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RESEARCH ARTICLE

Morphological and taxonomic overview of fruits in representatives of subclass *Caryophyllidae* in the flora of Ukraine

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Abstract. Subclass *Caryophyllidae* is a paraphyletic group among the clade of superasterids; its taxonomic circumscription has undergone major changes due to molecular phylogenetic results. The present study is aimed at analyzing the available information on the morphological diversity of fruits and the gynoecium structure in representatives of this subclass in the Ukrainian flora. Three basic fruit types are recognized in *Caryophyllidae*: capsular, berry-like, and one-seeded fruits. In the annotated list of morphological fruit types, the characteristics and morphological diversity of fruits according to different sources are reported for each family. The occurrence of apocarpous fruits, inferior fruits, and placentation types are analyzed, as also the functional types of fruits adapted to autochory, ballistochory, anemochory, and ornithochory. The carpological spectrum of basic fruit types at the levels of family, genus, and species demonstrates the widespread occurrence of capsular and one-seeded fruits (with a slighlt predominance of one-seeded fruits at the species level), while only four species have berry-like fruits.

Keywords: *Caryophyllales*, circumscissile capsule, free-central placentation, gynoecium, morphology, one-seeded fruit, superior ovary, *Santalales*

Introduction

The changing view in angiosperm systematics from the evolutionary-taxonomic to the molecular-phylogenetic paradigm caused several large-scale changes in the circumscription and taxonomic composition of the order *Caryophyllales* Juss. ex Bercht. & J. Presl (Walker et al., 2018; Yao et al., 2019; Morales-Briones et al., 2021). First, evolutionary relationships of families were revisited; as a result, the view on the ancestral group was re-evaluated. Second, a considerable expansion of the order was caused by the inclusion of the dialypetalae carnivorous plants, which resulted in the concept of the expanded *Caryophyllales* (Cuénoud, 2003; Walker et al., 2018). The third novelty is the shift of the order position from the basal-middle place among dicots (see Eckardt, 1976; Cronquist, 1981; Takhtajan, 2009) to the superasterid clade, close to the true asterids (APG IV, 2016). The close relationships of *Caryophyllales* with the small (in terms of the number of taxa included) order *Berberidopsidales* Doweld have been also supposed (Zeng et al., 2017).

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Currently, the order *Caryophyllales* is composed of core *Caryophyllales* (former *Centrospermae*) and non-core *Caryophyllales*; the latter group is subdivided into the carnivorous clade (*Droseraceae* Salisb., *Nepenthaceae* Dumort, *Drosophyllaceae* Chrtek & al., *Ancistrocladaceae* Planch. ex Walp., and *Dioncophyllaceae* Airy Shaw) and the FTPP clade (*Frankeniaceae* Desv., *Tamaricaceae* Link, *Plumbaginaceae* Juss., and *Polygonaceae* Juss.) (Walker et al., 2018; Yao et al., 2019). Core *Caryophyllales* are supposed to evolve in arid or semi-arid environments, thus obtaining common adaptations, such as often succulent leaves or stems, and salinity resistance (Cuénoud, 2003). Three synapomorphies were recognized for the core *Caryophyllales*, which refer to the reproductive features, namely, their free-central placentation, campylotropous ovule, and the perisperm in a seed (Eckardt, 1976; Bittrich, 1993a; Ronse De Craene, 2013). Other synapomorphies are betalaine pigments instead of anthocyanins, P3-type plastides in sieve elements, and the bound ferulic acid in unlignified cell walls (Eckardt, 1976; Cuénoud, 2003).

The paraphyletic group of superasterids, before branching out the asterids, comprises orders *Caryophyllales*, *Santalales* R. Br. ex Bercht. & J. Presl, and *Berberidopsidales* (APG IV, 2016). Currently, in the world flora, *Caryophyllales* contains 37 families, 749 genera, and 11620 species, while *Santalales* embraces 14 families, 151 genera, and 1992 species, and *Berberidopsidales* embraces 2 families, 3 genera, and 4 species, according to Stevens (2001). It looks like the orders *Caryophyllales*, *Santalales*, and *Berberidopsidales* have never been considered as closely related taxa before molecular phylogenetic studies (Takhtajan, 2009), as also the clades of core and non-core *Caryophyllales* (Cuénoud, 2003). Hence, the morphological diversity of floral parts and fruits has not been analyzed in detail for this set of taxa as a whole.

