Morphological and embryological investigation of
Daucus muricatus (L.) L. (Caucalideae: Umbelliferae)

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Abstract. The morphology and embryology of Daucus muricatus (L.) L. is studied. In the light of embryological characteristics, the systematic position of Daucus in the Umbelliferae is discussed.

Keywords. Morphology; embryology; Daucus muricatus.

1. Introduction

From the time of Bentham and Hooker (1867) there exists considerable confusion concerning the systematic position of the genus Daucus. The tribe Caucalideae of Bentham and Hooker (1867) and Boissier (1872) comprises a group of 14 genera. However, Drude (1897) distributed these genera between tribe Daucaceae and subtribe Caucalineae of tribe Scandiceae. Calestani (1905) distributed them into four different tribes: Caucalideae, Daucaceae, Scandiceae and Ligusticeae. Kosopoljansky (1915) included them in tribes: Caucalideae, Ligusticeae and Careae. Cerceau-Larrival (1971) distributed the genera in 8 new tribes: Orlayaeae, Cumineae, Artedieae, Torilineae, Turgenieae, Turgeniopsideae, Caucalideae and Daucaceae.

This confusion is due to the fact that classification of the family at tribal and generic level is based on morphology of fruits and vegetative structure. Recently, new characters have been used to solve the systematic problems such as embryology (Maheshwari 1945; Al-Attar 1974).

2. Material and methods

The seeds of Daucus muricatus were obtained from France (Nancy Laveuveville dt Nancy 220 m). The plants were grown in the Botanical Garden of Reading University, England. Samples of buds, flowers, fruits and seeds at different stages were collected, fixed in formalin–propionic–alcohol (1:1:18) and preserved in 70% alcohol. The method of study followed is the same as discussed previously (Al-Attar 1977). In addition, acetocarmine squash for pollen mother cells was prepared.
3. Observations

3.1. Floral morphology

The flowers of *D. muricatus* are borne in compound umbels, 15 rays of the first order umbels decrease to 10 in the highest order. Pedicel 20–8, 1–0·5 cm long. Involutures 8, 2·5–0·5 cm long, pinnatisect, covered by bristles; involucels 8, 1·5–0·5 cm long, linear to lanceolate, sometimes pinnatisect with bristles covering. Flowers 20 in the first order umbellete, reduced to 8 in the highest order. The peripheral 7–8 flowers are bisexual, zygomorphic, this is due to unequal size of petals (figure 1); others intergrade to merge with the inner whorls which show progressive decrease in zygomorphy and gradual suppression of gynoecia (figures 2, 3, 4). Sepals whitish green, lanceolate to deltoid, 0·4 mm long, distinct, ciliated margin, alternate with petals. Petals 5, whitish, polypetally, apically inflexed, unequal in size.

Stamens 5, inflexed in bud, spreading laterally at anthesis, alternate with petals and arising from the basal part of swollen epigynous disc (stylopodium). Pistil one, epigynous, bilocular, two ovules in each locule, one above the other, the upper usually abortive, the lower fertile, pendulous, anatropous, unitigmic (figure 14). Styles 2, 2·5 mm long at anthesis.

3.2. Organogeny

The development of umbellet in an umbel and the flowers in an umbellet appear in a centripetal sequence, but the arrangement is spiral rather than cyclic, as shown by the unequal sizes of primordia (figures 5, 6). The dome-shaped floral protuberance appears first as an undifferentiated (figure 7) mass of cells, but it broadens out and becomes differentiated into two tunica layers and a corpus (figures 8, 9). The site of initiation of petals and stamens primordia shows a rapid anticlinal division in the outer and mainly periclinal division in the inner tunica layer, resulting in almost simultaneous appearance of petals and stamens (figure 10). The tip of petals primordia grows rapidly by apical growth and curves over the floral apex (figures 11, 12), eventually all five petal tips meet at a point above the centre of the floral apex (figures 13, 14). At this time apical growth ceases. Marginal growth, which follows the earlier period of apical growth, proceeds until the margins of the petals just touch those of the other petals. After the apical and marginal growth, the middle ventral part of each petal bends inwardly to form a protrusion extending between adjacent stamens (figure 15). Primordia of the petals arise at the same time but inadequate rate of apical and marginal growth results in unequal size of mature petals (figure 15). As the stamens primordia grow, the apical part divide more actively, so it becomes broader and larger while the basal part remains smaller (figure 12).

The carpels primordia develop after stamens and petals primordia have attained a certain length, they grow upward in the form of crescent and incline at the tip to enclose a single ovarian cavity (figure 13).

The primordia, however, continue to grow and form two styles. Meanwhile the region around the base of the style grows enormously to form a swollen epigynous disc or stylopodium. The basal part of the carpels grows very fast inward and upward to form a partition called carpophore (figure 13). Meanwhile
the upper part of the carpels grows downwards at a slower rate to meet the carpophore at the summit of the ovarian locale forming a complete partition (figure 14). Two ovules develop in each locale one above the other on placenta at margins of carpels. Usually the upper two degenerate early while others develop to maturity (figures 14, 16). The sepals are last tiny floral organs to develop, but not until the primordia of stamens, petals and carpels have reached a certain height, do the sepal primordia become evident as small sepals outside and alternate with petals.

