

## Systematic treatment of morphological fruit types in plants of the class Liliopsida of the flora of Ukraine

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In this review, the scope of morphological diversity of fruits within the class Liliopsida belonging to the flora of Ukraine compared to the world flora diversity was analyzed. For the first time, the taxonomic diversity of monocot plants of the flora of Ukraine was analyzed, which includes 235 genera and about 1050 species, and the distribution of fruit types in the largest monocot families revealed. It was found that among monocot plants of the world flora, as also of the Ukrainian flora, more than 70% of generic and species diversity is taken up by the Orchidaceae, Poaceae, and Cyperaceae families having dry uniform fruits: inferior capsule (Orchidaceae) and one-seeded enveloped fruit (Poaceae and Cyperaceae). An annotated list of morphological fruit types was compiled for all 38 families of the natural and cultural flora of monocot plants of Ukraine. Among 12 families of the subclass Alismatidae, apocarpous polymorous or trimerous fruits, mostly with one-seeded fruitlets, occur in six families (Alismatidae, Butomaceae, Potamogetonaceae, Ruppiaceae, Scheuchzeriaceae, Zannichelliaceae). In 12 of 16 families of the subclass Liliidae, trimerous capsules are the most common (Agapanthaceae, Agavaceae, Alliaceae, Amaryllidaceae, Asphodelaceae, Colchicaceae, Hemerocallidaceae, Hyacinthaceae, Iridaceae, Liliaceae, Melanthiaceae, Orchidaceae), while in six families berry-like fruit occurs in all members or in the single genus (Asparagaceae, Rusaceae, Dioscoreaceae, Melanthiaceae (*Paris*), Liliaceae (*Streptopus*), Smilacaceae). Among 10 families of the subclass Commelinidae, in four families superior dry one-seeded fruits occur (Cyperaceae, Poaceae, Sparganiaceae, Typhaceae), while another four families have trimerous capsules (Cannaceae, Commelinaceae, Juncaceae, Pontederiaceae). In general, the most typical fruit on the familial taxonomical level is the capsule (17 families), berries occur in 10 families, aggregate fruits and one-seeded fruits are represented each in seven families, while the rarest fruit type is the schizocarp (Juncaginaceae). No monomerous follicles, poricidal and operculate capsules, winged fruits and loment were found. The most controversial fruit types are found in two groups of families, for both of them the problem is the gynoeceum type. These are families with one-seeded fruit (Araceae (*Lemna*), Cyperaceae, Hydrocharitaceae (*Najas*), Poaceae, Sparganiaceae, Typhaceae, Zosteraceae) and families with initial carpel fusion (Hydrocharitaceae (*Stratiotes*), Juncaginaceae, Melanthiaceae (*Veratrum*), Scheuchzeriaceae, Tofieldiaceae). As a result of our work, the key and the most relevant areas of carpological studies in Ukraine were defined, particularly, unifying the terminology, examination of the anatomical structure of the pericarp, revealing of the evolutionary and ecological aspects of fruit morphology.

**Keywords:** monocots; Alismatidae; Liliidae; Commelinidae; carpology; capsular fruit.

### Introduction

Fruit is defined as a terminal stage of differentiation and specialization of the gynoeceum together with persistent floral parts (Teryokhin, 2000). Although fruit characters are widely used in systematics (Cronquist, 1981; Takhtajan, 1987, 2009), this happens substantially less often than usage of the flower characters. This is due to the fact that fruit structure often undergoes parallel evolution and convergence in many clades, which makes it difficult to use carpological data in evolutionary morphology and systematics. It was stated that fruit are too versatile and have too many aspects to be divided into strict categories (Pijl, 1982). However, morpho-anatomical fruit structure is a combination of many apomorphic characters of plant species, related to their reproductive system, which emphasized the need to reveal homologous fruit features in different species and identify trends of fruit evolution (Bobrov et al., 2009). Such examinations are not possible without an unequivocal and adequate terminology on fruit structure and typology.

In Ukraine research on fruit structure began in the 1980s and has been carried out mainly in the relation to the systematics of defined families or plant introduction (Ziman & Bulakh, 2013). Predominantly, anatomical

features and ultrastructure of fruit surface were studied, as also taxonomically significant morphological fruit traits. The latest monograph studies on fruit in plants of the flora of Ukraine were carried out on the genus *Campanula* (Dremluga, 2013) and the Brassicaceae family (Ilyinska, 2016). However, generalized researches on morphological diversity and classification of fruits were absent. The necessity of such research is obvious to plant taxonomists, phytocoenologists, and ecologists using data on fruit adaptive and evolutionary-marker features in their studies. In this relation, in our neighbouring states structural carpological studies are actively proceeding in the XXI century, for instance, Slovakian botanists have published an atlas of seed and fruit morphology with descriptions of seeds and indehiscent fruits of 4,800 species (Bojňanský & Fargašová, 2007); in Poland, a bibliography of carpological works was published with more than 140 cited sources from Polish botanists (Latowski et al., 2015). Russian botanists are developing a morphogenetic approach and study of pericarp anatomy (Bobrov et al., 2009; Kravtsova, 2015; Bobrov & Romanov, 2019).

Contemporary researches pay great attention to ecology and consorcial relations of plants with frugivorous animals (Jordaan et al., 2011; Karimi et al., 2020; Sena et al., 2021), particularly, the significant role of

fleshy fruits of various woody plants in the diet of forest birds has been revealed (Pesotskaya et al., 2020). The fruit structure is studied in relation to the reproduction of plant species (Lebedeva et al., 2020), dispersion of plants by hydrochory (Boedeltje et al., 2008; Favre-Bac et al., 2017; Behren von & Yeakley, 2020), genetic regulation of fruit development (Dardick & Callahan, 2014), the evolutionary and adaptive significance of fleshy fruit metabolites (Balaguera-Lopez et al., 2020; Famiani et al., 2020) and fruit scent (Nevo & Ayasse, 2020).