In the pragmatic system of angiosperms proposed for the flora of Ukraine (Mosyakin, 2013), this paraphyletic group is treated as subclassis *Caryophyllidae* Takht. According to Mosyakin (2013), subclass *Caryophyllidae* in the flora of Ukraine embraces 18 families, which totally cover 103 genera and approximately 520 species (Mosyakin, Fedoronchuk, 1999); however, the number of species-rank taxa is possibly overestimated and will be reduced in the forthcoming list (Mosyakin, personal communication). Most of the included families belong to the order *Caryophyllales*, and two families belong to the order *Santalales*, namely, *Santalaceae* R. Br. and *Loranthaceae* Juss. The order *Berberidopsidales* is not represented in the Ukrainian flora. Six families are represented only by one to a few species that are cultivated or sometimes escaped (*Aizoaceae* Martinov, *Basellaceae* Raf., *Cactaceae* Juss., *Nyctaginaceae* Juss., *Phytolaccaceae* R. Br., *Plumbaginaceae* Juss. s. str.), some taxa are naturalized: e.g., *Mirabilis nyctaginea* (Michx.) MacMill. (*Oxybaphus nyctagineus* (Michx.) Sweet) of *Nyctaginaceae*, some species of *Opuntia* Mill. (*Cactaceae*).

The updated family composition and new placement of the *Caryophyllidae* among eudicots invoke the re-evaluation of the phenotypic features of the group in a new taxonomic context. The objective of this study is to analyze the morphological diversity of fruits in *Caryophyllidae* in the framework of the local taxonomic composition revealed in the flora of Ukraine. In the order *Caryophyllales*, various fruit types were earlier described: capsular fruits, achenes, berries, drupes, and nuts. Dry fruits more likely belong to the ancestral fruit type among core *Caryophyllales*, many representatives of which are adapted to arid environmental conditions (Bittrich, 1993a). Capsular fruits with loculicidal, septicidal, and circumscissile dehiscence predominate for basal representatives of the order, while dry indehiscent fruits appear in taxa with a reduced ovule number. Berries and drupes are found to be rare. No quantitative treatment of the occurrence of fruit types according to the common approach has been made so far.

Materials and methods

Descriptive and morphogenetic characteristics of fruits of the representatives of *Caryophyllidae* occurring in Ukraine were referred from Kaden (1965), Roth (1977), Spjut (1994), Takhtajan (2009), and other sources. The information on the gynoecium structure (carpel and ovule number, placentation) was obtained from Eichler (1875, 1878), Takhtajan (2009), as also from the treatments of families in *The Families and Genera of Vascular Plants*, Volumes 2, 5, and 12 edited by K. Kubitzki et al. (see **Results** for specific citations). Three basic fruit types were recognized for the *Caryophyllidae* of the flora of Ukraine, comparable with those recognized for the monocots (Odintsova et al., 2022) and rosids (Odintsova, 2023a). Fruit coverings (enveloped or covered) are described in the second article

mentioned above. These basic fruit types are outlined below.

Capsule — dry dehiscent fruit composed of united carpels. In *Caryophyllidae*, superior or semi-inferior, mostly multi-seeded capsules with various dehiscence modes occur. In many species of *Amaranthus* L., the capsule is few- to one-seeded, called "utricle" (*Ukr*. мішечок) and it transforms into indehiscent one-seeded fruit in the other species. Capsules are paracarpous, lysicarpous, or of combined types (syncarpous multilocular at the base and lysicarpous or paracarpous unilocular above). Placentation is axile (at the base), parietal, or free-central (above).

