THE REPRODUCTIVE STRUCTURES OF FRAXINUS VELUTINA (OLEACEAE)

HERBERT F. COPELAND

The observations on floral structure and embryogeny in *Fraxinus velutina* Torrey, called the Arizona ash, which are here presented, were undertaken because an abundance of material was available; and because the facts as to Oleaceae assembled in Schnarf's (1931) *Vergleichende Embryologie der Angiospermen* were fragmentary, including no reasonably complete account of any single species.

Material was collected from trees cultivated on the grounds of Sacramento City College during the years 1957 to 1959. It was treated by routine microtechnical methods: fixed in Bouin's fluid and stained with Delafield's haematoxylin, Heidenhain's haematoxylin, or safranine and light green.

In the library, consulted when a certain acquaintance with the plant had been attained, I found out that the microscopic reproductive features of the Oleaceae are no longer poorly known; also, that there has been disagreement as to the proper place of Oleaceae in the taxonomic system. These matters are discussed in later sections of this paper.

THE TREE

Fraxinus velutina occurs near springs and along streams in western Texas, New Mexico, Arizona, and southern California. Pratt (1922?) wrote of it as apparently new in cultivation and recommended it as resistant to alkali and drought. It is widely planted in northern California, where it is seen to survive with little or no irrigation, but to flourish in watered lawns.

Munz and Laudermilk (1949) refer all plants of this species which are native in California to var. *coriacea* (Watson) Rehder, and I have been uncertain of the identity of the cultivated material. Taylor (1945) found the species diploid (2n = 46) and the variety tetraploid (2n = 92). The cultivated trees are diploid (n = 23), and are to be referred to the species.

As a typical ash, this is a deciduous tree bearing opposite pinnate leaves and producing samaras. It belongs to the group of ashes in which the flowers are apetalous and dioecious. Flower clusters appear in the axils of the proximal fallen leaves of the previous year during the month of February. Pollination is evidently by wind. In March, the staminate flowers fall, and the leaves begin to unfold. The samaras grow to their full size by the end of May, but the seeds are not mature until autumn. The samaras are shed, along with the leaves, in autumn storms.

The flower clusters are dense glomerules. After anthesis, the axes of the pistillate clusters become elongate, and it is seen that they are freely branched in a decussate pattern. All of the flowers or fruits of a particular

cluster are at a particular time in nearly the same stage of development; most axes bear terminal flowers; hence, the clusters are to be construed as thyrses.

MALE STRUCTURES

The staminate flower (fig. 1) consists, beyond its receptacle, of a calyx which is reduced to a minute toothed cup and of two stamens having brief filaments and prominent basifixed extrorse anthers. The vascular supply of this flower (fig. 2) consists of a cylinder of tissue originating from the two sides of a bract gap, emitting a cycle of a small indefinite number of feebly developed traces to the calyx, and then splitting into two bundles which ascend the connectives of the anthers to their summits.

The anthers are of the structure usual in flowering plants. The cells of the endothecium duly develop ribbed walls, and the dehiscence of the anthers, which occurs through the usual two lengthwise clefts, is produced by their contraction. The tapetum is of the secretion type. The nuclei of the tapetal cells divide more than once, and then undergo fusions, with the result that just before the tapetum is absorbed its cells contain varying numbers of large nuclei with varying numbers of nucleoli (figs. 3, 4).

The haploid chromosome number, observed during meiosis in the pollen mother cells, is 23 (figs. 5, 6, 7). The pollen grains are separated by simultaneous furrowing. When mature, they are four-grooved, having the surfaces between the grooves finely pitted, and contain a tube nucleus and a generative cell (fig. 8).

THE PISTILLATE FLOWER

The pistillate flower (fig. 9) consists, beyond its receptacle, of a cup-shaped calyx with a dentate margin and a compound pistil of two carpels. The ovary contains two locules. The septum between the locules is punctured by a small cleft near its upper end: the upper ends of the locules are continuous. Each locule contains two ovules which are pendant from the distal area of the septum. The ovary is flattened contrary to the narrow septum (fig. 13); the flattening is moderate through most of the height of the ovary, but is greater in the upper part. The brief style is cylindrical. The stigma is of two lobes which are pressed together when the flowers are first exposed but become separate at anthesis. The stigmatic surface is papillose.

