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MORPHOLOGICAL AND TAXONOMICAL TREATMENTS OF FRUITS IN THE SUBCLASS ROSIDAE TAKHT. OF THE FLORA OF UKRAINE

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Introduction. Rosids is the pivotal clade of eudicots, whose taxonomic composition was significantly changed based on molecular phylogeny. Molecular insight led to the re-evaluation of many phenotypic features, especially in reproductive morphology. Although the floral structure and evolution within the current scope of rosids were actively investigated, the morphological structure of fruit was almost fully neglected. The present study aimed to survey the morphological diversity of fruits in rosids (subclass Rosidae) in the flora of Ukraine to reveal the most common fruit types, analyze the distribution of the basic fruit types among rosids, and survey some comparative-morphological features of gynoecium and fruit.

Materials and Methods. Fruit features have been surveyed based on many carpological sources. We also analyzed the gynoecium characteristics crucial for fruit development, *i.e.*, the type of ovary insertion, placentation, and ovule and locule number. For Rosidae, seven basic fruit types were recognized using the approach previously elaborated for the monocot plants of Ukraine: aggregate fruit, multi-seeded monocarp, capsule, berry, multi-seeded pyrenarium, schizocarp, and one-seeded fruit.

Results. As a result, the annotated list of morphological characteristics for each of the 54 families of Rosidae occurring in Ukraine was composed. In this list, the complementary and the most contrasting definitions of fruits from different sources were combined.

Discussion. According to our calculations, the subclass Rosidae in the flora of Ukraine is represented by 326 genera and at least 1617 species. Our results demonstrated that the most widespread fruit types at the family level seem to be capsular and one-seeded fruits, while at genus and species level the portion of multi-seeded monocarps and aggregate fruits is also significant. Nine families reveal more than one

basic fruit type in the flora of Ukraine. Some fruits are ambiguously classified into one or another fruit type because of their intermediate features. Thus, fuzzy boundaries between most fruit types are evident.

Conclusions. The obtained results have been compared with our previously reported results for the monocot clade in the flora of Ukraine. In both cases, the predominance of capsular fruits at the family-level spectrum of basic fruit types was clearly demonstrated. The results of our analysis suggest that the model of basic fruit types has the potential to be applied to the formal treatment of fruit structure in other groups of angiosperms.

Keywords: fabids, malvids, gynoecium, capsular fruit, one-seeded fruit, schizocarp

INTRODUCTION

Rosids is a large clade of eudicots comprising 17 orders, 135 families (APG IV, 2016) and ca. 90,000 species (Sun *et al.*, 2016). This clade hosts nearly a quarter of all angiosperm species. In the hierarchical system used for the flora of Ukraine (Mosyakin, 2013), rosids are considered as a subclass Rosidae Takht. of the class Rosopsida Batsch (Dicotyledonae) of the division Magnoliophyta Cronquist, Takht. & W. Zimmerm. ex Reveal (Angiospermae). In its current state, subclass Rosidae unites subclasses Rosidae, Dilleniidae Takht. ex Reveal & Takht. and Hamamelididae Takht. recognized by A. Takhtajan (2009) with exclusion of some orders. According to S. L. Mosyakin (2013), subclass Rosidae of the flora of Ukraine is represented by 54 families. Nearly half of them belong to the sub-clade fabids (28 families), while the others belong to the sister sub-clade malvids (25 families), and the family Vitaceae forms the basal clade (authors for all mentioned families are provided in the section **Results**).

In the last decades, the view on the taxonomic composition of the Rosidae changed following the progress in molecular studies (APG I, 1998; Zhu *et al.*, 2007; Wang *et al.*, 2009; Hilu *et al.*, 2014; APG IV, 2016; Sun *et al.*, 2016). Molecular insight led to the revision of phylogeny of this group, reevaluation of many phenotypic features and re-examination of previously accepted evolutionary-morphological concepts. Molecular phylogenetics also resulted in search of missing synapomorphies, especially in the reproductive morphology, for this pivotal group and its sub-clades (Endress & Friis, 2006; Endress & Matthews, 2006; 2012; Schönenberger & von Balthazar, 2006; Endress, 2014; Ickert-Bond *et al.*, 2014; Shivaprakash & Bawa, 2022).

Although the floral structure and evolution within the rosids were actively investigated, the morphological and taxonomical treatment of fruit in the frame of the whole clade was almost fully neglected. The present study aimed to survey the morphological diversity of fruits in the Rosidae in the flora of Ukraine to: (a) reveal the most common fruit types, (b) analyze the distribution of the basic fruit types among the studied families, genera and species of rosids, and (c) survey some comparative-morphological features of gynoecium and fruit.

MATERIALS AND METHODS

In our study, we referred to and analyzed characteristics of fruit in the subclass Rosidae of the flora of Ukraine. We surveyed the fruit features primarily from N. N. Kaden (1965), where the most precise characteristics of fruits in numerous families of the mid-

dle-European flora are provided. Also, data provided by I. Roth (1977), R. W. Spjut (1994), A. Takhtajan (2009), and other authors were taken into consideration. Following our concept of fruit morphogenesis (Odintsova, 2022), we included into the analysis the gynoecium characteristics significant for fruit development, namely, ovary insertion, placentation, and number of ovules and locules (Eichler, 1878; Takhtajan, 2009).

The number of species and genera in the flora of Ukraine (including the cultivated taxa) was calculated from the check-list of S. L. Mosyakin & M. M. Fedoronchuk (1999), with the addition of the data by S. L. Mosyakin (2013) and other recent surveys on certain families (Didukh *et al.*, 2004, 2010; Iljinska *et al.*, 2007; Fedoronchuk, 2017, 2018). Species names were synonymized according to POWO (https://powo.science.kew.org).

For unification and formalization of the data, we accepted the basic fruit types that occurred in the Rosidae as the less controversial ones applying the same approach as to monocots (Odintsova *et al.*, 2021). In particular, for the Rosidae, we recognized seven basic fruit types described below.

Aggregate fruit – polymerous or oligomerous fruit, developed from the apocarpous gynoecium, with multi-seeded or one-seeded carpels, occurring in Rosaceae (*i.e.*, achenecetum, cynarrhodium, multi-drupe, multi-follicle).

Multi-seeded monocarp – monomerous apocarpous, usually dehiscent fruit of follicle-type in Fabaceae (legume or pod). Some Fabaceae, however, have few-seeded, indehiscent, or irregularly dehiscent fruits, derived from legume (*e.g.*, articulated legume or loment). Indehiscent achene-like legume of some Fabaceae having one to few ovules are regarded as one-seeded fruit.

Capsule – syncarpous (*incl.* paracarpous) multi-seeded or oligo-seeded dehiscent fruit, usually dry and having lignified layers in the fruit wall. Multi-seeded fruits in Brassicaceae (*i.e.*, silique, silicle, and bilomentum) were included in this category, while indehiscent achene-like silicle we treated as one-seeded fruit.

Berry – completely fleshy, syncarpous (*incl.* paracarpous) indehiscent multi-seeded to oligo-seeded fruit.

Multi-seeded pyrenarium – pyrenarium with several pyrenes (*ukr*. bahatokistochkovyi pirenariy) or one pyrene having several locules; syncarpous drupe, syncarpous indehiscent fleshy or dry fruit with several stones (pyrenes), containing few to many seeds (*e.g.,* pome in the tribus Maleae Small of Rosaceae).

Schizocarp – syncarpous oligo-seeded indehiscent fruit, usually with dry or drupaceous fruit wall, which splits longitudinally into several closed usually one-seeded fragments (mericarps).

One-seeded fruit – indehiscent fruit containing one seed (rarely two), derived from the monomerous (uni-nucula, uni-achene, drupe), syncarpous, or pseudomonomerous (achene, nut, samara, one-seeded pyrenarium) gynoecium.

According to N. N. Kaden (1965), superior fruits are subdivided into three categories – covered (*lat*. velatus), enveloped (*lat*. tunicatus), and uncovered (*lat.* nudus). Covered fruits have persistent perianthium whorle (*e.g.*, calyx), which surrounds the ovary but does not completely hide it. Enveloped fruits are totally surrounded by the persistent perianthium or bracts. Uncovered fruits have missing perianthium or bracts.

RESULTS

The results were presented here as an annotated list of morphological fruit types and their characteristics. Families were listed according to S. L. Mosyakin (2013) and

clustered in sub-clades according to APG IV (2016). For each family, in the round brackets the names of a few taxa or, in case of numerous taxa, the number of genera and species occurring in the flora of Ukraine were indicated. Where it was not mentioned, the number of taxa corresponds to the information provided by S. L. Mosyakin & M. M. Fedoronchuk (1999). Asterisks (*) indicated the cultivated or escaped taxa. Alternative and complementary data on fruit morphology were arranged chronologically followed by the gynoecium characteristics. The data in the annotated list are not exhaustive; we rather intended to provide the most significant features and the most contrasting definitions of fruits.

Annotated list of morphological fruit types occurring in plants of the subclass Rosidae of the flora of Ukraine

Vitaceae* Juss. (3/13) – superior berry (uva), syncarpous, dimerous, uncovered, fleshy (Kaden, 1965); seeds 1–4 (Takhtajan, 2009). Ovules two per carpel, located near the base of the ovary in the symplicate zone (Ickert-Bond *et al.*, 2014).

1. Fabid sub-clade

Zygophyllaceae R. Br. (*Zygophyllum fabago* L.) – syncarpous superior pentamerous capsule, uncovered, dorsi-ventri-laterally dehiscent, with columella dividing into 5 strands composed of ventral vascular bundles of carpels, while valvae decline from them and fall out (Kaden, 1965). Fruit is a loculicidal capsule (Sheahan, 2007) with 4–5 locules (Hussein *et al.*, 2009).

1.1. Nitrogen-fixing clade

Fabaceae Lindl. (69/379–430) (Fedoronchuk, 2018) – legume (pod, *ukr.* bib), multiseeded superior monocarpium (Kaden, 1965; Roth, 1977; Van der Pijl, 1982). Following Kaden (1965), legume can be:

- bivalvate, dorsi-ventrally dehiscent, covered (most genera and species), or enveloped (*Ononis* L.);
- transversely septated, covered, dorsi-ventrally dehiscent (*Faba* Mill., *Phaseolus* L.);
- indehiscent uncovered (*Gleditsia* L.);
- folliculate, enveloped, ventrally dehiscent (many *Trifolium* Tourn. ex L. species, except those listed beneath); ventral dehiscence is slow, often incomplete or missing (Roth, 1977);
- enveloped, circumscissile dehiscent (*Trifolium alpestre* L., *T. borysthenicum* Grum., *T. incarnatum** L., *T. pratense* L., *T. rubens* L.);
- utriculate, enveloped, rupturing (*Trifolium arvense* L., *T. campestre* Schreb., *T. dubium* Sibth., *T. aureum* Pollich);
- articulated (loment fruit), covered (*Coronilla* L., *Securigera* DC., *Hedysarum* L., *Hippocrepis* L., *Ornithopus* L.);
- achene-like, indehiscent, covered (*Amorpha* L., *Glycyrrhiza echinata* L., *Medicago lupulina* L., *Melilotus* L., *Onobrychis* Mill.), or enveloped (*Anthyllis* L.) (Kaden, 1965). *Trigonella coerulea* (L.) Ser. and *T. spicata* Sibth. & Smith. have one- to few-seeded indehiscent legume while other species of *Trigonella* L. and *Medicago* L. have hardly dehiscent or coiling fruit (helicoid pod) (Roth, 1977);
- pseudo-bilocular, covered (*Astragalus* L., *Oxytropis* DC.), with the longitudinal false septum of different origin (Roth, 1977). Fruit is ventrally dehiscent (*A. dasyanthus* Pall., *O. pilosa* (L.) DC.), dorsi-ventrally dehiscent (*A. albicaulis* DC., *A. arenarius* L., *A. contortuplicatus* L.), incomplete dorsi-ventrally dehiscent (other

Astragalus and *Oxytropis* species), dorsally dehiscent (A. *testiculatus* Pall.) or indehiscent (*A. glycyphyllos* L.);

- necklace-like, fleshy (*Sophora* L.) (Zerov, 1965).

Polygalaceae Hoffmanns. & Link (*Polygala* L., 15 spp.) –syncarpous, superior, dimerous capsule with persistent calyx, dorsi-ventrally dehiscent (Kaden, 1965). Usually it is loculicidal capsule, however, in *Polygala vulgaris* L. fruit was treated as a one-seeded utricle, dehiscing after falling on the ground (Spjut, 1994). In *Polygala,* an ovary is composed of a synascidiate zone only; ovule is apical and median, and placentation is axile (Leinfellner, 1972). Capsule membraneous or fruit pseudomonomerous; ovule one per locule, pendent from the ovary roof where the septum and the wall converge, placentation seems to be parietal, based on vascular anatomy (Eriksen & Persson, 2007).

