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

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Introduction

Fruit is defined as a terminal stage of differentiation and specialization of the gynoecium 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 (Zirman & 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 Campylium (Dremliuga, 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, phytoecologists, 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 4,100 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 consor- tial relations of plants with frugivorous animals (Jordaın et al., 2011; Karimi et al., 2020; Sena et al., 2021), particularly, the significant role of fruit morphogenetics in the process of plant propagation and species diversity.
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 longing to the flora of Ukraine was defined including the cultivated taxa, (2013) or 30 families sensu Chase et al. (2016), which is about 40% of the monocot flora of Ukraine and main fruit types of the flora of Ukraine having the most controversial fruit types with a view to their further investigation.

**Table 1**

| The largest monocot families of 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                                 | Orchidaceae (29/29)                                                                             | Capsule fissuricidal    | Inferior trimerous dry multi-seeded dehiscent paracarp or fleshy indehiscent fruit |
| 2. Poaceae                                     | Poaceae (108/444)                                                                               | Caryopsis              | Superior dry one-seeded fruit in anthecium         |
| 3. Cyperaceae                                  | Cyperaceae (19/153)                                                                            | Cypsela                | Superior dry one-seeded fruit in envelope          |
| 4. Asparagaceae                                | Asparagaceae (15/57)                                                                           | Capsule or berry       | Superior trimerous dry multi-seeded dehiscent syncarpium or indehiscent fleshy fruit |
| 5. Arecaceae                                   | Arecaceae (11/25)                                                                              | Berry or utricle       | Superior oligomerous low-one-seeded fleshy indehiscent paracarp or low-one-seeded indehiscent fruit with undifferentiated pericarp |
| 6. Bromeliaceae                                | Bromeliaceae (3/13)                                                                            | Berry or capsule         | Inferior trimerous fleshy indehiscent fruit or dry dehiscent syncarpium |
| 7. Arecaceae                                   | Arecaceae (4/11)                                                                               | Drupe or date          | Superior trimerous low-seeded or one-seeded fleshy indehiscent apocarpium with stony endocarp, or papery endocarp |
| 8. Iridaceae                                   | Iridaceae (4/34)                                                                               | Capsule loculicidal    | Inferior trimerous dry multi-seeded dehiscent syncarpium |
| 9. Amaryllidaceae                              | Amaryllidaceae (7/61)                                                                          | Capsule loculicidal    | Inferior or superior trimerous dry or fleshy multi-seeded dehiscent syncarpium |
| 10. Zingiberaceae                              | Zingiberaceae (3/13)                                                                           | Capsule loculicidal    | Inferior trimerous dry multi-seeded dehiscent syncarpium |
| 11. Liliaceae                                  | Liliaceae (7/52)                                                                               | Capsule loculicidal or berry | Superior trimerous dry multi-seeded dehiscent syncarpium or fleshy indehiscent fruit |
| 12. Juncaceae                                  | Juncaceae (2/41)                                                                               | Capsule loculicidal    | Superior trimerous dry multi-seeded or three-seeded dehiscent syncarpium or paracarpium |
| 13. Potamogetonaceae                           | Potamogetonaceae (1/25)                                                                        | Oligo-druphe           | Superior apocarpus aggregate fruit of few one-seeded indehiscent fructules 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 & Fedorovych (1999) and Danielyk (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,
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 Alismatae, Liliidae, and Commelinidae within the framework of Moysakin (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 Alismatae

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 gyroecium 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 laminar to basal placation is observed as also from few ovules to a single ovule (Eames, 1961); carnarium – apocarpous polymorphanus fruit of dry multi-seeded indehiscent fruitlets, with seeds, do not fill the whole locale volume (Spjut, 1994).

Anacardiaceae (incl. Lennaecae) – superior berry-like one-low-seeded fruit (Takhtajan, 1985). In Calla fruit is a berry paracarpous, trimerous, non-covered, juicy, red, gathered in an inflorescence (Kaden, 1965). In Calla palustris there are 4–5 seeds in a berry (Belyakov et al., 2017). In Pista – capsule dry indehiscent (Takhtajan, 1985); monomorous low-seeded fruit with thin half-transparent pericarp (Takhtajan, 2009). In Lennaeaceae – capsule paracarpous (?), superior, trimerous (?), covered, broken (punctuation as in the original text) (Kaden, 1965); monomorous fruit, 1–seeded utricule (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 Spiryodella, fruit is 1–2-seeded, sometimes reddish, 1–2 mm long, with wing-like zone; monomorous achenial fruit with 1–7 seeds utricule, a unilocular un-seeded fruit with thin dehiscent fruit wall, releasing seeds (Spjut, 1994). Utricle, after Sput (1994), is composed by more than one carpel. Most Lennaeaceae have one-seeded fruits (Tippery & Les, 2020).

