

OVULE AND SEED STRUCTURE IN DATISCACEAE

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SUMMARY

The ovule primordium of *Datisca cannabina* is dizonate. The crassinucellate ovule has dermal, two-layered integuments that become crushed during their development, the exotesta excepted. The operculum contains the hilum and the micropyle and is lifted during germination without a special zone of rupture. The embryological and seed characteristics of Datisceae strongly support a close relationship with the Begoniaceae.

1. INTRODUCTION

The family Datisceae comprises the genera *Datisca*, *Octomeles* and *Tetrameles*. The monotypic genera *Octomeles* and *Tetrameles* represent tall trees which have an Indomalaysian distribution. The genus *Datisca* comprises two perennial herbaceous species of which *D. cannabina* occurs in Asia and *D. glomerata* in western Central America. All genera have many-seeded capsules opening with apical slits or splitting laterally.

The ovules and seeds of *Datisca cannabina* were studied by MONTEMARTINI (1905), HIMMELBAUER (1909), MAURITZON (1936), CRÉTÉ (1952) and KAMELINA (1983). SAND (1921) gives information about the ovule and developing seeds of *Tetrameles*.

NETOLITZKY (1926), DAVIS (1966) and CORNER (1976) have summarized the data on Datisceae. The ovules are bitegmic, anatropous and crassinucellate. In *Datisca cannabina* the lower of the two dyad cells develops into an embryo sac of the *Allium* type. The embryo constitutes the biggest part of the seed.

The endosperm is initially nuclear, and later becomes cellular. In the mature seed it is represented by only a single cell layer. All seed coat layers become crushed, except the exotesta of which only the inner and radial walls become lignified. The seeds of *Datisca* (KLEBS 1884, SAND 1921) have an operculum formed by the hilum and micropyle. The seeds are rather small and probably dispersed by wind or by water (DAVIDSON 1973). Already LINDLEY (1853) suggested a relationship between Datisceae and Begoniaceae on the basis of some shared morphological features. Later authors (SAND 1921, MAURITZON 1936, CRÉTÉ 1952) agree mainly on account of the embryological similarities between the two families. Despite their sound arguments there is still no consensus of opinion regarding the relationships of the Datisceae.

2. MATERIALS AND METHODS

Developmental stages of flowers and fruits of *Datisca cannabina* L. were collected in the Hortus Botanicus, University of Amsterdam. Seeds of *Datisca glomerata* (Presl) Baill. were collected by G. Hansen (1891), Flora of the Sequoia gigantea region and A. A. Heller (1902), Plants of California no. 5821. Seeds of *Octomeles sumatrana* Miq. were collected by Brouwer (1954), collectie Boswezen Nieuw-Guinea no. 1608, and G. Th. Iwanggin (1960), Boswezen Nederlands Nieuw-Guinea no. 9130. Seeds of *Tetrameles nudiflora* R. Br. were collected by Sutrisno (1957), Herb. Bog. no. 74, J. Sinclair (1959), Herb. Bot. Singapore, Flora of Java no. 9989 and F. C. Whitmore (1967), Flora of Malaya Fri no. 3502. All seeds originated from the Herbarium Leiden.

The material was dehydrated in a n-butyl alcohol series, embedded in methylmethacrylate, sectioned at 5 μ m and stained with periodic acid-Schiff's reagent and toluidin blue. In addition, phloroglucinol HCl, sudan IV, ruthenium red and IKI were used for specific colour tests. SEM observations were made with a Cambridge stereoscan mark II^a. The seeds were either directly or after critical point-drying sputter-coated with gold/palladium.

