Floral Morphology and Embryology of *Acer oblongum*

By

Ishwari Khushalani

Department of Botany, Birla College, Pilani (Rajasthan), India

With 66 Figures

Received May 30, 1963

Contents

1. Introduction

Bentham & Hooker 1862: 409 included *Acer* in *Sapindaceae* while some taxonomists have separated it from *Sapindaceae* and included under the family *Aceraceae* (Lawrence 1958, Hutchinson 1959, Copeland 1957, Porter 1959). Embryology of *Acer* is very little understood. Mottier 1893 worked out the development of embryo sac in *Acer rubrum*. However, some work has been done on the floral anatomy of the family. Saunders 1939, briefly described the floral anatomy of *Acer pseudoplatanus* and *A. negundo*. Hall 1951 has reviewed the earlier literature on *Aceraceae* and given a detailed account of the floral anatomy of *Acer*. On the basis of the floral anatomy Hall 1951 has divided nine species of *Acer* into six anatomical types, forming a single series, from the most primitive to the most highly evolved. Hall 1954 has described the variability in the floral anatomy of *Acer negundo*. Hall 1959 while studying the inflorescence in the *Aceraceae* confirmed the view that simpler inflorescence types have been derived phylogenetically from more complex ones through loss of branches and the shortening of internodes. *Aceraceae* provides an excellent material for such a study since they include a wide variety of inflorescence types within a group of closely related species.

2. Materials and methods

Acer oblongum was collected from Ootacamund and fixed in formalin-acetic-alcohol. Dehydration and imbedding were followed according to the usual alcohol xylol paraffin method. Sections were cut at 6—15 μ. For embryological purpose staining was done with combinations of safranin and fast green, safranin and light green and Heidenhains iron-alum haematoxylin. For the floral anatomy the combination erythrosine and crystal violet gave better results.

3. Observations

3. 1. External morphology

The small pedicellate flowers borne on panicles, are hypogynous and actinomorphic having five imbricate sepals and five free petals. A very distinctly lobed disc is present within the petals. The stamens are in two whorls, the outer whorl consists of five and the inner one of four stamens. The number of stamens varies from eight to nine but in all the cases, the antipetalous stames are suppressed. The ovary is superior, bicarpellary and compressed at right angles to the septum. There are two distinct and divergent styles, each having a terminal stigma.

3. 2. Floral anatomy

The floral anatomy described here is that of the functionally bisexual flower with five sepals, five petals, nine stamens occuring in two whorls of five and four respectively and a bicarpellary ovary (Fig. 1) *).

The pedicel consists of a siphonostele in the centre (Fig. 2). In the receptacular region the stele bulges out to give five traces which constitute the fused sepal and petal supply. Three out of these five traces are given off slightly at lower level (Figs. 3 and 4). Each of these traces is resolved into three branches (Figs. 5 & 6), the middle one of which forms the midrib of the sepal, while the lateral two branches once again bifurcate (Fig. 6). The inner branches of these enter the sepal, thus forming the two marginals of the same sepal while the outer ones move out tangentially. Two such branches of the adjacent sides unite and later on each of these fused bundles enters the petal (Fig. 7). The gaps created by the fused sepal and petal

---

*) Abbreviations in figures 1—66: anp = antipodal cells, cb = carpellary wall bundles, cd = carpel dorsal, cr = carpel, cv = carpel ventral, di = disc, ds = disc supply, eg = egg, end = endosperm, hyp = hypostase, ii = inner integument, lo = locules, nc = nucellar cap, nu = nucellus, ob = obturator, oi = outer integument, ot = ovular trace, pe = petal, pn = polar nuclei, pt = petal trace, pt' = pollen tube, se = sepal, sm = stamen, sn = secondary nucleus, spe = sepal lateral, spm = sepal dorsal, spt = sepal petal trace, st = staminal trace, syd = synergids, vb = vascular bundle.

are closed soon. At the higher level each petal has only one central bundle which does not divide further while each sepal is supplied with three.

