

UOT:581.4

MORPHOGENETIC TYPES AND MODIFICATIONS OF FRUITS IN THE *OLEACEAE* FAMILY

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DOI: <https://doi.org/10.30546/2958-8111.2025.3.1134>

Abstract

In this study, the morphogenetic types and modifications of fruits in various taxa belonging to eight genera of the *Oleaceae* family were investigated. During the research, the main criterion for differentiating the morphogenetic fruit types of the different genera of *Oleaceae* was the localization of lignified tissues in various histogenetic regions of the pericarp. It was determined that the studied species exhibit four fruit types: drupe (*Forestiera*, *Olea*), winged dry fruit (*Fraxinus*, *Fontanesia*), capsule (*Syringa*, *Ligustrum*, *Forsythia*), and berry (*Jasminum*). The study also analyzed the arrangement of mechanical tissues in the pericarp of the investigated genera, examining the location and functional significance of these tissues, which is reflected in the findings of this work. During the study, it was determined that in the fruits of species belonging to the genus *Forsythia*, mechanical tissues develop only within the mesophyll of the fruit leaves, while parenchyma cells form the endocarp. In general, the analyses conducted showed that the *Forsythia*-type fruit can be noted as the ancestor within the *Oleaceae* family. The anatomical structure of the fruits of taxa belonging to the tribe *Oleeae* showed that the fruits of plant species belonging to this tribe are typical *Olea*-type seeded xenocarp fruits. During the study, it was determined that mechanical stress in plants of species belonging to the genus *Jasminum* is not due to the presence of a distinct sclerenchyma region, but to the heterogeneity of the mesocarp parenchyma cells.

Keywords: *Oleaceae*, fruit, modification, morphogenetic type, carpology, pericarp

Introduction

The family *Oleaceae* is regarded as one of the most important and significant groups of angiosperms, encompassing a wide diversity of life forms and exhibiting a broad geographical distribution. The taxa included within this family are notable for their ecological and biological significance under both in situ and ex situ conditions. In this context, the investigation of fruit morphological and anatomical characteristics holds particular importance in carpological studies of taxa belonging to this family. The structural features of fruits are considered critical not only for taxonomic identification but also for elucidating the evolutionary relationships among species.

Species and varieties within the *Oleaceae* family differ markedly in terms of fruit morphogenetic types and shapes. These differences are closely associated with floral structure, ovary development, and the processes occurring during ontogenesis. The fruits of taxa belonging to the studied genera within *Oleaceae* are observed to develop into various forms, including winged fruits, drupes, and capsules. These morphogenetic fruit types arise as adaptive responses to diverse ecological conditions and are often accompanied by modifications that play a crucial role in seed and fruit dispersal.

The study of fruit morphogenetic types and their modifications represents a key aspect in clarifying the phylogenetic relationships among species of the *Oleaceae* family, refining their systematic positions, and understanding their evolutionary pathways. In this regard, a comparative morphological and anatomical analysis of fruits across different genera within *Oleaceae* is highly relevant for both fundamental and applied research.

Accordingly, the present study aims to provide a systematic and comparative analysis of the morphogenetic fruit types of taxa within the *Oleaceae* family, with particular emphasis on their developmental characteristics and associated modifications.

The fruits of *Oleaceae* have long attracted researchers' attention as sources of phylogenetic information. For example, the presence of fleshy, single-seeded drupes was used to distinguish the subfamily *Oleoideae* [7, p.1508-1513]. Similarly, in the sectional classification of the genus *Jasminum*, A. P. de Candolle (1844) considered the morphological characteristics of fruits, a criterion that remains relevant to this day [4, p.8-13; 6, p.4-25].

In general, the fruits of *Oleaceae* representatives have not been thoroughly or comprehensively studied in Azerbaijan. Moreover, the literature on the morphology and anatomy of fruits in this family contains contradictory information. For instance, *Olea europaea* L., a well-known and relatively well-studied taxon, is often described as producing drupes, while some studies indicate that its fruit is apocarpous [5, p.112-118]. Other sources state that all representatives of *Oleaceae* possess syncarpous fruits [4, p.8-13; 6, p.4-25].

These discrepancies demonstrate the need for further study of *Oleaceae* fruits. Such research is crucial not only for understanding fruit structure and determining morphogenetic types, but also for providing key information for reconstructing the phylogenetic system of the family. Additionally, carpological research is particularly valuable due to the economic importance of *Oleaceae*, which includes widely cultivated ornamental genera such as *Syringa*, *Forsythia*, *Ligustrum*, *Fraxinus*, *Olea*, and *Jasminum*. In general, carpological studies contribute not only to structural botany but also to solving broader botanical and phylogenetic problems [9, p.125-131].

