

BRIEF COMMUNICATION

OVULE DIMORPHISM IN *FICUS ASPERIFOLIA* MIQUÉL

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It is now known that in *Ficus* the variability in the form of the style ensures that not all female flowers are oviposited by pollinating fig wasps. In monoecious species (e.g. *F. ottoniifolia*), initially the ovules and ovaries are all identical. Due to gradual differences in style length, style thickness, and form of the stigma not all flowers have the same chance on oviposition, and after wasp activity the flowers either develop wasps or seeds (VERKERKE 1986). In contrast to this, the gynodioecious *F. asperifolia* is supplied with two specialized types of figs, viz., seed figs and gall figs. Seed figs contain female flowers that develop seeds (seed flowers); gall figs contain both male flowers and female flowers (gall flowers); in the latter the fig wasps develop. Seed flowers and gall flowers exhibit pronounced differences in the form of the style (VERKERKE, in preparation). Next to this, the ovules of seed flowers and gall flowers are different from the start, and the term ovule dimorphism is introduced to describe this situation.

In seed flowers (*figs. 1a, 2a-b*) the inner integument is initiated as a ring-shaped primordium, while the outer one appears as a half ring at the antiraphal side. The mature ovules are provided with an inner integument circumvallating the nucellus, while the outer integument invests the antiraphal side and fuses with the raphe. This is the common situation in anatropous and hemianatropous ovules (BOUMAN 1984).

The gall flowers have specialized ovules (*figs. 1b-d, 2c-d*). Initially, the integuments develop as in the female flowers of seed figs. Just before the tetrad is formed, subdermal periclinal divisions in the funicle form a wedge the swelling of which hampers an intercalary growth of the inner integument at the raphal side. The anatropous curvature starts earlier than in the ovules of seed flowers. As the ovule enlarges, the integuments expand and overgrow the nucellus at the lateral and antiraphal side, but at the raphal side the ovule enlargement is matched by periclinal divisions in the funicle, and the inner integument remains short. The intercalary funicular growth produces cell rows that run parallel with the raphal bundle, and render the raphe comparatively thick. In the embryo sac nuclear endosperm and early stages of embryo development are discernible.

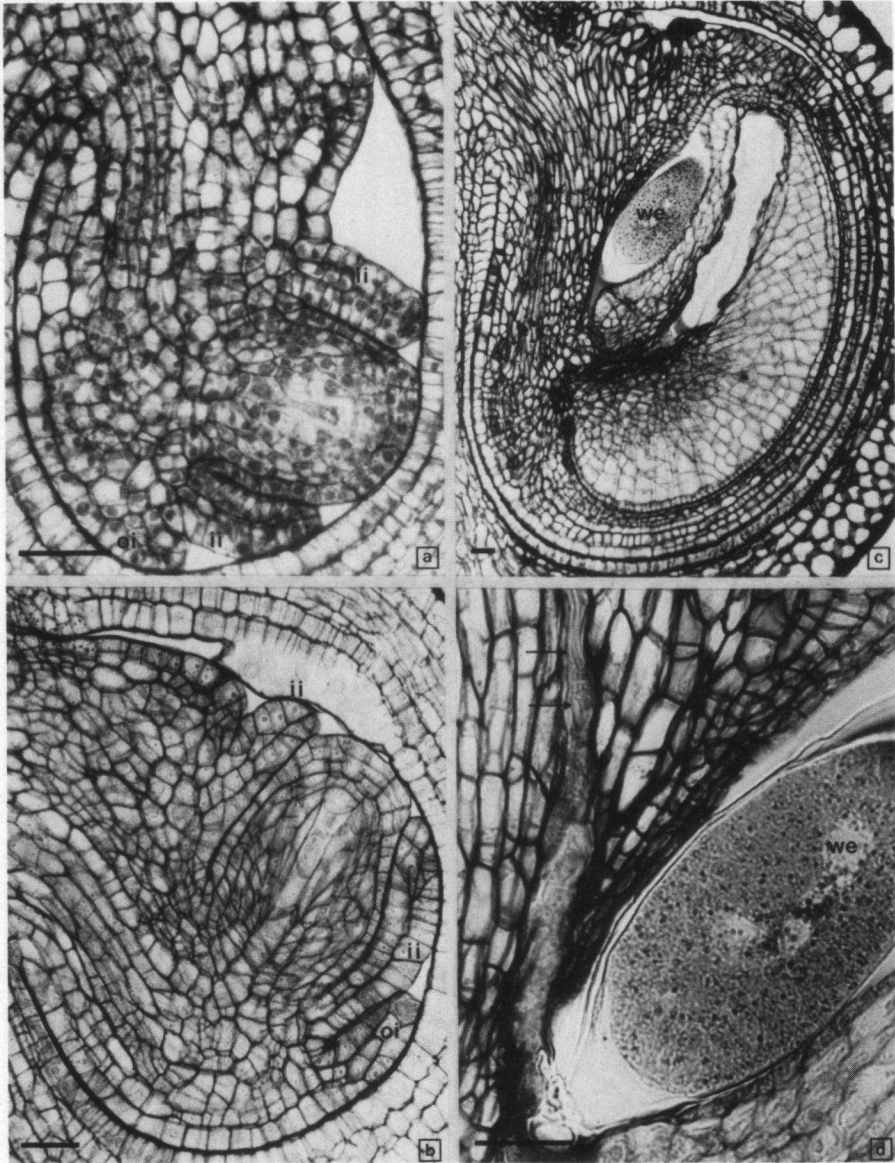


Fig. 1. *Ficus asperifolia*. Long sections of developing and mature ovules. a: young ovule, seed flower, with circumvallating inner integument; b: young ovule, gall flower, with short inner integument at the raphal side; c: mature ovule, gall flower, wasp egg deposited; d: detail of mature ovule, gall flower, arrows indicate track of ovipositor. ii = inner integument, oi = outer integument, we = wasp egg; scale bar indicates 20 μ m.