Berry — totally fleshy indehiscent fruit. The studied representatives of *Caryophyllidae* possess oligomerous and polymerous, superior and inferior berries (uva and bacca, correspondingly), composed of united carpels or partially united carpels (*Phytolacca acinosa* Roxb.), with axile, parietal or combined placentation, with many to one ovule per carpel.

One-seeded fruit — monomerous, oligomerous or pseudomonomerous indehiscent fruit containing typically one seed and dispersed as a disseminule or as a multiple fruit in the dense infructescence. Most fruits of this category are called nut or nut-like (utricle) fruits. We excluded from this category one-seeded capsular fruits of many species of *Amaranthus*, because in that case, a disseminule is a naked seed fallen out from the fruit. In *Caryophyllidae* of the flora of Ukraine, one-seeded fruits mostly develop from the uni-ovulate unilocular ovary, composed of 2–3(5) united carpels, with the basal placenta. Only in *Nyctaginaceae* the gynoecium is described as monocarpellate and apocarpous.

In the annotated list of morphological fruit types, we reported for each family the approximate number of representatives occurring in the flora of Ukraine (with genera and species numbers indicated). The numbers of taxa were referred from Mosyakin and Fedoronchuk (1999) (where it was not mentioned) and other mentioned sources. Cultivated or escaped taxa were marked with an asterisk (*). Families are recognized according to Mosyakin (2013) and listed in alphabetical order, grouped in the orders *Caryophyllales* and *Santalales*. Then, we counted families, genera and species that possess each basic fruit type and created a carpological spectrum for each taxonomic level.

Results

Order *CARYOPHYLLALES*

****Aizoaceae* Martinov** (*Mesembryanthemum* ×*vascosilvae* (Gideon F. Sm., E. Laguna, F. Verloove & P.P. Ferrer) Sáez & Aymerich [=*M. cordifolium* L. f. × *M. haeckelianum* A. Berger; *Aptenia* ×*vascosilvae* Gideon F. Sm., E. Laguna, F. Verloove & P.P. Ferrer]) (Mosyakin, Mosyakin, 2021). The fruit is a loculicidal hygrochastic capsule as in most *Mesembryanthemoideae* Ihlenfeldt, Schwantes, Straka; it is pentalocular in *Mesembryanthemum* L. and tetralocular in *Aptenia* N.E. Br. s. str. (now often included in *Mesembryanthemum* s. l.) (Hartmann, 1993; Spjut, 1994). Sometimes in *Mesembryanthemum* related species, false septas growing from the midribs of the carpels; the fruit is designated as loculicidal schizocarpous capsule, with several fruitlets which are formed by splitting of false septas, so each fruitlet is composed of two halves of neihboring carpels (Roth, 1977). The ovary is inferior, with carpels partly sunken into the cup-like receptacle; columella composed of conical axis covered with ascidiate parts of carpels (Roth, 1977). In *Aizoaceae* (as also in *Cactaceae*), the conical floral axis is extremely sunken (invaginates) during flower development and causes a shift of the placentas from the axile into basal and basal-laminar position. The other result is a shift from the superior ovary into the inferior or semi-inferior ovary (Leins, Erbar, 2010). The superior part of the ovary dehisces with valves when moistened (Eichler, 1878).

***Amaranthaceae* Juss. s. str.** (3/20) — utricle lysicarpous, di- or tri-merous, enveloped (Kaden, 1965). The ovary is superior, unilocular, with 2–3 stigmas, ovule mostly solitary, paired or numerous, placentation basal; the fruit is designated as dry thin-walled irregularly rupturing capsule (Townsend, 1993). The fruit features two bracteoles and a bract (Eichler, 1878).

A. The fruit is entitled a pyxidium-like utricle (*Ukr*. криночкоподібний мішечок) in most *Amaranthus* species; irregularly and circumscissile dehiscence of fruits occur (Kaden, 1965; Costea et al., 2001; Oyama et al., 2010). Spjut (1994) defined the fruit in most *Amaranthus* species as a pyxidium, while in *A. viridis* L. as an utricle — a small bladderlike fruit with one seed, thin fruit wall, dehiscent or indehiscent (Spjut, 1994: 121). In *Celosia* L., the fruit is circumscissile dehiscent, and has two or several seeds (Townsend, 1993). In *Celosia argentea* L.