Butomaceae (Botomus) – multi-follicle (hexa-follicle) superior, hemi-syncarpous, of 6–9 fruitlets, ventrally dehiscent, with covering (Kaden, 1965); oligomorous cyclic multi-follicle of 6–9 multi-seeded fruitlets with laminar placation (Takhtajan, 1985; Levina, 1987); dry cyclic 3–6-moronic multi-follicle, ventrally dehiscent (Bobrov et al., 2009). Carpels are fused postepically (www.mobot.org/MOBOT/research/APweb).

Hydrocharitaceae (incl. Najadaceae) – capsule inferior, fleshy, disrupting: syncarpous, hemisyncarpous (Hydrocharis, Stratiotes) or paracarpous trimerous (Elodora) (Kaden, 1965); inferior unilocular, berry-like indehiscent fruit or dehiscent by mucilage hydration, carpels are fused but have free margins (Takhtajan, 1985, 2009); inferior hemisyncarpous paracarpous berry (Stratiotes) or inferior hexamorous paracarpous (phragmocarpous) 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 hexamorous hemiparacarpous fruit.
pous berry, irregularly dehiscent by mucilage hydration (Eftremov et al., 2015b), in *Stratiotes aloides* fruit is defined as an inferior hexameros hermaphroditic syncarpous, with follicular dehiscence from top to bottom by three valves, in the last case, three wider valves are “fertile”, apically dehiscent (Takhtajan, 1985; 2009; Speta, 1998).

**Subclass Liliidae**

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

Asparagaceae (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, trilocular, 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).

Aliciae (Allium, Nectaroscordum) [Amaryllidaceae sensu Chase et al., 2016] – capsule superior, trilocular, low-seeded, with an envelope, leathery, dorsiventral (Kaden, 1965), or loculicidal (Takhtajan, 1985, 2009; Rahman, 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 (*Asphodole, Emerurus*) [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, septically-ventrally dehiscent (Kaden, 1962, 1965), septicidally dehiscent (Takhtajan, 1985; Artjuschenko & Theodorov, 1986); capsule multi-seeded, partially or totally syncarpous, septically-dehiscent (Nordenstamm, 1998).

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

Hemeroallidaceae* (Hemeroallis) [Asphodelaceae sensu Chase et al., 2016] – capsule dry, leathery, trilocular, with 9–12 seeds in a locale, loculicidal (Takhtajan, 1985, 2009; Clifford, 1998).

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

Iridaceae – capsule 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).

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

Melanthiaceae (*Veratrum, Paris*) – tri-follicle hermaphroditic syncarpous, covered, septically-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 septical ventricidal. In *Paris* – berry superior, trimerous, 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 fissicidal (Spjut, 1994).

Ruscaceae (incl. Convallariaceae) [Asparagaceae sensu Chase et al., 2016] – berry superior trimerous (*Convallaria, Polygonatum*) or dimerous fibrous endocarp (Spjut, 1994); uni-drupe or uni-nucula (Bobrov et al., 2009); fruit an achene/follicle (www.mobot.org/MOBOT/research/APweb).
(Majanthemum), non-covered (Kaden, 1965), unilocular, low-seeded (Ruscus), often red or orange (Takhtajan, 2009).

Smallacese* (Smalla) – 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 perigynium 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 – an 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 (baccatum) (Spujt, 1994).

Cannaceae* (Canna) – capsule inferior, trilocular, multi-seeded, with soft spines outside, localicidal, 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) (Spujt, 1994).

Commelinaceae* (Commelina, Tradescantia) – capsule hemiparacarpous, superior, dimerous, enveloped, dorsiventrally dehiscent (Kaden, 1965); capsule trilocular, sometimes unii-bilocular, localicidal (Takhtajan, 1985; 2009; Spujt, 1994).