The problem of fruit classification and evolution is closely related to the problems of the classification and evolution of the gynoecium, a structure bearing many adaptive and evolutionary significant fruit traits. In this article, we intend to analyze the known data on morphological fruit diversity within monocotyledonous plants, to compile fruit names applied to one taxon in home and foreign literature, to evaluate the occurrence of diverse morphological fruit types of the flora of Ukraine within the class Liliopsida Batsch, to reveal the most common fruit types, as also families of the flora of Ukraine having the most controversial fruit types with a view to their further investigation.

### Taxonomical diversity of the class Liliopsida in the flora of Ukraine and main fruit types

The class Liliopsida in the world flora comprises 78 families, 2612 genera, and from 56 310 (Thorne & Reveal, 2007) to 60 100 species (www.mobot.org/MOBOT/research/APweb). Monocotyledonous plants of the flora of Ukraine encompass 38 families, recognized by Mosyakin (2013) or 30 families sensu Chase et al. (2016), which is about 40% of the world monocot familial diversity. The extent of the class Liliopsida belonging to the flora of Ukraine was defined including the cultivated taxa,

as stated in the work of Mosyakin (2013). According to the published data (Mosyakin & Fedoronchuk, 1999), the monocot flora of Ukraine includes 235 genera and about 1050 species, which is less than 10% of genera and only about 1.5% of species of the world monocot flora. Taxonomical diversity of Liliopsida is five times less than dicotyledonous diversity (Thorne & Reveal, 2007), for this reason, we may expect a less expressed structural diversity of fruits within Liliopsida compared to the general diversity of angiosperm fruits. Within the class Liliopsida of the world flora, the first places in species richness are occupied by the families Orchidaceae, Poaceae, and Cyperaceae, embracing in total 74% of species and 70% of generic monocot richness. These families are characterized by uniform dry fruits: inferior capsule (Orchidaceae) and one-seeded enveloped fruits (Poaceae and Cyperaceae, Table 1). This fact results in the quantitative prevalence of corresponding fruit types in the class Liliopsida and even further restricts the limits of expected fruit diversity in the rest of the monocot taxa. Among the largest monocot families of the world flora, dry capsular fruits prevail, being the dominant or the most common fruit type in six of ten families. Within the top listed families, one-seeded fruits occur in addition to Poaceae and Cyperaceae also in Araceae and Araceae (in particular, Lemnaceae, included in Araceae). Berry-like fruits occur in some Asparagaceae, Araceae and Bromeliaceae (Table 1).

Within the class Liliopsida of the flora of Ukraine, the first places in species richness are occupied by seven of ten largest monocot families of the world flora, which means high representation of monocot plants of the flora of Ukraine on the familial level. The richest monocot families in the flora of Ukraine in terms of species diversity are the same three families as of the world flora, embracing totally 70–77% monocot species of the flora of Ukraine. Among the ten largest monocot families of the flora of Ukraine, capsular fruits are also found in six families (Table 1).

**Table 1**  
Fruit types in the ten largest monocot families of the world flora and flora of Ukraine

The largest monocot families of the world flora	Number of genera/species in the world flora	The largest monocot families of the flora of Ukraine (number of genera/species in the flora of Ukraine)	Descriptive fruit type	Principal morphological characteristics of the fruit
1. Orchidaceae	925/27135	Orchidaceae (29/92)	Capsule fissuricidal	Inferior trimerous dry multi-seeded dehiscent paracarpous fruit
2. Poaceae	777/11461	Poaceae (108/444)	Caryopsis	Superior dry one-seeded fruit in antherium
3. Cyperaceae	113/5732	Cyperaceae (19/153)	Cypsel	Superior dry one-seeded fruit in envelope
4. Asparagaceae	143/3632	Asparagaceae (15/57) incl.: Agavaceae (3/10) Asparagaceae (1/8) Hyacinthaceae (7/28) Ruscaceae (4/11)	Capsule or berry	Superior trimerous dry multi-seeded dehiscent syncarpium or indehiscent fleshy fruit
5. Araceae	113/3174	Araceae (6/13)	Berry or utricle	Superior oligomeric low/one-seeded fleshy indehiscent paracarpium or low/one-seeded indehiscent fruit with undifferentiated pericarp
6. Bromeliaceae	50/3160	Absent from the flora of Ukraine	Berry or capsule septicidal	Inferior trimerous fleshy indehiscent fruit or dry dehiscent syncarpium
7. Araceae	187/2466	Only in the cultural flora of Ukraine	Drupe or date	Superior trimerous low-seeded or one-seeded fleshy indehiscent apocarpium with stony endocarp, or papery endocarp
8. Iridaceae	80/2182	Iridaceae (4/34)	Capsule loculicidal	Inferior trimerous dry multi-seeded dehiscent syncarpium
9. Amaryllidaceae	79/2164	Amaryllidaceae (7/61) incl.: Agapanthaceae (1/1) Alliaceae (2/47) Amaryllidaceae s. s. (4/13)	Capsule loculicidal	Inferior or superior trimerous dry or fleshy multi-seeded dehiscent syncarpium
10. Zingiberaceae	52/1587	Absent from the flora of Ukraine	Capsule loculicidal	Inferior trimerous dry multi-seeded dehiscent syncarpium
11. Liliaceae	15/610	Liliaceae (7/52)	Capsule loculicidal or berry	Superior trimerous dry multi-seeded dehiscent syncarpium or fleshy indehiscent fruit
12. Juncaceae	8/442	Juncaceae (2/41)	Capsule loculicidal	Superior trimerous dry multi-seeded or three-seeded dehiscent syncarpium or paracarpium
13. Potamogetonaceae	4/111	Potamogetonaceae (1/25)	Oligo-drupe	Superior apocarpous aggregate fruit of few one-seeded indehiscent fruitlets with a stony endocarp

Note: families recognized after Chase et al. (2016); for the flora of Ukraine, families recognized by Mosyakin (2013) are noted; the number of genera and species in the world flora given after www.mobot.org/MOBOT/research/APweb, in the flora of Ukraine – after Mosyakin & Fedoronchuk (1999) and Danylyk (2012) for Cyperaceae.