Rosaceae Juss. (54/371 + *ca*. 120 cultivated species) (Fedoronchuk, 2017) – diverse fruits: aggregate fruits (achenecetum, cynarrhodium, multi-drupe, penta-follicle), one-seeded fruits (amaltaea and drupe; amaltaea can be also dimerous), or inferior multi-seeded pyrenarium (pome) (Kaden, 1965; 1968). Fruit evolution in Rosaceae seems to proceeded from dry aggregate fruits (*i.e.*, follicetum and achenecetum) to drupe and pome, and independently to drupetum (Xiang *et al.*, 2017). Further we follow N. N. Kaden (1965) with additions of other data:

- Achenetum (achenecetum, multi-nucula, *ukr*. bahatohorishok) can be: (a) acyclic covered (*e.g*., *Comarum* L., *Geum* L., *Potentilla* L., and *Dryas* L.), (b) cyclic, covered, designated as paucinucula (*ukr*. malohorishok) (*e.g*., *Filipendula* Mill.). In *Filipendula ulmaria* (L.) Maxim. ovary consists of 5–9 carpels, while in *F. vulgaris* Moench. it has 10–12 or even more carpels (Eichler, 1878). In *Holodiscus** (K. Koch) Maxim. fruit is covered penta-achene (Kaden, 1968). Placentation is basal (sub-basal) in *Potentilla* (Eames, 1961).
- Fragum (*ukr.:* sunychyna) – acyclic covered achenecetum in *Fragaria* L. and *Potentilla indica** (Andrews) Th. Wolf, supplied with fleshy conical fruiting receptacle (Kaden, 1968).
- Cynarrhodium – acyclic achenecetum, enveloped in fleshy hypanthium. It occurs in *Rosa* L.
- Amaltaea – di-achene or uni-achene enveloped in hypanthium. It can be: (a) dimerous in *Agrimonia* L., *Sanguisorba* L. (*incl*. *Poterium* L.); (b) monomerous in *Alchemilla* L. (Kaden, 1965). According to Eichler (1878), in *Agrimonia, Alchemila* (*incl. Aphanes* L.), *Aremonia* Neck. ex Nestl., *Poterium, Sanguisorba* 1–2(3) carpels occur. Fruits of *Aphanes* and *Alchemila* having mostly one carpel we treated as one-seeded fruit.
- Drupetum (multi-drupe) can be acyclic, covered (*Rubus* L.) or composed of few carpels. Specifically, in *Kerria* DC. fruit is penta-drupe (Kaden, 1968), carpels are one-seeded (Eichler, 1878). In *Rhodotypos scandens* (Thunb.) Makino fruit is covered tetra-drupe (Kaden, 1968) or carpels 2–4, two-seeded (Eichler, 1878).
- Drupe (uni-drupe) occurs in the tribus Amygdaleae DC., it can be uncovered fleshy (*Prunus* L., *incl*. *Cerasus* Mill. and *Padus* Mill.) or dry (*Prunus amygdalus* Batsch). In *Prinsepia** Royle drupe is covered (Kaden, 1968), ovules two, usually one is suppressed (Eichler, 1878).
- Multi-follicle is typically pentamerous (penta-follicle, sometimes tetra-follicle), cyclic, covered, many-seeded. It can be ventrally dehiscent (most species of *Spiraea* L.), or dorsi-ventrally dehiscent (*Physocarpus** (Cambess.) Raf., *Sorbaria** (Ser. ex DC.) A. Braun, *Spiraea chamaedryfolia* L., *S. salicifolia* L.) (Kaden, 1968).

In *Physocarpus, Spiraea,* and *Sibiraea** Maxim. carpels are basally united and adnate to hypanthium (Eames, 1961; Kaden, 1968). In *Physocarpus* carpels are shortly stalked, 2–4 ovules, few seeds (Kalkman, 2004). In *Exochorda** Lindl. fruit is hemisyncarpous penta-follicle with 1–2-seeded fruitlets (Kaden, 1968). In *Aruncus* Schaeff. fruit is covered tri-follicle. In *Neillia** D. Don, fruit is covered uni- or di-follicle (Kaden, 1968).

- Pome (*ukr*. yabluko) occuring in the tribus Maleae can be:
  (a) hemisyncarpous pentamerous (*Amelanchier* Medik., *Cydonia** Mill., *Malus* Mill., *Pyrus* L.) or oligomerous (*e.g.*, *Sorbus* L.). In *Sorbus,* an ovary is partly adnated to hypanthium, while in most other Malaea it is completely adnated (Eames, 1961). In *Cydonia, Malus,* and *Pyrus* pyrenes are leathery, cartilaginous, or parchment (Kaden, 1968);
  (b) pseudoapocarpous oligomerous (*Cotoneaster* Medik., *Mespilus* L., *Crataegus* L., except *Crataegus curvisepala* Lindm. (= *C. rhipidophylla* var. *rhipidophylla*), and *C. monogyna*). As carpellary tissue becomes fully lignified, the fruit must be treated as multi-nucula immersed in juicy hypantium with weakly united carpels; apocarpy seems to be secondary (Kaden, 1968);
  (c) monomerous (*Crataegus curvisepala* (= *C. rhipidophylla* var. *rhipidophylla*), *C. monogyna* Jacq. (Kaden, 1965), as also fruits in the species recognized for the flora of Ukraine: *C. fallacina* Klokov (= *C.* × *kyrtostyla* nothovar. *kyrtostyla*) and *C. pseudokyrtostyla* Klok. (= *C. rhipidophylla* var. *rhipidophylla*) (Dvirna *et al.*, 2021).

Generally, A. W. Eichler (1878) noted that 5 carpels are common for *Mespilus* L., *Cydonia** Mill., and *Pyrus* (sometimes four carpels); *Cotoneaster* and *Amelanchier* have 3–5 carpels, *Sorbus* has 2–3(4) carpels, and *Crataegus* has 1–5 carpels. Carpels are often bi-ovulate, sometimes poly-ovulate (*Cydonia, Chaenomeles* Lindl.) (Aldasoro *et al.*, 2005), or uni-ovulate (*Amelanchier*) (Eichler, 1878).

Elaeagnaceae Juss. (3/4) – sphalerocarpium (Kaden, 1965). N. N. Kaden & V. R. Kondorskaja (1967) revealed that in Elaeagnaceae carpel is solitary, surrounded with a tubular floral tube (hypanthium), one ovule (sometimes two in *Hippophae* L. and *Shepherdia** Nutt.), placed on the basal placenta attached to one of the carpellary margins. The fruit wall turns thin and membraneous, while fruiting hypanthium becomes fleshy and coloured. In *Elaeagnus** L., hypanthium becomes more or less fleshy, with lignified to a different degree inner zone resembling putamen. Thus, sphalerocarpium is treated as a one-seeded monocarpium enveloped by fleshy hypanthium imitating the inferior ovary, which resembles the fruit amaltaea in *Alchemilla* (Kaden & Kondorskaja, 1967). R. W. Spjut (1994) denominated such fruit as pseudodrupe: “anthocarpous fruit with pericarp surrounded by fleshy exocarp”. Fruit is an achene enveloped by the persistent base of the mealy or fleshy calyx tube (Takhtajan, 2009).

Rhamnaceae Juss. (5/13) – drupe syncarpous, superior, 2–3-merous, uncovered (*Rhamnus* L., *Frangula* Mill., *Ziziphus** Mill.) (Kaden, 1965). In *Ceanothus** L. fruit is entitled as coccarium – schizocarp, separating into three one-seeded dehiscent carpels (Spjut, 1994). From the other opinion, it is an explosive, semi-inferior, 3–4-locular capsule with one-seeded locules (Medan & Schirarend, 2004). In *Paliurus spina-christi* Mill., as it is evident from table 43 of vol. 1 in J. Gaertner (1788) and fig. 1 of table 1 in A. T. Brongniart (1826), fruit is semi-inferior 2–3-seeded pyrenarium, with 2–3 locules, seeds are basal and erect; the wing is attached above the middle height of the

ovary. Fruit in *P. spina-christi* is pome, disciform, depressed-globose, surrounded with a broad horizontal wing with an undulate surface (Bojňanský & Fargašová, 2007). Ovary position is variable in Rhamnaceae due to the activity of intercalary meristem forming gynoecial or perigynous hypanthium (Basso-Alves *et al.*, 2023).

Ulmaceae Mirb. (2/7) – fruit is samara (*ukr.* letyuchka) in *Ulmus* L.: one-seeded, syncarpous, superior, dimerous, covered, having a wing (Kaden, 1965); samara is uni-bilocular (Spjut, 1994). Locule – one, ovule – solitary, pendent, fruit is dry, usually more or less compressed (samaroid) or less often subdrupaceous (*Zelkova* Spach) (Takhtajan, 2009).

Cannabaceae Martinov (2/4) – superior dimerous paracarpous dry drupe, enveloped in perigonium (Kaden, 1965). In *Humulus* L. fruit is nut, in *Cannabis* L. – achene (Levina, 1987). In *Humulus* the fruit is designated as achenoconum – an infructescence composed of indehiscent fruits covered with scales and arranged in a cone (Spjut, 1994). In *Humulus* L. the fruit is entitled as achene (*ukr*. sim'yanka), in *Cannabis* L. – nutlet (*ukr*. horishok) (Didukh *et al.*, 2004).

Celtidaceae* Endl. [*Cannabaceae sensu* APG IV (2016)] (*Celtis* L., 4 spp.) – drupe, uni-bilocular, uncovered (Didukh *et al.*, 2004). Fruits are more or less globose, drupaceous, with thick-walled and well-lignified endocarp (Takhtajan, 2009). Gynoecium dimerous, mono-ovulate (Eichler, 1878).

Moraceae Gaudich. (4/5) – fruits are one-seeded, small, assembled in infructescence-coenosoma of various shapes (Levina, 1987). R. W. Spjut (1994) distinguised different fruit types in Moraceae: (a) pseudodrupe, an anthocarpous fruit with undifferentiated indurate pericarp surrounded with a fleshy or coriaceous exocarp; (b) sorosus (*Maclura* Nutt*., Morus* L.); (c) syconium (*Ficus* L.); (d) trymosum (*Broussonetia* L'Hér. ex Vent.) – a compound fruit (infructescence) enveloped by united bracts splitting at maturity to release simple fruits. Fruit in Moraceae is compound, drupe or achene, connated in a berry-like infructescence or embedded in a fleshy axis (*Ficus*); in *Morus* – false drupe (Didukh *et al.*, 2004). Fruit is an achene or drupaceous (dehiscent or indehiscent), free or adnate to the perianth, often forming a drupaceous whole with the fruiting perianth or also with the fleshy receptacle (Berg *et al.*, 2006). Fruit is drupaceous, sometimes with dehiscent exocarp; the ovary is unilocular or less often bilocular (Takhtajan, 2009). In *Morus* fruit is superior achene, enveloped in fleshy perigonium; in *Broussonetia* – dehiscent drupe, the endocarp body is ejected from the fruit (Berg *et al.*, 2006). In *Maclura* the true fruit is a drupe, enveloped in fleshy perigonium, ovary unicarpellate with permanent style, ovule apical (Arab *et al.*, 2019).

Urticaceae Juss. (2/11) – paracarpous, superior, dimerous drupe, fruit is dry and enveloped (Kaden, 1965). Achene (or nutlet), superior, one-seeded, one-locular (Didukh *et al.*, 2004). Fruit is nut-like (Takhtajan, 2009). Gynoecium is pseudomonomerous with single basal ovule (Eichler, 1878).

Fagaceae Dumort. (3/18) – one-seeded syncarpous inferior indehiscent fruit with a cupule (*ukr*. plyuska) (Kaden, 1965). The ovary is inferior tricarpellate (rarely with 6–12 carpels), with two pendulous ovules per locule (Eichler, 1878). In *Quercus* L. fruit was entitled as glans (*ukr*. zholud), in *Castanea** Mill. and *Fagus* L. as trymosum (Spjut, 1994) or one-seeded nut, subtended by accrescent cupule (Takhtajan, 2009). In *Castanea** the cupule encloses one or several fruits, in *Fagus* cupule is open, four-lobed, containing (1)2–4 fruits, while in *Quercus* cupule is open, unlobed, containing one fruit only (Takhtajan, 2009).

Myricaceae Rich. ex Kunth. (*Myrica gale* L.) – pseudodrupe (Spjut, 1994). There are 2–3 carpels, basal ovule, ovary wall is formed as a result of intercalary growth above and below the attached bracteoles (Macdonald & Sattler, 1973). In *Myrica gale,* ovary at anthesis is superior and becomes inferior owing to intercalary growth after pollination (Spjut, 1994). Ovary more or less inferior, uni-locular, with one basal erect ovule. Fruit is a drupe or almost a nut, sometimes enveloped in persistent, accrescent bracteoles (Takhtajan, 2009).

Juglandaceae* DC. ex Perleb (3/10) – one-seeded inferior fruit. In *Juglans* L. fruit is syncarpous inferior dry drupe (Levina, 1987) or pseudodrupe (Spjut, 1994). It is also described as a large drupe-like nut with a husk; bract and calyx fused with the ovary to its apex and involved in the husk; husk indehiscent or partially dehiscent (Manning, 1978). In *Carya* Nutt. husk is dehiscent, composed of the involucre only (Manning, 1978). Such fruit is defined as tryma – an anthocarpous fruit with an active (splitting) hypanthium (Spjut, 1994). In *Pterocarya* Kunth fruit is a winged nutlet with two bracteolar wings attached to the fruit (Manning, 1978), or, according to Spjut (1994), fruit is pseudosamara – a winged fruit-anthocarp, with the wings formed by accrescent fruit parts, perianth or bracts. Gynoecium in Juglandaceae is composed of two united carpels, ovary inferior, bilocular below and unilocular above, ovule solitary erect (Leroy, 1955). Placentation modified axile (Manning, 1978).

Betulaceae Gray (6/21) – syncarpous inferior dimerous fruit (Kaden, 1965). The ovary is bilocular, with one ovule in each locule, both ovules born on the anterior septa (nearby to the bract) (Eichler, 1878). Ovules are axile, pendulous (Kubizki, 1993). The fruit in Betulaceae can be:

- Samara – a dry winged fruit (*Betula* L., *Alnus Mill., incl. Duschekia* Opiz) (Kaden, 1965). It is also denominated as achenoconum, like in *Humulus* (Spjut, 1994). Fruit is small, compressed, laterally winged, and not enclosed in the foliaceous involucre (Takhtajan, 2009).
- Nut with a cupule occurs in *Corylus* L. (Kaden, 1965). It is also entitled diclesium – one-seeded fruit covered with the fruiting perianth (Spjut, 1994), or a large nut, surrounded with leaflike involucre of accrescent bract and bracteoles (Takhtajan, 2009).
- Pseudosamara – a winged fruit-anthocarp in *Carpinus* L. and *Ostrya* Scop. (Spjut, 1994). This fruit is described as a small nut subtended by a large tri-lobed or coarsely dentate bract (*Carpinus*) or enclosed in tubular or bladderlike involucre (*Ostrya*) (Takhtajan, 2009).

Cucurbitaceae Juss. (12/17) – inferior paracarpous trimerous fleshy fruit, pepo (*ukr*. harbuzyna), or bacca (*Bryonia* L.) (Kaden, 1965), or fruit is berry-like (Didukh, *et al.*, 2010). Fruits in Cucurbitaceae are represented by berry or pepo (firm-walled berry with hardened pericarp), less often dry or fleshy capsule (Takhtajan, 2009). In *Ecballium elaterium* (L.) A. Rich. fruit is pyxidium – a capsular fruit dehiscing by a single pore or lid (Spjut, 1994). Fruit in *Echinocystis lobata** (Michx.) Torr. & A. Gray can be regarded as a fleshy capsule with four seeds, dehiscent with four short valves (**Fig. 1*A, B***). The ovary is 2–5-merous in *Cucurbita** L., trimerous in *Ecballium, Bryonia, Cucumis** L.; and dimerous in *Echinocystis lobata.* In *Sicyos angulatus** L. the ovary is unilocular uniovulate with one hanged ovule; stigmas (representing carpel tips) are 3–5 (Eichler, 1878).

