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Embryological features of some *Piperales*

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Abstract

Embryological investigation of some *Piperales* (*Piperaceae* and *Saururaceae*) as well as analysis of the available data confirm the ancient origin and natural character of this order. Similarity of the seed structure and a great variety of modes of formation of the embryo sac, endosperm and embryo are found in *Piperales*.

The order of *Piperales*, which includes 2 families (*Piperaceae* and *Saururaceae*) is usually placed at the bottom of the system, but its relation with other orders needs further study. *Piperales* show some features in common with the monocotyledons. Thus, important for understanding the phylogenesis of *Piperales* are more detailed data on the development of their reproductive organs. Comprehensive research of these structures was done by Johnson (1900a, b, 1902, 1914 and others). Later studies of species of *Peperomia, Piper, Heckeria (Piperaceae), Saururus, Houttuynia* (*Saururaceae*) were fragmentary. We also investigated some of the species of these genera, except *Saururus*.

From literature and the results of our study we can present general characteristics of these families (Nikitícheva, 1981).

1. The ovule is orthotropous, crassinucellate, with one or two integuments, the outer integument showing signs of reduction to the extent of its absence in *Peperomia*.

2. The parietal tissue of the nucellus consists of 3-6 layers in *Peperomia, Piper, Heckeria,* it is reduced in *Houttuynia.*

3. The embryo sac is of *Peperomia* type (*Peperomia*) or *Fritillaria* type (*Piper, Heckeria*); bisporic (probably, *Saururus*) or of normal type (*Houttuynia*).

4. The antipodal cells vary in number, arrangement and life-span.

5. The endosperm is of nuclear type (*Piper*) or cellular type, the latter may be without a haustorium (*Peperomia, Heckeria*) or with a chalazal haustorium (*Saururus, Houttuynia*).

6. Embryogenesis is of *Peperomia* type (*Peperomia*), Asterad type (*Houttuynia*) or other types, the suspensor is either undifferentiated (*Peperomia, Heckeria*) or differentiated (*Piper, Houttuynia*).
7. In the mature seed there is abundant perisperm, containing starch, little endosperm with proteins and a minute undifferentiated embryo. Thus, there is a great variety of embryological characteristics in this small order.

Our aim was to analyze the developing seed structures and to explain their causative relation. We also tried to find the relative level of the structural specialization of *Piperales.*

Peperomia has a crassinucellate ovule with parietal and massive chalazal tissue of the nucellus. *Peperomia* has a tetrasporic 16-nucleate embryo sac, characterized by a peculiar arrangement of its cells (Johanson, 1902a, 1914). It was previously considered to have a two-celled egg apparatus with a single synergid and a lateral position of the antipodal cells. Our investigation, made jointly with Plushch and Yakovlev (1981) confirmed the tetrasporic nature of the 16-nucleate embryo sac. However, all species studied (*Peperomia blanda, P. maculosa, P. obtusifolia, P. pellucida*) showed a three- nucleate egg apparatus. Its cells are slightly differentiated and have no cellulose cell walls. Probably this is the reason why the three cells have not been discovered before. After fertilization the embryo sac shows the remains of one destroyed synergid, the other synergid and the zygote become pronounced due to the formation of cellulose walls. The egg apparatus is on the micropylar pole. The antipodals occupy a lateral unfixed position and vary from 0 to 8. The number of central cell nuclei varies from 5 to 13. The peculiar arrangement of the elements of the *Peperomia* embryo sac (Fig. 1) is associated with its specific rounded form and, probably, with the homogeneity of its nucellar tissue at the lateral and chalazal sides of the embryo sac. Besides, the cellular endosperm of *Peperomia* is also a homogeneous structure without any differentiation of special digesting tissues. Hence, one can

Fig. 1. Embryo sac and ovule of *Peperomia*

think that their absence is compensated by the polyploid nature (6-14 n) of the endosperm, and the characteristic lens-like shape which increases contact with the perisperm.

The embryo sac of *Piper* and *Heckeria* is tetrasporic, of *Fritillaria* type and has a bipolar structure. Under the embryo sac in *Piper majusculum* and *Heckeria umbellata* we found elongated cells of the nucellus which can be regarded as a weakly specialized conducting system. During endosperm development the embryo sac widens but, in contrast to *Peperomia*, it preserves its bipolar structure due to survival of the antipodals at the chalazal pole. In *Heckeria* the antipodals can divide. Our data show that when the *Piper* endosperm passes to the cellular stage, smaller cells are formed at its chalazal pole. We consider this phenomenon to be the primary differentiation of the endosperm tissues having various functions.

More distinct differentiation of some embryonic structures can be observed in *Houttuynia cordata*. We found that in the nucellus the central strand formed by elongated and slightly specialized cells is more pronounced than in *Piper* and *Heckeria*. The structure of the embryo sac and the endosperm corresponds to this difference. The monosporic 8-nucleate embryo sac is elongated, 3 antipodals are at the chalazal pole (Fig. 2). The endosperm is triploid. *Saururus cernuus* also develops a chalazal haustorium (Johnson, 1900). Thus, some features of the embryo sac, endosperm and, embryo are interrelated with those of the surrounding tissue of the nucellus. The globular zygote and the embryo have a large basis adjacent to multilayer parietal tissue which occurs in *Peperomia, Piper, Heckeria*. On the contrary, the *Houttuynia* ovule has reduced parietal tissue, the embryo attaches to the nucellar epidermis by a narrow 1-celled suspensor. Therefore, we can suggest, that the parietal tissue is likely to play a special role in supplying the undifferentiated embryo with nutritive substances.

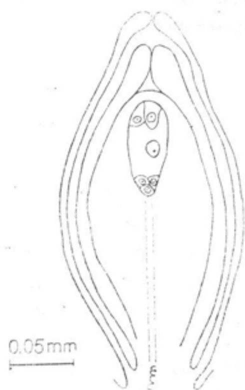

Fig. 2. Embryo sac and ovule of *Houttuynia*

The *Piperales* investigated all have the same transformation of the inner integument. During seed development some tannins accumulate in the cells. In the micropylar part of the fertilized ovule the adjacent cell walls of the integument and nucellus form finger-like growths into each other. Probably, increased contact between these tissues causes intensification of their metabolism in that part of the ovule.

Piperaceae and *Saururaceae* species are quite similar in their mature seed features (Fig. 3): 1) stored nutritive substances in the nucellus (perisperm); 2) slightly differentiated embryo, continuing its differentiation during germination; 3) the small endosperm, which is the intermediary between the embryo and the perisperm and surviving during germination until the starch of the perisperm has been absorbed.

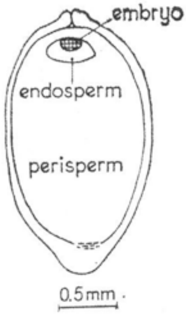

Fig. 3. Mature seed of *Piperales*

The analysis of the development of the *Piperales* embryological structures confirms the ancient origin and the natural character of this taxon. In spite of the similarity in seed structure, there are striking differences in the mode of formation of the ovule, embryo sac, endosperm and embryo. These differences are likely to reflect primary evolutional directions in the "search" for the most effective relation between the structures of the developing seed. The 16-nucleate embryo sac slightly differentiated before fertilization and the polyploid homogenous endosperm of *Peperomia* are the least efficient of all. These type are seldom found among angiosperms.

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