The ovary bears a moderate number of peltate trichomes (figs. 15, 16) which are of the same nature as those which occur on leaves of *Syringa* and *Ligustrum*. The pedicel and flower bear also a few simple hairs, mostly on the margin of the calyx.

The vascular system supplying this flower is as follows (figs. 11, 12). The usual cylinder of vascular tissue ascends the pedicel. The calyx contains a whorl of a varying number of feebly developed bundles which fade out below. This means that the stele in the pedicel supplies only the pistil. The stele gives rise to an outer whorl of about fourteen bundles including (a) two well-marked carpel-dorsals, respectively ascending the
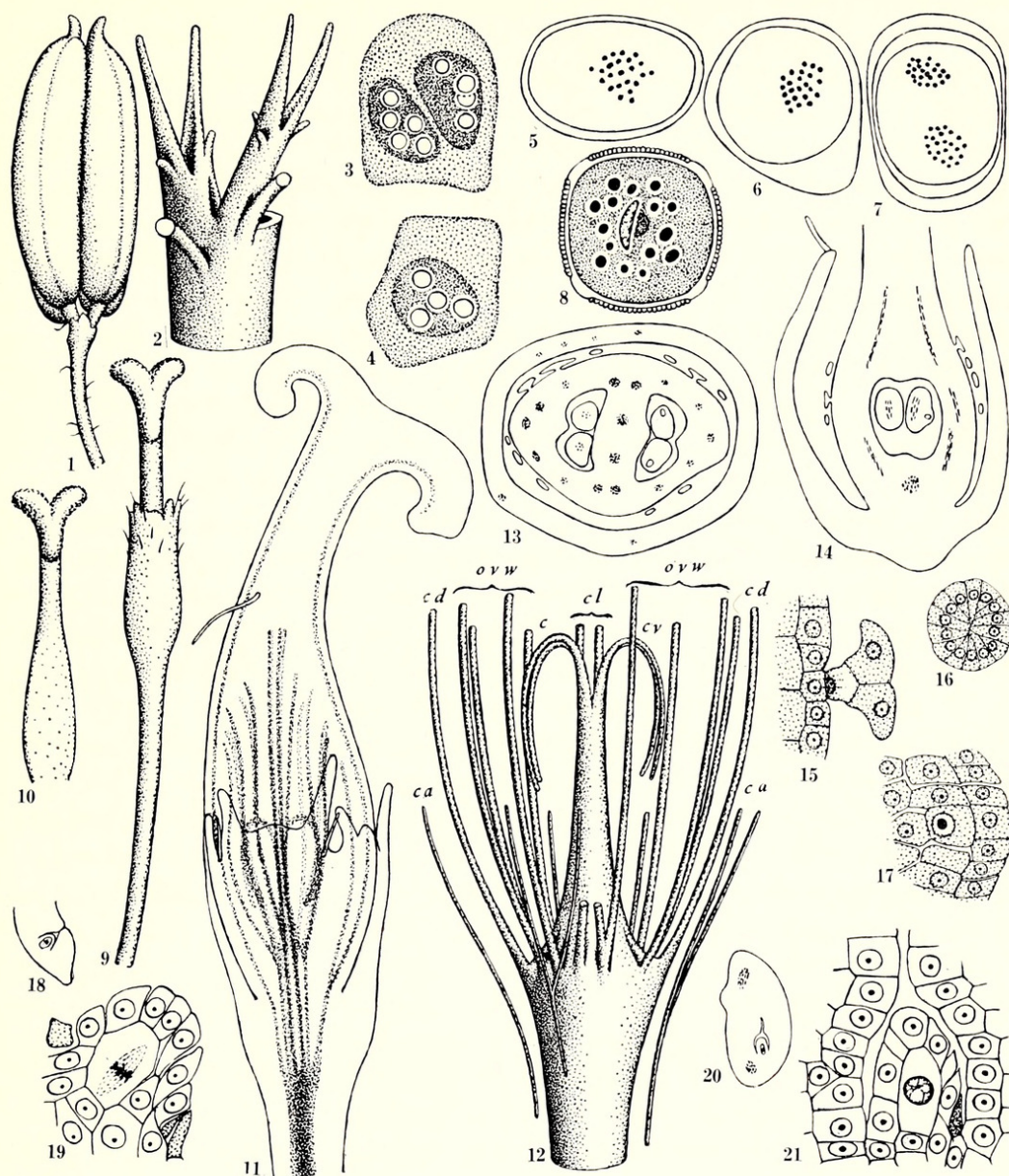
FIGS. 1–21. *Fraxinus velutina*: 1, staminate flower ×8; 2, vascular supply of two staminate flowers, × 40; 3, 4, mature cells of the tapetum, × 720; 5, 6, pollen mother cells with nucleus in heterotypic metaphase, × 720; 7, pollen mother cell with nucleus in heterotypic anaphase, × 720; 8, pollen grain, × 720; 9, pistillate flower, × 8; 10, pistil, × 8; 11, pistillate flower cleared in chlorine water, × 20; 12, model of vascular system in lower part of the pistillate flower, × 40; 13, cross section of young ovary, × 40; 14, longitudinal section of young overy, × 40; 15, 16, radial section and surface view of scale of ovary, × 320; 17, archesporial cell of young ovule, × 320; 18,19, longitudinal section of developing ovule, × 40, and nucellus of same showing megaspore mother nucleus in heterotypic metaphase, × 320; 20, 21, longitudinal section of ovule, × 40, and nucellus of same showing megaspore mother cell, × 320. *ca,* sepal bundles; *cd,* carpel dorsal bundles; *cl,* carpel lateral bundles; *cv,* carpel ventral bundles; *ovw,* ovary wall bundles.