(=*C. cristata* L.) the ovary is tricarpellate, ovules are numerous on basal-central placenta (Eichler, 1878). In *Gomphrena globosa* L., the ovary is dimerous (Eichler, 1878). In *Gomphrena* L., ovules are solitary and basal (Takhtajan, 2009).

B. Indehiscent or irregularly dehiscent fruit — in *Amaranthus blitum* L. and some other taxa of *Amaranthus*.

****Basellaceae*** **Raf.** (*Anredera cordifolia* (Ten.) Steenis). The fruit is an indehiscent, thin-walled nutlet, surrounded by two persistent winged sepals, sometimes they are considered as winged persistent bracteoles (Sperling, Bittrich, 1993; Takhtajan, 2009). Fruit is a **diclesium** — dry or fleshy one-seeded fruit covered or enveloped by fruiting perianthium (Spjut, 1994). Carpels three, ovary superior, unilocular; ovule solitary, basal (Eichler, 1878). Ovule is considered to be cauline in *Basella alba* L. (incl. *B. rubra* L.) (Sattler, Lacroix, 1988) or, alternatively, of carpellary origin (Sperling, Bittrich, 1993).

****Cactaceae*** **Juss.** (*Opuntia humifusa* Raf.; several other species are also reported as locally escaped). The fruit is an inferior unilocular multi-seeded conspicuous berry, composed of three or more carpels. Seeds are embedded in a fleshy pulp; the ovary is surrounded by pericarpel — a stem tissue enclosing the carpels; placentas are formed separately from the septa and alternating with them (hypanthial placentation) (Barthlott, Hunt, 1993). Pericarpel has no homologs in other taxa of *Caryophyllales*, it is evidence for the receptacular origin of the inferior ovary wall (Rosas-Reinhold et al., 2021). The fruit is an **arcosarcum** — indehiscent fruit with an undifferentiated fruit wall surrounded with an accrescent fleshy exocarp derived from perianthium or receptacle, synonim to inferior berry (Spjut, 1994). Placentas are basal-laminar, very flat, and broadened; see *Aizoaceae* (Leins, Erbar, 2010).

Caryophyllaceae **Juss.** (We accepted 46/209 taxa from the list of 49/231 taxa according to Fedoronchuk (2023), with the exclusion of 18 subspecies and taxa which need confirmation). Fruits are a capsule (mostly with loculicidal and/or septicidal dehiscence), berry, dry nutlet, or achene (Bittrich, 1993b). The ovary is superior (weaky inferior in *Paronychia* Mill.), sometimes on a short gynophore (anthophore) (Bittrich, 1993b). According to Eichler (1878), isomerous 5-merous (exceptional 4-merous) gynoecium with episepalous carpels appears in *Arenaria* L., and other *Alsineae* DC., *Cerastium* L., *Coronaria* Guett. (often included in *Silene* L. s. l.; see also taxa mentioned below), *Lychnis* L. (*Silene* s. l.), *Melandrium* Roehl. (*Silene* s. l.), *Silene* p. p., and *Viscaria* Bernh. Carpels are epipetalous in *Agrostemma* L. and *Spergula* L. with a 5-merous gynoecium, and in *Sagina* L., *Spergella* Rchb. (*Sagina* s. l.) with a 4-merous gynoecium. Gynoecium is trimerous in *Alsine* L. (*Stellaria* s. l.), *Arenaria*, *Corrigiola* L., *Cucubalus* L. (*Silene* s. l.), *Heliosperma* (Rchb.) Rchb., *Holosteum umbellatum* L., *Moehringia* L., *Silene* s. str. (most species), *Spergularia* (Pers.) J. Presl & C. Presl, and *Stellaria* L. s. str. Gynoecium is dimerous in *Dianthus* L., *Gypsophila* L., *Herniaria* L., *Moehringia muscosa* L., *Paronychia*, *Saponaria* L., *Scleranthus annuus* L., *S. perennis* L., *Vaccaria* Wolf (now included in *Gypsophila* s. l.). In the trimerous gynoecium, the odd carpel is posterior; in the dimerous gynoecium, carpels are always median (Eichler, 1878).