The survey of the published data on fruit diversity in monocots is complicated by the application of molecular genetic methods in taxonomy during the last two decades, which has substantially changed the system of

the class Liliopsida. These methods have revealed substantial differences between traditional evolutionary systems of the end of the XX century and the new scenario of clade phylogenesis (Chase, 2004; Thorne & Reveal,

2007; Mosyakin, 2013; Chase et al., 2016). As a result, the extent of subclasses, some orders and families was changed; especially it concerns the families of the order Asparagales (Mosyakin & Buyun, 2013). In this relation, it is desirable to analyze the fruit traits as potential synapomorphies of newly recognized clades as also to retain their representation in the flora of Ukraine.

### Characteristics of main fruit types in the monocots

The names of fruit types are given based on different principles of fruit classification (Kaden, 1965; Roth, 1977; Artjuschenko & Theodorov, 1986; Levina, 1987; Spjut, 1994; Bobrov et al., 2009; Bobrov & Romanov, 2019). The lack of a formalized terminology in the carpological literature causes many difficulties during the analysis of multisource data for one taxon, and during comparison of data for several taxa. For instance, the phrases: “capsule inferior syncarpous dorsiventral” (Kaden, 1965), “capsule dehiscent by valves” (Takhtajan, 1985), and “capsule loculicidal” (Goldblatt et al., 1998), given for Iridaceae, have the same meaning.

To make possible the treatment of published data on the distribution of fruit types inside the class Liliopsida of the flora of Ukraine, we compiled an annotated list of names of fruit types, used in specialized home and foreign literature. This list has shown a range of diversity of fruit types in each family and the diversity of names given for fruit in each taxon. We did not examine in detail the morphogenetic (Bobrov et al., 2009; Bobrov & Romanov, 2019) and carpological (Spjut, 1994) approaches to fruit classification because these concepts need a special discussion, however, some data cited from those works for some taxa are taken without discussion. We distributed fruit names in the annotated list according to descriptive and comparative-morphological principles (Artjuschenko & Theodorov, 1986; Levina, 1987; Bobrov et al., 2009) into five principal fruit categories, given below. Then, we treated these categories in monocot subclasses and families.

Polymerous apocarpous fruit, aggregate fruit (ukr. zbirnyi plid) – the most primitive fruit, formed from apocarpous gynoecium of many or some carpels, correspondingly one can distinguish polymerous and oligomerous apocarpium or indicate the number of carpels in the fruit name by prefix multi-, oligo- (for example, hexamerous multi-follicle, tri-follicle). An element of the aggregate fruit is named fruitlet (ukr. plodyk), that can be many-, low-, one-seeded, dehiscent or indehiscent, with various pericarp consistency. Aggregate fruit most often can be one of three types: multi-nucula or polyachene (ukr. bahatorishok), multi-drupe (ukr. bahatokistyanka), multi-follicle (ukr. bahatolystyanka).

Capsular fruit, capsule (ukr. korobochka) – syncarpous (as well coenocarpous and paracarpous), multi-seeded, dehiscent, dry, seldom fleshy, superior or inferior, uni-locular or multi-locular fruit, with various dehiscence modes and mechanisms, as also complicated pericarp anatomy.

Berry-like fruit, berry (ukr. yahoda) – apocarpous or syncarpous indehiscent fruit with fully unligified fleshy pericarp. The berry can be polymerous, oligomerous or monomerous, many-, low-, one-seeded, superior or inferior.

Schizocarp (ukr. skhizokarpnyy, drobnyi plid) – syncarpous low-seeded fruit splitting longitudinally into a few unicarpellate units (mericarps). Such fruit is considered to be derived from capsular fruit or pyrenarium, having an advantage in that seeds are dispersed with pericarp covering.

One-seeded fruit – unilocular fruit developed from the monomerous or pseudomonomerous gynoecium, bearing only one seed, as a rule indehiscent, with various pericarp consistency. It is the most difficult fruit type for interpretation because it is the result of reduction in the number of carpel and seeds in the apocarpous or syncarpous gynoecium. This category embraces fruits, called achene, cypsela (ukr. sim'yanka), nutlet (ukr. horishok), nut (ukr. horikh), caryopsis (ukr. zemivka), utricle (ukr. mishechok), and drupe (ukr. kistyanka). Drupaceous fruit or drupe (ukr. kistyanka), is characterized by strong differentiation of the inner mechanical zone of the pericarp, forming a stone (putamen). It is as a rule an indehiscent one-seeded fruit or fruitlet. Syncarpous drupe is called pyrenarium. Because a drupe is reliably recognized only by the anatomical study of the pericarp, which is not always taken into consideration in taxonomical works, we classified multi-drupe as an aggregate fruit and uni-drupe and pyrenarium as one-seeded fruit.

### Annotated list of morphological fruit types of monocot plants of the flora of Ukraine

In this list, for all monocot families of the flora of Ukraine, the descriptive and morphological fruit traits were outlined, as also ovary insertion (superior or inferior), seed number, placentation, presence of envelope, and mode of dehiscence, if such information is known from published sources. Fruit types are presented only for genera occurring in the flora of Ukraine. Families are listed alphabetically and distributed in subclasses Alismatidae, Liliidae, and Commelinidae within the framework of Mosyakin (2013), where authors of names of taxa are given. Asterisked (\*) are the families of cultural flora or those which have escaped to the wild. Alternative data for one taxon are separated by a semicolon (;). We submitted only basic sources for each family, since the informational pool for some taxa substantially exceeds the volume of a journal article.

#### Subclass Alismatidae

Acoraceae (*Acorus*) – berry syncarpous, superior, trimerous, low-seeded, with thin leathery pericarp, red, enveloped in tepals (Kaden, 1965; Takhtajan, 2009). In the natural populations, fruits do not develop remaining green, with sterile seeds inside. For *Acorus* a congenitally syncarpous gynoecium is characteristic, which is unexpected because this genus is recognized as a sister clade to all other monocots (Endress, 1995; Chen et al., 2004; Igersheim et al., 2008).