3. RESULTS

3.1. Ovule ontogenesis

The ovule primordium of *Datisca cannabina* is dizonate (figs. 1A, B). The initiation takes place by periclinal divisions in the second layer (l_2) of the placenta and the resulting bulge is covered by the at first only anticlinally dividing dermatogen (l_1). The subdermal archesporous cell divides into a primary parietal cell and a megaspore mother cell. A megaspore tetrad has not been observed. The lower of the two dyad cells develops into the 8-nucleate embryo sac (fig. 1H), the upper one degenerating. The primary parietal cell undergoes further divisions (figs. 1H, 2C). The nucellus is rather massive. When the anatropous curvature is about 90°, the inner integument (ii) is initiated, soon followed by the outer integument (oi). Both integuments are initiated in rings of two dermal cells (figs. 1C, D, E). The i.i. starts as a complete ring wall, the o.i. appears as an incomplete, later as an asymmetric ring wall (figs. 1F, G, H). The o.i. soon overtakes the i.i. (fig. 1G). Both integuments remain two-layered from the beginning, only the tip of the o.i. becoming multilayered (figs. 1H, 2C). During the development of the ovule first the outer epidermal raphal cells and later those of the o.i. enlarge substantially. These cells are not or hardly tanniferous. At maturity they form the exotestal layer of the seed coat. At the level of the exostome the outer epidermal cells of the raphe show periclinal divisions to form a bulge (figs. 1F-H, 2C). Already before the ovule is mature longitudinally oriented intercellular spaces form at the sides of the raphal bundle and in the chalazal region (figs. 1H, 3A).