Materials and methods

In this study, mature fruits of species belonging to eight genera of the *Oleaceae* family were used as research material. For many species, fruits at different stages of development were examined. For several genera (e.g., *Forsythia*, *Jasminum*, *Olea*, etc.), studies on the histogenesis of the pericarp at various stages of fruit development were conducted. Flowers and floral buds at different developmental stages were also examined for *Jasminum arborensis*, *J. fruticans*, *J. nudiflorum*, and *J. officinale*.

During the course of the study, 20 samples were collected from each taxon. This sample size was considered sufficient for statistical analysis, and efforts were made to ensure equal sampling

across all studied taxa to enable reliable comparison.

For microscopic examination, four sections were prepared from the fruits of each taxon. Microtome sections were obtained at a thickness of 10–20 µm. In the analysis of the anatomical structure of fruits in taxa belonging to the *Oleaceae* family, it was observed that cell size and the thickness of tissue layers do not remain constant, but vary depending on species, fruit type, and developmental stage.

The average anatomical parameters recorded for taxa within the *Oleaceae* family were as follows: exocarp cell size ranged from 10 to 30 µm, with a cuticle thickness of 2–10 µm; mesocarp cell size ranged from 30 to 150 µm, with a layer thickness of 0.2–2 mm; and endocarp cell size ranged from 10 to 100 µm, with a layer thickness of 0.2–0.3 mm, depending on fruit type.

A comparative analysis of the morphogenetic traits and anatomical characteristics of the fruits of the studied taxa is presented in this research.

The research material was collected by the authors from the Institute of Dendrology of the Ministry of Science and Education of the Republic of Azerbaijan, the Central Botanical Garden, as well as from parks and gardens in Baku city.

For anatomical studies of the pericarp, preparations were made for observation under a light microscope. A MS-2 microtome was used for sectioning. Fresh, fleshy fruits were initially fixed in 70% ethanol. Mature dry fruits, as well as fruits from carpological and herbarium collections, were stored prior to analysis in Strasburger's mixture (distilled water: 96% ethanol: glycerin, 1:1:1). The duration of storage in Strasburger's mixture ranged from 10 to 30 days, depending on the size of the fruit and the thickness of the sclerenchyma tissue.

For sectioning, the plant material was embedded in paraffin blocks without prior treatment. Transverse sections were prepared from the middle portion of the fruit to study the pericarp anatomy, as these provide highly informative parameters for anatomical analysis [16, p.69-75; 17, p.59-67]. In some cases, longitudinal sections were also prepared to clarify structural features. Anatomical observations were carried out using a Mikmed-1 light microscope.

Fixation of the material, staining of sections, histochemical reactions, as well as localization of secondary metabolites, were performed following standard protocols [3, p.19-21]. Of particular importance were the observations of mechanical elements processed with phloroglucinol and concentrated hydrochloric acid, which provided information on cell shape and degree of lignification. Drawings of the preparations were produced using a PA-5 drawing apparatus. The ultrastructure of the dry fruit surface was examined using a Hitachi S-405A scanning electron microscope. Preparation for electron microscopy followed standard methods [3, p.19-21].

During the description of the pericarp, absolute cell size was not the main focus. Instead, emphasis was placed on the size of parenchyma cells in fleshy fruits, their formation, and changes in response to environmental conditions during maturation.

In the research work, mathematical and statistical calculations of experimental results were carried out using G.N. Zaytsev and statistical analyses were carried out using GraphPad Prism 7 and Microsoft Excel 2010 programs [20]. The formulas mentioned below were used.

1. Arithmetic $M = \sum x / N$
2. Variance: $\sum^2 = \sum (x-M)^2 / N-1$
3. Standard deviation: $\bar{\sigma} = \sqrt{\sum^2}$
4. Arithmetic mean deviation: $m = \bar{\sigma} / N$
5. Coefficient of variation: $\gamma = 100 \times \bar{\sigma} / M$

Results and discussions

During the analysis of the obtained data, the morphogenetic fruit types of the studied taxa were determined. As noted in the introduction, the morphogenetic type of a fruit can only be established after its anatomical structure has been thoroughly examined [1, p.71-74; 13, p.1-5]. Therefore, to differentiate between various morphogenetic fruit types, the primary criterion is the localization of lignified tissues within the distinct histogenetic zones of the pericarp. This approach en-

tures more accurate and reliable results. Analysis of the fruit structure of taxa belonging to the *Oleaceae* family allowed the identification of their morphogenetic types, and their main structural characteristics are summarized in Table 1.