3.3. Microsporogenesis and male gametophyte

The anther primordia arise as undifferentiated mass of cells but later become differentiated into two and four lobes (figures 17, 18, 23). In each lobe, archesporium appears as a single hypodermal layer of cells (figure 24). The primary parietal and primary sporogenous layers originate by periclinal division of the archesporial cells (figures 19, 24, 25). The former undergoes further periclinal division to form two secondary parietal layers which intervene between the epidermis and the sporogenous tissue (figures 20, 26). The outer secondary parietal layer gives rise to two layers, the outermost forming the endothecium and the innermost forming a middle layer. The inner secondary parietal layer develops directly into tapetum (figures 21, 27, 28). In the mature anther, the endothelial layer develops thickening on the radial and the inner tangential walls (figures 30, 31, 32). The epidermis persists in the mature anther and its outer tangential wall becomes slightly elevated (figure 30). The middle layer degenerates by the end of the pollen tetrad stage (figure 29). The tapetal cells do indicate any degeneration until separation of pollen tetrads but it becomes disorganised by the time 3-celled pollen grains are formed (figure 30). The tapetal cells become prominent and their nuclei undergo mitotic division, therefore frequently two or three nuclei are present in cell (figure 29).

The primary sporogenous cells are large in size with dense cytoplasm and conspicuous nuclei. They divide mitotically to produce microspore mother cells (figure 33). In the material examined, the reduction division in the microspore mother cells is nonsynchronous in different anthers of the same flower as well as in different sacs of the same anther. During meiosis (figures 34, 35) a tendency towards nonsynchrony was also observed in the same sac (figures 22, 28); however, the formation of the pollen tetrad and their arrangement in tetrahedral or decussate manner was simultaneous (figures 29, 36, 37). While the microspores are in a tetrad a densely staining mucilaginous material surrounds the tetrad (figure 29). After separation from tetrad, the somewhat triangular microspore becomes spherical, oval and later ellipsoidal (figures 38, 39).

The nucleus of the microspore moves to one pole before it undergoes any division due to the appearance of vacuole at the centre (figure 40). It divides in this position forming a large vegetative nucleus which moves to the equatorial position and a small generative nucleus (figure 41), which divides (figure 42) at one pole forming two male gametes, one of them remaining in this position while the other moves to the opposite pole. The average polar axis (P-axis) of the trinucleate pollen grains is 21 μ with an average of 14 μ in equatorial axis (E-axis).
3.4. Ovule, megasporogenesis and female gametophyte

The pendulous ovule becomes inverted or anatropous during development. At about the 8-nucleate stage of the embryo sac, the funicular epidermis enlarges and elongates radially and gets transformed into obturator (figure 52). The chalazal part of the developing ovule shows a dark staining group of cells; the hypostase vanishes after fertilisation.

The nucellar epidermis surrounds the megaspore mother cell—tenuinucellate type (figures 43, 44). It degenerates at about four-nucleate embryo sac stage; therefore the embryo sac comes in direct contact with the inner layer of the integument (figure 49), which elongates radially and functions as the endothelium (figures 50, 51); the archesporial cell functions directly as the megaspore mother cell (figures 43, 44), and after two transverse meiotic divisions, forms a linear of four megaspores (figures 45, 46). As the chalazal megaspore of the tetrad gives rise to the embryo sac, the other three megaspores degenerate (figures 47, 48). Typically the embryo sac is 8-nucleate, three-celled egg at the micropylar end, three antipodal cells at the chalazal end and two polar nuclei (figure 51). The poles move into the centre of the embryo sac and fuse. The diploid and enlarged secondary nucleus migrates towards the micropylar end and comes near the 3-celled egg apparatus consisting of two synergids and one egg (figure 51).

3.5. Endosperm and embryogeny

The fertilised egg is surrounded by pear-shaped synergids. The synergids stain darkly and possess a small vacuole at basal ends (figure 52). During penetration of the pollen tube, one of the synergids comes in contact with it and deteriorates rapidly, while the other one persists a little longer (figures 55, 56). The primary endosperm nucleus is the largest nucleus in the embryo sac (figure 53), and it lies adjacent to the zygote. It undergoes several free nuclear divisions, the first few divisions are synchronous (figures 54, 55) but later the divisions become nonsynchronous (figures 56, 57). The derivatives of some of these nuclei accumulate near the zygote while others become distributed on the periphery of the embryo sac (figures 55, 56). The nuclei on the raphe side divide more actively than those on anti-raphe side, so that when one or two layers of nuclei occur at the anti-raphe side, there are two or three layers of nuclei on raphe side (figures 56, 57). At about 8-celled stage of the proembryo, there are five to six layers of nuclei on the raphe side. A centripetal wall formation is initiated, the walls being first laid down in the micropylar region and proceed downwards, as well as inwards (figure 58). Ultimately the whole endosperm becomes cellular when the proembryo is at the early globular stage (figure 59). At this stage the cell wall of peripheral endosperm cells becomes thin and cellulosic and their protoplasts vacuolated but the central endosperm is at an early stage of wall formation. By the end of the heart-shaped embryo (figures 65, 66), the wall of endosperm cells becomes thick and accumulates oil globules, druses and aleurone grains.