The central stele, at a slightly higher level, gives out eight traces which constitute the supply of disc, stamens and ovary wall (Fig. 8). Small irregular branches are given off from these traces towards the outer side for the disc (Figs. 9, 10). At a slightly higher level, the staminal traces are separated from the two dorsals and several carpellary wall traces to which they were fused at the lower level (Fig. 10). All the staminal traces arise at the same level.

In the centre now are left two bundles which are fused ventrals of the two carpels (Figs. 8—11). At this level the lower portions of the locules are marked off (Fig. 12). Before supplying the ovules each of the fused ventral divides (Fig. 13) into two and these become inversely oriented (Fig. 14). After giving off the traces to the ovules these ventral bundles move to the septal radii where they fuse with the carpellary wall bundles (Fig. 15). At the terminus of the ovular region the ventral bundles travel along with the two dorsals through the stylar region (Figs. 16—18). At a higher level one dorsal and the two ventrals of one carpel fuse together. Thus, in the tip region each stigmatic lobe has a single bundle.

3.3. Organography and Organogeny

Unicellular hairs are present on some of the floral parts. The cell destined to develop into a hair gets differentiated from the rest of the cells (Fig. 19) by a large nucleus and its large size. Later on, it becomes papillate (Fig. 20), increases in length, and becomes vacuolated (Fig. 21). Along with the unicellular hairs, stalked multicellular glands are also present on the outer side of the ovary wall.

The precursor of a gland becomes differentiated from the rest of the cells with a prominent nucleus and protrudes out slightly (Fig. 22). It divides transversely forming an outer and an inner cell (Fig. 23), the inner one being in continuation with the epidermis. The outer cell divides first transversely and later in various planes to form the stalk and head of the gland (Figs. 24, 25).

In this plant two types of ovaries are found, one with stunted growth having papillate hairs on the stigma and another which is with a normal growth, the latter being more common. Though the ovay may be stunted, the embryo sacs in the ovules of these ovaries are quite normal and even fertilization has been found to have taken place. The funicular obturator is present and its cells are elongated and vacuolated.

There are two anatropus, superimposed ovules in each locule of the normal ovary. The funicular obturator is present and its cells are elongated and vacuolated.

The floral organs develop in the sequence, sepals, petals, disc, stamens and carpels (Figs. 26—28).

3. 4. Microsporogenesis and male gametophyte

The young anther of the flower is four-lobed (Fig. 29). The primary partietal layer cut off by the archesporium divides to form four layers of cells beneath the epidermis. The cells of epidermis become tangentially elongated and their cytoplasm is gathered on one side. The subepidermal layer develops into the endothecium, the cells of which become radially elongated and develop the characteristic fibrous thickenings when uninucleate pollen grains are formed in the microsporangium (Fig. 30). Just beneath the endothecium are two middle layers, which get crushed and absorbed. No trace of them is found when the pollen grains are uninucleate (Fig. 30).

The innermost wall layer is the tapetum. Its cells are uninucleate at first but they become two-three-nucleate at the time of the meiotic divisions in the microspore mother cells. Some of the tapetal nuclei are very large and contain a varying number of nucleoli. The nuclei often fuse with each other. The tapetum is of glandular type (Fig. 31). When the uninucleate pollen grains are distinguished in the anther, the tapetal cells show signs of degeneration.