Begoniaceae* C. Agardh (*Begonia* L., at least 7 cultivated species) (Anufrieva, 2013) – loculicidal, inferior capsule; gynoecium of (2)–3–(6) carpels, numerous ovules (Eichler, 1878; Takhtajan, 2009). Parietal placentation (Ickert-Bond *et al.*, 2014).

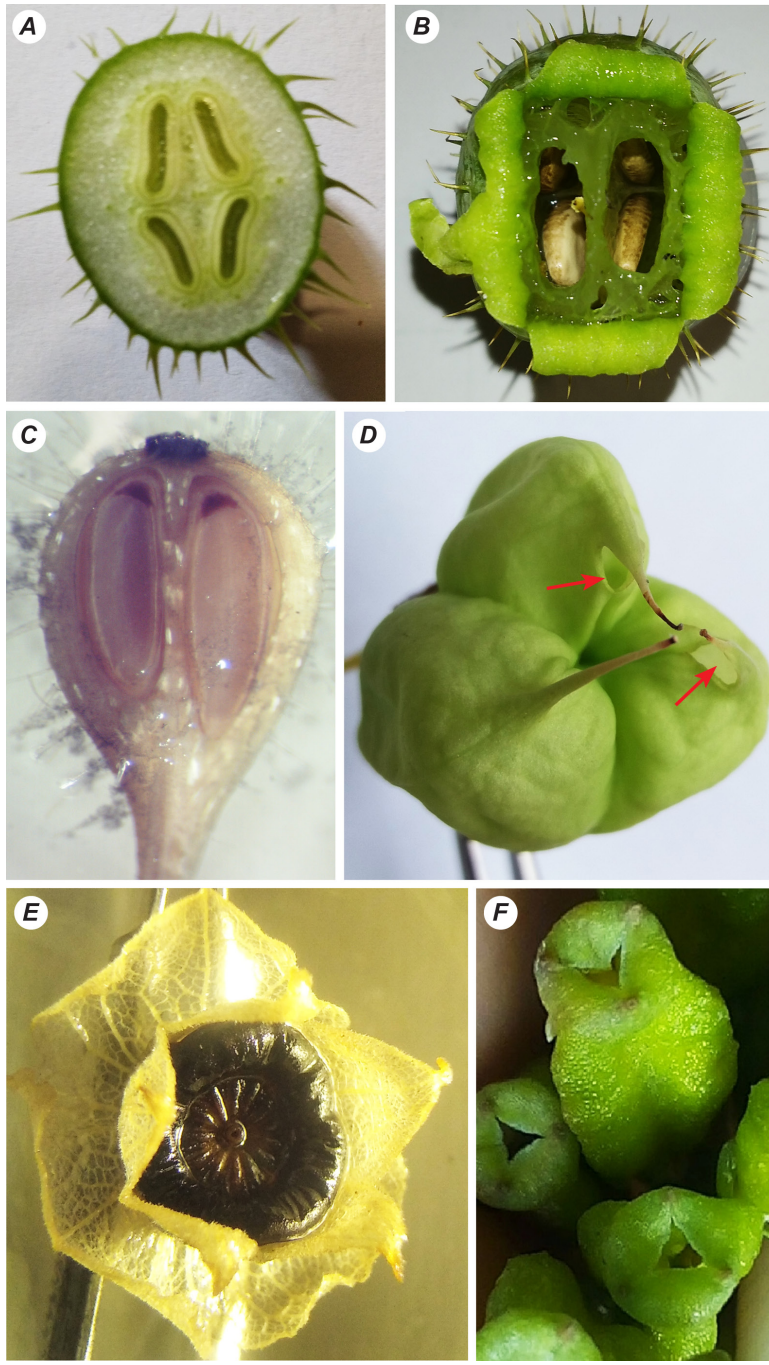

Fig. 1. Peculiar fruits of rosids: *Echinocystis lobata* (Michx.) Torr. & A.Gray, unripe fruit with baccate fruit wall, TS (***A***), and opened fruit from the tip (***B***), *Circaea lutetiana* L., LS, fruit with two one-seeded locules (***C***), *Staphylea pinnata* L. (***D***), ventral openings of partly united carpels are arrowed; *Malva trimestris* (L.) Salisb splitting fruit covered with expanded style base (***E***), *Reseda lutea* L. (***F***), ventral splits forming a common triangular opening at the capsule tip are visible

1.2. COM-clade

Celastraceae R. Br. (*Celastrus scandens** L. and 10 species of *Euonymus* L. of native and cultivated flora of Ukraine) – syncarpous superior, tetramerous, covered capsule, dorsi-ventrally dehiscent (Kaden, 1965). In *Euonymus latifolius* (L.) Mill. ovary is inferior on four-fifth of its length, completely synascidiate, with the apical septum; placenta apical-lateral; ovules two in each locule, pendant (Matthews & Endress, 2005).

Parnassiaceae Martinov [Celastraceae *sensu* APG IV (2016)] (*Parnassia palustris* L.) – paracarpous superior tetramerous, covered capsule, with incomplete dorsal dehiscence (Kaden, 1965). Ovary is synascidiate at the base and symplicate higher, with incomplete septas and laking apical septas; placentation is parietal, protruding-diffuse in the most part of ovary, while axile at its base; numerous ovules (Matthews & Endress, 2005).

Oxalidaceae R. Br. (2/7) – syncarpous superior pentamerous, covered capsule, with dorsal dehiscence (Kaden, 1965).

Passifloraceae* Juss. ex Roussel (*Passiflora** L., S. L. Mosyakin (2013) mentioned this family without number of species) – amphisarcum, fruit indehiscent, multiseeded, with lignified external layer and a fleshy internal layer of fruit wall (Spjut, 1994). Indehiscent or rarely irregularly dehiscent fruit, baccate, very short gynophore; fleshy or membranous berry (Feuillet & MacDougal, 2007).

Salicaceae Mirb. (2/43) – paracarpous superior dimerous, uncovered capsule, with dorsal dehiscence (Kaden, 1965). Gynoecium consists of two united carpels (less often of 3–4 united carpels in certain species of *Populus* L.). Ovary is unilocular, sessile or situated on a short or rarely long gynophore; numerous ovules or rarely only one ovule in the ovary (some *Salix* L. species). Fruit is capsule with 2–4 valves (Takhtajan, 2009).

Violaceae Batsch (*Viola* L.*, ca.* 40 spp., and some hybrid species) (Didukh *et al.*, 2010) – paracarpous superior trimerous, covered capsule, with dorsal dehiscence (Kaden, 1965). Placentation is parietal, ovary superior, unilocular, with one to many ovules; loculicidal fruit and valvular capsule (Takhtajan, 2009).

Hypericaceae Juss. (*Hypericum* L., 15 spp.) – hemiparacarpous superior, trimerous, covered capsule, with septicidal-lateral dehiscence (Kaden, 1965). Capsule is leathery, splitting into 3–5 valves (Didukh *et al.*, 2010).

Elatinaceae Dumort. (*Elatine* L., 5 spp.) – syncarpous superior, covered capsule, with septicidal-lateral dehiscence: (a) tetramerous (*E. alsinastrum* L.*, E. hungarica* Moesz*, E. hydropiper* L.); (b) trimerous (*E. ambigua* Wight, *E. triandra* Schkuhr) (Kaden, 1965; Sramkó *et al.*, 2016). Capsule septicidal (Spjut, 1994; Takhtajan, 2009). Gynoecium is syncarpous, 2–5-locular, with numerous ovules on axile placentas. (Takhtajan, 2009).

Euphorbiaceae Juss. (5/71) – regma (syncarpous, superior, uncovered schizocarp, with septicidal-dorsal and fenestral dehiscence (Kaden, 1964a; 1965): (a) trimerous (*Acalypha australis** L., *Ricinus communis** L., *Chrozophora* Neck. ex Juss. and *Euphorbia* L. species) or (b) dimerous (*Mercurialis* L.). For *Euphorbia*, a septicidal-lateral-dorsal dehiscence was outlined when septas detach the columella (Kaden, 1962). Fruit in Euphorbiaceae is coccarium (see Rhamnaceae) (Spjut, 1994). Fruit is typically a capsular schizocarp, with carpels (cocci) elastically dehiscent from a persistent columella; one ovule per locule (Takhtajan, 2009). Fruit is an explosively dehiscent capsule (schizocarp) splitting into three one-seeded segments (cocci) with the central axis remaining as a columella after seed dispersion (Webster, 2014). Fruit is a schizocarp

with dehiscent mericarps. Dehiscence and abscission occur between the carpels in the radius of the septa, and along the dorsal line, as well as from the central column (Gagliardi *et al.*, 2014).

Phyllanthaceae Martinov (*Andrachne telephioides* L.*, Flueggea suffruticosa** (Pall.) Baillon) – trimerous (2–6-merous) superior capsule. Fruit septicidal capsule, ovules two per locule (Takhtajan, 2009). Fruit is explosively dehiscent (Gagliardi *et al.*, 2014; Webster, 2014).

Linaceae DC. ex Perleb (2/28) – syncarpous superior, covered capsule, with septicidal-dorsi-ventral dehiscence: (a) pentamerous pseudo-decalocular (*Linum* L.); (b) tetramerous pseudo-octolocular (*Radiola* Hill) (Kaden, 1965).

2. Malvid sub-clade

Geraniaceae Juss. (3/36) – sterigma (fruit syncarpous, superior, pentamerous, covered with sepals), axile placentation; ovules two per carpel, but only one develops the seed (Kaden, 1964b). Fruit dehisces by (a) hippocrepiform slits on persistent valvae (*Geranium collinum* Stephan*, G. linearilobum* DC*, G. palustre* L.*, G. pratense* L., *G. sanguineum* L., *G. sibiricum* L., *G. silvaticum* L.) or (b) by circumscissile slits with deciduous valvae (*Erodium* L'Her.*, Pelargonium* L'Her. ex Aiton and other species of *Geranium* L.) (Kaden, 1962; 1964b; 1965). Capsular fruit with persistent columella and five actopetally detached valvae (Levina, 1987). R. W. Spjut (1994) defined this fruit as polachenarium (*syn*. cremocarpium) – schizocarpous fruit with fruitlets remaining attached to a carpophore or columella, dehiscent or indehiscent. Three mechanisms of seed discharge were recognized in *Geranium* by P. F. Yeo (1984) and re-examined by Th. Marcussen & A. S. Meseguer (2017): (a) "ballistic expulsion" or "seed-ejection type" (subgenus *Geranium*); (b) „forsible discharge" (subgenus *Robertium*) or "carpel-projection type" (with rostrum and locules detached), considered together with "inoperative type" (not-splitting fruit) (sect. *Divaricata*); and (c) monocarps with rostrum detached from the columella (subgenus *Erodioeae*) or "Erodium-type", correspondingly. Fruit in *Geranium* is considered a schizocarp of five one-seeded mericarps, detached from the columella and having a long rostrum (Deniz *et al.*, 2018).

Lythraceae J. St.-Hil. [*incl*. Lythraceae *s. str.*, Punicaceae Bercht. & J. Presl, Trapaceae Dumort.] (7/27) – syncarpous fruits, diverse in the former three families:

- In Lythraceae *s. str.* – superior, dimerous capsule, enveloped with hypanthium, dehiscent: (a) incomplete septicidal-lateral (*Lythrum* L.); (b) incomplete dorsi-lateral (*Middendorfia* Trautv.); or (c) rupturing (*Peplis* L.) (Kaden, 1965). Bilocular ovary with axile placentas (Odintsova, 2008). Ovary stipitate, placentas axile, globose; capsule septicidal (Graham & Graham, 2014).
- In *Punica* L. – fruit is an irregularly dehiscing capsule with juicy seeds and persistent calyx; ovary - inferior, with two or possibly three concentric whorls of carpels; axile placentation, but due to the receptacle invagination after insertion of carpels, placentas of the outer carpels shift to the ovary wall and thus become parietally located (Roth, 1977). Other names of the *Punica* fruit are balausta (*ukr.*: hranatyna) (Spjut, 1994), or inferior multi-seeded indehiscent berry, crowned with persistent sepals (Graham & Graham, 2014).
- In *Trapa* L. – semi-inferior, dimerous, dry drupe (Kaden, 1965). Ovary is two-locular, ovules one per locule, pendant; fruit drupe-like, one-seeded, with 2–4 horns (Graham & Graham, 2014). Fruit is named pseudodrupe or pome (Spjut, 1994).

Onagraceae Juss. (6/38) – fruits syncarpous inferior:

- Capsule tetramerous, dorsi-laterally dehiscent (Kaden, 1965) that is denoted as dorsi-septifragally dehiscent (Odintsova, 2016; Odintsova & Klimovich, 2017) – in most genera;
- Drupe dimerous, dry (Kaden 1965) – in *Circaea* L. In *C. lutetiana* L. there are two one-seeded locules surrounded by thin lignified layer (**Fig. 1*C***), in *C. alpina* L. fruit is one-locular, while in *C.* × *intermedia* Ehrh. only one of two locules is fertile.

Myrtaceae* Juss. (*Myrtus communis* L.) – inferior tri-locular, trimerous berry; numerous ovules on axile placentas (Eichler, 1878). Ovary unilocular, placentation is parietal, and axile at the base (Harthman *et al.*, 2018).

Staphyleaceae Martinov (*Staphylea* L.*,* 3 spp.) – *Staphylea* has a "bladder-fruit" adapted for flying (Roth, 1977), thus it is presumed that fruit with few seeds inside is a disseminule. Fruits are inflated, membranous, bladder-like capsules, dehiscent or indehiscent, or multifollicles, dehiscing along the ventral suture (**Fig. 1*D***); ovary superior to partially inferior, 2–3(4)-carpellate, the carpels almost free or united, placentation axile, ovules few to many in two series on ventral suture (Simmons, 2007). Fruit – multifollicle or inflated capsule opened at the tip, laterally and sometimes also apically lobed, with 6–12 ovules per locule (Takhtajan, 2009).