Alismataceae – multi-nucula with envelope: acyclic (*Sagittaria*) or cyclic (*Alisma*) (Kaden, 1965); multi-nucula of small fruitlets, sometimes with lignified endocarp (*Caldesia*) (Takhtajan, 1985); achenetum (Spjut, 1994); achene (Takhtajan, 2009); multi-nucula (*Sagittaria*), poly-laurine (*Alisma*), multi-drupe (*Caldesia*) (Bobrov et al., 2009). *Laurine* is considered to be a follicle-derived fruit with lignified endocarp, analogically to drupe. In *Damasonium*, fruit is a syncarpous multi-follicle (Takhtajan, 1985); hemisyncarpous multi-follicle with ventral dehiscence (Bobrov et al., 2009); basally dehiscent follicles (Takhtajan, 2009). In *Damasonium*, the transition from laminal to basal placentation is observed as also from few ovules to a single ovule (Eames, 1961); camaretum – apocarpous polymerous fruit of dry multi-seeded indehiscent fruitlets, with seeds, do not fill the whole locule volume (Spjut, 1994).

Araceae (incl. Lemnaceae) – superior berry-like one-low-seeded fruit (Takhtajan, 1985). In *Calla* fruit is a berry paracarpous, trimerous, non-covered, juicy, red, gathered in an infructescence (Kaden, 1965). In *Calla palustris* there are 4–5 seeds in a berry (Belyakov et al., 2017). In *Pistia* – capsule dry indehiscent (Takhtajan, 1985); monomerous low-seeded fruit with thin half-transparent pericarp (Takhtajan, 2009). In Lemnaceae – capsule paracarpous (?), superior, trimerous (?), covered, broken [punctuation as in the original text] (Kaden, 1965); monomerous fruit, 1–6-seeded utricle (Takhtajan, 2009); utriculate indehiscent one-seeded (*Lemna minor*, *L. trisulca*) or 1–6-seeded (*L. gibba*) fruit with soft, membranous pericarp and a beak on place of fallen style (Takhtajan, 1985; Zhmylev et al., 1995). In *Spirodela*, fruit is 1–2-seeded, sometimes reddish, 1–2 mm long, with wing-like zone; monomerous achenial fruit with 1–7 seeds; utricle, a unilocular uni-seeded fruit with thin dehiscent fruit wall, releasing seeds (Spjut, 1994). Utricle, after Spjut (1994), is composed by more than one carpel. Most Lemnaceae have one-seeded fruits (Tippery & Les, 2020).

Butomaceae (*Butomus*) – multi-follicle (hexa-follicle) superior, hemisyncarpous, of 6–9 fruitlets, ventrally dehiscent, with covering (Kaden, 1965); oligomerous cyclic multi-follicle of 6–9 multi-seeded fruitlets with laminal placentation (Takhtajan, 1985; Levina, 1987); dry cyclic 3–6-merous multi-follicle, ventrally dehiscent (Bobrov et al., 2009). Carpels are fused postgenitally ([www.mobot.org/MOBOT/research/APweb](http://www.mobot.org/MOBOT/research/APweb)).

Hydrocharitaceae (incl. Najadaceae) – capsule inferior, fleshy, disrupting: syncarpous, hexamerous (*Hydrocharis*, *Stratiotes*) or paracarpous trimerous (*Elodea*) (Kaden, 1965); inferior unilocular, berry-like indehiscent fruit or dehiscent by mucilage hydration, carpels are fused but have free margins (Takhtajan, 1985, 2009); inferior hexamerous hemiparacarpous berry (*Stratiotes*) or inferior hexamerous paracarpous (phragmocarpaceous) berry, sometimes with an envelope, fruit sometimes irregularly cracking by drying (*Elodea*, *Hydrocharis*, *Vallisneria*) (Bobrov et al., 2009). In *Hydrocharis* fruit is defined as an inferior hexamerous hemiparacarpous

pous berry, irregularly dehiscent by mucilage hydration (Efremov et al., 2015b), in *Stratiotes aloides* fruit is defined as an inferior hexamerous hemisyncarpous multi-follicle with unilocular ovary and incomplete septa, laminar-diffuse placentation with aerial cavities in the mesocarp (Efremov et al., 2015a); fruit fleshy, capsular/dehiscence irregular/indehiscent. The fruit may be follicular or achenial, or in *Hydrocharis* opening because of the mucilage developing inside it ([www.mobot.org/MOBOT/research/APweb](http://www.mobot.org/MOBOT/research/APweb)). In Najadaceae fruit – uninucula in an envelope (apocarpous, monomerous, indehiscent fruit) (Kaden, 1965); one-seeded indehiscent fruit with thin soft pericarp (Takhtajan, 1985); uninucula (Levina, 1987; Bobrov et al., 2009); achene (Spjut, 1994); carpel is solitary (Eames, 1961); pseudomonomerous, coenocarpous nut, however, pericarp remains juicy for a long time (Singh, 1965 cit. by Bobrov et al., 2009); monomerous or pseudomonomerous fruit, superior, one-seeded, with thin transparent pericarp, closely adnated to basal seed, dehiscing by decay (Takhtajan, 2009); gynoecium ostensibly monomerous, superior, carpel one-ovular, fruit non-fleshy, the fruiting carpel indehiscent, an achene, pericarp thin ([www.delta-intkey.com](http://www.delta-intkey.com)).

Juncaginaceae (*Triglochin*) – fruit is a schizocarp syncarpous, superior, hexamerous, not covered (Kaden, 1965, 1971); multi-follicle of free or fused to some degree one-seeded indehiscent fruitlets; fruit splits up from the bottom to top on three particles, remaining connected for some time above by central columella. In *Triglochin palustre* units of fruit have a long spike (Takhtajan, 1985); schizocarpous fruit, splitting into three one-seeded indehiscent fruitlets, without columella (camarium) or columnar (polachenarium), columella is formed by three sterile carpels (Spjut, 1994); poly-achene of 3 or 6 fruitlets, sometimes basically fused, but over time splitting (Takhtajan, 2009); apocarpous fruit with elongated receptacle or schizocarp with a columella (Lock et al., 2011); schizocarpous drupe, fruitlets have lignified endocarp, barely adjoined one to another, detached from the columella during drying (Thadeo et al., 2015); fruit schizocarpic/drupaceous/achenial/ (hooked, winged) ([www.mobot.org/MOBOT/research/APweb](http://www.mobot.org/MOBOT/research/APweb)).