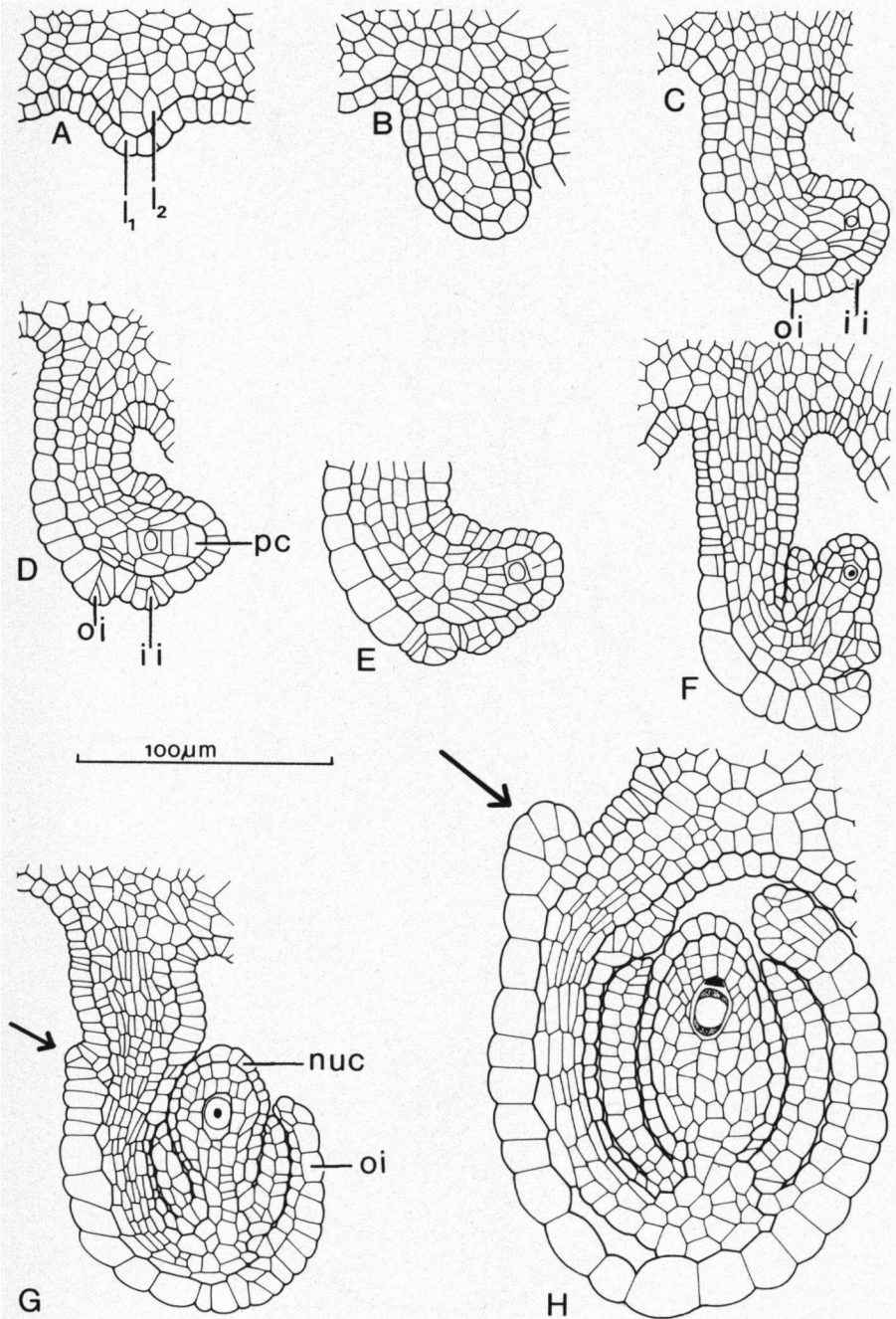


Fig. 1A-H. *Datisca cannabina*. L.s. of developmental stages of the ovule. Arrows point at the raphal bulge which later becomes part of the operculum.

Nuc = nucellus; ii = inner integument; oi = outer integument; pc = parietal cells; ex = exostome.