Table 1. Morphogenetic fruit types of the studied genera of the *Oleaceae* family and the distribution of mechanical tissues in their pericarp

Fruit Type	Mechanical Tissue	Location of Tissue in Pericarp	Function / Importance
Drupe (stone fruit)	Sclereids	Endocarp	Protects the seed
Winged dry fruit	Sclerenchyma (fibers)	Mesocarp, Endocarp	Dispersal by wind
Capsule fruit	Sclerenchyma	Endocarp (dehiscence region)	Fruit opens (dehiscence)
Berry	Sclereids (weak)	Mesocarp (local areas)	Dispersal by animals

Genus *Forsythia* Vahl According to the literature, species of the genus *Forsythia* produce dehiscent dry capsule fruits. Each fruit can contain 8 to 20 seeds. Upon maturation, the fruits naturally split open, allowing seeds to disperse. Because they are characterized by loculicidal dehiscence (opening along the back of the fruit leaves).

Table 2. Morphological and Anatomical Structure of *Forsythia suspense* Fruit

General Feature of Fruit	Morphological Characteristics	Anatomical Characteristics
Type	Capsule fruit	Pericarp consists of 3 layers
Shape	Oblong with pointed ends	Outer layer cells are compact
Size	1.5–2 cm	Cell layers are tightly connected; cell walls are thick
Color	Brownish-yellow	–
Fruit dehiscence	Capsule opening with two valves (dehiscent capsule)	Well-developed mechanical tissues in the dehiscence zone
Number of seeds	Numerous	Seeds are located in the ovary cavity
Pericarp layers	Exocarp, mesocarp, endocarp	Exocarp – epidermal cells; mesocarp – parenchyma and mechanical tissues; endocarp – sclerenchyma cells
Mechanical tissues	Strengthen the fruit wall	Sclerenchyma, sclereids
Seed structure	Winged edges, flat	Seed coat composed of thick-walled cells

However, using the term “capsule” to describe fruits with dehiscence along the dorsal side of the carpels for all *Oleaceae* species is not entirely correct. Fruits with loculicidal dehiscence are highly diverse; they can be syncarpous or paracarpous, and superior or inferior. Most importantly, the anatomical structure of the pericarp in fruits with loculicidal dehiscence is very different. The fruit opening mechanism follows the same principle—uneven contraction of pericarp tissues during drying—but this process occurs differently across various taxonomic groups. The mechanical tissues that mediate fruit dehiscence can develop from different histogenetic zones of the carpels, which can lead to the formation of entirely different morphogenetic fruit types.

Consequently, it is not correct to directly compare the dried fruits of species in *Forsythia Vahl.* with those of another genus, such as *Parrotia C.A.Mey.*, because these genera differ in multi-

ple fundamental morphological and anatomical characteristics.

In species of the genus *Forsythia Vahl.*, mechanical tissues develop only within the mesophyll of the carpels, while the parenchyma cells form the endocarp (Table 2).

The arrangement of mechanical elements in this way, along with the lignification of the multilayered endocarp, forms the basis for identifying a distinct morphogenetic fruit type, the *Forsythia*-type capsule [9, p.125-131].

Overall, analyses have shown that the *Forsythia*-type fruit can be considered ancestral within the *Oleaceae* family. Based on the floral structure of taxa in the genus *Forsythia*, it closely resembles the hypothetical ancestral flower of *Oleaceae*, as suggested by T. F. Weber. This view has been supported by several researchers [6, p.4-25; 10, p.37- 41; 11, p.476-509; 12, p.8-11].

A notable feature indicating the primitiveness of the fruit structure in *Forsythia* species is that the dehiscence (fruit opening) zones are perforated with numerous parenchyma strands and reinforced by a thickened sklerenchyma region [10, p.31-37]. In contrast, taxa with larger fruits (e.g., *Nathusia Hochst.*) have relatively thinner sklerenchyma regions and more delicate parenchyma strands [10, p.41-43]. Another evidence of the primitive fruit structure is the high variability in ovule number, both within individuals and among taxa in the genus *Forsythia*.

Syringa L. – genus-The fruits of taxa in the genus *Syringa L.* are also capsules, similar to those of the genus *Forsythia*. Literature sources generally describe lilac fruits as capsules; however, several researchers have noted that this characterization may be inaccurate [14, p.577-592; 15, p.19-23; 18, p.1827-1841].