Nitrariaceae Lindl. (*Nitraria schoberi* L.) – syncarpous, trimerous, superior, covered drupe (Kaden, 1965). In *Nitraria* L. "Gynoecium composed of three or rarely six carpels... Fruits drupaceous, one-seeded, derived from a single fertile locule" (Takhtajan, 2009). The ovary is trilocular, fruit is a drupe (Hussein *et al.*, 2009). The gynoecium is syncarpous, ovary trilocular, ovule one per locule, pendant (Decraene & Smets, 1991). At the transition level between the synascidiate and the symplicate zones, one margin of each carpel bears an axile lateral placenta with a single apical ovule; some locules become empty at anthesis (Bachelier *et al.*, 2011).

Tetradiclidaceae Takht. [Nitrariaceae *sensu* APG IV (2016)] (*Tetradiclis tenella* (Ehrend.) Litv., *Tribulus terrestris* L.) – diverse fruits:

- In *Tetradiclis* Steven ex M. Bieb., fruit is syncarpous, superior tri- or tetramerous, uncovered capsule, septicidal-lateral dehiscent (Kaden, 1965). Takhtajan (2009) mentioned the unique structure of the gynoecium, placentation, and fruit dehiscence in *Tetradiclis*. He outlined that the fruit is fleshy and becomes dry, capsule-like, opened at first loculicidally and then, by mechanical rupture of the tissues around the seed (Takhtajan, 2009). Ovary with a long apical septum, placentas lateral, basal, and erect, bearing three (sometimes fewer) ovules (Bachelier *et al.*, 2011).
- In *Tribulus* L., fruit is pentamerous syncarpous superior uncovered schizocarp (Kaden, 1965). This fruit is also defined as camarium, – schizocarpous, deeply lobed fruit with indehiscent or irregularly dehiscent fruitlets, containing one or more seeds (Spjut, 1994). In the ovary, a persistent central column remains, ovules usually 2–5 per locule, ovary sessile, covered with long erect hairs, 5-lobed, 5-locular, with 3–10 superposed ovules per locule. Fruit separates into indehiscent, spiny mericarps with up to five seeds in each mericarp; columella is missing (Sheahan, 2007). The ovary is 5-locular, fruit is a schizocarp (Hussein *et al.*, 2009). Fruit in *Tribulus* divides by oblique transverse septas into 3–5 one-seeded compartments (Takhtajan, 2009).

Peganaceae Tiegh. ex Takht. [Nitrariaceae *sensu* APG IV (2016)] (*Peganum harmala* L.) – trimerous, covered, dorsi-ventral dehiscent capsule (Kaden, 1965). The ovary is trilocular, fruit is a capsule (Hussein *et al.*, 2009). Fruit is a loculicidal capsule (Takhtajan, 2009). Placentation is considered axile but from fig. 38 in Decraene *et al.* (1996) seems to be rather parietal. Gynoecium syncarpous, ovary has a short and stout gynophore, globose, trilocular, with conspicuous dorsal bulges surrounding and hiding the base of a style, with apical septas. Placentas axile lateral paired in each locule, bearing ca. 10 ovules (Bachelier *et al.*, 2011).

Anacardiaceae R. Br. (4/9) – syncarpous, superior, dry drupe (Levina, 1987). In *Cotinus coggygria* Scop fruit is cypsela (Spjut, 1994). Gynoecium is composed of three united carpels, but two carpels are represented only by their stylodia; the ovary is one-locular, with a single ovule, fruit is usually drupaceous, pseudomonomerous (Bachelier & Endress, 2009; Takhtajan, 2009). In *Cotinus* Mill.*, Pistacia* L.*, Rhus* L., *Toxicodendron** Mill. fruit is unilocular drupe with one apical and pendulous to basal and erect ovule in each carpel (Pell *et al.*, 2010).

Xanthoceraceae* Buerki, Callm. & Lowry [Sapindaceae *sensu* APG IV (2016)] (*Xanthoceras sorbifolium* Bunge) – superior trilocular capsule with 6–8 ovules per locule (Rosado *et al.*, 2022).

Aceraceae Juss. (*Acer* L.*,* 18 spp.) [Sapindaceae *sensu* APG IV (2016)] – fruit is disamara (*ukr.* dvokrylatka), schizocarpous syncarpous superior dimerous uncovered fruit with columella (Kaden, 1965). R. W. Spjut (1994) designated this fruit as samarium – schizocarpous fruit of several indehiscent winged mericarps (samaras).

Hippocastanaceae* A.Rich. (*Aesculus* L., 7 spp.) [Sapindaceae *sensu* APG IV (2016)] – syncarpous superior trimerous, uncovered capsule, dorsi-ventrally dehiscent (Kaden, 1965). Ovary is composed of synascidiate and symplicate zones (El Ottra, *et al.*, 2022).

Sapindaceae Juss.* (*Koelreuteria paniculata* Laxm.) – superior, trimerous, papery, loculicidal capsule. Placentation is parietal; ovules two per locule, but only one seed develops (Decraene *et al.*, 2000). Ovary is composed of synascidiate and symplicate zones (El Ottra *et al.*, 2022).

Rutaceae Juss. (7/13) – fruit syncarpous or hemisyncarpous, superior, however, gynoecium development expresses apocarpous or syncarpous patterns; ovary is composed of synascidiate and symplicate zones (El Ottra *et al.*, 2022). The family is very diverse in gynoecium and fruit structure (Appelhans *et al.*, 2021; Paschoalini *et al.*, 2022):

- Pentafollicle hemisyncarpous superior covered, ventrally dehiscent (*Dictamnus* L.) (Kaden, 1965). Gynoecium syncarpous, on short gynophore, anacrostylous; ovary 5-lobed, ovules 3(4) per carpel. Fruit capsular, disintegrating into five mericarps remaining coherent only at their bases; endocarp discharged explosively with seeds at dehiscence. Seeds 3 per mericarp (Kubitzki *et al.*, 2010). For the formalization, we treat this poorly understood fruit as capsular (not aggregate fruit) because of significant carpel fusion and the common style of the ovary.
- Capsule (*Haplophyllum* A. Juss., *Ruta* L.) – fruit of 4–5 separate carpels, divided when ripe, with loculicidal dehiscence (Takhtajan, 2009). Fruit is a capsule, dehiscing from the inner side of the apex; seeds are several per locule; gynoecium syncarpous, anacrostylous; ovary lobed (Kubitzki *et al.*, 2010). In *Haplophyllum* A. Juss. fruit is 3–5-carpellate, sometimes indehiscent, almost anacrostylous, located on a short gynophore. Seeds are few per locule (Kubitzki *et al.*, 2010).

- Hesperidium – berry-like fruit in *Citrus** L. and *Poncirus trifoliata** (L.) Raf. (Takhtajan, 2009). Fruit is a sarcocarp (hesperidium), usually large to very large; its pericarp differentiated into thin exocarp, mesocarp composed of the outer leathery part (flavedo) and spongy inner part (albedo), and endocarp with juicy pulp vesicles. Locules (2)5–15(18), ovules (2)4–8 (Kubitzki *et al.*, 2010).
- Samara 1–2 seeded in *Ptelea trifoliata** L. – dry and winged fruit; gynoecium of 2–5 united carpels, each with 1–2 ovules (Takhtajan, 2009). Fruit is a subcircular, 2(3)-locular samara with a broad dorsal wing on each carpel. Seed is one per carpel; carpels 2(3); ovary compressed perpendicular to septum, usually narrowly 2-winged (Kubitzki *et al.*, 2010).
- Pyrenarium with five stones (*Phellodendron amurense** Rupr.) – fruit is a 5-angled drupe, with five compressed, cartilaginous pyrenes; gynoecium is completely syncarpous with short gynophore; ovule is one per carpel (Kubitzki *et al.*, 2010).

Meliaceae* Juss. (*Melia azeradach* L.) – drupe thin-walled, with one to few one-seeded stones (Baillon, 1874). Drupe 3–8-locular; endocarp thick, bony, deeply dimpled at base and apex; loculi 1(2)-seeded (Mabberley, 2010). Ovary with five locules (sometimes six), ovules two per locule, axile (Eichler, 1878).

Simaroubaceae* DC. (*Ailanthus altissima* (Mill.) Swingle) – tri-achene, aggregate fruit (Levina, 1987). Fruit is samarium, as in *Acer* (Spjut, 1994). Fruit superior, schizocarpous, composed of 1–5 samaroid mericarps with elongate, membranous wings, pericarp dry, carpels 2–5, placentation axile (Clayton, 2010). Fruit is winged samaroid composed of peculiarly twisted samarids, developed from partially fused carpels (Alves *et al.*, 2022). Gynoecium is almost apocarpous; ovary contains short synascidiate zone in the gynophore and ovary base, symplicate zone is missing, but young carpels fuse postgenitally at the centre of the ovary (El Ottra *et al.*, 2022). Fruitlets separate from each other at early stages (El Ottra *et al.*, 2022). Ovule one per carpel; fruit is samaroid (Eichler, 1878).

Malvaceae Juss. (13/44) – fruits superior, diverse (Kaden, 1965). F. Areces-Berazain & J. D. Ackerman (2017) revealed that the ancestral fruit for Malvaceae was pentamerous capsule.

- Capsule syncarpous pentamerous, enveloped, dorsi-ventrally dehiscent (*Gossipium** L., *Hibiscus** L.) (Kaden, 1965); loculicidal capsule (Spjut, 1994; Bayer & Kubitzki, 2003).
- Multi-follicle – cyclic syncarpous covered fruit, completely dorsi-ventrally dehiscent (*Abutilon* Mill.) (Kaden, 1965). In *Abutilon* fruit is camarium (Spjut, 1994). Fruit schizocarpic (*ukr*. drobnyi plid), but mericarps of *Abutilon* contain up to eight seeds, are partially dehiscent and functionally capsular (Areces-Berazain & Ackerman, 2017). In *Abutilon* species mericarps are 8–14, partially dehiscent, covered by calyx, seeds 4–9 (Bayer & Kubitzki, 2003; Masullo *et al.*, 2020).
- Dieresilis (*ukr.* kalachyk) – schizocarpous, syncarpous, polymerous, enveloped fruit (*Malva* L. and related genera) (Kaden, 1965). In *Malva* fruit is typical camarium with opened mericarps (Spjut, 1994). Fruit is aggregate, composed of many or at least five dry achenes arranged in a circle (Didukh *et al.*, 2010). Dehiscent mericarps of schizocarpic fruit outlined for all Malveae J.Presl, including species of *Alcea* L., *Althaea* L., *Kitaibelia** Willd., *Lavatera* L., *Malope** L., *Malvella* Jaub. & Spach., and *Sida* L. (Areces-Berazain & Ackerman, 2017; Masullo *et al.*, 2020). In *Sida*, mericarps are 7–12, partially dehiscent, enveloped by calyx, and

one-seeded; the dehiscence of the mericarp does not allow for seed dispersal; therefore, the mericarp itself functions as a diaspora (Masullo *et al.*, 2020). In the former *Lavatera* L. species (now *Malva thuringiaca* (L.) Vis. and *M. trimestris* (L.) Salisb.), mericarps incompletely enclose the seed from the sides (Bayer & Kubitzki, 2003) and are covered with expanded discoid style base (**Fig. 1*E***).

- Schizocarp of irregularly arranged numerous mericarps, apparently superposed, forming a head (*Kitaibelia vinifolia** Willd and *Malope trifida** *Cav.*); mericarps indehiscent or dehiscent (Bayer & Kubitzki, 2003); or fruit is treated as achenarium (*Malope*) (Spjut, 1994).

Tiliaceae Juss. [Malvaceae *sensu* APG IV (2016)] (*Tilia* L., 16 spp.) – carcerulus: syncarpous, superior, pentamerous, uncovered, and indehiscent fruit (Kaden, 1965). Fruit is also defined as nut-like coenocarpium (Levina, 1987), pseudosamara (Spjut, 1994), or achene derived from a capsule, 1–2-locular (Didukh *et al.*, 2010).

Thymelaeaceae Juss. (2/6) (Didukh *et al.*, 2010) – paracarpous pseudomonomerous drupe, fleshy (*Daphne* L.), or dry (*Thymelaea* Mill.) (Kaden, 1965). Fruit is drupaceous, usually enclosed in the base of the persistent calyx tube; two carpels, with one pendulous ovule per locule (Takhtajan, 2009). Unilocular drupe (*Daphne*) or pyriform achene with a beak (*Thymelaea*) (Didukh *et al.*, 2010). A. W. Eichler (1878) treated the Thymelaeaceae gynoecium as monomerous monovulate with a hanged ovule.

Cistaceae Juss. (3/20) (Didukh *et al.*, 2010) have superior paracarpous, trimerous, enveloped capsule, dorsally dehiscent, as was mentioned for *Helianthemum* Mill. (Kaden, 1965). In Cistaceae ovary is 3–5-merous, placentation is parietal, with incomplete septas, fruit loculicidally dehiscent (Eichler, 1878). In *Cistus* L. carpels 5–(6–12); in *Fumana* (Dunal) Spach (incl. *Fumanopsis* Pomel) the ovary is tricarpellate, with 6–9 seeds. Placentation is parietal, but placentas are deeply intruded, and then appear axile; sepals are persistent (Arrington & Kubitzki, 2003).

Tropaeolaceae* Juss. ex DC. (*Tropaeolum* L., 2 spp.) – trimerous superior schizocarp with one-seeded, enclosed mericarps; columella is missing (Kaden, 1964). R. W. Spjut (1994) treated this fruit as baccarium – a schizocarpic berry, consisting of fleshy indehiscent fruitlets.

Resedaceae Martinov (*Reseda* L., 4 spp.) – paracarpous, superior, trimerous, covered capsule, incomplete-disjunctively dehiscent (Kaden, 1965). Pyxidium – capsular fruit dehiscing at the apex (Spjut, 1994). According to our personal observation, the capsule dehisces apically along the ventral sutures on persistent stylodia (**Fig. 1*F***). Placentation is parietal; ovary is unilocular, with triangular flaps visible at the ovary tip (Arber, 1942).