Potamogetonaceae (Potamogeton) – tetra-achene with a cover (apocarpous, superior, tetramerous, indehiscent fruit) (Kaden, 1965); multi-drupe of 1–4 fruitlets (Takhtajan, 1985); achenetum (Spjut, 1994); fruit drupaceous (Bobrov et al., 2009; Takhtajan, 2009; Thadeo et al., 2015).

Ruppiaceae (*Ruppia*) – oligomerous drupe with one-seeded fruitlets, asymmetrical, pendulous on long and thin peduncles (Takhtajan, 1985, 2009; Levina, 1987; Spjut, 1994); polyaurine or oligo-laurine (Bobrov et al., 2009).

Scheuchzeriaceae (*Scheuchzeria*) – tri-follicle hemisyncarpous, dorsiventral dehiscent (Kaden, 1965); oligomerous cyclic follicle, carpels are fused at a base, with 1–2 seeds, remain open for a long time (Takhtajan, 1985, 2009; Levina, 1987); multi-follicle (Spjut, 1994); dry inflated multi-follicle (tri-follicle), with 1–2-seeded fruitlets, to some degree fused at the base, ventrally dehiscent “from the inner side” (Minaeva, 1997); dry cyclic 3–6-merous one-low-seeded multi-follicle with ventral dehiscence (Bobrov et al., 2009); gynoecium of 3 (2–6) two-ovulate carpels, fused at the base, fruit a superior dry hemisyncarpous capsule with fertile symplicate zone, and dorsiventral dehiscence (Remizowa & Sokoloff, 2014).

Tofieldiaceae (*Tofieldia*) – capsule superior syncarpous trimerous, covered, septicidal-ventrally dehiscent (Kaden, 1965); transitional type between multi-follicle and septicidal capsule (Takhtajan, 1985); capsule trimerous, septicidal, or tri-follicle (Takhtajan, 2009); carpels 3–5, stipitate, basally fused, postgenitally united in its upper portion (Eames, 1961; Remizowa et al., 2006).

Zannicheliaceae (*Zannichelia*) [Potamogetonaceae sensu Chase et al., 2016] – drupaceous fruit of one or few fruitlets, indehiscent, one-seeded, stipitate (Takhtajan, 1985, 2009); achenetum (Spjut, 1994); monolaurine (Bobrov et al., 2009).

Zosteraceae (*Zostera*) – paracarpous pseudomonomerous pyrenarium, developed from dimerous pseudomonomerous gynoecium (Cronquist, 1981); small monomerous one-seeded fruit with thin papery dehiscent fruit wall (Takhtajan, 1985; 2009), covered by a spathe, destroyed by rupture, releasing a seed (Ackerman, 1997); one-seeded brownish, non-covered, ovate, juicy follicle, 3–4 mm long, longitudinally dehiscent (Vekhov, 1992); camara, “indehiscent follicle” – apocarpous monomerous indehiscent fruit with undifferentiated pericarp, with soft exocarp and hard

fibrous endocarp (Spjut, 1994); uni-drupe or uni-nucula (Bobrov et al., 2009); fruit an achene/follicle ([www.mobot.org/MOBOT/research/APweb](http://www.mobot.org/MOBOT/research/APweb)).

## Subclass Liliidae

Agapanthaceae\* (*Agapanthus*) [Amaryllidaceae sensu Chase et al., 2016] – capsule superior, trimerous, multi-seeded, loculicidal (Kubitzki, 1998a; Takhtajan, 2009).

Agavaceae (*Anthericum*, *Hosta*\*, *Yucca*\*) [Asparagaceae sensu Chase et al., 2016] – capsule superior trimerous, covered, dorsiventral (*Anthericum*) (Kaden, 1965); capsule superior trimerous multi-seeded loculicidal (Takhtajan, 1985); apically dehiscent (Conran, 1998a; Takhtajan, 2009). In *Hosta* – capsule superior, trilobular, multi-seeded, pendent, loculicidal, dehiscent from top to bottom by three valves (Takhtajan, 1985; Kubitzki, 1998b). In *Yucca* – capsule superior, loculicidal or septicidal (Takhtajan, 2009).

Alliaceae (*Allium*, *Nectaroscordum*) [Amaryllidaceae sensu Chase et al., 2016] – capsule superior, trilobular, low-seeded, with an envelope, leathery, dorsiventral (Kaden, 1965), or loculicidal (Takhtajan, 1985, 2009; Rahn, 1998).

Amaryllidaceae – capsule inferior, trimerous, dry or fleshy, loculicidal or fruit is fleshy berry-like, indehiscent (Takhtajan, 1985, 2009; Meerow & Snijman, 1998).

Asparagaceae (*Asparagus*) – berry trimerous superior, not covered, one-low-seeded (Kaden, 1965; Takhtajan, 1985, 2009; Kubitzki & Rudall, 1998).

Asphodelaceae (*Asphodeline*, *Eremurus*) [Xanthorrhoeaceae sensu Stevens (2017)] – capsule superior one-low-seeded, thick-walled, loculicidal (Takhtajan, 1985; 2009; Smyth & van Wyk, 1998); capsule superior syncarpous, loculicidal, dehiscent by three apical valves (Bobrov et al., 2009).

Colchicaceae (*Bulbocodium*, *Colchicum*) – capsule superior syncarpous trimerous, covered, septicidal-ventrally dehiscent (Kaden, 1962, 1965), septicidally dehiscent (Takhtajan, 1985; Artjuschenko & Theodorov, 1986); capsule multi-seeded, partially or totally syncarpous, septicidally dehiscent (Nordenstam, 1998).

Dioscoreaceae (*Tamus*) – berry inferior trimerous, with 1–6 seeds, red (Takhtajan, 1985; Levina, 1987).

Hemerocallidaceae\* (*Hemerocallis*) [Asphodelaceae sensu Chase et al., 2016] – capsule dry, leathery, trilobular, with 9–12 seeds in a locule, loculicidal (Takhtajan, 1985, 2009; Clifford, 1998).

