ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 58, nr 1-2: 273-277
1981

## The contribution of embryogeny to the systematics of *Polycarpicae* and *Helobiae*

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## Abstract

The study of embryogenesis in 27 genera of *Polycarpicae* and *Helobiae* allows to determine the embryological characters of these two taxa and determine their phylogenetic bonds by comparison with other morphologic criteria. This study suggests that there is no direct relationship between *Ranunculales* and *Helobiae*, whereas the latter, in spite of their appearance, show some relationship with *Magnoliaceae*.

Embryological studies which analyse the segmentation process from the zygote to the mature embryo in the seed are becoming less numerous. The reading of "Biological Abstracts" is convincing enough. It is true that such detailed studies require some hundred hours of microscopic observation and that it is more sensible to devote time to the biomolecular aspect of differentiation than to the process of development at the level of the whole plant or its embryo. None the less, we are convinced that embryological studies are still useful and can provide the taxonomist with many valuable data.

We have recently been studying *Polycarpicae* and *Helobiae* which are brought together by several authors: is the genus *Ranalisma* not a concrete example of similarity between the *Ranunculus* and *Alisma* genera belonging to the *Ranunculaceae* and *Alismataceae* families respectively?

We have investigated embryogenesis in 27 genera, fourteen among Ranunculaceae, seven in the group of Ranunculales and Magnoliales and seven again in Helobiae (Ly Thi Ba, 1974, 1976; Ly Thi Ba et al., 1970, 1973, 1978; Ly Thi Ba, Guignard, 1976a, b).

We have in particular made a synthesis which has never yet been attempted of all of the embryogenic data concerning these groups. In fact, we see that at the level of *Helobiae* and, to a lesser degree, at that of *Magnoliales-Ranunculales* we have in our possession quite a large number of observations. But these latter have been laken down in a disparate way often using various terminologies for description. We there-

fore collected and recorded all these facts, gave up, along the way, some outdated notions of descriptive embryogeny, used other known morphologic criteria (structure of the vessels, structure of the pollen grain, serodiagnostic...) and thus came to a coherent whole.

The most important results which we have achieved can be summarized as follows.

Magnoliales — This taxon is characterized by embryos of a primitive type with a "delayed histogen differentiation" as Haccius and Bhandari (1975) named it or with a "dilatated ontogeny" according to Vallade (1978). The tetrad is most often globula and considered archaic. The suspensors are generally multicellular and massive. Embryogeny shows in another way that the Trochodendraceae occupy an isolated position among Magnoliales and that Cercidiphyllaceae exhibit similarities to Hammamelidales.

Ranunculales — All of the examined species of Ranunculaceae belong to the group according to Soueges' embryogenic classification to the IV megarchetype. Thus, embryogenic results corroborate the homogeneity of the family.

The embryogenic pattern, and more particularly the variable character of the formation of the tetrad at the second generation allow us to distinguish seven embryogenic groups:

- among Helleboroideae, the three groups "Actaea", "Delphinium" and "Nigella" which come from an archaic stock now represented by the sole genus Helleborus.
- among Ranunculaea, the four groups "Adonis", "Hepatica", "Myosurus" and "Clematis", set in a progressive order according to their state of evolution.

The character of "family by chaining" of Ranunculaceae is still found at the level of embryogeny and, in general, embryogenic features agree with other morphologic ones. Some differences can nevertheless be noted: the embryogenic criterion, which applies to young structures recapitulating more or less directly the phylogeny of the group, is a fundamental one but it is possible that this criterion "maximizes" the distances between genera and species: a similar fact is observed in Ranunculaceae with the structure of the seedling (Decamps, 1976).

The tribe of *Paeoniaea*, often included in *Ranunculaceae*, has particular embryogenic characters (especially the proembryo has a coenocytic structure) and must be raised to the rank of an independent family.

Berberidaceae and, to a lesser degree, Menispermaceae show an embryogenic pattern close to the one found in Ranunculaceae and, more particularly, in Helleboroideae.

Nymphaeales (often included in Ranunculales) — The embryogenesis of Nymphaeales shows characters recognized as primitive: a globular tetrad,

a massive mature embryo. Moreover, all of the embryological data prove that the three sub-families, Nymphaeoideae, Cabomboideae and Nelumbonoideae could be considered as autonomus families. Ceratophyllaceae, in spite of their vegetative type which differs from that of Nymphaeaceae, must be joined to this group because of the embryogenic criterion.

The monocotyloid characters observed in Nymphaeales (the lyorhyze root; the processus of germination...) show, on one hand the nearness of this group to the ancestral stock at the origin of Monocotyledones and, on the other hand, convergences due to their aquatic habitat. But the embryo is definitely of the dicotyloid type and Nymphaeales are part of Dicotyledones.

Helobiae — This group has a very constant embryological pattern (tetrad of the A category, presence of a vesicular haustorial cell, belonging to the same group of Soueges' embryogenic classification) to which some embryologic particularities such as an intermediate type of endosperm in the seed are added. These facts suggest that we have here a very well defined taxon.

The formation of the shoot apex of the embryo is done according two patterns — "terminal" or "lateral" — and these two models allow to divide *Helobiae* into two great phyla:

— Potamogetonales including the Hydrocharitaceae, Najadaceae, Zannichelliaceae, Potamogetonaceae, Ruppiaceae and Zosteraceae families; — Alismatales including the Butomaceae, Alismataceae, Scheuchzeriaceae, Juncaginaceae and Aponogetonaceae families.

Relationship of the *Helobiae* with *Polycarpicae*. In spite of their appearance — resulting essentially from the fact that *Helobiae* are herbaceus plants which are often aquatic and that *Magnoliales* are above all ligneous — the two phyla show some similarities which bring them close to each other: they have monocolpate pollen grains and a tetracellular embryo of an archaic type. However since are to be considered as more advanced than *Magnoliales*, which is also proven by the presence of trinucleate pollen admitted as more developed than pollen with two nuclei.

Returning to Ranunculales, we think that it most probably separated early from the parent stock of Polycarpicae. The presence of tricolpate pollen in Ranunculales and monocolpate pollen in Helobiae corroborates the precocious individualization of these two phyla. Here the embryogenic and palynologic criteria differ from the data given by the anatomic and morphologic ones and plead in favor of the absence of affinities between Helobiae and Ranunculales. The often quoted similarities between Alismataceae and Ranunculaceae would only be a convergence.

However it remains that Helobiae and Ranunculales come from a stock that is common to Monocotyledones, which is shown in Nymphaeales and certain Ranunculaceae by a tendency to monocotily.

The contribution of embryogeny to the classification and the phylogeny of *Polycarpae* and *Helobiae* appears to be most valuable, and, all the more so, as the latest attempts at phylogenic classification such as those by Emberger and Chadefaud (1960), Cronquist (1968), Takhtajn (1969), de Meeuse (1970), Walker (1976), Dahlgren (1977) take into account anatomic (vessels, pollen) and chimitaxonomic criteria, but very little do they include embryogenic ones.

We are therefore convinced that, beside experimental embryogeny which we are trying to take up by the technique of *in vitro* culture of plant cells and embryoids, there still remain some beautiful studies in classical embryogeny to carry out.

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