Capparaceae Juss. (*Capparis spinosa var. herbacea* (Willd.) Fici) – paracarpous, superior, fleshy capsule, irregularly dehiscent (Levina, 1987). Fruit in *Capparis* L. is amphisarcum, – many-seeded, crustaceous fruit, while in *C. spinosa* it is utricle, – small bladderlike or vase-like fruit, thin-walled, composed of more than one carpel, unilocular, often inflated, one-seeded, dehiscent or indehiscent (Spjut, 1994). Fruit polymerous, indehiscent, berry or amphisarcum, with postgenitally fused placentas (Brückner, 2000). Capsule oblong, berry-like (Iljinska *et al.*, 2007). There are 10–12 carpels, gynophore is long, fruit is berry-like (Eichler, 1878). Carpel number in Capparaceae is considered to have increased from the initial bi-carpellate state (Decraene & Smets, 1997).

Cleomaceae Bercht. & J. Presl (*Cleome* L., 3 spp.) – fruit is typical ceratium in *Cleome viscosa* L.: “capsular fruit that opens by separation or break in the pericarp layers, usually

the inner parts – replum, styles, parietal placentas – persistent and often setaceous, skeletal or partitional...” (Spjut, 1994). Fruit is an elongated multi-seeded silique composed of two detaching valvae and seed-bearing replum, which apically bifurcates after valvae drop down; uncovered (Brückner, 2000). Fruit is unilocular multi-seeded silique-like capsule (Iljinska *et al*., 2007). Carpophore 4–8 cm long, capsule elongated, dehiscent in *Cleome houtteana** Schltdl., while in other species carpophore is very short, and capsule indehiscent (Iljinska, 2014). Two carpels, lateral, ovary with gynophore (Eichler, 1878).

Brassicaceae Burnett (71/246) (Iljinska *et al*., 2007) – silique, siliqua (*ukr*. struchok) and silicle, silicula (*ukr*. struchechok) – fruit paracarpous superior, dimerous, pseudobilocular, uncovered (in *Alyssum calycinum* L. fruit with a covering) (Kaden, 1965). Compared to ceratium, silique has a false septum attached between the placentas. In silicle, the fruit lengths is four (Spjut, 1994) or three times bigger (Brückner, 2000) than the width. Dehiscence is mainly acropetal, less often basipetal; valves fall down (Brückner, 2000). The evolution of silique is trended from valvate to nutlike indehiscent fruit, or biloment (Brückner, 2000). Heterocarpous and heteroarthrocarpous fruits occur (Voytenko, 1989). Carpophore occurs in *Barbarea* R. Br., *Brassica* L.*, Diplotaxis* DC.*, Lunaria* L.*, Pseudoarabidopsis toxophylla* (M. Bieb.) Al-Shehbaz, O’Kane & R.A. Price, and *Rorippa* Scop. In some Brassicaceae, the distal narrowed part of the ovary forms the rostrum (*ukr*. nosyk) (Iljinska, 2013*a*). Detailed investigation on fruit morphological diversity in Brassicaceae of the flora of Ukraine was realized by A. P. Iljinska (Iljinska *et al.*, 2007; Iljinska, 2013*a*; 2013b; 2016). Further, we follow Kaden’s (1965) classification:

- Silique: (a) bivalvate, with fenestrale dehiscence (most genera), (b) with fenestral-articulated dehiscence (*Chorispora* R. Br. ex DC.), (c) silique articulated (bilomentum) (*Raphanus raphanistrum* L.)*;* (d) silique indehiscent (*Raphanus sativus* L.) (Kaden, 1965). In *Cardamine* L.*,* turgor explosive fruit dehiscence occurs (Roth, 1977).
- Silicle: (a) fenestrale dehiscent, with two variants of shape proportion: (1) latiseptate form (with wide septum) (*Alyssum* L., *Armoracia* G. Gaertn., B. Mey. & Scherb., *Berteroa* DC., *Camelina* Crantz*, Draba* L.*, Erophila* DC.*, Lunaria* L.*, Meniocus* Desv.*, Rorippa amphibia* (L.) Besser*, R. austriaca* (Crantz) Besser*, R. brachycarpa* (C.A. Mey.) Hayek*, Schivereckia* Andrz. ex DC.); (2) angustiseptate form (with narrow septum) (*Capsella* Medik.*, Hymenolobus* Nutt. ex Torr. & A. Gray*, Lepidium* L.*, Subularia* L.*, Thlaspi* L.); (b) indehiscent (*Cardaria* Desv.); (c) articulated, biloment (*Crambe* L.*, Rapistrum* Crantz); (d) nut-like (*e.g*.: *Bunias* L.*, Euclidium* R.Br.*, Isatis* L.*, Neslia* Desv.) (Kaden, 1965). One-seeded indehiscent silicles appear in *Crambe, Rapistrum*, *Calepina* Adans., *Myagrum* L., *Clypeola* L., *Goldbachia* DC., *Sobolewskia* M.Bieb., *Coronopus* Zinn. (Zerov, 1965; Ilyinska, 2013b). *Cakile* Mill. has two one-seeded segments, sometimes the lower segment is sterile (Zerov, 1965). In *Biscutella laevigata* L. fruit is one-seeded (Eichler, 1878).

DISCUSSION

Gynoecium structure and morphogenetic characteristics of fruits in Rosidae. The referred data evidence a significant morphological diversity of fruits among representatives of Rosidae in the flora of Ukraine. Among rosids, there are few cases of initial carpel fusion in ovaries (*e.g.*, in *Spiraea* and *Staphylea*), as well as incomplete adnation of the ovary to the hypanthium (*e.g.*, in *Spiraea, Sorbus, Myrica,* and *Trapa*). Some fruits with incomplete fusion between carpels or early separation of carpels (*e.g.,*

in *Abutilon* and *Dictamnus*) are ambiguously treated as schizocarpous, or capsular, or hemisyncarpous follicular. In Rosaceae, Malvaceae, and many Sapindales, the obvious cases of apocarpy, which is usually considered a primitive state, are proposed to be a derived condition from syncarpy (Endress *et al.*, 1983; Endress, 2011). Thus, the current state of understanding of the gynoecium's and fruit's structure in these rosid taxa is not still sufficient.

Syncarpous fruits were found to be dimerous (Brassicaceae, Lythraceae, Fagaceae, Betulaceae, Salicaceae, *Circaea*), trimerous (Rhamnaceae, Fagaceae, Cucurbitaceae, *Begonia*, Oxalidaceae, *Hypericum, Celastrus*, *Viola*, *Euphorbia*, Phyllanthaceae, *Nitraria, Peganum*, Sapindaceae, *Staphyllea, Reseda*, Cistaceae), tetramerous (*Euonymus, Parnassia, Tetradiclis,* Onagraceae), or pentamerous (*Zygophyllum*, Geraniaceae, *Tribulus*, Rutaceae, Malvaceae). Trimerous gynoecium and parietal placentation are common in Malpighiales Juss. ex Bercht. & J.Presl, the largest order of COM-clade, while two pendant ovules in the carpel on the axile placenta are a unique feature for the whole COM-clade (Endress *et al.*, 2013). Polymerous syncarpous fruits occur in the Malvaceae and *Punica granatum* (in dicyclic condition). The difference in the appearance of multi-carpellate gynoecia was previously found between malvids and fabids (Endress, 2014), as well as the formation of free or united carpels.

One-seeded fruits of rosids are manifold: nut, nutlet (nucula), achene, drupe, and samara. Most of them develop from the pseudomonomerous gynoecium (Eckardt, 1937), found in many fabid (Ulmaceae, Celtidaceae Urticaceae, Cannabeceae, Moraceae, Rhamnaceae, Juglandaceae), and malvid families (Anacardiaceae, Thymelaeaceae). They possess a one-locular one-seeded ovary with two stigmas (Eichler, 1878). Some other one-seeded fruits develop from the syncarpous plurilocular and pluriovular ovaries (Fagaceae, Betulaceae, *Nitraria*, *Tilia, Trapa*), indicating their recent origin from other basic fruit types. The monomerous one-seeded fruit was found in Elaeagnaceae, some Rosaceae and Fabaceae*,* where intermediate conditions from dimerous aggregate fruit (Rosaceae) or multi-seeded monocarp (Fabaceae) to one-seeded monocarp still occur.

Gynophore or androgynophore persisting in a fruit occur in many families of malvid orders Sapindales, Malvales and Brassicales. For Sapindales, anacrogynous style is usual (El Ottra *et al.*, 2022).

Inferior fruits are not abundant in Rosids, they occur in 12 of 54 families (22 %), nine of which belong to fabid sub-clade. Most of the inferior fruits are indehiscent (**Table 1**). Half of the inferior fruits in rosids occur in cultivated or alien taxa, which arose in other floristic zones and continents (Juglandaceae, Begoniaceae, Myrtaceae, some Onagraceae, and *Punica*).

Placentation in studied rosid families is mostly axile, less often parietal, and probably equally distributed among fabid and malvid clades (Takhtajan, 2009; Ickert-Bond *et al.*, 2014; Shivaprakash & Bawa, 2022). In many cases, the gynoecium is syncarpous, multi-locular (2–5-locular), with as many locules as carpels, and has combined placentation (axile beneath, parietal above) or parietal placentation with protruding septas contacting in the ovary center. Paracarpous gynoecium with typical parietal placentation also occurs (Cucurbitaceae, Parnassiaceae, Salicaceae, Violaceae, Hypericaceae, Cistaceae, Resedaceae, Capparidaceae, Brassicaceae). In few-seeded carpels, both basal (*Elaeagnus, Juglans, Myrica, Rhamnus, Urtica*) and apical (*Cannabis, Ulmus, Zelkova, Celtis, Morus,* Betulaceae*, Sicyos, Thymelaea, Tropaeolum*) placentation types occur.

Table 1. **Inferior fruits in the subclass Rosidae of the flora of Ukraine**

Family	Sub-clade	Fruit names
Rosaceae (tribus Malaea)	fabids	Multi-seeded pyrenarium, pome
Rhamnaceae (*Paliurus spina-christi*)	fabids	Multi-seeded semi-inferior pyrenarium
Cucurbitaceae	fabids	Berry, capsule, pepo, one-seeded fruit
Begoniaceae	fabids	Capsule
Celastraceae (*Euonymus*)	fabids	Capsule partly inferior
Fagaceae	fabids	One-seeded fruit, nut, glans
Betulaceae	fabids	One-seeded fruit, nut, samara
Juglandaceae	fabids	One-seeded fruit, nut, pyrenarium
Myricaceae	fabids	One-seeded semi-inferior fruit, nut
Onagraceae	malvids	Capsule, pyrenarium (*Circaea*)
Myrtaceae	malvids	Berry
Lythraceae (*Trapa, Punica*)	malvids	One-seeded semi-inferior fruit (*Trapa*); berry-like polycyclic fruit, balausta (*Punica*)

Some genera and species of Rosidae represent a unique combination of fruit features and thus obtained individual names – *e.g.,* amalthaea, balausta, cynarrhodium, pome, regma, sphalerocarpium, sterigma and others (see R. W. Spjut (1994) for historical records). Family-specific fruits in rosids are the legume, pepo, and silique, while some fruits represent variants of wide-recognized fruit types: carcerulus, ceratium, dieresilis (articulate silique), and loment (articulate pod). A significant diversity and abundance of peculiar fruits among Rosidae emphasizes the unique evolutionary history of fruit development in many rosid taxa.

Appearance of basic fruit types in families and sub-clades. According to our calculations based on the checklist of S. L. Mosyakin & M. M. Fedoronchuk (1999) and other mentioned sources, the subclass Rosidae in the flora of Ukraine is represented by 321 genera and at least by 1617 species (the number of species and infraspecific taxa cultivated in botanical gardens may load additionally nearly 10 %). Among them, three families (Fabaceae, Rosaceae, and Brassicaceae) comprise each over 250 species in the flora of Ukraine, another 21 families are represented by 11–71 species, and 30 families are represented by 1–10 species. The species and genera number of the three largest families together compose ca. 60 % of the total species and genera number of the Rosidae in the flora of Ukraine. Among them, Fabaceae is the only family where multiseeded monocarp occurs, a rare fruit type among angiosperms (**Table 2**). Apocarpous fruits occur only among fabid sub-clade: in Rosaceae, Fabaceae, and Elaeagnaceae. They reveal poly-, iso-, oligo-, and also monomerous conditions. Rosaceae is an extremely diverse family regarding the gynoecium and fruit morphology (ovary insertion, carpel fusion, carpel and ovule number, pericarp consistency, and fruit covering) (Dardick & Callahan, 2014). Brassicaceae and Fabaceae are similar in having stable ground-plan of the gynoecium and fruit, while diverse radiation of exomorphic fruit characters. In last two families, convergent trends of fruit evolution appear, namely, the formation of one-seeded fruit, articulate fruit, heteroartrocarpy, inflated fruits, etc.

Table 2. **Basic fruit types in the families of the subclass Rosidae of the flora of Ukraine**

Basic fruit type	Family
Aggregate fruit	**Fabids:** Rosaceae *p. p.* **Malvids:** not found
Multi-seeded monocarp	**Fabids:** Fabaceae *p. p.* **Malvids:** not found
Capsule	**Fabids:** Begoniaceae, Celastraceae, Cucurbitaceae (*Ecbalium, Echinocystis*), Elatinaceae, Euphorbiaceae, Hypericaceae, Linaceae, Oxalidaceae, Parnassiaceae, Phyllanthaceae, Polygalaceae, Rhamnaceae (*Ceanothus*), Salicaceae, Violaceae, Zygophyllaceae **Malvids:** Brassicaceae *p. p.,* Capparaceae, Cistaceae, Cleomaceae, Geraniaceae, Hippocastanaceae, Lythraceae *p. p.,* Malvaceae *p. p.,* Onagraceae *p .p.,* Peganaceae, Resedaceae, Rutaceae *p. p.,* Sapindaceae, Staphyleaceae, Tetradiclidaceae (*Tetradiclis*), Xanthoceraceae
Berry (uva/bacca)	Vitaceae **Fabids:** *Cucurbitaceae p. p.,* Passifloraceae **Malvids:** Lythraceae (*Punica*), Myrtaceae, Rutaceae (*Citrus, Poncirus*)
Schizocarp	**Fabids:** not found **Malvids:** Aceraceae, Malvaceae *p. p.,* Simaroubaceae, Tetradiclidaceae (*Tribulus*), Tropaeolaceae
Multi-seeded pyrenarium	**Fabids:** Rosaceae (tribus Malaea), Rhamnaceae (*Paliurus*) **Malvids:** Meliaceae, Onagraceae (*Circaea lutetiana*), Rutaceae (*Phellodendron*)
One-seeded fruit	**Fabids:** Betulaceae, Cannabaceae, Celtidaceae, Cucurbitaceae (*Sycios*), Elaeagnaceae, Fabaceae *p. p.,* Fagaceae, Juglandaceae, Moraceae, Myricaceae, Rhamnaceae, Rosaceae *p. p.,* Ulmaceae, Urticaceae **Malvids:** Anacardiaceae, Brassicaceae *p. p.,* Lythraceae (*Trapa*), Nitrariaceae, Onagraceae (*Circaea alpina*), Rutaceae (*Ptelea*), Thymelaeaceae, Tiliaceae

Note. Basic fruit types are defined according to our arguments outlined in **Materials and Methods**

Fabids and malvids are almost equal in occurring of the four basic fruit types: capsule, berry, multi-seeded pyrenarium and one-seeded fruits. Aggregate fruits and multi-seeded monocarps are found only in fabid, while true schizocarps – are only in malvid sub-clades (**Table 2**). Some families in the flora of Ukraine (Fabaceae, Rosaceae, Rhamnaceae, Malvaceae, Tetradiclidaceae, Rutaceae, Lythraceae, Onagraceae, Brassicaceae) reveal more than one basic fruit type.