margins of the ovary and continuing up the style into the stigmatic lobes; (b) a total of about eight ovary wall bundles, being about two on each

side of each carpel dorsal; and (c) a pair of well-marked carpel-laterals at each margin of the septum. Above the level of the locules, the ovary wall bundles and carpel laterals spread apart to form two fan-like layers toward the respective surfaces of the flattened upper part of the ovary. These bundles do not enter the style, but fade out. The vascular tissue which ascends beyond the departure of the whorl just described takes the form of an attenuate cone ascending the septum of the ovary. The cone splits to form two bundles located toward the margins of the septum, and each of these, toward the summit of the septum, splits in turn into two bundles which diverge and turn down to supply two ovules lying in different locules.

Ovule and Embryo Sac

When the pistillate flowers are first exposed, before the stigmatic lobes swing apart and become receptive, one finds in each locule two immature ovules (figs. 13, 14) of the form of downward-pointing fingers. Each one contains a strand of immature vascular tissue. Each contains one hypodermal archesporial cell (fig. 17). The archesporial cells are located on the sides of the ovules which are away from the plane of the carpel-dorsal bundles: one sees them best in sections cut parallel to the septum.

The archesporial cell is itself the megaspore mother cell. It becomes elongate, and the epidermis covering it is pushed up as a scanty nucellus (figs. 19, 21). The tissue on all sides of the nucellus grows forth to form an integument. The growth is greatest on the side of the nucellus toward the original tip of the ovule, which now becomes the chalaza. The effect of this growth is to turn the nucellus toward the summit of the ovary, and to enclose it except for a narrow micropyle leading up from it (the growth of the ovule is illustrated only by two little diagrams, figs. 18, 20). The mature ovule is somewhat flattened between the septum and the ovary wall.

During the growth of the ovule as just described, spiral tracheids appear in the main bundle which runs down the raphe to the chalaza. At the same time, several additional bundles begin to undergo differentiation in the integument. These latter bundles, few but not of definite number, usually three or four, extend the length of the ovule from the end of the original bundle, in the chalaza, nearly to the level of the micropyle.

While the integument is growing up about the nucellus (fig. 18), the meiotic divisions of the nucleus of the megaspore mother cell, and the accompanying cell divisions, begin to take place (figs. 19, 22-24). A T-shaped tetrad of megaspores is produced. The spore at the chalazal end is functional.