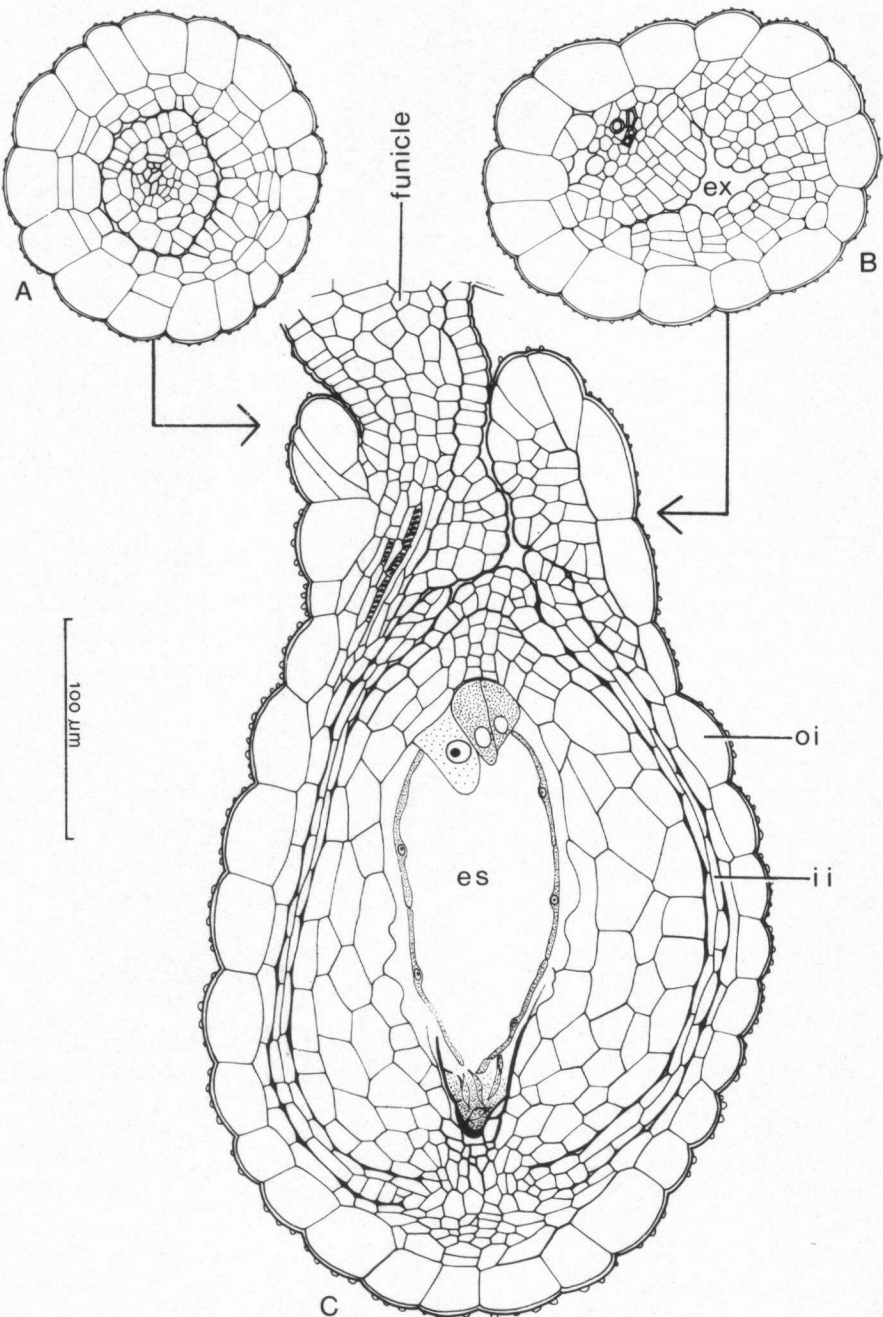


Fig. 2A–C. *Datisca cannabina*. Mature ovule, shortly after fertilisation. A: Cross section of funicle area passing through ring wall; B: cross section of the raphe somewhat below that of fig. 2A; (the arrows indicate the levels of the two cross sections) C. l.s. of ovule.

3.2. The mature ovule

The mature ovule is anatropous, bitegmic and crassinucellate. The embryo sac starts to resorb the rather large nucellus. The parietal tissue has become 4- to 5-layered. The dermal cells of the nucellar apex form a small nucellar cap of 3 to 5 cells layers (*fig. 2C*). The opening at the top of the i.i. does not close completely, so that the micropyle is formed by the o.i. only. The apex of the o.i. becomes multilayered by repeated divisions of its inner layer.

The exostome (micropyle) has a roughly triangular form (*fig. 2B*); in cross section the raphal bulge is continuous with the apex of the o.i. so that an orbicular rim surrounding the funicle is formed (*figs. 2A, C*). This situation persists in the mature seed, where the hilum lies sunk in the middle of the ring wall (*figs. 4A, B*). The xylem elements in the amphicribral funicular and raphal bundle differentiate into spiral and ring tracheids. At both sides of the raphal bundle and in the chalaza large intercellulars develop. The mature ovule contains starch, mainly in the nucellar tissue surrounding the e.s. but also in other ovular parts.

3.3. Seed development and mature seed

The endosperm is of the nuclear type and initially forms a thin multinucleate layer at the periphery of the e.s. (*fig. 2C*). Later, after wall formation, the main part is resorbed except its outer layer, which persists in the mature seed (*fig. 3C*). According to CRÉTÉ (1952), wall formation begins around the proembryo. Gradually the nucellus is compressed and resorbed, but the crushed remains, covered by a previously formed, prominent cuticle, remain conspicuous in the mature seed (*fig. 3C*). The cells of the i.i. and those of the inner layer of the o.i. remain rather small and are represented in the mature seed coat by somewhat thick-walled, brown, crushed cells (*figs. 3B, C*). The cells of the outer layer of the o.i. enlarge substantially (*figs. 2C, 3A, B*) and develop into the mechanical layer of the seed (*fig. 3C*). The inner and radial walls of these cells are thickened, pitted and lignified. The outer wall, which is covered by an inconspicuous cuticle and reacts with sudan IV and ruthenium red, has collapsed against the thickened inner walls (*figs. 4A-D*). Sometimes this collapsed outer wall is so strongly adpressed against the pitted wall thickenings that the pits can be observed in the outer wall.

The brown-coloured seed of *D. cannabina* measures $0.8-0.9 \times 0.3-0.4$ mm. The polygonal testa cells are arranged in rows (*figs. 4A, B*). The rim surrounding the hilum functions in conjunction with the hilar region as an operculum facilitating germination (*figs. 4E, F*). The straight and relatively large embryo (*fig. 3E*) is rich in oils and aleurone and free of starch. Also the endosperm contains appreciable quantities of lipids and aleurone. The seeds of *Datisca glomerata* correspond rather closely with those of *D. cannabina*, but in the former the testa cells are not so clearly arranged in rows, the anticlinal walls of the testa seem thicker (*figs. 5A, B*), and the cuticular folds are more pronounced. The seed measures $0.8-0.9 \times 0.3-0.4$ mm. The seed of *Octomeles sumatrana* is smaller than that of *Datisca* ($0.75-1.0 \times 0.2$ mm) but resembles it rather closely (*figs. 3D, 5C*). The testa cells are also arranged in rows. The cuticular structure (the

