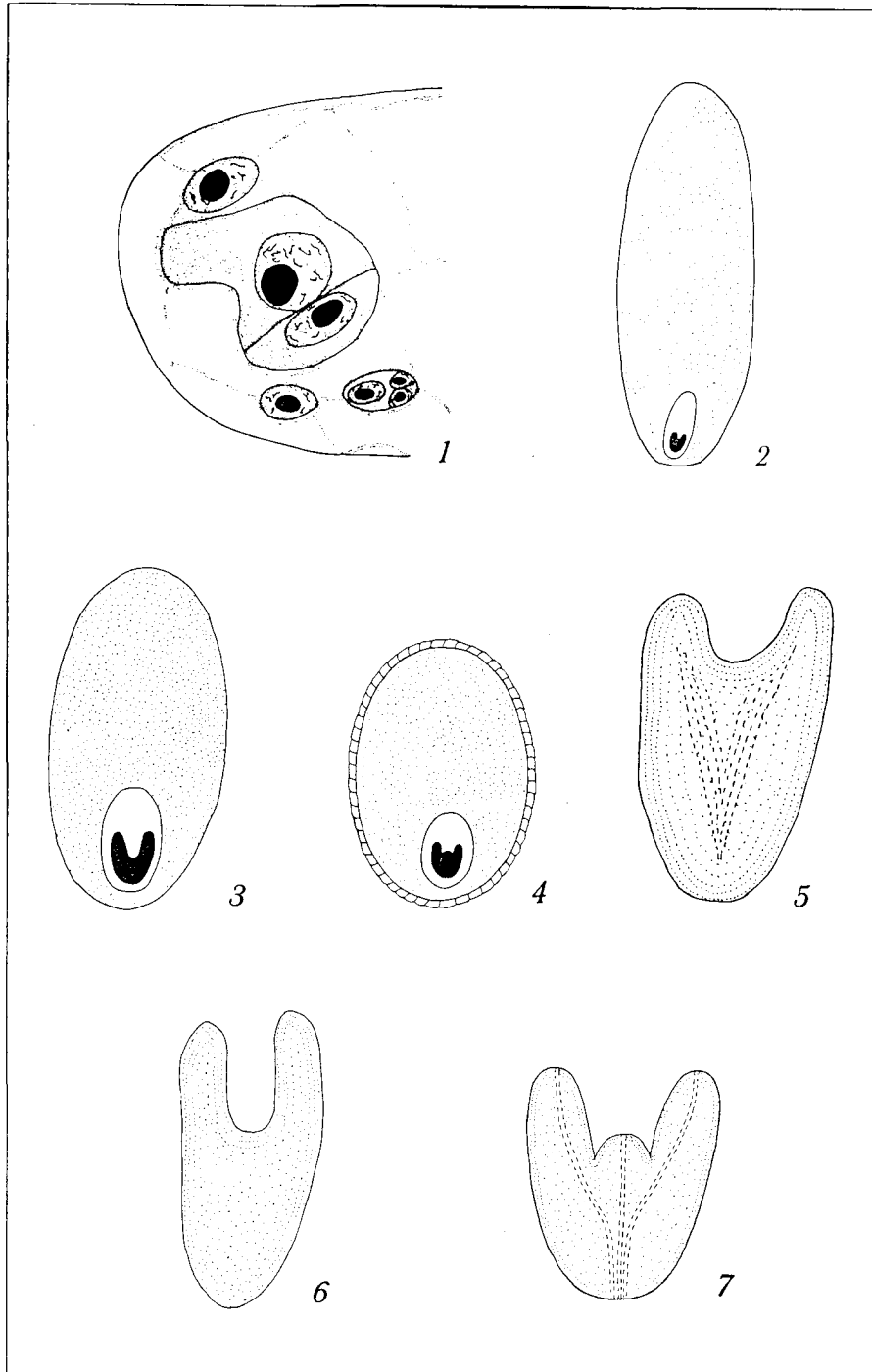
The first division of the primary endosperm nucleus is not followed by wall formation, and the endosperm is nuclear as in all other *Thalictrum* species studied so far (Overton 1904, Vijayaraghavan & Bhandari 1970) and, generally, in all *Ranunculaceae* (Tamura 1965).

The first division of the zygote is transversal, as in all other members of the family (Davis 1966), and terminal and basal cells are formed (Fig. 1). The further embryogeny conforms to the Onograd type, considered to be primitive (Fig. 2).

In the mature seed, the endosperm occupies the whole cavity (Fig. 2-4), surrounding a small, typically dicotyledonous embryo (Fig. 1-3) which consists of a short massive

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Fig. 1-7. Seed formation in Bulgarian *Thalictrum* species. – 1, First division of the zygote in *T. foetidum* (× 2000); 2, seed of *T. aquilegifolium* (× 200); 3, seed of *T. flavum* (× 200); 4, seed of *T. simplex* (× 200); 5, mature embryo in *T. flavum* (× 1500); 6, mature embryo in *T. minus* (× 1500); 7, mature embryo in *T. simplex* (× 1500).



suspensor, a radicle, a hypocotyl, a shoot apex, and cotyledons. According to these characteristics the mature seeds are similar to the "rudimentary type" in Martin's (1946) seed classification, which is considered to be the most primitive type in angiosperms. As a rule, the embryo is not differentiated when it is detached.

In the mature seed, however, some progressive features were found that are unevenly distributed over the studied taxa, among which the degrees of correlation between embryo and whole seed and of cotyledonary development vary. The weakest correlation and lowermost degree of cotyledonary development were found in *Thalictrum aquilegiifolium* subsp. *aquilegiifolium* (T-11237, Fig. 2), followed in this order by *T. lucidum* (T-12505), *T. flavum* (T-13507, Fig. 3, 5), *T. foetidum* (T-1406), and *T. minus* (T-11203, Fig. 6). The strongest correlation between embryo and whole seed, and the highest degree of cotyledonary development – features that are considered as advanced – were found in *T. simplex* subsp. *rhodopaeum* (T-1199, Fig. 4).

According to our results, and due to the observed formation of a primordial plumula and procambial vessels (Fig. 7), the mature seeds of *Thalictrum simplex* subsp. *rhodopaeum* would represent the highest evolutionary level known so far, not only in the genus *Thalictrum* (Overton 1904, Vijayaraghavan & Bhandari 1970, Ivanova 1971), but in the *Ranunculaceae* as a whole (Sokolovskaja 1981).

The foregoing results, when combined with further embryological data established by us (Daskalova 1984), demonstrate that the evolution of cytoembryological features within the genus *Thalictrum* shows both parallelism and heterobathmy.

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Address of the author:

Dr Cvetana Daskalova, Institute of Botany, Bulgarian Academy of Sciences, Akad. G. Bončev Str. 23, BG-1113 Sofija, Bulgaria.