Hyacinthaceae [Asparagaceae sensu Chase et al., 2016] – capsule superior, trimerous, loculicidal, dry or fleshy, erect or pendent, perfectly or apically dehiscent (Takhtajan, 1985; 2009; Speta, 1998).

Iridaceae – carpule syncarpous, inferior, trimerous, multi-seeded, leathery, dorsiventral (Kaden, 1962, 1965), dehiscent by valves or longitudinal fissures (Takhtajan, 1985); loculicidal capsule (Spjut, 1994; Goldblatt et al., 1998; Takhtajan, 2009).

Liliaceae – capsule syncarpous, superior, trimerous, non covered (most of the genera) or covered (*Gagea*), dorsiventrally dehiscent (Kaden, 1965); capsule trilobular loculicidal (Takhtajan, 1985, 2009; Spjut, 1994; Tamura, 1998b). In *Streptopus* – berry syncarpous superior, trilobular multi-seeded (Tamura, 1998a; Takhtajan, 2009).

Melanthiaceae (*Veratrum*, *Paris*) – tri-follicle hemisyncarpous, covered, septicidal-ventrally dehiscent (*Veratrum*) (Kaden, 1965); capsule multi-seeded loculicidal (Takhtajan, 1985); capsule syncarpous, ventrally dehiscent, trilobate, of fused to some degree carpels, semi-inferior, multi-seeded (Tamura, 1998c; Takhtajan, 2009); capsule semi-inferior septicidal/ventricidal. In *Paris* – berry superior, tetramerous, covered (Kaden, 1965; Tamura, 1998d).

Orchidaceae – capsule paracarpous (sometimes syncarpous) inferior, trimerous, multi-seeded, laterally dehiscent on six valves, among them three wide “dorsal” and other three narrow “placental” valves, sometimes vice versa; valves detach from the top, or the bottom, or the middle-height, releasing seeds (Kaden, 1962, 1965); capsule unilocular, dehiscent by drying onto three or six valves, in the last case, three wider valves are “fertile”, bear placenta and other three valves are “sterile” (Roth, 1977); capsule fissuricidal (Spjut, 1994).

Ruscaceae (incl. *Convallariaceae*) [Asparagaceae sensu Chase et al., 2016] – berry superior trimerous (*Convallaria*, *Polygonatum*) or dimerous

(*Majanthemum*), non-covered (Kaden, 1965), unilocular, low-seeded (*Ruscus*), often red or orange (Takhtajan, 2009).

Smilacaceae\* (*Smilax*) – berry superior trimerous, unilocular, with 1–2 seeds (Conran, 1998b; Takhtajan, 2009), or 1–3, 6 seeds (Takhtajan, 1985).

### Subclass Commelinidae

Arecaceae\* (*Chamaerops*, *Trachycarpus*, *Phoenix*) – apocarpous superior, trimerous fruit of one-seeded fruitlets, covered by lignified perigonium at a base (Eames, 1961); drupe dry or fleshy, mostly one-seeded (Takhtajan, 1985); drupe of “coryphoid” type, with early lignified mesocarp with compound many-layered structure, fruits apocarpous, rarely 2–3-merous (*Chamaerops humilis*), often monomerous (*Trachycarpus*) (Bobrov et al., 2009). In *Phoenix* fruit is a date – apocarpous superior mono-oligomerous one-seeded fleshy fruit, with a layer of stony cells under hypoderm and membranous endocarp (Levina, 1987; Bobrov et al., 2009). Date is a berry-like, one-seeded fruit with tanniniferous mesocarp (Roth, 1977); aggregate berry-like fruit (baccetum) (Spjut, 1994).

Cannaceae\* (*Canna*) – capsule inferior, trilobular, multi-seeded, with soft spines outside, loculicidal, opened by valves or teeth, or indehiscent (Takhtajan, 1985); capsule opening by the collapse of the pericarp (Takhtajan, 2009); carcerula (indehiscent capsule), fissuricidal capsule (*Canna indica*) (Spjut, 1994).

Commelinaceae\* (*Commelina*, *Tradescantia*) – capsule hemiparacarpous, superior, dimerous, enveloped, dorsiventrally dehiscent (Kaden, 1965); capsule trilobular, sometimes uni-bilobular, loculicidal (Takhtajan, 1985; 2009; Spjut, 1994).

Cyperaceae – drupe (pyrenarium) paracarpous, superior, di-trimerous, dry, non covered or covered by perigonium in a form of bristles (most genera); enveloped in utricle formed by prophyll or bract (*Carex*) (Kaden, 1965); fruit is nut-like, with hard pericarp, sometimes pyrenarium-like, triangular or twice convex (Takhtajan, 1985); achene with perigonium and a modified bract in a form of utricle (*Carex*) (Artjuschenko & Theodorov, 1986); achene or nut, depending on lignification extent of the pericarp (Levina, 1987). In some forest sedges (*Carex digitata*, *C. ornithopoda*) the basal part of the utricle becomes fleshy, acting as elaiosome, attracting ants-disseminators (Levina, 1987); fruits achene-like or rarely drupaceous (Takhtajan, 2009); achene with perigonium in the form of bristles (cypsel) (*Elaeocharis*) or non-covered achene, or fruit is pseudanthecium – fruit covered by extra-floral structures (*Carex*) (Spjut, 1994).

Juncaceae – capsule syncarpous, superior, trimerous, covered, dorsiventrally dehiscent (*Juncus*) or paracarpous, dorsally dehiscent (*Luzula*) (Kaden, 1965); capsule loculicidal (Takhtajan, 1985, 2009; Spjut, 1994), multi-seeded (*Juncus*) or three-seeded (*Luzula*) (Takhtajan, 2009).

Musaceae\* (*Musa*) – berry inferior, trimerous multi-seeded, elongated, with leathery exocarp; fruit expresses negative geotropic reaction by rupturing (turns up) (Roth, 1977); “rind” of a fruit easily removed due to a layer of aerial parenchyma in the fruit wall (Esau, 1977).