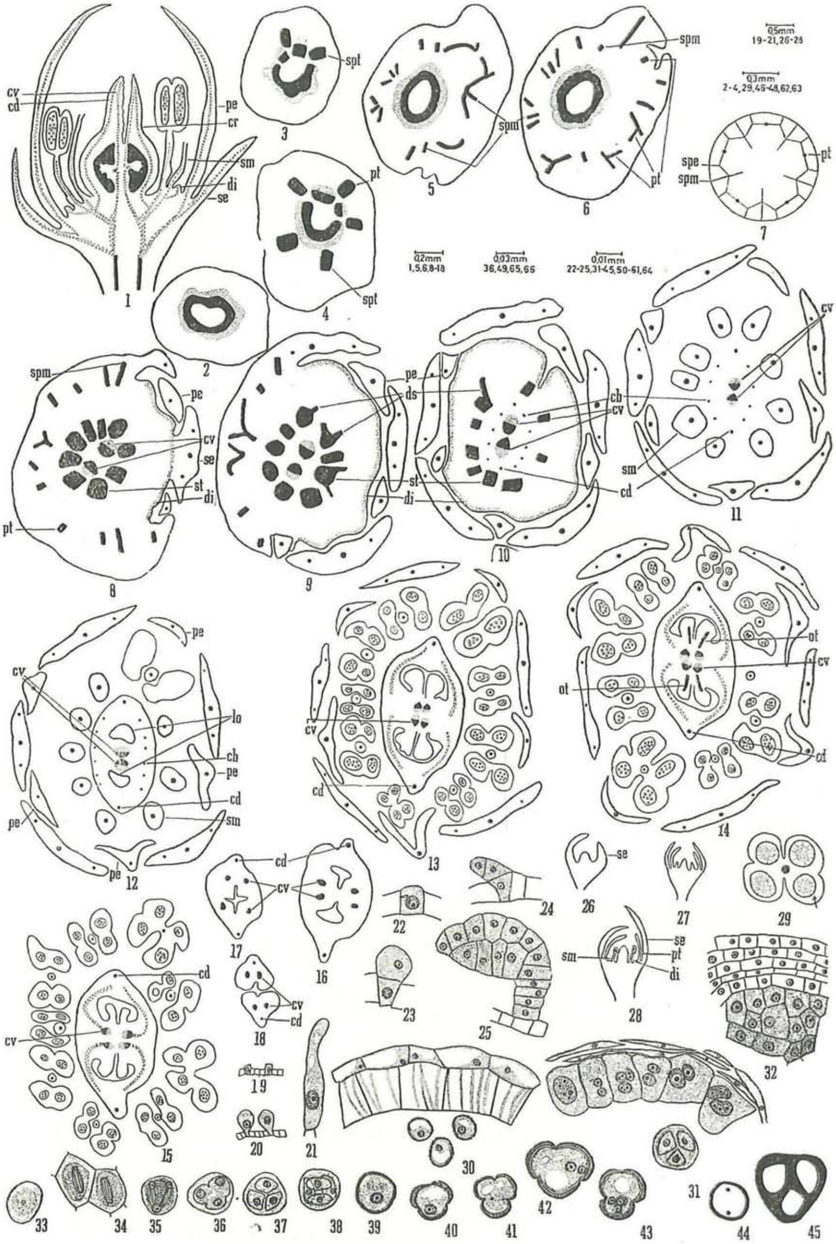
The primary sporogenous cells function directly as the spore mother cells (Fig. 32).

The mother cells undergo usual meiotic divisions in a simultaneous manner, forming isobilateral and tetrahedral tetrads, the latter being more predominant. The divisions are not synchronous in the four lobes of the anther. Quadripartition takes place by centripetal furrowing (Figs. 33—38). Later the microspores acquire their own walls. The young microspore has a dense cytoplasm and a centrally placed large nucleus (Fig. 39). The development of male gametophyte is in a normal way. Generally the pollen

---

Explanation of figures

Figs. 1—45, *Acer oblongum*. — Fig. 1, L. S. of the flower. — Fig. 7, A diagrammatic representation. Figs. 2—7 and 8—18, Serial transection of the flower from pedicel onwards. (Sepals and petals avoided in Fig. 15). — Fig. 19—21, Development of the hairs, which are found on the inner side of the ovary wall. — Figs. 22—25, Development of the gland. — Figs. 26—28, Development of floral organs. — Fig. 29, T. S. of young anther. — Fig. 30, Fibrous thickenings in the endothecium. — Fig. 31, Multinucleate, multinucleolate and vacuolated tapetal cells are seen, along with the degenerating middle layers. — Fig. 32, It is an enlargement of the portion marked by arrow in Fig. 29. It shows the wall layers and the sporogenous tissue. — Figs. 33—36, Meiotic divisions of the microspore mother cell. — Figs. 37—38, Tetrahedral and isobilateral tetrads. — Fig. 39—40, Uninucleate pollen grains. — Fig. 41, Division of the nucleus in the microspore. — Fig. 42, Bicelled pollen grain. — Fig. 43, Three-celled pollen grain. — Figs. 44—45, Degeneration taking place after the first and the second division in the microspore mother cell.