We found that the most widespread fruit types at the family level are capsular and one-seeded fruits (**Fig. 2*A***), while at genus and species level, the portion of multi-seeded monocarpous and aggregate fruits is also significant (**Fig. 2*B, C***). The most common fruit type in the studied rosids appears to be a capsular fruit. Berries are the less abundant fruit type in Rosidae, they occur mostly in cultivated and alien species.

Some fruits are ambiguously interpreted because of the intermediate features of the fruit: capsular or baccate (*Capparis, Echinocystis, Ecballium, Punica*), multi-follicle, capsule or schizocarp (Rutaceae, Euphorbiaceae, Malvaceae, Geraniaceae), capsule

or syncarpous multi-follicle (*Staphylea*). For example, fruit regma in Euphorbiaceae and sterigma in Geraniaceae could be conditionally classified as capsular fruits (not schizocarps) because mericarps are open and, in most cases, the naked seed is a disseminule. The formal definition of these fruits is arbitrary, based on one or another argument. For upcoming formal analysis, such fruits could be treated in the frame of continuum morphology ("fuzzy" logic) rather than classical morphology (either/or logic) (Sattler & Rutishauser, 2022).

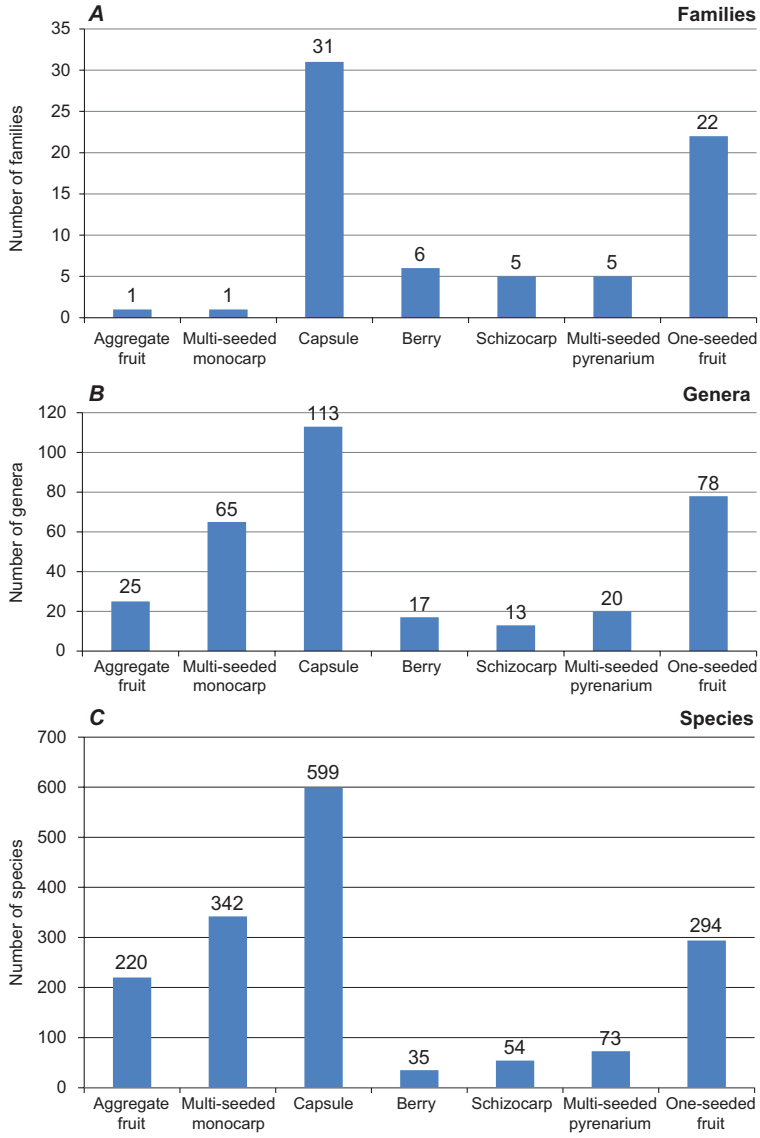

Fig. 2. Number of taxa of the subclass Rosidae of the flora of Ukraine, representing basic fruit types, occuring at the family (***A***), genus (***B***) and species (***C***) levels. The total number of families and genera above the columns is greater than that indicated in this article because in some families and genera several fruit types occur

Another dubiousness of the fruit classification is the regular variability of fruit characteristics at individual and species levels, the so called intraspecific and interspecific trait variability, an important way to promote taxonomic and functional diversity (Albert *et al.*, 2010; He *et al.*, 2021). For example, there are some species having one kind of uncertainty: one or two carpels in the flower, one or two seeds in the ovary, fruit opening proceeds or not, which makes the fuzzy boundary between monocarp and dimerous aggregate fruit, one-seeded and multi-seeded pyrenarium, capsule and berry, and more.

The obtained results on the taxonomic representativeness of basic fruit types in the families of the subclass Rosidae have been compared with those for the monocot clade in the flora of Ukraine, surveyed by us previously (Odintsova *et al.*, 2021). In both cases, the predominance of capsular fruits at the family-level spectrum was clearly demonstrated. Specifically, capsular fruit is found in 17 of 38 families of monocots and in 31 of 54 families of rosids of the flora of Ukraine. The results of our analysis suggest that fruits dispersing the naked seeds are found in each second family among the two large and unrelated clades of angiosperms. The model of basic fruit types seems to have the potential to be applied to the formal treatment of fruit structure in other groups of angiosperms.

CONCLUSIONS

The present investigation makes evident the huge morphological diversity of fruits in the subclass Rosidae in the flora of Ukraine. All fruits were classified into seven basic fruit types and the occurrence of each fruit type among families, genera, and species of Rosidae were elucidated. We also surveyed the occurrence of some gynoecium traits crucial for fruit structure, namely, gynoecium merosity, ovary position, locule and ovule number, and type of placentation. As a result of the present examination, we revealed a wide distribution of capsular fruits, occuring in each second family of rosids. The other conclusion is predominance of capsules, multi-seeded monocarps, one-seeded and aggregate fruits at genus and species taxonomic levels. This predominance seems to be associated with the high species richness of Fabaceae, Rosaceae, and Brassicaceae in the flora of Ukraine. Rosaceae is confirmed to be the most diverse family on fruit types among rosids, the Rutaceae and Malvaceae are also highly diverse. Overall nine families revealed more than one basic fruit type in the flora of Ukraine. Some fruits can be ambiguously classified as one or another type because of their intermediate features. Thus, fuzzy boundaries between most fruit types are evident. Fabids and malvids differed in occurrence of apocarpous (polymerous and monomerous) and schizocarpous fruits. The fruit morphological structure in most families of rosids seems to be clearly defined and precisely studied. Further studies of fruits could be focused on those fruits obtaining the most controversial definitions due to their intermediate features or insufficient exploration level.

COMPLIANCE WITH ETHICAL STANDARDS

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REFERENCES

Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S., & Lavorel, S. (2010). A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology*, 24(6), 1192–1201. doi:10.1111/j.1365-2435.2010.01727.x Crossref ● Google Scholar

Aldasoro, J. J., Aedo, C., & Navarro, C. (2005). Phylogenetic and phytogeographical relationships in Maloideae (Rosaceae) based on morphological and anatomical characters. *Blumea – Biodiversity, Evolution and Biogeography of Plants*, 50(1), 3–32. doi:10.3767/000651905x623256 Crossref ● Google Scholar

Alves, G. G. N., Fonseca, L. H. M., Devecchi, M. F., El Ottra, J. H. L., Demarco, D., & Pirani, J. R. (2022). What reproductive traits tell us about the evolution and diversification of the tree-of-heaven family, Simaroubaceae. *Brazilian Journal of Botany*, 45(1), 367–397. doi:10.1007/s40415-021-00768-y Crossref ● Google Scholar

Anufrieva, S. V. (2013). *Entsyklopediya roslyn. Sadovi ta kimnatni* [*Encyclopedia of plants. Garden and indoor*]. Donetsk: Gloria. Retrieved from https://shron1.chtyvo.org.ua/Anufriieva_Svitlana/Entsyklopediia_roslyn_sadovykh_ta_kimnatnykh.pdf? (In Ukrainian)

APG I (The Angiosperm Phylogeny Group). (1998). An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden*, 85(4), 531–553. doi:10.2307/2992015 Crossref ● Google Scholar

APG IV. (2016). Chase, M. W., Christenhusz, M. J. M., Fay, M. F., Byng, J. W., Judd, W. S., Soltis, D. E., Mabberley, D. J., Sennikov, A. N., Soltis, P. S., & Stevens, P. F. The Angiosperm phylogeny group. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants APG IV. *Botanical Journal of the Linnean Society*, 181, 1–20. doi:10.1111/boj.12385 Crossref ● Google Scholar

Appelhans, M. S., Bayly, M. J., Heslewood, M. M., Groppo, M., Verboom, G. A., Forster, P. I., Kallunki, J. A., & Duretto, M. F. (2021). A new subfamily classification of the *Citrus* family (Rutaceae) based on six nuclear and plastid markers. *Taxon*, 70(5), 1035–1061. doi:10.1002/tax.12543 Crossref ● Google Scholar

Arab, R., Majd, A., Tajadod, G., Rezanejad, F., & Mirzaei, M. (2019). The morphological and anatomical studies of inflorescence, flower, embryo and fruit development in *Maclura pomifera* (Moraceae). *Cogent Biology*, 5(1), 1663698. doi:10.1080/23312025.2019.1663698 Crossref ● Google Scholar

Arber, A. (1942). Studies in flower structure. VII. On the gynoecium of *Reseda*, with a consideration of paracarpy. *Annals of Botany*, *New Series*, 6(21), 43–48. doi:10.1093/oxfordjournals.aob.a088400 Crossref ● Google Scholar

Areces-Berazain, F., & Ackerman, J. D. (2017). Diversification and fruit evolution in eumalvoids (Malvaceae). *Botanical Journal of the Linnean Society*, 184(4), 401–417. doi:10.1093/botlinnean/box035 Crossref ● Google Scholar

Arrington, J. M., & Kubitzki, K. (2003). Cistaceae. In: K. Kubitzki, & C. Bayer (Eds.). *The families and genera of vascular plants. Vol. V. Flowering plants. Dicotyledons. Malvales, Capparales and non-betalain Caryophyllales* (pp. 62–70). Berlin, Heidelberg: Springer. doi:10.1007/978-3-662-07255-4_15 Crossref ● Google Scholar

Artyushenko, Z. T., & Fedorov, A. A. (1986). *Atlas po opisatel'noj morfologii vysshih rastenij. Plod* [*Atlas of comparative morphology of higher plants. The Fruit*]. Leningrad: Nauka (In Russian) Google Scholar

Bachelier, J. B., & Endress, P. K. (2009). Comparative floral morphology and anatomy of Anacardiaceae and Burseraceae (Sapindales), with a special focus on gynoecium structure and evolution. *Botanical Journal of the Linnean Society*, 159(4), 499–571. doi:10.1111/j.1095-8339.2009.00959.x
Crossref ● Google Scholar

Bachelier, J. B., Endress, P. K., & Craene, L. P. R. D. (2011). Comparative floral structure and development of *Nitrariaceae* (*Sapindales*) and systematic implications. In L. Wanntorp, & L. Ronse De Craene (Eds.). *Flowers on the tree of life* (pp.181–217). Cambridge: Cambridge University Press. doi:10.1017/cbo9781139013321.008
Crossref ● Google Scholar

Baillon, H. E. (1874). *Histoire des plantes* (Vol. 5). Paris: Librairie Hachette. doi:10.5962/bhl.title.40796
Crossref ● Google Scholar

Basso-Alves, J. P., Ribeiro, C. C., & Teixeira, S. P. (2023). Floral development of Rhamnaceae and origin of its unique floral features. *Plants*, 12(2), 247. doi:10.3390/plants12020247
Crossref ● PubMed ● PMC ● Google Scholar

Bayer, C., & Kubitzki, K. (2003). Malvaceae. In K. Kubitzki, & C. Bayer (Eds.). *The families and genera of vascular plants. Vol. V. Flowering plants. Dicotyledons. Malvales, Capparales and non-betalain Caryophyllales* (pp. 225–311). Berlin, Heidelberg: Springer. doi:10.1007/978-3-662-07255-4_28
Crossref ● Google Scholar

Berg, C. C., Corner, E. J. H., & Jarrett, F. M. (2006). Moraceae (genera other than *Ficus*). *Flora Malesiana*, *Series I*, 17(1), 1–152.
Google Scholar

Bojňanský, V., & Fargašová, A. (2007). *Atlas of seeds and fruits of Central and East-European flora the Carpathian Mountains Region*. Dordrecht: Springer. doi:10.1007/978-1-4020-5362-7
Crossref ● Google Scholar

Brongniart, A. T. (1826). *Mémoire sur la famille des Rhamnées, ou, histoire naturelle et médicale des genres qui composent ce groupe de plantes*. Paris: Didot Le Jeune. doi:10.5962/bhl.title.97298
Crossref ● Google Scholar