Table 3. Morphological and Anatomical Structure of *Syringa vulgaris* Fruit

General fruit characteristic	Botanical description
Fruit type	Dehiscent capsule
Fruit shape	Ovoid
Fruit size	1.5–2 cm
Color	Brown
Type of dehiscence	Capsule opening with two valves
Number of seeds	2–4
Seed shape	Flattened, winged
Seed dispersal	Wind-dispersed

Table 4. Anatomical structure of the pericarp of *Syringa vulgaris*

Layers of the fruit pericarp	Anatomical structure of the fruit
Exocarp	Composed of a single layer of cells, serving a protective function
Mesocarp	Mainly composed of parenchyma cells, occasionally containing mechanical tissues
Endocarp	Made of densely structured cells, playing a role in fruit dehiscence
Mechanical tissues	Sclerenchyma cells located in the walls of the capsule fruit, providing strength

Species of the genus *Syringa* exhibit fruit development characteristics similar to those of taxa in the genus *Nathusia Hochst.*. This similarity is evidenced by the presence of a normally formed dehiscence mechanism and a consistent number of ovules [18, p.1827-1841]. Anatomical studies of the pericarp in *Syringa* species have shown that, like other *Oleaceae*, the pericarp consists of three layers, with each layer composed of distinct cell types.

Genus *Ligustrum L.*

In general, the fruits of species in the genus *Ligustrum* have traditionally been considered capsule fruits [5, p.218-221]. However, analysis of the literature indicates that these fruits are more

diverse than they initially appear. Most *Ligustrum* species have fleshy fruits that have lost their dehiscence ability, though traces of the opening mechanism remain. The anatomical structure of *Ligustrum* fruits is similar to the characteristics described above.

It has been proposed that the fruit type of *Ligustrum* taxa can be considered as *Olea*-type pyrenaria (drupe-like fruits) [5, p.228-231]. By “pyrenaria,” we refer to syncarpous fruits with a single distinct stone. *Olea*-type pyrenaria are distinguished from other stone fruits by the localization of mechanical elements in the inner part of the mesocarp. It is suggested that the *Olea*-type stone fruit may have evolved directly from the *Forsythia*-type capsule fruit through compaction of the parenchyma in the pericarp and reduction of the dehiscence mechanism.

Although the fruits of *Ligustrum* taxa resemble the anatomical structure of *Syringa* fruits, *Ligustrum ibota* can still be classified as a typical *Forsythia*-type drupe (pyrenaria, stone fruit). At maturity, the parenchyma in the pericarp of *L. ibota* remains moist and, under various influences, can rapidly disintegrate. As a result, like *Syringa* taxa, the seeds are released into the environment via loculicidal dehiscence.

In fact, the fruits of *Ligustrum ibota* represent a stable transitional stage between *Forsythia*-type capsule fruits and *Olea*-type stone fruits (pyrenaria). Additionally, taxa in the genus *Ligustrum* exhibit a slight reduction in the number of ovary locules and ovules. Consequently, the fruits may occur as two-stoned, four-ovule pyrenaria; two-stoned, two-ovule pyrenaria; one-stoned, one-ovule pyrenaria; or as single-stoned syncarpous fruits [4, p.8-13].

In typical single-ovule plants, the reduction in the number of ovary locules or developed seeds to one reflects the general evolutionary trend in *Angiospermae* fruits, representing a transition to a single-seeded dispersal unit that facilitates seed distribution [5, p.43-51].

In *Ligustrum vulgare*, a different developmental pattern of fruit formation is observed, indicating variation within the genus.

Table 5. Morphological and anatomical structure of the fruit of *Ligustrum vulgare*

General characteristics of the fruit	Morphological characteristics of the fruit	Anatomical characteristics of the fruit
Fruit type	Berry	Pericarp consists of three layers
Fruit shape	Ovoid	Composed of densely packed parenchyma cells
Fruit size (diameter)	5–9 mm	Composed of thin-walled cells
Fruit color	Dark purple	Pigment substances present in epidermal cells
Exocarp	Thin-skinned	Single-layered epidermis with thick cuticle
Mesocarp	Juicy mesophyll	Mainly composed of parenchyma cells; occasionally mechanical tissues are present
Endocarp	Surrounds the seeds	Composed of dense cells
Number of seeds	1–3	Seed coat composed of thick-walled cells
Seed position	In the center of the fruit	Endosperm and embryo are well developed

The pericarp of the fruit in this species is entirely composed of parenchyma cells, which leads to the loss of both the dehiscence mechanism and the seed. The rudiments of the seed are distributed in groups of sclereids within the inner layers of the mesocarp parenchyma. As a result, the plant produces a syncarpous berry. By berry, we mean a fruit that lacks the sclerenchyma region in the pericarp. It should be noted that although the fruits of *Ligustrum vulgare* have evolved different-

ly from most other taxa in the genus, the number of developed seeds is reduced (one seed) (Table 5). The fruits of *Ligustrum ibota* represent the most primitive structure within the genus *Ligustrum* L., whereas the fruits of *Ligustrum vulgare* are the most developed. This view is also supported by several researchers [4, p.8-13; 8, p.360-377].