Cyperaceae – drupe (pyrenarium) paracarpous, superior, di-trimerous, dry, non-covered or covered by perigynium in a form of bristles (most genera); enveloped in utricle formed by prophyll or bract (Kaden, 1965); podocarpus, inferior, di-trimerous, enveloped, dorsiventrally dehiscent (Kaden, 1965); uninucula in infruitescence, apocarpous, secondary monomerous (Eckardt, 1937; Levina, 1987). In some genera the pericarp is membranous, two-layered (endocarp with thick-walled cells), splitting after the fruit falls in water (Mavrodie, 1997); monomerous fruit, a berry-like and achene-like before dehiscence, long stipeitate, with two-layered pericarp, the inner layer with thick-walled cells (Takhtajan, 2009).

Juncaceae – capsule syncarpous, superior, trimerous, covered, dorsiventrally dehiscent (Juncus) or paracarpous, dorsally dehiscent (Luzula) (Kaden, 1965); capsule localicidal (Takhtajan, 1985; 2009; Spujt, 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 (Shehyag-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 paraparous (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); apo-carpous fruit, secondary monomerous, falls out together with spikelet scales (lamina, 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); Spujt (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) indeliscent nut-like fruit; sclerenchyma, often atypical, located in all pericarp layers. Caryopsis is characterized by diverse attachments (Bobrov et al., 2009). In Cyprip and Helcochloa Caryopsis is follicle-like (Kaden, 1965); in Cyprip fruit is utricule-like, with a free papery fruit wall (Takhtajan, 2009).

Pontederiaceae (Monochoria) – capsule superior trimerous, multi-seeded, localicidal (Takhtajan, 2009); capsule fissuricidal (Spujt, 1994).

Sparganiaceae (Sparganium) [Typhaeaceae 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, indelisent, drupaceous, over time becomes nut-like with a spongy, smallfleshly exocarp and hard endocarp (Takhtajan, 1987); Spujt (1994) classified fruit in Sparganium as achenomus – infrutescence of dry indelisent one-seeded fruitlets, with thin pericarp, closely adjacent to seed; fruit with 1–2 carpels, monomerous or syncarpous (pseudomonomerous), bilocular, 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) – uni-nucula 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); uni-nucula in infrutescence, apocarpous, secondary monomerous (Eckardt, 1937; Levina, 1987); fruit small, dry, spindel-like, coenocarpous pseudomonomerous (almost monomerous) one-seeded, splitting to the time of full ripening (Takhtajan, 1987); after Spujt (1994), fruit in Typha is a cypsela due to exotegmic 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 (Mavrodie, 1997); monomerous fruit, a berry-like but tiny and achene-like before dehiscence, long stipeitate, 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 polymereous 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 Lilaceae, Paris in Melanthiaceae). In some genera, deviations from trimerous groundplan occur (tetrameric, monomerous or syncarpous capsules) in four families of the subclass Alismatidae of the flora of Ukraine, considered 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 Lilaceae, Paris in Melanthiaceae). In some genera, deviations from trimerous groundplan occur (tetramerous, monomerous or syncarpous capsules) in four families of the subclass Alismatidae of the flora of Ukraine, considered by Mosyakin (2013).
tones, 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 nest 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 monomorphic foli- lies) belong to the subclass Liliidae and have trimerous capsular or berry-For example, the different definitions can concern the dehiscence mode of which however can differ in minor traits according to different sources. Table 2

| Fruit types | Subclasses and families |
|-------------|-------------------------|
| Aggregate   | Alismatidae: Alismataceae, Butomaceae, Potamogetonaceae, Ruppiaceae, Schoenoplectaceae, Zannichelliaceae |
| Capsule     | Alismatidae: Tofieldiaceae, Liliidae: Agapanthaceae*, Agavaceae*, Alliaceae, Amryllidaceae, Asphodelaceae, Cohlecia, Hemerocallidaceae, Hypecia, Indiceae, Liliaceae p. p., Melanthiaceae (Veratrum), Orchidaceae |
| Berry       | Alismatidae: Acoraceae, Anacardiaceae, Asterales, Dioscoreaceae, Melanthiaceae (Paris), Liliaceae (Streptopus), Smilacaceae* |
| Schizocarp  | Alismatidae: Juncaginaceae |
| One-seeded  | Alismatidae: Acanthaceae, Asparagaceae, Commelinidae, Cypripedioideae, Poaceae, Sparganiaceae, Typhaceae |