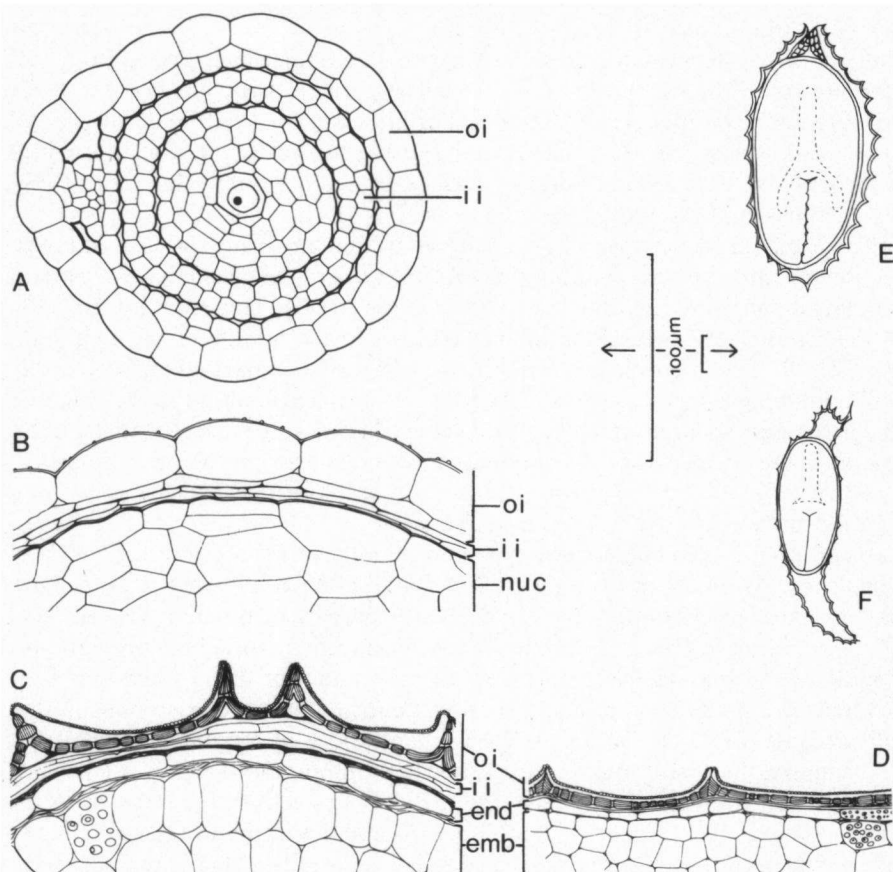
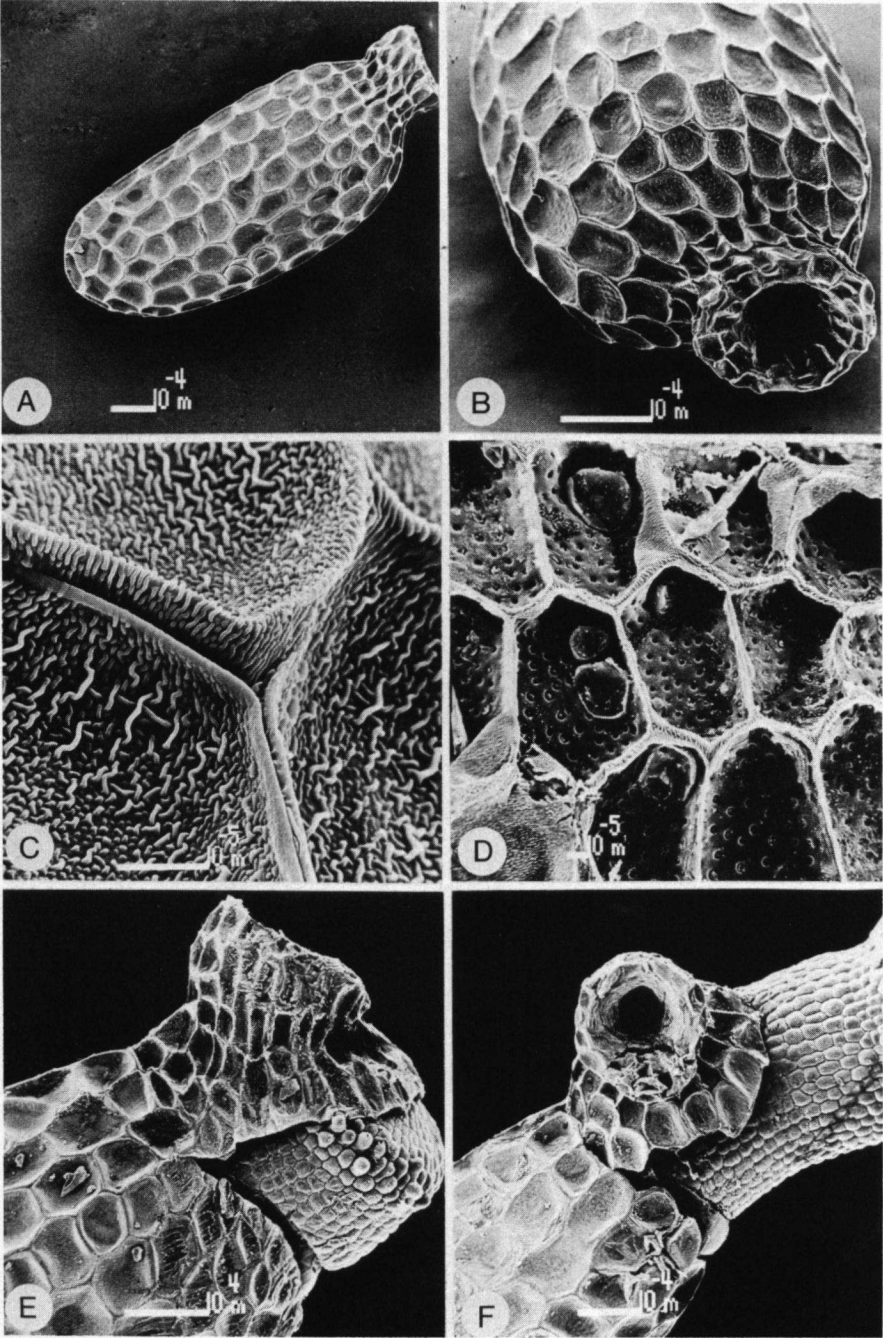