Tribe *Oleeae* Hoffmanns. & Link ex Dumort, 1827 – *Oleeae* tribe

This tribe, which includes 12 genera (such as *Forestiera*, *Olea*, etc.), differs from other tribes in terms of fruit formation and structure [9, p.125-131]. In the literature, the fruits of all genera within this tribe are generally described as stone fruits (*Olea europaea* type) [5, p.69-75]. However, this characterization can be considered inaccurate, as was also noted for taxa in the genus *Ligustrum*, because the main reason is that a stone fruit is actually an apocarpous fruit [17, p.59-67]. In fact, there are no taxa within the *Oleaceae* family that produce truly apocarpous fruits. This view is supported by several researchers in their studies [9, p.125-131].

Table 6. Morphological and Anatomical Structure of Fruits of Some Species Belonging to the *Oleeae* Tribe

Taxon	Fruit Type	Fruit Shape	Pericarp Structure	Number of Seeds	Anatomical Features of the Fruit
<i>Olea europaea</i>	Drupe (stone fruit)	Ovoid, fleshy mesocarp	Exocarp: thin epidermis; Mesocarp: parenchyma; Endocarp: lignified cells	1	Endocarp composed of lignified sclerenchyma cells
<i>Forestiera neomexicana</i>	Drupe (stone fruit)	Small, fleshy fruit	Exocarp: thin epidermis; Mesocarp: parenchyma; Endocarp: lignified sclerenchyma cells	1	Endocarp forms a hard protective lignified layer

The anatomical structure of fruits in the tribe *Oleeae* shows that the species within this tribe produce typical *Olea*-type drupaceous syncarp (pyrenaria) fruits (Table 6). Minor variations, such as the presence of isolated sclereids in the mesocarp parenchyma or radially elongated cells in the mesocarp parenchyma, do not significantly affect the overall pericarp structure. The presence of traces of a dehiscence mechanism in the inner mesocarp indicates the evolutionary transition from Forsythia-type capsule fruits to *Olea*-type drupaceous syncarp fruits.

Unlike taxa in the genus *Ligustrum*, representatives of the *Oleeae* tribe do not show intermediate forms that indicate sequential reductions in seed number [4, p.8-13; 9, p.125-131]. Within this tribe, the parenchymatous layers of the pericarp undergo complex development, which is closely associated with seed dispersal by animals [13, p.1-5]. Based on the data obtained on the fruits of *Oleeae*, their fruits can be considered more advanced compared to those of *Ligustrum* taxa. Among all genera in the *Oleeae* tribe, species of the genus *Forestiera* possess the most developed fruit characteristics, as no traces of a dehiscence mechanism are observed in their fruits.

Genus *Fraxinus* L.

The fruits of species in the genus *Fraxinus* L. have traditionally been classified as winged dry fruits (Table 7). As noted in the literature, these fruits are not only winged but also represent a fruit type in which lignification occurs in all histogenetic regions of the pericarp [15, p.287-298]. In the fruits of taxa within *Fraxinus*, lignification is observed primarily in the inner part of the mesocarp, where sclerenchyma cells are distributed in an organized pattern.

Table 7. Anatomical structure of the pericarp of *Fraxinus excelsior*

Morphological Feature of the Fruit	Botanical Description of the Fruit
Fruit type	Winged dry fruit
Shape	Egg-shaped, flattened with one broad wing
Size (length)	2.5–4 cm
Number of seeds	1
Pericarp type	Thin and dry
Exocarp	Composed of a single layer of epidermal cells
Mesocarp	Mainly composed of parenchyma cells, sometimes with mechanical tissues
Endocarp	Protective layer of dense and thickened cells
Mechanical tissues	Sclerenchyma cells located in the winged part of the fruit
Winged part	Flattened and expanded section of the pericarp that helps the fruit stay in the air
Seed coat	Thin, providing strength to the seed coat
Dispersal type	By wind

Overall, the fruits of representatives belonging to the genus *Fraxinus* L. can be considered *Olea*-type syncarpous stone fruits; however, ash fruits do not exhibit all the characteristics of typical syncarpous stone fruits. There are several reasons to believe that the fruits of ash species evolved directly from *Olea*-type syncarpous stone fruits. The fruits of ash plants have acquired adaptations for wind dispersal (anemochory) [17, p.59-67; 19, p.287-298]. Specifically, in these taxa, the number of parenchyma and sclerenchyma layers in the pericarp has decreased, and the seed mass has been reduced from an evolutionary perspective [2, p.8-13]. From an evolutionary standpoint, these adaptations can be considered part of the general evolutionary trajectory of all fruits within the Angiospermae division.