The nucleus of the functional megaspore undergoes three successive divisions, while the three non-functional spores and the nucellus are absorbed (figs. 25, 26; the stage with eight free nuclei has not been seen). An embryo sac with an egg and two synergids, two polar nuclei and three antipodal cells, is organized (fig. 27). The antipodal cells appear moribund from the time when they are set apart, and soon disappear. During
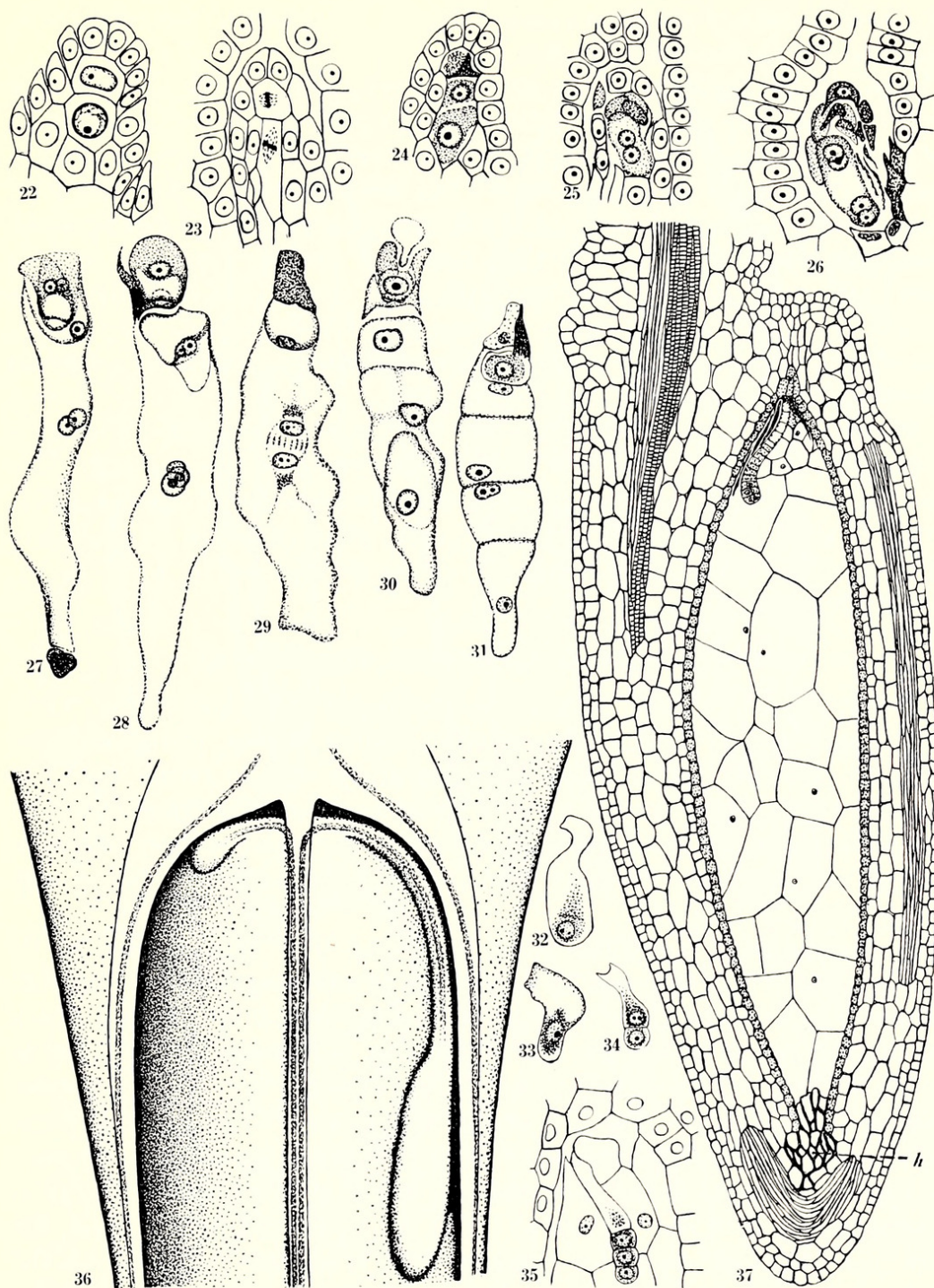
FIGS. 22–37. *Fraxinus velutina*: 22, nucellus showing diad cells, × 320; 23, homeo-typic metaphase, × 320; 24, tetrad of megaspores, × 320; 25, 2-nucleate embryo sac, ×320; 26, 4-nucleate embryo sac, ×320; 27, mature embryo sac, × 320; 28, fertiliza-tion, ×320; 29, first division of endosperm nucleus, × 320; 30, 31, zygote and endo-sperm in 4-celled stage, ×320; 32, 33, zygote about one month after fertilization, × 320; 34, first division of zygote, × 320; 35, four-celled embryo in many-celled endo-sperm, × 320; 36, dissection of lower part of fruit about two months after fertiliza-tion, × 20; 37, longitudinal section of seed at same stage as in fig. 36, × 80. *h,* hypostase.

the development of the embryo sac, the inner epidermis of the integument takes on the character of a jacket layer.