The zygote divides transversely forming the apical cell (ca) and basal cell (cb) (figure 60). Both ca and cb divide transversely. The cell ca gives rise to l and l′ and cb forms m and ci. Thus a 4-celled linear proembryo is obtained (figure 61). The cells l, l′, m and ci divide transversely but one of the resultant cells from l′ further divides obliquely, thus forming a 9-celled filamentous proembryo (figure 62).
The divisions in the derivatives of cells ci and m are transverse while the derivatives of l divide both transversely and longitudinally the cells of l divide only longitudinally (figure 63). By subsequent transverse and longitudinal divisions the cells ci and m contribute to the formation of multiseriate suspensor and root cap; the cells l form root tip and hypocotyl, the cells l give rise to the cotyledons and stem apex (figure 64). According to Souèges (1926, 1954, 1958) classification, the development of the embryo conforms to the Solanad type. Passing through globular and heart-shaped stages the embryo becomes dicotyledonous (figure 67).

4. Discussion

The flowers of *D. muricatus* are small and borne in compound umbels. The total number of the flowers in the first order umbels shows a continuous decrease in the subsequently higher order umbels. This is similar to that found elsewhere in the Causalidae. The centripetal arrangement of the floral primordia observed in *Daucus* has been reported in several other species of the tribe (Borthwick 1931a Al-Attar 1974; Majumdar 1942, 1947; Rodrigues 1957). So far as sequence of initiation of the floral whorls is concerned, *D. muricatus* resemble *D. carota* (Borthwick 1931a) and *Chaetos-ciadium trichospermum*, *Pseudoryya pumila* and *Torilis nodosa* (Al-Attar 1974) in that stamens and petals are initiated approximately at the same time, followed by carpel. This is in contrast to two other types of floral developments described by Sieler (1870). In all umbelliferous species each locule contains two ovules except *Hydrocotyle farmosana* where one develops in each locule (Tseng 1965). Other characters common to those of Bentham and Hooker group of genera investigated resemble in many embryological characters such as presence of chalazal hypostase, funicular obturator, a single megaspore mother cell and presence of endothelium (Gupta 1964; Sehgal 1965; Borthwick 1931b; Paliwal 1950; Al-Attar 1974; Adatia and Shah 1952). All three major types of embryo sac developments were described by Håkansson (1923, 1952) and other investigators in umbelliferae. The first type to which *Daucus* belongs has an embryo sac of monosporic, 8-nucleate polygonum type. Sixty genera of apioidae, four genera of saniculoideae and four genera of Hydrocotylodeae show this common type. The second type to which *Bupleurum aureum* belongs has 8-nucleate bisporic allium type. The third type to which Drusa, Bowlesia and Azorella belong has tetrasporic 16-nucleate.

*Azorella* is *Penaea* type while Drusa and Bowlesia are Drusa type. However, the Causalidae of Bentham and Hooker group of genera investigated exhibit the normal monosporic 8-nucleate polygonum type (Håkansson 1923, 1952; Al-Attar 1974; Gupta 1964; Sehgal 1965; Borthwick 1931b).

The development of microsporangia and microspores is uniform in the family and the pollen grains are 3-celled at the time of shedding. The endosperm is of nuclear type, later it becomes cellular (Singh and Gupta 1956; Nordheim 1930; Gupta and Gupta 1964; Gupta 1964; Håkansson 1923; Al-Attar 1977). Although the investigators agree that mostly the embryogeny in the family is of Solanad type, there do exist some variations. Borthwick (1931b), who investigated *D. carota*, contradicted Souèges (1954, 1958) interpretation that the fate and contribution of the cells of the 4-celled proembryo is always fixed. Håkansson (1952) has also supported Borthwick (1931b) in his study on *Bowlesia tenera*. 
5. Summary and conclusions

The flowers in *D. muricatus* (L.) L. are borne in compound umbels and generally hermaphrodite. A few flowers develop into males owing to the abortion of the ovary, style and stigma. The ovary is inferior, bicarpellary, syncarpous and bilocular. There are two pendulous ovules initiated in each carpel; however, the lower only develops to maturity. The ovules are unitegmic and tenuinucellate. The inner epidermis of the integument is differentiated into an endothelium. There is a hypostase in the chalazal region of the ovule below the embryo sac. The funicular epidermis develops into obturator, there is one hypodermal archesporial cell which functions as the megaspore mother cell. It divides meiotically to form a linear tetrad of megaspore. The chalazal megaspore develops into mature embryo sac while others degenerate. The development of anther wall conforms to the dicotyledonous type. The microspore mother cells show nonsynchronous division in the four locules of an anther or a tendency towards nonsynchronous division within the same locule was also observed. The development of the embryo sac is of polygonum type. The endosperm is of nuclear type, it becomes cellular later. The embryogeny conforms to the Solanad type. It is suggested that *Daucus* be placed in the tribe Caucalideae of Bentham and Hooker.

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