Brückner, C. (2000). Clarification of the carpel number in Papaverales, Capparales, and Berberidaceae. *The Botanical Review*, 66(2), 155–307. doi:10.1007/bf02858151
Crossref ● Google Scholar

Clayton, J. W. (2010). Simaroubaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Volume X. Flowering plants. Eudicots. Sapindales, Cucurbitales, Myrtales* (pp. 408–423). Berlin, Heidelberg: Springer. doi:10.1007/978-3-642-14397-7_18
Crossref ● Google Scholar

Deniz, İ., Yildiz, K., & Çirpici, A. (2018). Taxonomical study of seeds and fruit micromorphology of the *Geranium* (Geraniaceae) species in the Thrace region of Turkey (Europe). *Phytologia Balcanica*, 24(1), 35–43.
Google Scholar

Dvirna, T., Futorna, O., Minarchenko, V., & Tymchenko, I. (2021). Morphological features of fruits and seeds of some species of the genus *Crataegus* L. of the flora of Ukraine. *Acta Agrobotanica*, 74. doi:10.5586/aa.7418
Crossref ● Google Scholar

Eames, A. J. (1961). *Morphology of the angiosperms*. New-York, Toronto: McGraw-Hill. doi:10.5962/bhl.title.5986
Crossref ● Google Scholar

Eckardt, Th. (1937). Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung des pseudomonomeren Gynoeceums. *Nova Acta Leopoldina* (NF5), 26, 1–112.
Google Scholar

Decraene, L. P. R., & Smets, E. F. (1991). Morphological studies in Zygophyllaceae. I. The floral development and vascular anatomy of *Nitraria retusa*. *American Journal of Botany*, 78(10), 1438–1448. doi:10.1002/j.1537-2197.1991.tb12610.x
Crossref ● Google Scholar

Decraene, L. P. R., & Smets, E. F. (1997). Evidence for carpel multiplications in the Capparaceae. *Belgian Journal of Botany,* 130(1), 59–67.
Google Scholar

Decraene, L. P. R., Laet, J. D., & Smets, E. F. (1996). Morphological studies in Zygophyllaceae. II. The floral development and vascular anatomy of *Peganum harmala*. *American Journal of Botany*, 83(2), 201–215. doi:0.1002/j.1537-2197.1996.tb12698.x
Crossref ● Google Scholar

Decraene, L. P. R., Smets, E., & Clinckemaillie, D. (2000). Floral ontogeny and anatomy in *Koelreuteria* with special emphasis on monosymmetry and septal cavities. *Plant Systematics and Evolution*, 223(1–2), 91–107. doi:10.1007/bf00985329
Crossref ● Google Scholar

Didukh, Ya. (Ed.), Burda, R., Ziman, S., Korotchenko, I., Fedoronchyk, M., & Fitsailo, T. (2004). *Ekoflora Ukrainy* [*Ecoflora of Ukraine*] (Vol. 2). Kyiv: Phytosociocentre. (In Ukrainian)
Google Scholar

Didukh, Ya. (Ed.), Korotchenko, I., Fitsailo, T., Burda, R., Moysiyenko, I., Pashkevich, N., Yakushenko, D., & Shevera, M. (2006). *Ekoflora Ukrainy* [*Ecoflora of Ukraine*] (Vol. 6). Kyiv: Phytosociocentre. (In Ukrainian)
Google Scholar

Eichler, A. W. (1878). *Blüthendiagramme construirt und erlautert: enthaltend die apetalen und choripetalen Dicotylen* (Vol. 2). Leipzig: Engelmann. doi:10.5962/bhl.title.12323
Crossref ● Google Scholar

El Ottra, J. H. L., de Albuquerque Melo-de-Pinna, G. F., Demarco, D., Pirani, J. R., & Ronse De Craene, L. P. (2022). Gynoecium structure in Sapindales and a case study of *Trichilia pallens* (Meliaceae). *Journal of Plant Research*, 135(2), 157–190. doi:10.1007/s10265-022-01375-y
Crossref ● PubMed ● Google Scholar

Endress, P. K. (2010). Flower structure and trends of evolution in eudicots and their major subclades. *Annals of the Missouri Botanical Garden*, 97(4), 541–583. doi:10.3417/2009139
Crossref ● Google Scholar

Endress, P. K. (2011). Evolutionary diversification of the flowers in angiosperms. *American Journal of Botany*, 98(3), 370–396. doi:10.3732/ajb.1000299
Crossref ● PubMed ● Google Scholar

Endress, P. K. (2013). Multicarpellate gynoecia in angiosperms: occurrence, development, organization and architectural constraints. *Botanical Journal of the Linnean Society*, 174(1), 1–43. doi:10.1111/boj.12099
Crossref ● Google Scholar

Endress, P. K., & Friis, E. M. (2006). Rosids – reproductive structures, fossil and extant, and their bearing on deep relationships: introduction. *Plant Systematics and Evolution*, 260(2–4), 83–85. doi:10.1007/s00606-006-0438-5
Crossref ● Google Scholar

Endress, P. K., & Matthews, M. L. (2006). First steps towards a floral structural characterization of the major rosid subclades. *Plant Systematics and Evolution*, 260(2–4), 223–251. doi:10.1007/s00606-006-0444-7
Crossref ● Google Scholar

Endress, P. K., & Matthews, M. L. (2012). Progress and problems in the assessment of flower morphology in higher-level systematics. *Plant Systematics and Evolution*, 298(2), 257–276. doi:10.1007/s00606-011-0576-2
Crossref ● Google Scholar

Endress, P. K., Jenny, M., & Fallen, M. E. (1983). Convergent elaboration of apocarpous gynoecia in higher advanced dicotyledons (Sapindales, Malvales, Gentianales). *Nordic Journal of Botany*, 3(3), 293–300. doi:10.1111/j.1756-1051.1983.tb01941.x
Crossref ● Google Scholar

Endress, P. K., Davis, C. C., & Matthews, M. L. (2013). Advances in the floral structural characterization of the major subclades of Malpighiales, one of the largest orders of flowering plants. *Annals of Botany*, 111(5), 969–985. doi:10.1093/aob/mct056
Crossref ● PubMed ● PMC ● Google Scholar

Eriksen, B., & Persson, C. (2007). Polygalaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. IX. Flowering plants*. *Eudicots* (pp. 345–363). Berlin, Heidelberg: Springer.
Google Scholar

Farinati, S., Rasori, A., Varotto, S., & Bonghi, C. (2017). Rosaceae fruit development, ripening and post-harvest: an epigenetic perspective. *Frontiers in Plant Science*, 8. doi:10.3389/fpls.2017.01247
Crossref ● PubMed ● PMC ● Google Scholar

Fedoronchuk, M. M. (2017). Taxa of Rosaceae of the Ukrainian flora: position in a new system of the family according to molecular phylogenetic data. *Ukrainian Botanical Journal*, 74(1), 3–15. doi:10.15407/ukrbotj74.01.003 (In Ukrainian)
Crossref ● Google Scholar

Fedoronchuk, M. M. (2018). A synopsis of the family Fabaceae in the flora of Ukraine. I. Subfamilies Caesalpinoideae, Mimosoideae, Faboideae (tribes Sophoreae, Tephrosieae, Robinieae, Desmodieae, Phaseoleae, Psoraleae, Amorpheae, and Aeschynomeneae). *Ukrainian Botanical Journal*, 75(3), 238–247. doi:10.15407/ukrbotj75.03.238 (In Ukrainian)
Crossref ● Google Scholar

Feuillet, C., & MacDougal, J. M. (2007). Passifloraceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. IX. Flowering plants*. *Eudicots* (pp. 270–281). Berlin, Heidelberg: Springer. doi:10.1007/978-3-540-32219-1_35
Crossref ● Google Scholar

Gaertner, J. (1788). *De fructibus et seminibus plantarum* (Vol. 1). (Table 43). Stutgardiae: Typis Academiae Carolinae. doi:10.5962/bhl.title.53838
Crossref ● Google Scholar

Gagliardi, K. B., de Souza, L. A., & Albiero, A. L. M. (2013). Comparative fruit development in some Euphorbiaceae and Phyllanthaceae. *Plant Systematics and Evolution*, 300(5), 775–782. doi:10.1007/s00606-013-0918-3
Crossref ● Google Scholar

Graham, S. A., & Graham, A. (2014). Ovary, fruit, and seed morphology of the Lythraceae. *International Journal of Plant Sciences*, 175(2), 202–240. doi:10.1086/674316
Crossref ● Google Scholar

Harthman, V. de C., de Souza, L. A., & Lucas, E. J. (2018). Characters of the inferior ovary of Myrteae (Myrtaceae) and their implication in the evolutionary history of the tribe. *Australian Systematic Botany*, 31(3), 252–261. doi:10.1071/sb17059
Crossref ● Google Scholar

He, D., Biswas, S. R., Xu, M., Yang, T., You, W., & Yan, E. (2020). The importance of intraspecific trait variability in promoting functional niche dimensionality. *Ecography*, 44(3), 380–390. doi:10.1111/ecog.05254
Crossref ● Google Scholar

Hilu, K. W., Black, C. M., & Oza, D. (2014). Impact of gene molecular evolution on phylogenetic reconstruction: a case study in the rosids (Superorder Rosanae, Angiosperms). *PLoS One*, 9(6), e99725. doi:10.1371/journal.pone.0099725
Crossref ● PubMed ● PMC ● Google Scholar

Hussein, S. R., Kawashty, S. A., Tantawy, M. E., & Saleh, N. A. M. (2009). Chemosystematic studies of *Nitraria retusa* and selected taxa of Zygophyllaceae in Egypt. *Plant Systematics and Evolution*, 277(3–4), 251–264. doi:10.1007/s00606-008-0108-x
Crossref ● Google Scholar

IIckert-Bond, S. M., Gerrath, J., & Wen, J. (2014). Gynoecial structure of Vitales and implications for the evolution of placentation in the rosids. *International Journal of Plant Sciences*, 175(9), 998–1032. doi:10.1086/678086
Crossref ● Google Scholar

Iljinska, A., Didukh, Ya. (Ed.), Burda, R., & Korotchenko, I. (2007). *Ekoflora Ukrainy* [*Ecoflora of Ukraine*] (Vol. 5). Kyiv: Phytosociocentre. (In Ukrainian)
Google Scholar
Iljinska, A. P. (2013a). The structural diversity of fruits of species of Brassicaceae in the flora of Ukraine. *Ukrainian Botanical Journal,* 70(2), 168–177. (In Ukrainian)
Google Scholar
Iljinska, A. P. (2013b). Modern approaches to classificationof fruits of Brassicaceae: a case study of taxa occurring in Ukraine. *Ukrainian Botanical Journal,* 70(4), 467–478. (In Ukrainian)
Google Scholar
Iljinska, A. P. (2014). The family Cleomaceae in the flora of Ukraine. *Ukrainian Botanical Journal*, 71(1), 29–35. doi:10.15407/ukrbotj71.01.029 (In Ukrainian)
Crossref ● Google Scholar
Iljinska, A. P. (2016). The range of morphological characters of Brassicaceae s. l.: fruit and seeds. *Ukrainian Botanical Journal*, 73(3), 219–233. (In Ukrainian)
Google Scholar
Kaden, N. N. (1962). Tipy prodolnogo vskryvaniya plodov [The types of longitudinal dehiscense of fruits]. *Botanicheskii Zhurnal*, 47(4), 495–505. (In Russian)
Google Scholar
Kaden, N. N. (1964a). K voprosu o drobnykh plodakh [On the question of schizocarp fruits]. *Botanicheskii Zhurnal*, 49(7), 966–973. (In Russian)
Google Scholar
Kaden, N. N. (1964b). Morfologiya plodov geranievykh [Morphology of fruits in Geraniaceae]. *Nauchnye doklady vysshej shkoly. Biologicheskie nauki*, 2, 97–102. (In Russian)
Google Scholar
Kaden, N. N. (1965). Tipy plodov rasteniy sredney polosy evropeyskoy chasti SSSR [The fruit types of plants inhabiting the middle zone of the European part of the USSR]. *Botanicheskii Zhurnal*, 50(6), 775–787. (In Russian)
Google Scholar
Kaden, N. N. (1968). Evolyutsiya plodov rozotsvetnykh [Evolution of the fruits of Rosales]. *Bulletin of Moscow Society of Naturalists. Biological series*, 73(2), 127–135. (In Russian)
Google Scholar
Kaden, N. N., & Kondorskaja, V. R. (1967). Morfologiya tsvetka i ploda lokhovykh [Morphology of flower and fruit in oleaster family]. In A. N. Sladkov (Ed.). *Morfologiya rasteniy: sbornik statey posvyaschennyiy pamyati professora K. I. Meyera* [*Morphology of plants: collection of articles dedicated to the memory of professor K. I. Meyer*] (pp.102–118). Moskow: Nauka. (In Russian)
Google Scholar
Kubitzki, K. (1993). *Betulaceae*. In K. Kubitzki, J. G. Rohwer, & V. Bittrich (Eds.). *The families and genera of vascular plants. Vol. II. Flowering plants. Dicotyledons: Magnoliid, Hamamelid and Caryophyllid families* (pp. 152–157). Berlin, Heidelberg: Springer. doi:10.1007/978-3-662-02899-5_15
Crossref ● Google Scholar
Kubitzki K., Kallunki, J. A., Duretto, M., & Wilson, P. G. (2010). Rutaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. X. Flowering plants. Eudicots: Sapindales, Cucurbitales, Myrtaceae* (pp. 276–356). Berlin, Heidelberg: Springer. doi:10.1007/978-3-642-14397-7_16
Crossref ● Google Scholar
Leinfellner, W. (1950). Der Bauplan des synkarpen Gynözeums. *Österreichische Botanische Zeitschrift*, 97(3–5), 403–436. doi:10.1007/bf01763317
Crossref ● Google Scholar
Leinfellner, W. (1972). Zur Morphologie des Gynözeums der Polygalaceen. *Österreichische Botanische Zeitschrift*, 120(1–2), 51–76. doi:10.1007/bf01373258
Crossref ● Google Scholar
Leroy, J. F. (1955). *Étude sur les Juglandacea: à la recherche d'une conception morphologique de la fleur femelle et du fruit* (Vol. 6). Paris: Muséum national d'Histoire naturelle.
Google Scholar

Leins, P., & Erbar, C. (2010). *Flower and fruit: morphology, ontogeny, phylogeny, function and ecology*. Stuttgart: Schweizerbart.
Google Scholar