The meiotic divisions appear always to take place earlier in one of the four ovules of the ovary than in the others (figs. 18, 19 show the beginning of meiosis before the integument is fully developed; figs. 20, 21 show a fully formed ovule in which meiosis has not begun). Through all later stages, one ovule is always found in a more advanced stage of development than the others. More ovules than one may develop complete embryo sacs; pollen tubes may enter more than one ovule; but only the ovule which developed most rapidly is capable of maintaining an embryo. Developed embryo sacs in other ovules undergo degeneration by a process of collapse which begins at the chalazal end.

When the embryo sac is ready for fertilization, the ovule contains a hypostase, consisting of a small body of differentiated chalazal cells. It is recognizable by cell walls which are relatively retentive of the dye safranine; in sections stained with haematoxylin alone, it is not recognizable. It is separated from the chalazal end of the embryo sac by a few undifferentiated cells.

Fertilization, Endosperm, and Embryo

Pollen tubes have been seen in the micropyles of various ovules. Their discharged tips, of the form of heavily staining masses, have been seen between pairs of synergids in which the nuclei remain recognizable: it appears that both synergids survive for some time after the entrance of the pollen tube. On several slides, one sperm nucleus has been seen near the egg nucleus, while the other sperm nucleus is in process of fusing with the polar nuclei (fig. 28).

The endosperm is cellular from its origin. The first division of its nucleus (fig. 29) is followed by deposition of a transverse wall. The divisions of its daughter nuclei are followed by the deposition of walls which are transverse or nearly so: the endosperm passes through a stage in which it is a linear (or nearly linear) tetrad of cells (figs. 30, 31). During further multiplication, the cells of the endosperm do not become differentiated except for the crushing of some of them at the micropylar end; no haustoria are produced. The chalazal end of the endosperm digests or crushes the cells of the chalaza as far as the hypostase. For the rest, the endosperm does not digest the adjacent cells. It appears to press upon the jacket layer and the hypostase, and the integument grows along with the endosperm.