Poaceae – caryopsis, apocarpous, superior, monomerous fruit, it can be leptodermal with a cover (most genera), with an envelope (*Zea*), non-covered (e.g. *Eragrostis*, *Secale cereale*, *Triticum aestivum*, *T. durum*) (Kaden, 1965); fruit is composed of two- or three-carpellate ovary (Shelyag-Sosonko, 1977); fruit has a thin pericarp of parenchymatous outer layers, drying by maturing, and two inner mechanical layers: a subepidermal layer of cross cells and the incomplete epidermal layer of tube cells (Esau, 1977); caryopsis is a one-seeded fruit with membranous or coriaceous pericarp, closely adjacent to the seed coat, often with longitudinal groove, sometimes with connected scales, sometimes “sac-like” (Takhtajan, 1985); nut-like paracarpous (coenocarpous) one-seeded fruit of three carpels, covered by scales (bracts and bracteoles) as also inflorescence axis. Covering can be close adjoined to caryopsis or surround it entirely, and connected with a pericarp (Artjuschenko & Theodorov, 1986); apocarpous fruit, secondary monomerous, falls out together with spikelet scales (lemma, palea, glumes) and spikelet axis (rachilla). Caryopsis together with adjacent parts of inflorescence compose a kind of diaspore – anthecium (Levina, 1987); pseudomonomerous fruit of 2–3 carpels, ovary superior unilocular, one-seeded (Takhtajan, 1987, 2009); Spjut (1994) recognized for Poaceae besides caryopsis, another ten fruit types, most of them are variants of an anthecium; coenocarpous (paracarpous) superior

dimerous one-seeded (pseudomonomerous) indehiscent nut-like fruit; sclerenchyma, often atypic, located in all pericarp layers. Caryopsis is characterized by diverse attachments (Bobrov et al., 2009). In *Crypsis* and *Heleochloa* caryopsis is follicle-like (Kaden, 1965); in *Crypsis* fruit is utricle-like, with a free papery fruit wall (Takhtajan, 2009).

Pontederiaceae (*Monochoria*) – capsule superior trimerous, multi-seeded, loculicidal (Takhtajan, 2009); capsule fissuricidal (Spjut, 1994).

Sparganiaceae (*Sparganium*) [Typhaceae sensu Chase et al., 2016] – uni-nucula in envelope (apocarpous superior fruit) (Kaden, 1965); pseudomonomerous dry drupe (Takhtajan, 1985); coenocarpous superior dry drupe in infrutescence (Levina, 1987); secondary monomerous fruit (Eckardt 1937); coenocarpous pseudomonomerous fruit, with 1–3 seeds, pyramidal, indehiscent, drupaceous, over time becomes nut-like with a spongy, seldom fleshy exocarp and hard endocarp (Takhtajan, 1987); Spjut (1994) classified fruit in *Sparganium* as achenosum – infrutescence of dry indehiscent one-seeded fruitlets, with thin pericarp, closely adjacent to seed; fruit with 1–2 carpels, monomerous or syncarpous (pseudomonomerous), bilobular, with one fertile and one sterile carpel, sessile, one-seeded, drupaceous or nucular, with stout exocarp, spongy mesocarp and stony endocarp (Takhtajan, 2009); superior syncarpous (pseudomonomerous) one-stoned pyrenarium; fruit is unilocular, sometimes with 2–3 sterile locules, one-seeded, rarely 2–3 seeded (Bobrov et al., 2009).

Typhaceae (*Typha*) – uninucula in envelop (apocarpous superior monomerous fruit) (Kaden, 1965; Bobrov et al., 2009); tiny, dry one-seeded fruit, falls with peduncle and ring of hairs, forming a fly-apparatus (Takhtajan, 1985); uninucula in infrutescence, apocarpous, secondary monomerous (Eckardt, 1937; Levina, 1987); fruit small, dry, spindle-like, coenocarpous pseudomonomerous (almost monomerous) one-seeded, splitting to the time of full ripening (Takhtajan, 1987); after Spjut (1994), fruit in *Typha* is a cypsel due to extragynecial structures in a form of a bundle of hairs; ovary with one hanging seed; on a stipe, elongated after anthesis, with a ring of hairs, the pericarp is membranous, two-layered (endocarp with thick-walled cells), splitting after the fruit falls in water (Mavrodiev, 1997); monomerous fruit, a follicle but tiny and achene-like before dehiscence, long stipitate, with two-layered pericarp, the inner layer with thick-walled cells (Takhtajan, 2009).

### Distribution of the main morphological fruit types in monocot subclasses and families

As a result of the treatment of the published data, we revealed apocarpous polymerous or trimerous fruits (aggregate fruits) mostly with one-seeded fruitlets in six of twelve families of the subclass Alismatidae of the flora of Ukraine recognized by Mosyakin (2013). A few families have berry-like, one-seeded fruits, capsules, and schizocarp (Table 2). We did not consider as capsule some fruits in members of the Araceae and Hydrocharitaceae families, for which other fruit types were referred to in most later publications. Within 16 families of the subclass Liliidae trimerous capsules are the most common fruits in 12 families, in four families the fruit is berry-like, and two families with capsular fruit have berry-like fruits in the solitary genus (*Streptopus* in Liliaceae, *Paris* in Melanthiaceae). In some genera, deviations from trimerous groundplan occur (tetramerous fruit in *Paris*, dimerous fruit in *Ruscus* and *Majanthemum* of Ruscaceae). Within 10 families of the subclass Commelinidae, in four families superior dry one-seeded fruits occur (Cyperaceae, Poaceae, Sparganiaceae, Typhaceae), while another four families have trimerous capsule (Cannaceae, Commelinaceae, Juncaceae, Pontederiaceae). The families Arecaceae and Musaceae which are only cultivated in Ukraine possess drupaceous and berry-like fruits correspondingly. The most diverse subclass in terms of fruit morphology is Alismatidae, where all five main fruit types are revealed. In Commelinidae there are four main fruit types, while in Liliidae only two fruit types, capsule and berry, were revealed (Fig. 1).