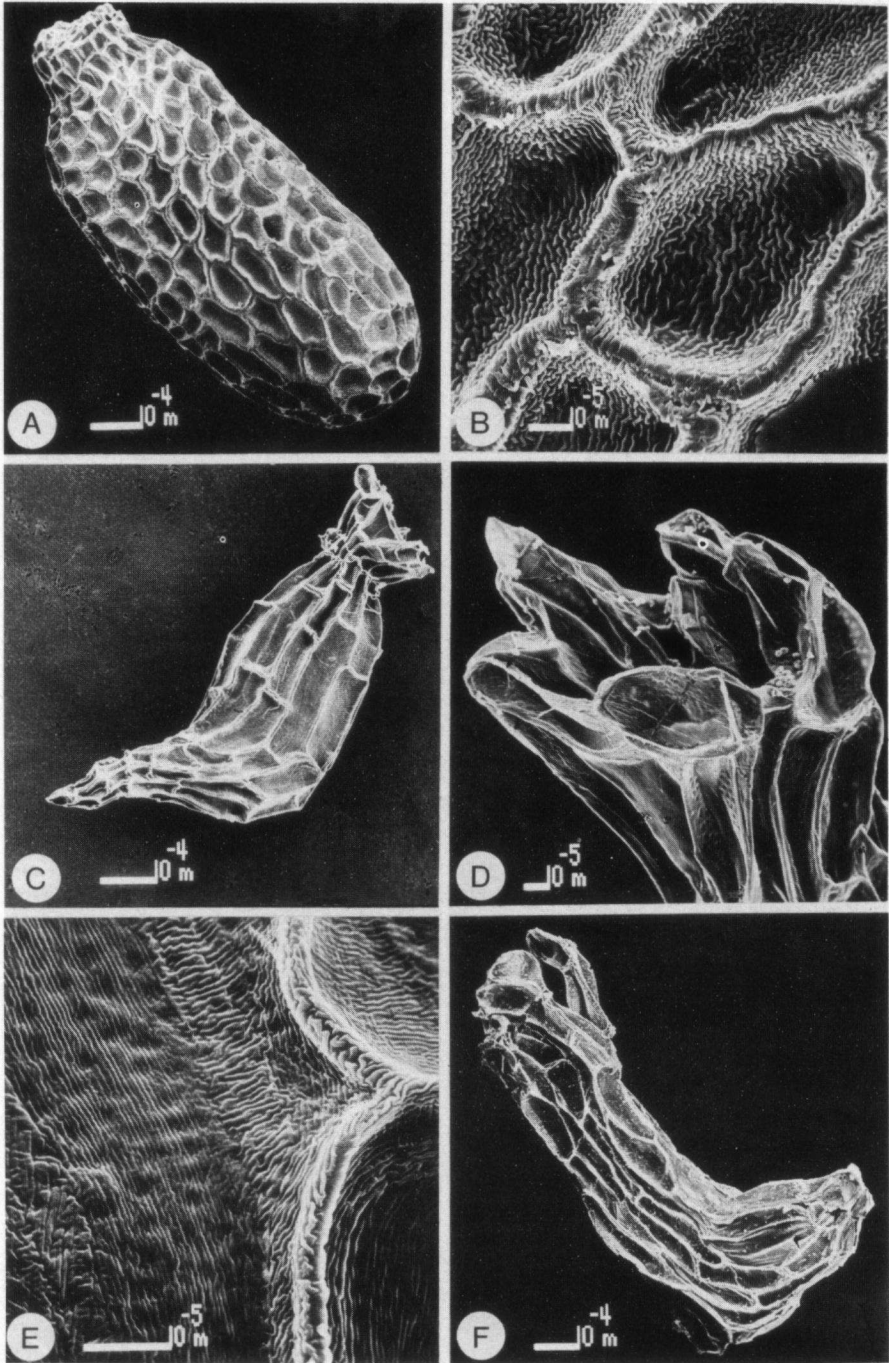
Fig. 3A, B, C, E. *Datisca cannabina*, D, F. *Octomeles sumatrana*. A: Cross section of immature ovule showing intercellular spaces next to the raphe; B: t.s. of developing seed coat; C, D: t.s. of mature seed coat; E, F: l.s. of mature seed.