Fontanesia Labill. – Species of this genus show fruit morphology and anatomy very similar to those of *Fraxinus*. Although some literature incorrectly describes their fruits as winged fruits, the fruits of *Fontanesia* species are actually *Olea*-type syncarpous stone fruits [5, p.77-81]. The fruits of this genus are elongated and oval, with a thin membranous wing along the lateral side of the fruit. Analysis has shown that species of *Fontanesia* and *Fraxinus* have evolved fruit structures that provide adaptations for dispersal, allowing their diaspores to remain airborne for extended periods [15, p.288-298].

Table 8. Morphological and Anatomical Structure of the Fruit of *Fontanesia fortune*

Morphological Feature of the Fruit	Botanical Description of the Fruit
Fruit type	Indehiscent winged dry fruit
Fruit shape	Ovoid, flattened, with one side having a broad thin wing
Size (diameter)	1.5–3 cm
Color	Yellowish-brown
Number of seeds	1
Pericarp type	Thin and dry
Exocarp	Composed of thin epidermal cells
Mesocarp	Mainly composed of parenchyma cells, sometimes containing mechanical tissues
Endocarp	Thick cell layers surrounding the seed
Mechanical tissues	Sclerenchyma cells in the mesocarp and endocarp

Wing structure	Thin membranous wing formed by the expansion of the fruit's lateral side
Function	Wind dispersal

The main point here is that in most representatives of the Angiospermae, there is an increase in the number of pericarp layers and the development of fruit wings. In addition, it should be noted that in taxa of the genus *Fontanesia*, each ovary locule contains only one ovule, which indicates that the fruits of *Fontanesia* species have an independent origin and do not derive from *Forsythia*-type capsule fruits [5, p.234-238]. The fruits of taxa belonging to this genus are indehiscent winged dry fruits, each containing a single seed (Table 8). When mature, the fruits turn light or yellowish-brown. In *Fontanesia* fruits, the pericarp is mainly thin, and the mechanical tissues are weakly developed, primarily in the winged part of the fruit. The lignification process in the endocarp is weak.

Analysis of the literature shows that there is considerable variability in the terminology used to describe the fruits of taxa in the genus *Jasminum* L.. Some authors classify these fruits as capsules (dehiscent fruits) [7, p.1508-1513]. It should also be noted that the difference between the fleshy fruits of *Jasminum* and the capsule fruits of *Forsythia* is substantial, comparable to the difference between a capsule and a fleshy drupe.

On the other hand, some literature sources describe the fruits of *Jasminum* taxa as berries [4, p.8-13]. In general, there is a wide variety of opinions regarding the fruit structure and type within the *Oleaceae* family. The pericarp of *Jasminum* species is relatively thin and rarely exceeds 10 cell layers, but the seeds have a very thick sarcotesta (fleshy outer layer). Therefore, classifying these fruits as fleshy is not accurate [4, p.8-13]. Overall, the fruits of *Jasminum* taxa can be divided into two morphogenetic types, depending on whether they dry out or remain fleshy.

The dehiscent fruits of *Jasminum* are not *Forsythia*-type capsules but rather *Galanthus*-type capsules, because they lack the topographically distinct sclerenchyma zones in the pericarp that are characteristic of *Forsythia*-type capsules [4, p.8-13; 5, p.158-173]. In contrast, *Galanthus*-type capsules contain distinct sclerenchyma regions in the pericarp. Thus, the opening (dehiscence) of *Jasminum* fruits occurs as a result of mechanical forces acting on the pericarp tissues during fruit drying.

Table 9. Morphological and anatomical structure of fruits of *Jasminum officinale*

Biological Characteristics	Botanical Description
Fruit type	Berry
Fruit shape	Elongated, oval
Fruit size	4–7 mm
Fruit color	Dark bluish-black
Pericarp structure	Thin and fleshy, weak mechanical tissue
Exocarp	Thin epidermis with waxy coating
Mesocarp	Slightly fleshy, parenchymatous
Endocarp	Slightly differentiated, weak lignification
Number of seeds per fruit	1–3
Seed shape	Ovoid
Fruit dehiscence	Indehiscent
Fruit dispersal	By birds
Position within Oleaceae family	Berry-type fruit

In species of the genus *Jasminum*, mechanical stress in the fruit is not associated with a distinct sclerenchyma region, but rather with the heterogeneity of the mesocarp parenchyma cells (Table 9). The presence of parenchyma cells of highly variable size and shape, as well as numerous cells with thickened but non-lignified walls in the fruit's dehiscence zone, ensures uneven compres-

sion of the pericarp during fruit drying, which in turn triggers its opening.