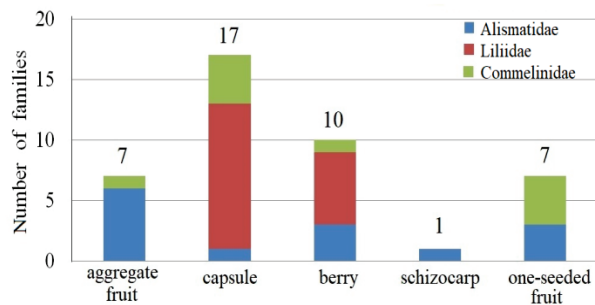
Among families of the class Liliopsida of the flora of Ukraine, trimerous capsules are the most common type (17 of 38 families), occurring in all subclasses (Fig. 1). However, considering the great species richness of the Poaceae and Cyperaceae families, the most numerous fruit can be supposed to be one-seeded fruit, monocarpous or pseudomonocarpous, occurring in seven families. One-seeded fruitlets of aggregate fruits are also very common, particularly, in Alismataceae, Arecaceae, Potamo-

tonaceae, Ruppiaceae, Zannichelliaceae. Berries occur in 10 monocot families, however, these families are not large or there are solitary genera within families with capsular fruit. The rarest fruit type for monocot plants of Ukraine is schizocarp (Fig. 1), appearing only in one genus *Triglochin* (Juncaginaceae). Among the studied taxa there are no monomerous foli- cles, poricide and operculate capsules, winged fruits and loment revealed that occur in dicotyledonous plants (Levina, 1987). Most monocot families in the flora of Ukraine are homogenous in carpological traits. This presumably results from the fact that few taxa represent many monocot families in the flora of Ukraine. However, in six families several fruit types were revealed (Alismataceae, Araceae, Araceae, Hydrocharitaceae, Liliaceae, Melanthiaceae).

**Table 2**  
Main fruit types in the monocot plants of the flora of Ukraine

Fruit types	Subclasses and families
Aggregate fruit	Alismatidae: Alismataceae, Butomaceae, Potamogetonaceae, Ruppiaceae, Scheuchzeriaceae, Zannichelliaceae Commelinidae: Araceae*
Capsule	Alismatidae: Tofieldiaceae Liliidae: Agapanthaceae*, Agavaceae*, Alliaceae, Amaryllidaceae, Asphodelaceae, Colchicaceae, Hemerocallidaceae*, Hyacinthaceae, Iridaceae, Liliaceae <i>p. p.</i> , Melanthiaceae ( <i>Veratrum</i> ), Orchidaceae Commelinidae: Cannaceae*, Commelinaceae*, Juncaceae, Pontederiaceae
Berry	Alismatidae: Acoraceae, Araceae <i>p. p.</i> , Hydrocharitaceae <i>p. p.</i> Liliidae: Asparagaceae, Ruscaceae, Dioscoreaceae, Melanthiaceae ( <i>Paris</i> ), Liliaceae ( <i>Streptopus</i> ), Smilacaceae* Commelinidae: Musaceae*
Schizocarp	Alismatidae: Juncaginaceae
One-seeded fruit	Alismatidae: Araceae <i>p. p.</i> , Hydrocharitaceae ( <i>Najas</i> ), Zosteraceae Commelinidae: Cyperaceae, Poaceae, Sparganiaceae, Typhaceae

Note: families recognized after Mosyakin (2013); \* – cultural flora.



**Fig. 1.** Fruit types in monocot families of the flora of Ukraine: the total number of families above columns is greater than 38 because in some families two fruit types are recognized

Many monocot families have unambiguously defined fruit types, which however can differ in minor traits according to different sources. For example, the different definitions can concern the dehiscence mode of the capsule or pericarp consistency. Most of these families (15 of 27 families) belong to the subclass Liliidae and have trimerous capsular or berry-like fruits. For 11 families (29% of families), two or more interpretations of morphological fruit type exist. Among them, one case is a group of families with initial carpel fusion (Hydrocharitaceae (*Stratiotes*), Juncaginaceae, Melanthiaceae (*Veratrum*), Scheuchzeriaceae, Tofieldiaceae), resulting in fruit type being formed of a transitional stage between apocarpous and syncarpous and that is why it is defined as multi-follicle (apocarpous fruit) or capsule and schizocarp (syncarpous fruit). The other group of families unites families with one-seeded fruit, being treated as monomerous apocarpium or pseudomonocarpium because of the absence of transitional stages between one-seeded and ancestral fruit (Araceae (*Lemna*), Cyperaceae, Hydrocharitaceae (*Najas*), Poaceae, Sparganiaceae, Typhaceae, Zosteraceae). In both cases, the reason for the controversial interpretation of the fruit type concerns gynoecium structure, which is still problematic (Remizowa et al., 2006, 2010; Sokoloff, 2016; Sokoloff et al., 2017). It is interesting that the Hydrocharitaceae family appears in both lists of controversial fruit types, and fruit in *Stratiotes* is

unique through the combination of almost unfused carpels and inferior ovary (Efremov et al., 2015a). The examination of gynoecium structure and pericarp anatomy in various monocot plants of the flora of Ukraine is a ground for future research on evolutionary fruit morphology and fruit adaptations to dissemination.

## Conclusions

As a result of our study, it becomes clear that the taxonomical diversity of monocotyledonous plants of the flora of Ukraine represents well the diversity of the world monocot flora, with an almost equally high portion of the largest families that define the spectrum of fruit types in the class Liliopsida. The morphological diversity of fruits within the class Liliopsida in the flora of Ukraine is characterized by the predominance of trimerous capsules on the familial level and one-seeded fruits and fruitlets on the generic level. Fruits in many families have alternative names due to the lack of unified carpological terminology, different degrees of knowledge of the fruit structure and different opinions on the gynoecium and fruit classification in taxa that are problematic from the morphological viewpoints. The most controversial fruit types are in plants with one-seeded fruit (monocarpium or pseudomonocarpium). The problem also arises for the definition of fruit type in plants with initial carpel fusion. The great number of families with trimerous capsules led to the need to apply anatomical methods in the study of pericarp structure aimed at differentiating the convergent variants of fruits. Meanwhile, for the most problematic taxa, it is necessary to find principles of classification of the fruits with undefined gynoecium type. In general, the monocot plants of the flora of Ukraine are characterized by limited diversity of morphological fruit types and poor knowledge of the fruit structure, which makes further carpological studies in Ukraine a highly relevant topic for research.

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