folding) is rather similar to that of *Datisca* seeds (fig. 5E). The seed coat and the internal structures of the seed are also rather similar to those of *Datisca* (fig. 3F) and even a micropylar ring wall (operculum?) is present (fig. 5D). The formation of chalazal intercellulars has gone so far that at maturity an air bladder has formed at the tapering chalazal end of the seed.

As far as can be deduced from the seed of *Tetrameles*, it is of the same type and dimensions as that of *Octomeles*. There is also a micropylar ring wall and the outer walls have collapsed (fig. 5F). The seed setting may have been abnormal in the material of *Tetrameles* at my disposal, or the seeds may be immature.

Fig. 4. SEM micrographs of *Datisca cannabina*. A, B: mature seeds; C: detail of seed coat with cuticular structure; D: seed coat with outer wall removed, showing the pitted, thick inner walls; E, F: stages of seed germination showing the operculum and emerging radicle.





4. DISCUSSION

The ovule and seed of *D. cannabina* are very similar to those of *Begonia* (BOESEWINKEL & DE LANGE 1983).

The ovule and seeds are of rather simple construction. The ovule primordia are dizonate and the integuments are two layered from the very beginning. The operculate seed has an almost completely crushed exotestal seed coat, the straight embryo is relatively large, and the endosperm is only one cell layer thick. These similarities are strongly indicative of the close relationship between the Datisceae and Begoniaceae. The main differences between the ovules and seeds of the two families are: the larger nucellus in *Datisca*, the lack of the enlarged cells of the nucellar epidermis (pseudoentelium) found in Begoniaceae and the lack of the so-called collar cells (BOESEWINKEL & DE LANGE 1983). These collar cells are in Begoniaceae longitudinally oriented cells and arranged in a transverse ring around the operculum. At germination the operculum is lifted, often along the splitting of the middle lamellae of the cell walls between operculum and collar cells. In *Datisca* no such special rupture layer is present.