Figs. 1 – 45. For explanation see opposite page.

grains are shed at two-celled stage but in one case, a three-celled pollen grain was observed (Fig. 43).

Pollen grains are tricolporate. Sterility of pollen grains is very high. Some of the dyads and tetrads were also degenerating (Figs. 44—45).

3. 5. Megasporogenesis and female gametophyte

The ovules are bitegmic, crassinucellate and anatropous. The ovular protuberance is erect at the earlier stages (Fig. 46). Soon it curves (Fig. 47), and at the eight-nucleate embryo sac stage, it becomes anatropous (Fig. 48). The inner integument develops when the hypodermal archesporium is distinguished in the young nucellus. The outer one also develops soon. The micropyle is formed by the inner integument. A nucellar cap is present which is eight to ten cell layers in thickness at the mature embryo sac stage (Fig. 49).

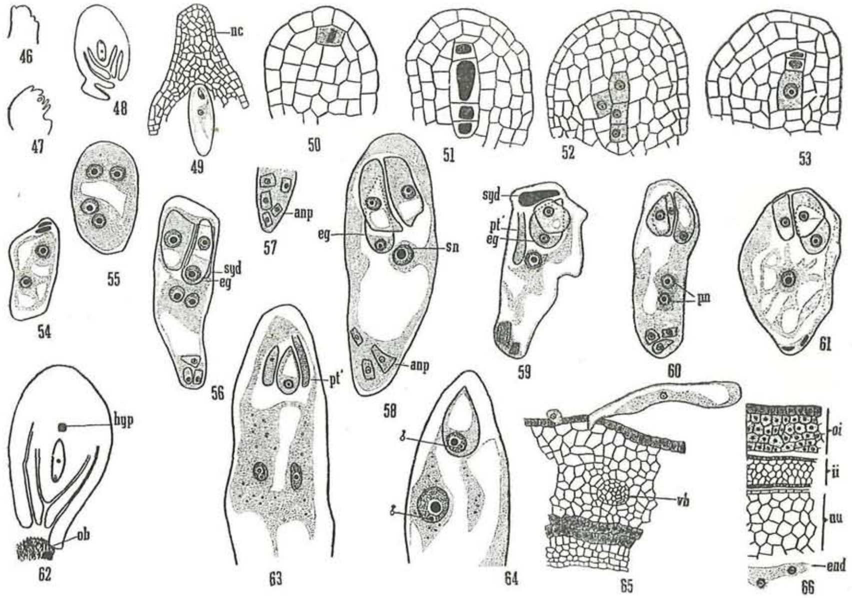
The single hypodermal archesporial cell divides periclinally to form a primary parietal cell and a primary sporogenous cell (Fig. 50). The primary parietal cell undergoes further periclinal divisions while the primary sporogenous cell functions directly as the megaspore mother cell.

The megaspore mother cell increases in size and undergoes the usual meiotic divisions to form the tetrad. In most of the cases linear tetrads are formed but in one case an almost T-shaped tetrad was observed (Fig. 52). In one case of the linear tetrad all the spores had degenerated (Fig. 51). The chalazal megaspore is usually functional. In Fig. 53, two degenerating spores at the micropylar end were observed. The development of the embryo sac conforms to the *Polygonum*-type (Figs. 54—56). The mature embryo sac has a narrow chalazal end and a broad micropylar end. The synergids are hooked and the egg is flask-shaped. The three antipodal cells may degenerate soon. More than three antipodal cells have also been observed (Fig. 57). The embryo sac contains numerous starch grains (Fig. 63). The two polar nuclei meet slightly above the centre (Fig. 58). In the ovaries with stunted growth, the embryo sacs were of a normal type. Even a pollen tube has been observed lying in the embryo sac in one case (Fig. 59). Figures 60 and 61 show mature embryo sacs. The funicular obturator is seen crushed in the later stages. A well marked hypostase is present (Fig. 62).