Fertilization having taken place early in March, the zygote remains undivided until about the beginning of May, by which time the endosperm is already many-celled. Before the zygote divides, it may become enlarged (figs. 32, 33). After it divides, the enlargement disappears; there is no exceptionally swollen cell at the base of the suspensor (figs. 34, 35). Dividing transversely, the zygote and its progeny produce a uniseriate filament of a dozen or more cells (figs. 37-39). The definitive embryo
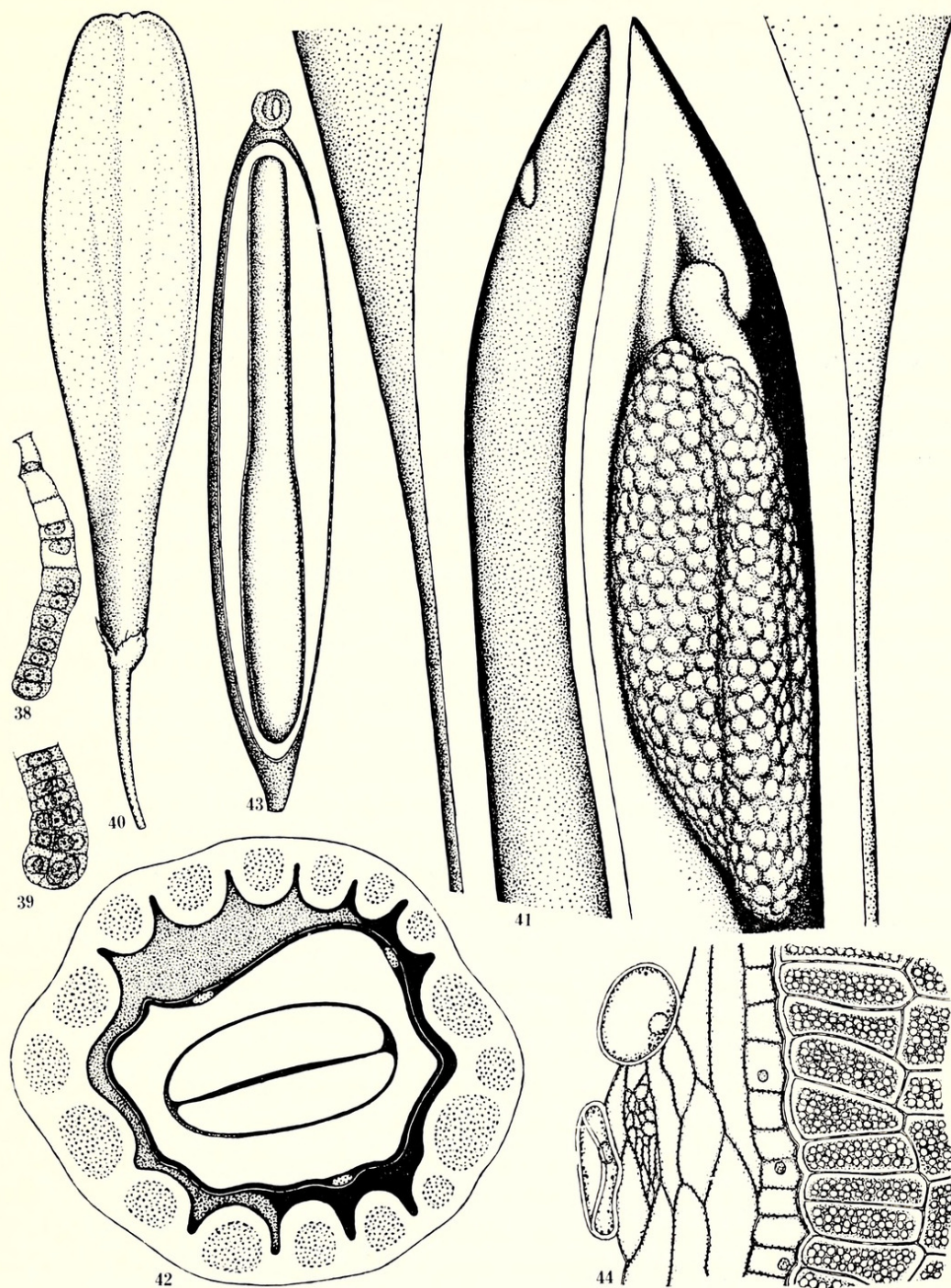
Figs. 38–44. *Fraxinus velutina*: 38, 39, embryos from same collection as figs. 36 and 37, × 320; 40, mature fruit, × 4; 41, dissection of lower part of mature fruit, × 20; 42, cross section of lower part of mature fruit, × 20; 43, dissection of seed (much longer than the one in fig. 41), × 8; 44, section of outer part of seed, seed coat to the left and endosperm to the right, × 320.

originates by longitudinal divisions in several cells at the distal end of this filament. The proximal cells lose their stainable contents, shrink, and disappear.

Fruit and Seed

Between early March and late May, growth of the ovary produces a samara of mature size. There are great differences in rate of growth between different parts of the ovary and different dimensions of the parts. The lower part of the ovary, originally a small moderately flattened cylinder, retains this shape while growing to seven or eight times its original dimensions. The upper part, while undergoing slight increase in thickness, grows to some fifteen times its original width and fifty times its original length. Thus it produces the wing of the samara. The wing is not derived from the style, which persists, if at all, as a withered terminal scrap.

The internal septum of the ovary, originally a wall with nearly plane surfaces, undergoes swelling immediately after fertilization and becomes fusiform. The bundles of the ovary wall become greatly enlarged by the differentiation of masses of fibers and form vertical ribs on the inner surface. Septum and ribs fill the locules, leaving scant clefts of complicated form.

Of the four ovules which are hung from the upper part of the septum, three undergo no growth, but turn dark and shrivel. The fourth develops at its proximal end a long funiculus which holds the main body of the developing seed at about the middle of the height of the septum (fig. 36). During the growth of the funiculus, its surface is thrown into microscopic transverse ridges.

The seed proper, enlarging principally after the beginning of July, reaches dimensions approximately half of those of the lower part of the fruit, that is, of the fruit apart from the wing (fig. 41). In the course of this growth, the seed presses into, and largely crushes, the enlarged septum. It pushes back the funiculus, throwing it into coils. The surface of the mature seed is yellow to brown, shiny, and minutely papillate.