Datisceae are less specialized than Begoniaceae because they have a larger, less reduced nucellus, without strikingly swollen epidermal cells and because there is no special rupture layer aiding the lifting of the operculum. Also the vegetative characters of the Datisceae are not so much reduced and specialised as they are in Begoniaceae. The small spindle-shaped seeds of *Octomeles* exhibit much of the characters of the seeds of *Datisca*. SAND (1921) observed that the ovular structure and behaviour of the endosperm of *Tetrameles nudiflora* also correspond closely with those of *Datisca*. The immature seed of *Tetrameles* in surface is reminiscent of that of *Octomeles*. These correspondences obviously indicate that the genera *Datisca*, *Octomeles* and *Tetrameles* are closely related and seem to be correctly placed in the same family. Despite their woody habit the genera *Octomeles* and *Tetrameles* possess the smallest and most specialised seeds of the family. The seeds of *Datisca* and *Octomeles* possess intercellular spaces in the raphal and chalazal regions, which in *Octomeles* even develop into a chalazal air bladder. The small seeds of *Datisca*, *Octomeles* and *Tetrameles* are likely to be primarily dispersed by air currents. The somewhat larger seeds of *Datisca* may be polychorous as they are assumed to be dispersed also by water currents or on the legs or in the feathers of birds in the riparian habitat (DAVIDSON 1973). Despite the correspondences between the seeds of Datisceae and the also wind-dispersed seeds of Begoniaceae the relationships of the Datisceae are still subject to disagreement. According to VAN STEENIS (1953) there is no consensus of opinion concerning the systematic position of the family which has been compared with several other ones. DAVIDSON (1973) reports "that little anatomical correspondence is present between Datisceae and the possibly related Begoniaceae because of the great specialization of the members of the latter

Fig. 5.A, B. *Datisca glomerata*: mature seed and detail of seed coat; C, D: *Octomeles sumatrana*: mature seed and detail of micropylar part of seed; E: *Octomeles sumatrana*: detail of cuticular structure; F: seed of *Tetrameles nudiflora*.

family, but both may be related through a common ancestry with Flacourtiaceae”.

The families Datisceae and Begoniaceae clearly show that the morphology of ovules and seeds may be more conservative than that of the vegetative parts of the plant (which are more subject to selection and environmental specialisation). As a result ovules and seeds are often better indicators of relationships than the vegetative parts. In recent systems the Datisceae are usually placed next to the Begoniaceae, which suggests a close relationship between these two families. The Cucurbitaceae are often also considered to be related with Begoniaceae and Datisceae, but the large crassinucellate ovules and the more complex seed structure (with a vascularized o.i.) render a close affinity rather doubtful. It is questionable whether the Datisceae and Begoniaceae belong to the parietalian alliance (BOESEWINKEL & DE LANGE 1983). Also CORNER (1976) remarks that the exotestal seeds of Begoniaceae and Datisceae seem to indicate a different line of evolution. MERXMÜLLER & LEINS (1971) and LEINS & BONNERY-BRACHTENDORF (1977) have pointed out that the different mode of development of the androecium in the Begoniaceae and Datisceae renders a position of these families in the Parietales very doubtful. LAWRENCE (1951) states: “The available evidence indicates that the order Parietales is not a phylogenetic taxon, and the re-alignment of the families into several orders is to be expected”.

In order to unravel the relationships of the Datisceae it seems promising to study the ovules and seeds of some other families of the Parietales such as the Caryocaraceae, Elatinaceae, Droseraceae and Frankeniaceae. The Droseraceae also have ovules with swollen nucellar epidermal cells closely resembling those of Begoniaceae. The seeds of Droseraceae are rather conform those of Datisceae and Begoniaceae. The significance of the in some respects similar ovular morphology of Saxifragaceae (Parnassiaceae) and Crassulaceae in this connection is as yet not clear.

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