Table 2

Main fruit types in the monocot plants of the flora of Ukraine

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 is a group of families with initial carpel fusion (Hydrocharitaceae (Stratiotes), Juncaginaceae, Melanthiaceae (Veratrum), Schoenoplectaceae, Tofieldiaceae), resulting in fruit type being formed of a transitional stage between apocarpous and syncarpous and that is why it is defined as multi-filicule (apo-carpous fruit) or capsule and schizocarp (syncarpous fruit). The other group of families unites families with one-seeded fruit, being treated as monomeroous apocarpium or pseudomonocarpium because of the ab-sence of transitional stages between one-seeded and ancestral fruit (Anacardiaceae (Lemna), Cypripedioideae, 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 (Remizova 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

Conclusions

As a result of our study, it becomes clear that the taxonomical diversi-

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References

Ackerman, J. D. (1997). Submarine pollination in the marine angiosperm Zostera marina (Zosteraceae). The influence of fruit morphology on fluid flow. American Journal of Botany, 84(4), 1099–1109.

Arturaschenko, Z. T., & Theodorov, A. A. (1986). Atlas po opisatelnoy morfolo- gyi vysshikh rasteni. Plod [Atlas of descriptive morphology of higher plants. Fruit] [Organographia illustrata plantarum Vascularium. Fruits]. Nauka, Le- ningrad (in Russian).

Bulgaro-Kopa, H. E., Fischer, G., & Magnitsky, S. (2020). Seed-fruit relation-

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References

Ackerman, J. D. (1997). Submarine pollination in the marine angiosperm Zostera marina (Zosteraceae). The influence of fruit morphology on fluid flow. American Journal of Botany, 84(4), 1099–1109.

Arturaschenko, Z. T., & Theodorov, A. A. (1986). Atlas po opisatelnoy morfolo-gyi vysshikh rasteni. Plod [Atlas of descriptive morphology of higher plants. Fruit] [Organographia illustrata plantarum Vascularium. Fruits]. Nauka, Le-ningrad (in Russian).

Bulgaro-Kopa, H. E., Fischer, G., & Magnitsky, S. (2020). Seed-fruit relation-ships in fishes’ fruit species: Role of hormones. A review. Revista Colombiana de Ciencias Horticolas, 14(1), 90–103.

Behren, C., & Yeselak, J. A. (2020). Hydrochorous seed dispersal in riparian forests altered by urbanization. Ecosphere, 11(2), e03849.

Belyakov, E. A., Laprov, A. G., & Lebedeva, O. A. (2017). Ekologiya prorastaniya semen i osobennosti ontogenezy splavinoobrazuyushchego gigrogelofita Calla palustris (Araceae) v laboratornykh uslovijakh [Ecology of seed germination and features of ontogeny of floating mat-forming hydrophyte Calla palustris (Araceae) under laboratory conditions]. Biosystems Diversity, 25(4), 282–288 (in Russian).

Bobrov, A. V. F. C., & Romanov, M. S. (2019). Morphogenesis of fruits and types of fruit of angiosperms. Botany Letters, 166(3), 366–399.

Bobrov, A. V., Mel'kyan, A. P., & Romanov, M. S. (2009). Morphogenesis of plodov Magnolypi (Morphogenesis of fruits of Magnoliophyta). Librokom, Mos- cow (in Russian).

Boudelche, G., Ozma, W. A., & Prinzing, A. (2008). The trade-off between vegeta-tive and generative reproduction among angiosperms influences regional hyd-rochorous propagule pressure. Global Ecology and Biogeography, 17, 50–58.

Bojarski, V., & Farghalov, A. (2007). Atlas of seeds and Fruits of Central and East-European flora the Carpathian Mountains Region. Springer, Dordrecht.

Chase, M. W. (2004). Monocot relationships: An overview. American Journal of Botany, 91(10), 1645–1655.

Chase, M. W., Christenhusz, M. J. M., Fay, M. F., Byng, J. W., Judd, W. S., Soltis, D. E., Malbrerley, D. J., Sennikov, A. N., Soltis, P. S., & Stevens, F. P. (2016). The angiosperm phylogeny group. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants. APG IV. Botan-ical Journal of the Linnean Society, 181, 1–20.