Dissection shows the seed to have a thin coat covering an endosperm in which lies a large cylindrical embryo divided through the distal half of its length into two cotyledons (figs. 42, 43). The papillae on the surface of the seed are enlarged epidermal cells. The jacket layer, that is, the internal epidermis of the integument, remains intact. With the exception of the papillae, the jacket layer, and small bodies of fibers in the four or five longitudinal bundles, the cells of the integument are compressed and nearly empty. A definite continuous wall at the outer margin of the endosperm belongs to the endosperm, not to the jacket layer. The cells of the endosperm are packed with granules (fig. 44). These are definitely not of starch; they appear to be of protein.

Discussion

Schnarf's account of the embryology of Oleaceae consisted of scattered observations upon *Forsythia*, *Jasminum*, *Ligustrum*, and *Fraxinus* in the classic general papers of Hofmeister (1858), Warming (1878), Guignard (1882), Billings (1901), Juel (1915), and Dahlgren (1923, 1927). Sommer (1929) had studied *Fraxinus excelsior* among various plants in which

a distinction among the ovules of a single ovary, some continuing their development and others undergoing abortion, appears suddenly at a certain stage of development. Eames (1931) included *Syringa* and *Forsythia* among plants in which he studied the vascular supply of the pistil. Subsequent embryological studies include those of Andersson (1931) on a wide variety of Oleaceae, and of King (1938) and Messeri (1950) on the domestic olive, *Olea europaea*. Johnson (1941) included *Forsythia* among plants in which he studied the cytology of the male gametophyte. Fotidar (1942) studied the floral anatomy of *Nyctanthes*. Numerous counts of chromosomes are reported by Sax (1930), O'Mara (1930), Sax and Abbe (1932), Taylor (1945), and Dutt (1952); the contribution of Taylor is particularly interesting as including counts for *Fraxinus velutina* and its varieties, and as proposing to limit the subfamily Oleoideae to genera in which the basic chromosome number is 23, thus excluding *Jasminum* and *Menodora*.

The observations on *Fraxinus velutina* here presented are in very nearly complete agreement with the facts as to Oleaceae in general as stated in the literature just cited. Andersson noted in various Oleaceae the peculiar tapetum, characteristic of widely scattered presumably derived groups, in which the nuclei divide more than once. Johnson found the pollen grains of *Forsythia* binucleate. The vascular supply of the pistil, alike in *Syringa, Ligustrum, Nyctanthes,* and *Fraxinus,* exhibits slight variations upon a common pattern which is precisely that of the typical bicarpellate compound pistil according to the theory of Eames. The pattern of the vascular supply to the ovules is identical in *Olea* and *Fraxinus.* Billings was presumably mistaken in describing, in the ovule of *Fraxinus excelsior,* a single vascular strand which descends the raphe to the chalaza and ascends the integument on the side opposite the raphe. In *F. velutina,* as noted, a varying small number of bundles, in positions which vary from one ovule to another, run up from the chalaza; Fotidar observed the same structure in *Nyctanthes.* Also, as Dahlgren suspected, Billings was surely mistaken in figuring an ovule in which the megaspore mother cell is covered by more than one layer of cells of the nucellus: this appearance represents an oblique section of the ovule. In most Oleaceae, the embryo sac is of normal type and the definitive embryo develops from several distal cells of a filamentous early embryo. In these points, *Olea* appears exceptional: its embryo sac is said to be of *Scilla*-type and its filamentous early embryo is very short.

The proper location of Oleaceae in the taxonomic system is next to be discussed. The traditional place of the family is in an order named Contortae. The order was established by Linnaeus (1764) to include the plants subsequently assembled as families Apocynaceae and Asclepiadaceae. Of *Olea* and its allies, Linnaeus made a separate order Sepiariae; he placed *Gentiana* among primulaceous plants in his order Rotaceae. Eichler (1886) and Engler (1892) are responsible for assembling as order Contortae the families Oleaceae, Loganiaceae, Gentianaceae,

Apocynaceae, and Asclepiadaceae. In earlier presentations of the Englerian system, one finds the small tropical family Salvadoraceae placed next to Oleaceae; in later presentations it is dismissed from this neighborhood, surely correctly, since the ovules of Salvadoraceae have two integuments and a nucellus of more than one layer of cells (David, 1938). Wettstein (1908) followed Linnaeus and most pre-Englerian authors in placing Oleaceae in an order (he called it Ligustrales) separate from Contortae. Schnarf followed Wettstein, although expressing doubt that the families remaining in Contortae belong together as a natural group. Wettstein (1908) is authority for family Menyanthaceae, a segregate from Gentianaceae, and Schnarf (1931) is authority for family Buddleiaceae, a segregate from Loganiaceae. Tournay and Lawalrée (1952) transferred Menyanthaceae and Buddleiaceae from Contortae to Ligustrales.