In general, taxa with dehiscent fruits have a clearly defined area in the pericarp that transforms into a dehiscence zone consisting of heterogeneous parenchyma. In indehiscent fruits, such a zone is usually absent, although clusters of cells with thickened walls and small parenchyma cells are present. The area of the pericarp with the highest concentration of such cells usually corresponds to the site of fruit opening.

It should also be noted that in *Jasminum* fruits, the pericarp from the distal (apical) to the median (ventral) region is very thin (3–5 cell layers), which is why these fruits rarely split in the middle. In contrast, in fully dehiscent fruits, opening occurs in the thickest pericarp region (10–15 cell layers).

Although the opening mechanism of fruits in other *Oleaceae* genera (e.g., *Forsythia*, *Syringa*) is based on similar principles, it is more complex and involves a clearly differentiated tissue zone (sclerenchyma) [2, p.1-34].

Fruits of *Jasminum* taxa that have lost their dehiscence capability are characterized by the absence of topographically distinct sclerenchyma zones in the pericarp, and in this regard, these fruits can be classified as *Psysena*-type nuts. These fruits are derivatives of *Galanthus*-type capsules [5, p.321-332]. Anatomically, *Psysena*-type nuts differ from *Galanthus*-type capsules by being composed of more uniform parenchyma cells, where the parenchyma is more clearly visible.

It can be inferred that both *Galanthus*-type capsules and *Psysena*-type nuts diverged from the ancestral *Forsythia*-type capsule forms at early stages of morphogenesis. Nevertheless, both *Galanthus*-type capsules and *Psysena*-type nuts are sufficiently specialized and evolutionarily advanced [5, p.159-170].

A comparative statistical analysis of the anatomical structure of fruits of taxa belonging to the studied genera within the family *Oleaceae* is presented in Table 10.

Table 10. Comparative statistics of the anatomical structure of fruits of taxa belonging to the family *Oleaceae*

Genus	Cell diameter (µm)	Exocarp cell size (µm)	Exocarp thickness (µm)	Mesocarp thickness (µm)	Endocarp thickness (µm)	Seed coat thickness (µm)	Total number of layers (average)
<i>Olea</i> L.	26,5±2,9	27,5±3,0	25 ± 2,8	2750±300	1650±180	200±21,8	27±2,9
<i>Fraxinus</i> L.	23±2,5	24±2,6	18 ± 2,0	1400±150	108 ± 12	130±15	26±2,8
<i>Syringa</i> L.	30±3,2	22±2,4	15 ± 1,6	550±60	100±11	100±11	19±2,0
<i>Ligustrum</i> L.	35±3,8	31±3,3	22 ± 2,4	400±44	96 ± 11	185±21	14±1,5
<i>Jasminum</i> L.	22±2,4	24±2,6	20 ± 2,1	800±87	75 ± 9,0	85±9	17±1,8
<i>Forsythia</i> Vahl	28±3,0	22±2,4	17 ± 1,8	1000±105	108 ± 12	115±13	13±1,4
<i>Fontanesia</i> Labill.	25±2,7	26±2,8	16 ± 1,7	475±52	50±5,4	130±15	11±1,2

As shown in Table 10, the thickest exocarp was observed in taxa belonging to the genus *Olea*. The relatively thick exocarp in these taxa indicates a strong protective function of the fruit. Increased mesocarp and endocarp thickness were also recorded in representatives of the genus *Olea*, a characteristic typical of fleshy drupaceous fruits. The well-developed endocarp provides effective protection of the seed against mechanical damage in members of this genus.

A comparative analysis of seed coat thickness across the studied genera revealed that taxa belonging to *Olea* again exhibited the highest values, whereas the lowest seed coat thickness was recorded in *Jasminum* and *Syringa*. These findings indicate that fruits of *Olea* taxa within the *Olea*-

ceae family are distinguished from other genera by a more highly differentiated and thicker pericarp. The lowest total number of tissue layers was observed in representatives of the genera *Fontanisia* and *Forsythia*.

Conclusion

- Four morphogenetic fruit types were identified among the taxa of the studied genera within the *Oleaceae* family, namely pome fruits, berries, capsule fruits, and winged fruits;
- The formation of morphogenetic fruit types is closely associated with ovary structure, while pericarp differentiation occurs in different developmental directions;
- Fruit modifications in the studied taxa are influenced by ecological factors;
- Morphogenetic characteristics of the fruits reflect phylogenetic relationships among taxa;
- Statistical analyses confirm the reliability and validity of the obtained results.

In conclusion, the morphogenetic fruit types and their modifications within the *Oleaceae* family exhibit a high degree of diversity, which is determined by morphological-anatomical, ecological, and evolutionary factors. Fruit structural characteristics possess significant diagnostic value for determining the systematic position of taxa.