The entry of the pollen tube is through the micropyle. The remnants of the pollen tube have been observed (Fig. 63). In one case, one male gamete is seen fusing with the egg and another with the secondary nucleus (Fig. 63).

3. 6. Endosperm

The endosperm is of the Nuclear type (Fig. 65). The development of the embryo is arrested for a long time. The seeds from the fruits which were naturally shed showed only undivided zygotes with many endosperm nuclei.



Figs. 46—66, *Acer oblongum* (contd.). — Figs. 46—48, Development of an ovule. — Fig. 49, Formation of the nucellar cap. — Fig. 50, A hypodermal archesporium. — Fig. 51, Linear degenerating tetrad of the megaspores. — Fig. 52, An almost T-shaped tetrad. — Fig. 53, Functioning megaspore. — Figs. 54, 55, Bi-nucleate and four-nucleate embryo sacs. — Fig. 56, Mature embryo sac. — Fig. 57, Chalazal portion showing five antipodal cells. — Figs. 58—61, Mature embryo sacs. — Fig. 62, An ouvle after fertilisation, obturator cells are crushed. — Fig. 63, Shows the remnants of the pollen tube and synergids and also the two endosperm nuclei have been formed. — Fig. 64, Syngamy and triple fusion is seen. — Fig. 65, Pericarp with vascular bundle and the hairs. — Fig. 66, Portion of the seed coat shown in L. S.

3. 7. Pericarp and seed

Figure 66 shows the section of the ovary wall before the fertilisation has taken place. The young seeds have an outer integument of seven to eight layers. The inner integument consists of four to five layers, the massive nucellus is nine layers thick (Fig. 66).

4. Discussion

The five sepals are free. The traces of the sepals and petals are combined only in the cortex region. Each trace divides into three. Median branch forms the sepal dorsal, while the lateral branches of the trace bifurcate. The inner branches of these form the sepal laterals and the two outer branches of the two adjacent traces fuse and form a petal trace. This phenomenon raises a question as to whether it is brought about by shifting of the sepal laterals to petal trace or vice-versa? Or it is the internode between the lateral sepal traces and petal traces reduced thus bringing together the two whorls of the traces and ultimately bringing about the fusion? Earlier, PURI 1942 and 1954 having observed a similar condition in *Moringaceae* and *Cucurbitaceae* has propounded the view that it is a case of adnation where bundles arising very closely to each other or in the same sector often remain united for shorter or longer distances.

The petal trace in *Acer oblongum* does not divide in the petal even at the higher level. The disc receives the supply from the staminal traces. It will not be proper on the part of the author to draw any conclusions regarding the nature of the disc only on the basis of one species.

The stamens are in two whorls, with five stamens in the outer whorl and four in the inner. Since the vascular bundles to all the stamens diverge out at the same level from the central stele, then it may be assumed that the original two whorls of the traces of stamens have been compressed into one whorl due to the lack of the space. Reduction in the number of the stamens has involved the antipetalous whorl in *Acer oblongum*.

The ovary is bicarpellary and syncarpous. The syncarpy affects the vascular system also. The single dorsal bundle was distinguished by its prominent size among the carpellary wall branches given off by the staminal traces, but the secondary marginals were not observed.

The ovary is bicarpellary and ovules are borne on the dorsal radii. The placental strands are formed by the ventrals of the same carpels and they lie opposite the dorsal bundles. Hence the placentation is axile in view of PURI's 1952 interpretation.

ALMSTEDT 1933 has proposed a phylogenetic series in *Aceraceae* on the basis of inflorescence. *Acer oblongum* is the most primitive type according to this series, the flowers being in loose panicles. Similarly the primitiveness of *Acer oblongum* is substantiated by basic vascularisation of the flower being similar to the 1st type of HALL's 1951 anatomical series. According to him the presence of disc is an additional factor in support of the primitiveness of the family *Aceraceae*. Considering all these aspects, *Acer oblongum* seems to be quite primitive in nature.