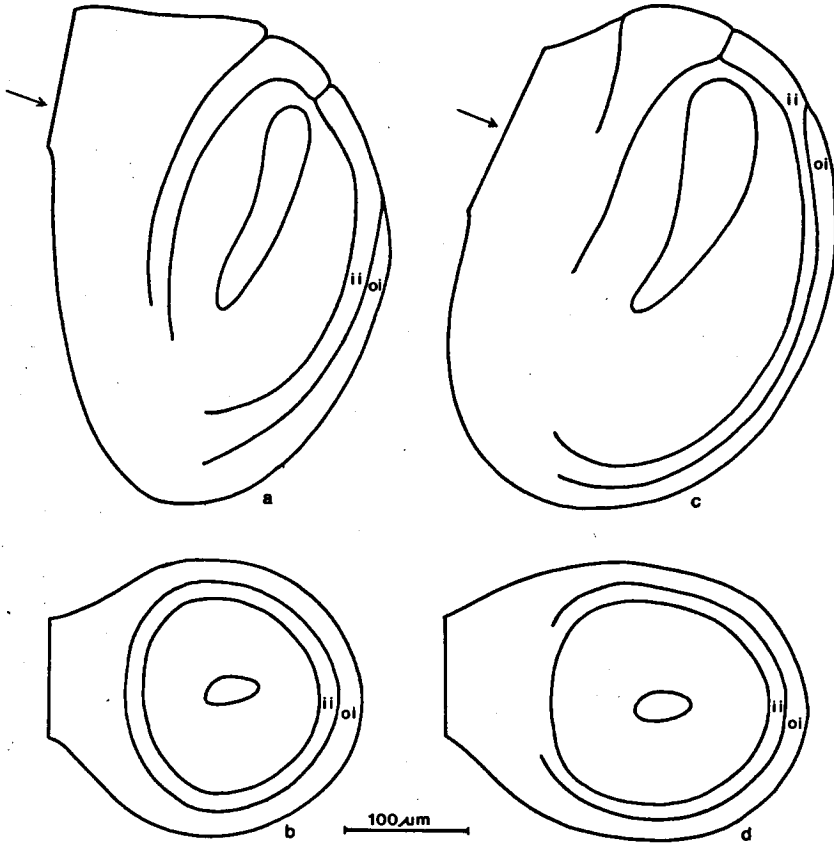


Fig. 2. *Ficus asperifolia*. Schematic long sections (a, c) and cross sections (b, d) of mature ovules, arrows indicate the level of the cross sections. a, b: seed flower; c, d: gall flower.

The ovule dimorphism can clearly be related to the different functions of the ovules in gall and seed flowers. Upon fertilization, the ovules of seed flowers produce a seed, while oviposition in gall flowers leads to fig wasp development. In all *Ficus* spp. studied the wasp egg is deposited next to the nucellar epidermis; the exceptions of this are on account of parasites (see VERKERKE 1986). Apparently, the insect senses the barrier of the nucellar cuticle with its ovipositor and deposits the egg. The egg feeds the first days on nucellar cells, then it develops into a larva which migrates towards the embryo sac, and starts feeding on the endosperm. If the inner integument would circumvallate the nucellus, it is probable that the egg would be deposited between the raphe and the inner integument, since it is unlikely that the ovipositor could distinguish between the surface of the inner integument and the nucellar epidermis. Both the food supply during the first days and the migration towards the endosperm would be more complicated by the presence of a circumvallating, fully developed inner integument.

On the other hand, the aberrant ovule development in gall flowers leads to a thicker raphe with cells running parallel with the vascular bundle and the direction of oviposition. For oviposition, the insect inserts the ovipositor in the styler canal, punctures the raphe and manipulates the ovipositor between these cells, whose orientation guides the ovipositor to the nucellar epidermis. It is concluded that the specialized features of the gall flower ovule facilitate puncturing of the raphal tissue, ensure a successful egg development, and fit the gall flowers as an oviposition site for fig wasps. It remains not clear why never seeds develop in gall flowers. A discussion of the importance of ovule dimorphism in *F. asperifolia* is at hand (VERKERKE, in preparation). In *F. asperifolia*, both style and ovule dimorphism contribute to the different functions of gall and seed flowers. *F. asperifolia* represents the first case in which ovule dimorphism is described. The aberrant ovule development in the gall flowers resembles the process of integumentary shifting (BOUMAN 1984), but differs in the unequal length of the inner integument at the different sides of the ovule. The present ontogenetic observations explain the different descriptions of the ovular anatomy of other *Ficus* spp. in the older literature (see VERKERKE 1986). The ovule dimorphism of *F. asperifolia* is directly related with the pollination and oviposition by fig wasps, and this contrasts with the seed and fruit dimorphism known from e.g. Chenopodiaceae, Compositae, and Cruciferae (HARPER et al. 1970) which is related to dispersal or germination.

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