The ovary is septate during flower development in most species (Bittrich, 1993b), but becomes unilocular at anthesis (sometimes only basally multilocular), with free-central placentation (only in *Paronychieae* (Juss.) Dumort. the central column is short, the ovule is often solitary and basal) (Eichler, 1878). During the flower development, septas are dissolved from top to bottom, and sometimes the basal part of the ovary remains septate (Bittrich, 1993b). In the ovary, synascidiate and symplicate zones are present, the ovules in pluriovulate ovaries may be inserted in both zones but in *Paronychieae* the placenta is restricted to the synascidiate zone (Bittrich, 1993b). Ovules in *Sileneae* DC. are numerous, in *Alsineae* there are often only two ovules per carpel; ovules are arranged in two series in each carpel (Eichler, 1878; Bittrich, 1993b).

A. Capsule — fruit which occurs in most genera. The capsule is often denticidal — it dehisces regularly, incompletely, by teeth not more than one-fifth of its length (Spjut, 1994) with various combinations of dorsal and septicidal slits (Fig. 1A–R).

Classification of capsular fruits follows Kaden (1965).

1. Syncarpous trimerous covered, dorsi-laterally dehiscent — *Alsine*.
2. Hemi-lysicarpous.
   1) pentamerous, enveloped, incomplete disjunctive dehiscent — *Viscaria*;
   2) trimerous, enveloped, incomplete disjunctive-dorsally dehiscent — *Silene*;

3) dimerous, enveloped, incomplete disjunctive-dorsally dehiscent — *Vaccaria.*

3. Lysicarpous.

1) pentamerous, covered;

a) incomplete disjunctive-dorsally dehiscent — *Cerastium*, *Dichodon* (Bartl. ex Rchb.) Rchb. (except *D. viscidum* (M. Bieb.) Holub [*Cerastium dubium* (Bastard) Guepin], *Myosoton* Moench. (*Stellaria* s. l.);

b) disjunctive dehiscent — *Sagina nodosa* (L.) Fenzl., *Spergula* (except *Spergula arvensis* L. subsp. *linicola* (Boreau) Janch.);

c) indehiscent or rupturing — *Spergula arvensis* L. subsp. *linicola* (Boreau) Janch.;

2) pentamerous, enveloped;

a) incomplete disjunctive dehiscent — *Agrostemma*, *Coronaria*, *Lychnis*;

b) incomplete disjunctive-dorsal dehiscent — *Melandrium*;

3) tetramerous, covered, disjunctive dehiscent — *Sagina procumbens* L.;

4) trimerous, covered;

a) disjunctive dehiscent — *Minuartia*, *Spergularia*;

b) disjunctive-dorsal dehiscent — *Moehringia*, *Stellaria*;

c) incomplete disjunctive-dorsal dehiscent — *Arenaria*, *Dichodon viscidum* (M. Bieb.) Holub [*Cerastium dubium* (Bastard) Guepin], *Holosteum* Dill. ex L.;

5) trimerous, enveloped, incomplete disjunctive-dorsal dehiscent — *Elisanthe* (Fenzl ex Endl.) Rchb. (*Silene* s. l.);

6) dimerous, enveloped, incomplete disjunctive-dorsal dehiscent — *Dianthus*, *Gypsophila*, *Saponaria.*

B. Berry — fruit is trimerous in *Cucubalus baccifer* L. [now mainly accepted as *Silene baccifera* (L.) Durande] (Bittrich, 1993b). According to Kaden (1965), *C. baccifer* has a lysicarpous trimerous covered capsule, indehiscent or rupturing. Morphologically, the fruit in *C. baccifer* resembles the capsular fruit in *Silene* s. str.: it is trimerous, with free-central placenta and gynophore. However, it has a fleshy fruit wall, and is indehiscent. In the sectioned fruit, the remnants of septas on the thin fruit wall are visible, as well as three free-central placentas (Fig. 2A, B).