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OLEACEAE FƏSİLƏSİNƏ AİD TAKSONLARIN MEYVƏLƏRİNİN MORFOGENETİK TİPLƏRİ VƏ MODİFİKASIYALARI

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Xülasə

Tədqiqat işində *Oleaceae* fəsiləsinin 8 cinsinə aid müxtəlif taksonların meyvələrinin morfoqenetik tipləri və şəkildəyişmələri tədqiq olunmuşdur. Tədqiqat zamanı *Oleaceae* fəsiləsinə aid fərqli cinslərin morfoqenetik meyvə tiplərini fərqləndirmək üçün əsas göstərici kimi perikarpın müxtəlif histogenetik sahələrdə ligninləşmiş toxumaların lokalizasiyası olmuşdur. Məlum olmuşdur ki, tədqiq olunan növlərdə dörd meyvə tipinin (çəyirdəkli meyvə- *Forestiera*, *Olea*; qanadlı quru meyvə- *Fraxinus*, *Fontanesia*; qutucuq meyvə- *Syringa*, *Ligustrum*, *Forsythia*; giləmeyvə- *Jasminum*) olduğu müəyyən edilmişdir. Tədqiqat işində *Oleaceae* fəsiləsinə aid tədqiq olunan cins nümayəndələrində olan meyvələrinin perikarpında mexaniki toxumaların yerləşməsi, toxumanın perikarpda yerləşdiyi yer və əhəmiyyəti öyrənilərək əsərdə öz əksini tapmışdır. Tədqiqat zamanı *Forsythia* cinsinə aid növlərin meyvələrində mexaniki toxumaların yalnız meyvə yarpaqlarının mezofili daxilində inkişaf etdiyi, parenxim hüceyrələri isə endokarpı formalaşdırdığı müəyyən olunmuşdur. Ümumiyyətlə aparılan təhlillər onu göstərmişdir ki, *Oleaceae* fəsiləsi içərisində

Forsythia tipli meyvəni əcdad kimi qeyd etmək olar. *Oleaceae* tribasına aid taksonların meyvələrinin anatomik quruluşu onu göstərmişdir ki, bu tribaya aid bitki növlərinin meyvələri tipik *Olea* tipli çəyirdəkli senokarp meyvələrdir. Tədqiqat zamanı müəyyən edilmişdir ki, *Jasminum* cinsinə aid növlərdə bitkilərinə mexaniki stres, fərqli bir sklerenxim bölgəsinin olması ilə deyil, mezokarp parenxim hüceyrələrinin heterogenliyi ilə əlaqədardır.

Açar sözlər: *Oleaceae*, meyvə, modifikasiya, morfoqenetik tip, karpologiya, perikarp

МОРФОГЕНЕТИЧЕСКИЕ ТИПЫ И МОДИФИКАЦИИ ПЛОДОВ РАЗЛИЧНЫХ ТАКСОНОВ СЕМЕЙСТВА OLEACEAE

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Аннотация

В исследовании изучались морфогенетические типы и морфологические изменения плодов различных таксонов 8 родов семейства *Oleaceae*. В ходе исследования локализация одревесневших тканей в различных гистогенетических областях перикара являлась основным показателем для различения морфогенетических типов плодов разных родов, принадлежащих к семейству *Oleaceae*. Известно, что у изученных видов было определено четыре типов плодов: косточковый плод - *Forestiera*, *Olea*; крылатый сухой плод - *Fraxinus*, *Fontanesia*; коробочка - *Syringa*, *Ligustrum*, *Forsythia*; ягоды - *Jasminum*. В ходе исследования изучалось и отражалось в работе расположение механических тканей в перикарпии плодов представителей изучаемых родов семейства *Oleaceae*, а также местоположение и значение тканей в перикарпии. В ходе исследования было установлено, что у плодов видов рода *Forsythia* механические ткани развиваются только в мезофилле листьев плода, тогда как паренхимные клетки образуют эндокарп. В целом, проведенные анализы показали, что плод типа *Forsythia* можно считать предком в семействе *Oleaceae*. Анатомическое строение плодов таксонов, принадлежащих к трибе *Oleeae*, показало, что плоды видов растений, принадлежащих к этой трибе, представляют собой типичные ксенокарпные плоды с семенами типа *Olea*. В ходе исследования было установлено, что механическое напряжение у растений видов рода *Jasminum* обусловлено не наличием четко выраженной склеренхимной области, а гетерогенностью паренхимных клеток мезокарпа.

Ключевые слова: *Oleaceae*, плод, модификация, морфогенетический тип, карпология, перикарп

Daxil oldu:
19.01.2026

Çap edildi:
25.05.2026