Levina, R. E. (1987). *Morfologiya i ekologiya plodov* [*Morphology and ecology of fruit*]. Nauka, Leningrad. (In Russian)
Google Scholar

Lorts, C. M., Briggeman, T., & Sang, T. (2008). Evolution of fruit types and seed dispersal: a phylogenetic and ecological snapshot. *Journal of Systematics and Evolution,* 46(3), 396–404.
Google Scholar

Mabberley, D. J. (2010). Meliaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. X. Flowering plants*. *Eudicots: Sapindales, Cucurbitales, Myrtaceae* (pp. 185–211). Berlin, Heidelberg: Springer. doi:10.1007/978-3-642-14397-7_13
Crossref ● Google Scholar

Macdonald, A. D., & Sattler, R. (1973). Floral development of *Myrica gale* and the controversy over floral concepts. *Canadian Journal of Botany*, 51(10), 1965–1975. doi:10.1139/b73-251
Crossref ● Google Scholar

Mangla, Y., Tandon, R., Goel, S., & Raina, S. N. (2013). Structural organization of the gynoecium and pollen tube path in Himalayan sea buckthorn, *Hippophae rhamnoides* (Elaeagnaceae). *AoB Plants*, 5, plt015. doi:10.1093/aobpla/plt015
Crossref ● PMC ● Google Scholar

Manning, W. E. (1978). The classification within the Juglandaceae. *Annals of the Missouri Botanical Garden*, 65(4), 1058–1087. doi:10.2307/2398782
Crossref ● Google Scholar

Marcussen, T., & Meseguer, A. S. (2017). Species-level phylogeny, fruit evolution and diversification history of *Geranium* (Geraniaceae). *Molecular Phylogenetics and Evolution*, 110, 134–149. doi:10.1016/j.ympev.2017.03.012
Crossref ● PubMed ● Google Scholar

Masullo, F. de A., Siqueira, S. F. H., Barros, C. F., Bovini, M. G., & Toni, K. L. G. D. (2020). Fruits of neotropical species of the tribe Malveae (Malvoideae-Malvaceae): macro- and micromorphology. *Acta Botanica Brasilica*, 34(2), 301–311. doi:10.1590/0102-33062019abb0293
Crossref ● Google Scholar

Matthews, M. L., & Endress, P. K. (2005). Comparative floral structure and systematics in Celastrales (Celastraceae, Parnassiaceae, Lepidobotryaceae). *Botanical Journal of the Linnean Society*, 149(2), 129–194. doi:10.1111/j.1095-8339.2005.00445.x
Crossref ● Google Scholar

Medan, D. & Schirarend C. (2004). Rhamnaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. VI. Flowering plants. Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales* (pp. 320–338). Berlin, Heidelberg: Springer. doi:10.1007/978-3-662-07257-8_37
Crossref ● Google Scholar

Mosyakin, S. L., & Fedoronchuk, M. M. (1999). *Vascular plants of Ukraine: a nomenclatorial checklist.* Kiev: National Academy of Sciences of Ukraine, M. G. Kholodny Institute of Botany.
Google Scholar

Mosyakin, S. L. (2013). Families and orders of angiosperms of the flora of Ukraine: a pragmatic classification and placement in the phylogenetic system. *Ukrainian Botanical Journal*, 70(3), 289–307. doi:10.15407/ukrbotj70.03.289 (In Ukrainian)
Crossref ● Google Scholar

Odintsova, A. V. (2008). Porivnyalnyi analiz morfolohii ta vaskulyarnoi anatomii hinetseya v rodyni Lythraceae [Comparative analysis of gynoecium morphology and vascular anatomy in the family Lythraceae]. *Ukrainian Botanical Journal*, 65(5), 687–695. (In Ukrainian)
Google Scholar

Odintsova, A. (2016). Loculicidal dehiscence of superior and inferior capsular fruits in Myrtales. *Studia Biologica*, 10(3–4), 129–140. doi:10.30970/sbi.1003.504 (In Ukrainian)
Crossref ● Google Scholar

Odintsova, A. V. (2022). Morphogenesis of fruit as a subject matter for the carpological studies. *Ukrainian Botanical Journal*, 79(3), 169–183. doi:10.15407/ukrbotj79.03.169 (In Ukrainian)
Crossref ● Google Scholar

Odintsova, A., & Klimovych, N. (2017). Anatomical and morphological fruit structure in *Epilobium hirsutum* and *E. angustifolium* (Onagraceae). *Ukrainian Botanical Journal*, 74(6), 582–593. doi:10.15407/ukrbotj74.06.582 (In Ukrainian)
Crossref ● Google Scholar

Odintsova, A. V., Fishchuk, O. S., Scrypec, K. I., & Danylyk, I. M. (2021). Systematic treatment of morphological fruit types in plants of the class Liliopsida of the flora of Ukraine. *Regulatory Mechanisms in Biosystems*, 12(3), 375–382. doi:10.15421/022151
Crossref ● Google Scholar

Paschoalini, G. de O., Pirani, J. R., Demarco, D., & El Ottra, J. H. L. (2022). Revisiting pericarp structure, dehiscence and seed dispersal in Galipeeae (Zanthoxyloideae, Rutaceae). *Brazilian Journal of Botany*, 45(1), 415–429. doi:10.1007/s40415-021-00779-9
Crossref ● Google Scholar

Pell, S. K., Mitchell, J. D., Lobova, T., & Miller A. J. (2010). Anacardiaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. X. Flowering plants. Eudicots: Sapindales, Cucurbitales, Myrtaceae* (pp. 7–50). Berlin, Heidelberg: Springer. doi:10.1007/978-3-642-14397-7_3
Crossref ● Google Scholar

POWO (2022). Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Retrieved from http://www.plantsoftheworldonline.org (https://powo.science.kew.org). Accessed 21 March, 2023.

Rosado, A., de Souza, M. R., Milaneze, M. A., & de Souza, L. A. (2022). *Sapindaceae: biologia reprodutiva e sua importância para os insetos na região norte do Paraná, Brasil*. São Paulo: Presidente Prudente. Retrieved from https://www.researchgate.net/publication/366237839_Sapindaceae_-_Biologia_reprodutiva_e_sua_importancia_para_os_insetos_na_regiao_norte_do_Parana_Brasil

Roth, I. (1977). Fruits of angiosperms. Encyclopedia of plant anatomy (Vol. 10, Part 1). Berlin, Stuttgart: Gebrüder Borntraeger.
Google Scholar

Sattler, R., & Rutishauser, R. (2022). Fundamentals of plant morphology and plant evo-devo (evolutionary developmental morphology). *Plants*, 12(1), 118. doi:10.3390/plants12010118
Crossref ● PubMed ● PMC ● Google Scholar

Schönenberger, J., & Balthazar, M. von. (2006). Reproductive structures and phylogenetic framework of the rosids-progress and prospects. *Plant Systematics and Evolution*, 260(2–4), 87–106. doi:10.1007/s00606-006-0439-4
Crossref ● Google Scholar

Sheahan, M. C. (2007). Zygophyllaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. IX. Flowering plants. Eudicots* (pp. 488–500). Berlin, Heidelberg: Springer. doi:10.1007/978-3-540-32219-1_56
Crossref ● Google Scholar

Shivaprakash, K. N., & Bawa, K. S. (2022). The evolution of placentation in flowering plants: a possible role for kin selection. *Frontiers in Ecology and Evolution*, 10, 784077. doi:10.3389/fevo.2022.784077
Crossref ● Google Scholar

Simmons, S. L. (2007). Staphyleaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. IX. Flowering plants. Eudicots* (pp. 440–445). Berlin, Heidelberg: Springer. doi:10.1007/978-3-540-32219-1_49
Crossref ● Google Scholar

Spjut, R. W. (1994). *A systematic treatment of fruit types*. New York: New York Botanical Garden. Retrieved from http://www.worldbotanical.com/fruit_types.htm#Classification
Google Scholar

Sramkó, G., Molnár V., A., Tóth, J. P., Laczkó, L., Kalinka, A., Horváth, O., Skuza, L., Lukács, B. A., & Popiela, A. (2016). Molecular phylogenetics, seed morphometrics, chromosome number

evolution and systematics of European *Elatine* L. (Elatinaceae) species. *PeerJ*, 4, e2800. doi:10.7717/peerj.2800
Crossref ● PubMed ● PMC ● Google Scholar

Sun, M., Naeem, R., Su, J.-X., Cao, Z.-Y., Burleigh, J. G., Soltis, P. S., Soltis, D. E., & Chen, Z.-D. (2016). Phylogeny of the Rosidae: a dense taxon sampling analysis. *Journal of Systematics and Evolution*, 54(4), 363–391. doi:10.1111/jse.12211
Crossref ● Google Scholar

Takhtajan, A. (Ed.). (2009). *Flowering plants*. Springer Dordrecht. doi:10.1007/978-1-4020-9609-9
Crossref ● Google Scholar

Van der Pijl, L. (1982). *Principles of dispersal in higher plants*. Berlin, Heidelberg: Springer. doi:10.1007/978-3-642-87925-8
Crossref ● Google Scholar

Voytenko, V. F. (1989). Geterokarpiya (geterodiasporiya) u pokrytosemennykh rasteniy: analiz ponyatiya, klassifikatsiya, terminologiya [Heterocarpy (heterodiaspory) in angiosperms: concept analysis, classification and terminology]. *Botanicheskii Zhurnal,* 74(3), 281–297. (In Russian)
Google Scholar

Wang, H., Moore, M. J., Soltis, P. S., Bell, C. D., Brockington, S. F., Alexandre, R., Davis, C. C., Latvis, M., Manchester, S. R., & Soltis, D. E. (2009). Rosid radiation and the rapid rise of angiosperm-dominated forests. *Proceedings of the National Academy of Sciences*, 106(10), 3853–3858. doi:10.1073/pnas.0813376106
Crossref ● PubMed ● PMC ● Google Scholar

Webster, G. L. (2014). Euphorbiaceae. In K. Kubitzki (Ed.). *The families and genera of vascular plants. Vol. XI. Flowering plants. Eudicots: Malpighiales* (pp. 51–216). Berlin, Heidelberg: Springer. doi:10.1007/978-3-642-39417-1_10
Crossref ● Google Scholar

Xiang, Y., Huang, C.-H., Hu, Y., Wen, J., Li, S., Yi, T., Chen, H., Xiang, J., & Ma, H. (2017). Evolution of Rosaceae fruit types based on nuclear phylogeny in the context of geological times and genome duplication. *Molecular Biology and Evolution*, 34(2), 262–281. doi:10.1093/molbev/msw242
Crossref ● PubMed ● PMC ● Google Scholar

Yeo, P. F. (1984). Fruit-discharge-type in *Geranium* (Geraniaceae): its use in classification and its evolutionary implications. *Botanical Journal of the Linnean Society*, 89(1), 1–36. doi:10.1111/j.1095-8339.1984.tb00998.x
Crossref ● Google Scholar

Zerov, D. K. (Ed.). (1965). *Vyznachnyk roslyn Ukrainy* [*Determiner of plants of Ukraine*]. Kyiv: Urozhaj. (In Ukrainian)
Google Scholar

Zhu, X.-Y., Chase, M. W., Qiu, Y.-L., Kong, H.-Z., Dilcher, D. L., Li, J.-H., & Chen, Z.-D. (2007). Mitochondrial *matR* sequences help to resolve deep phylogenetic relationships in rosids. *BMC Evolutionary Biology*, 7(1), 217. doi:10.1186/1471-2148-7-217
Crossref ● PubMed ● PMC ● Google Scholar

МОРФОЛОГІЧНИЙ І ТАКСОНОМІЧНИЙ АНАЛІЗ ПЛОДІВ У ПІДКЛАСІ ROSIDAE ТАКНТ. ФЛОРИ УКРАЇНИ

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Вступ. Розиди є ключовою кладою еудикотів, чий таксономічний склад був значно змінений на підставі вивчення молекулярної філогенії. Молекулярні дані призвели до переоцінки багатьох фенотипічних ознак, особливо у репродуктивній

сфері. Попри те, що структуру й еволюцію квітки активно вивчали, морфологічну структуру плодів майже не досліджували в межах цілого підкласу. Це дослідження мало на меті з'ясувати морфологічну різноманітність плодів у представників розидів (підкласу Rosidae) на прикладі рослин флори України для того, щоби встановити найбільш поширені типи плодів, проаналізувати розподіл базових типів плодів серед розидів і з'ясувати деякі порівняльно-морфологічні особливості гінецею та плоду.

Матеріали та методи. Характеристики плодів ми наводили з різних карпологічних зведень. Подано також характеристики гінецея, важливі для розвитку плоду, а саме: положення зав'язі, плацентація, кількість насінинних зачатків і гнізд зав'язі. У межах підкласу ми виділили сім основних типів плодів, використовуючи підхід, розроблений нами для аналізу плодів однодольних рослин флори України: збірний плід, багатонасінний монокарпій, коробочка, ягода, багатонасінний піренарій, схізокарпій і однонасінний плід.

Результати. В результаті був укладений анотований список морфологічних характеристик плодів для кожної з 54 родин підкласу Rosidae*,* які наведені для України. У цьому списку подано взаємодоповнюючі дані та найбільш контрастуючі визначення плодів із різних джерел інформації.

Обговорення. Згідно з нашими підрахунками, підклас Rosidae у флорі України представлений 326 родами і щонайменше 1617 видами. Наші дані демонструють, що найбільш поширеними типами плодів на рівні родини є коробчасті й однонасінні плоди, однак на рівні роду та виду частка багатонасінних монокарпіїв і збірних плодів також значна. У дев'яти родинах флори України виявлено кілька базових типів плодів. Деякі плоди неоднозначно класифікують до того чи іншого типу через їхні проміжні характеристики. Отже, явно демонструються нечіткі межі між більшістю типів плодів.

Висновки. Отримані результати ми порівняли з нашими попередніми даними з вивчення плодів однодольних рослин флори України. В обох випадках було чітко показано домінування коробчастих плодів на рівні родини. Результати нашого аналізу дають підстави стверджувати, що модель базових типів плодів можна потенційно використовувати для формального аналізу структури плодів у інших групах покритонасінних.

Ключові слова: фабіди, мальвіди, гінецей, коробчастий плід, однонасінний плід, схізокарпій

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