PAX 1885 suggested that *Acer* has been evolved from ancestors that were pentamerous in all whorls. Evidence in support of this interpretation was found in the androeceum of the flowers. The author supports PAYER 1857 who found evidence in the ontogeny of *A. tatarium* which has a complete pentamerous antisepalous whorl of which two or three stamens have been lost phylogenetically.

MOTTIER 1893 while studying the development of the embryo sac in *Acer rubrum* states that "The mother cell in all probability arises from a single hypodermal cell, but as growth proceeds it becomes more deeply situated in the nucellus by the multiplication of epidermal cells by tangential or periclinal division." The above statement indicates that the mother cell is deeply situated due the repeated division of the epidermis. While describing the mode of the division of the megaspore mother cell in *Acer rubrum* MOTTIER 1893 states "this cell which has now elongated considerably divides by a wall at right angles to its long axis. The upper cell divides again in a similar manner so that there are three cells resulting from the mother cell. The lower one of these three now enlarges gradually absorbing the two upper, its large nucleus soon divides".

A T-shaped tetrad was seen in *A. oblongum.* Five antipodal cells were observed in one case only. MOTTIER 1893 in *A. rubrum* reported only three antipodal cells and in one case he observed three antipodal cells lying close to each other without any walls.

5. Summary

The flowers of *Acer oblongum* are pentamerous. Sepal and petal supply arise conjointly. The disc is supplied by the staminal traces. The stamens are in two whorls but their traces are given off at the same level. The dorsals and the carpellary wall bundles are fused with the staminal traces at an earlier stage. The placentation is axile.

The tapetum is secretory, the division of the microspore mother cells is simultaneous and the pollen grains are shed mostly at the two-celled stage. The ovules are bitegmic, crassinucellate and anatropous. Micropyle is formed by the inner integument. The development of the embryo sac conforms to *Polygonum*-type. The triple fusion has been observed. The endosperm is of the Nuclear type. *Acer oblongum* is considered to be the primitive species of the genus.

The author wishes to express her sincere thanks to Prof. B. N. MULAY for his valuable suggestions and interest in the work.

6. Literature cited

ALMSTEDT M. F. 1933. An anatomical study of inflorescence of certain species of *Acer.* — Thesis Cornell University.

BENTHAM G. & HOOKER J. D. 1862. Genera Plantarum, 1 (1). London.

COPELAND H. F. 1957. Forecast of a system of the dicotyledons. — Madroño, 14: 1—9.

HALL B. A. 1951. The floral anatomy of the genus *Acer.* — Amer. J. Bot. 38: 793—799.

— 1954. Variability in the floral anatomy of *Acer negundo.*

— 1959. Inflorescences in the *Aceraceae.* — IX. International bot. Congr. Proc. 2, 2a.

HUTCHINSON J. 1959. The families of flowering plants, I. Dicotyledons. Oxford.

LAWRENCE G. H. M. 1958. Taxonomy of vascular plants. New York.

MOTTIER D. M. 1893. Development of the embryo sac in *Acer rubrum.* — Bot. Gaz. 18: 375—377.

*) Pax F. 1885. Monographie der Gattung *Acer*. — Bot. Jb. 6: 287—374.

*) Payer J. B. 1857. Traité d' organogénie comparée de la fleur. Paris.

Porter C. L. 1959. Taxonomy of flowering plants. San Francisco and London.

Puri V. 1942. Studies in floral anatomy, II. Floral anatomy of the *Moringaceae* with reference to gynaecium constitution. — Proc. Nat. Inst. Sci. India, 8: 71—88.

— 1952. Placentation in Angiosperms. — Bot. Rev. 18: 603—651.

— 1954. Studies in floral anatomy, VII. On the placentation in the *Cucurbitaceae*. — Phytomorphology 4: 278—299.

Saunders K. 1939. Floral Morphology. A New outlook. Cambridge.

*) Not seen in original.

Zeitschrift/Journal: Phyton, Annales Rei Botanicae, Horn

Jahr/Year: 1963

Band/Volume: 10_3_4

Autor(en)/Author(s): Khushalani Ishwari

Artikel/Article: Floral Morphology and Embryology of Acer oblongum. 275-284