Schnarf, and Tournay and Lawalrée, were influenced by embryological knowledge, including particularly the following point. The endosperm is nuclear in proper Loganiaceae and Gentianaceae, and in Apocynaceae and Asclepiadaceae. It is cellular in Buddleioideae, Menyanthoideae, and Oleaceae.

Assuming that the production of a nuclear endosperm is a primitive character from which the production of the cellular endosperm has repeatedly been derived, the presence of both types in a particular order or family is not by itself sufficient reason for dividing the group. We can interpret Loganioideae, Gentianoideae, Apocynaceae, and Asclepiadaceae as a natural series in which the primitive type of endosperm is retained, and Buddleioideae and Menyanthoideae as offshoots from it in which the derived type of endosperm has developed independently. This appears to be the idea of Moore (1947), who considers Loganiaceae to be an immediate ally or derivative of some primitive stock from which have evolved also the Tubiflorae (among which a repeated evolution of the cellular endosperm is evident) and the Rubiales (which retain the nuclear endosperm).

The Buddleioideae have a cellular endosperm with haustoria (Moore describes these as absent in *Polypremnum*, but one of his figures shows structures to which no other term can be applied) and an embryo developed from two cells terminal upon a three-celled suspensor (Souèges, 1940; Moore, 1948).

Of Menyanthoideae, the writer has learned nothing beyond what was known to Schnarf. A tapetum in which the nuclei divide more than once; an embryo sac of normal type, with fugitive antipodal cells; a cellular endosperm in which cell divisions beyond the first are transverse, and which lacks haustoria; and an early embryo of the form of a many-celled filament: all of these are characters in precise agreement with Oleaceae. To present knowledge it appears probable that the Oleaceae are derived from the Menyanthoideae and should be placed after that group.

SUMMARY

1. *Fraxinus velutina* Torrey, the Arizona ash, a tree of the southwest-

ern United States, is a typical ash of the group having dioecious apetalous flowers. The flowers and their vascular systems are described. The vascular system of the pistillate flower is very nearly that of the typical bicarpellate compound pistil according to the theory of Eames.

2. Staminate flowers consist of little more than two stamens with ribbed endothecia and tapeta in which the nuclei divide more than once and then undergo random fusions. The haploid chromosome number is 23. Pollen grains are 4-grooved, binucleate.

3. The ovules are unitegmous and tenuinucellate. They have several longitudinal bundles in the integument and an obscure hypostase in the chalaza. The inner epidermis of the integument becomes a jacket layer. Of four ovules in the ovary, only one becomes a seed.

4. The embryo sac is of normal type, the antipodal cells disappearing quickly.

5. Double fertilization was observed.

6. The endosperm is of cellular type. The first cell division is by a transverse wall; the second cell divisions are by walls which are transverse or nearly so. No haustoria are produced.

7. The zygote, after remaining undivided for several weeks, produces a filament of many cells. The embryo proper is derived from several cells at the distal end of this filament.

8. The single seed of the samara crowds aside or crushes other structures within the ovary and becomes mature in autumn. Papillae upon its surface are enlarged epidermal cells. The jacket layer persists to this stage. A continuous wall within the jacket layer is the outer cell wall of the endosperm. There is a large straight dicotyledonous embryo.

9. These observations, compared with others in the literature, tend to substantiate the naturalness of the family Oleaceae and the order Contortae. Among other Contortae, the Menyanthoideae appear most similar to Oleaceae in embryological characters.

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Sacramento City College
Sacramento 22, California
</div>

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A NEW SILENE FROM NORTHWESTERN CALIFORNIA

A. R. Kruckeberg[1]

Long past is the era in California botany when a collector could count among his season's haul a good proportion of undescribed species. Most areas of the state are sufficiently well known so as to limit the likelihood of uncovering anything new. Nowadays, range extensions, records of new adventives, and the discovery of some inconspicuous annual that fails to