C. Nut (achene or utricle) — fruit lysicarpous dimerous, enveloped, indehiscent in 10 species of genera *Herniaria*, *Scleranthus* L., *Paronychia cephalotes* (M. Bieb.) Besser, and *Queria hispanica* L.

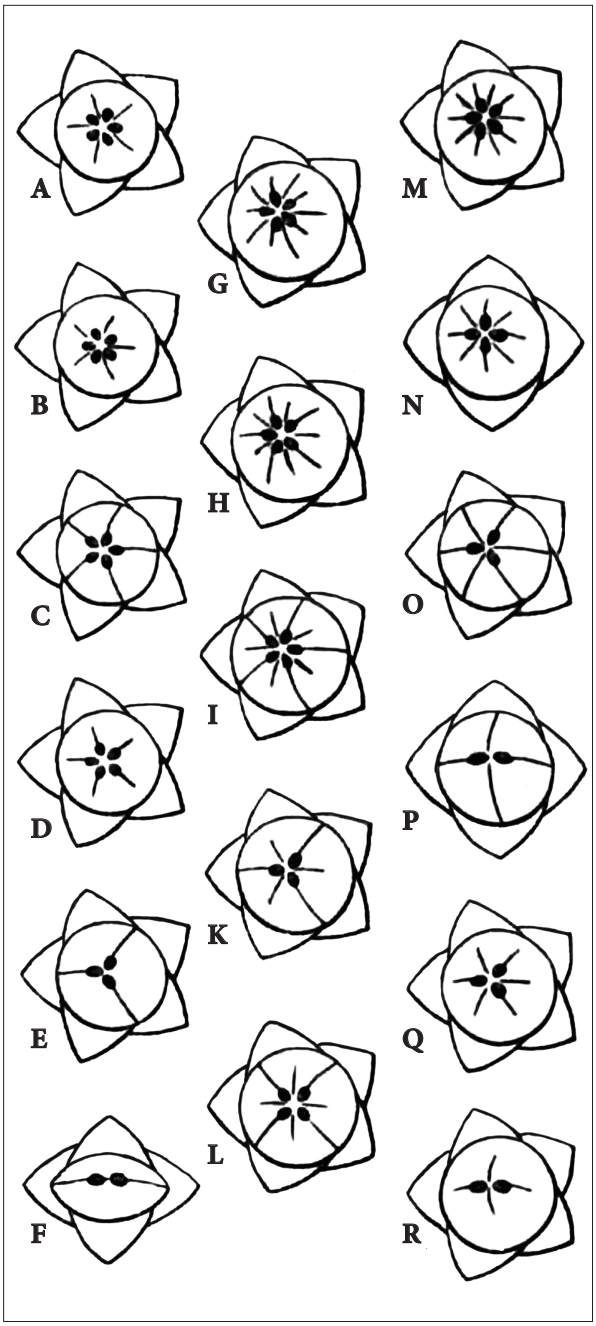

Fig. 1. Arrangement of dehiscence slits in fruits of *Caryophyllaceae* (after Eichler, 1878), names of taxa are given according to the original work. A: *Agrostemma*; B: *Lychnis*; C: *Spergula*; D: *Viscaria*; E: *Alsine*; F: *Bufonia*; G: *Melandrium vespertinum*; H: *M. sibiricum*; I: *Malachium*; K, L: *Arenaria*; M: *Cerastium*; N: *C. quaternellum*; O: *Stellaria*; P: *Moehringia muscosa*; Q: *Silene*; R: *Dianthus*. Sepals are presented in figures surrounding the fruit; black circles in the center of the capsule mark the carpels' tips

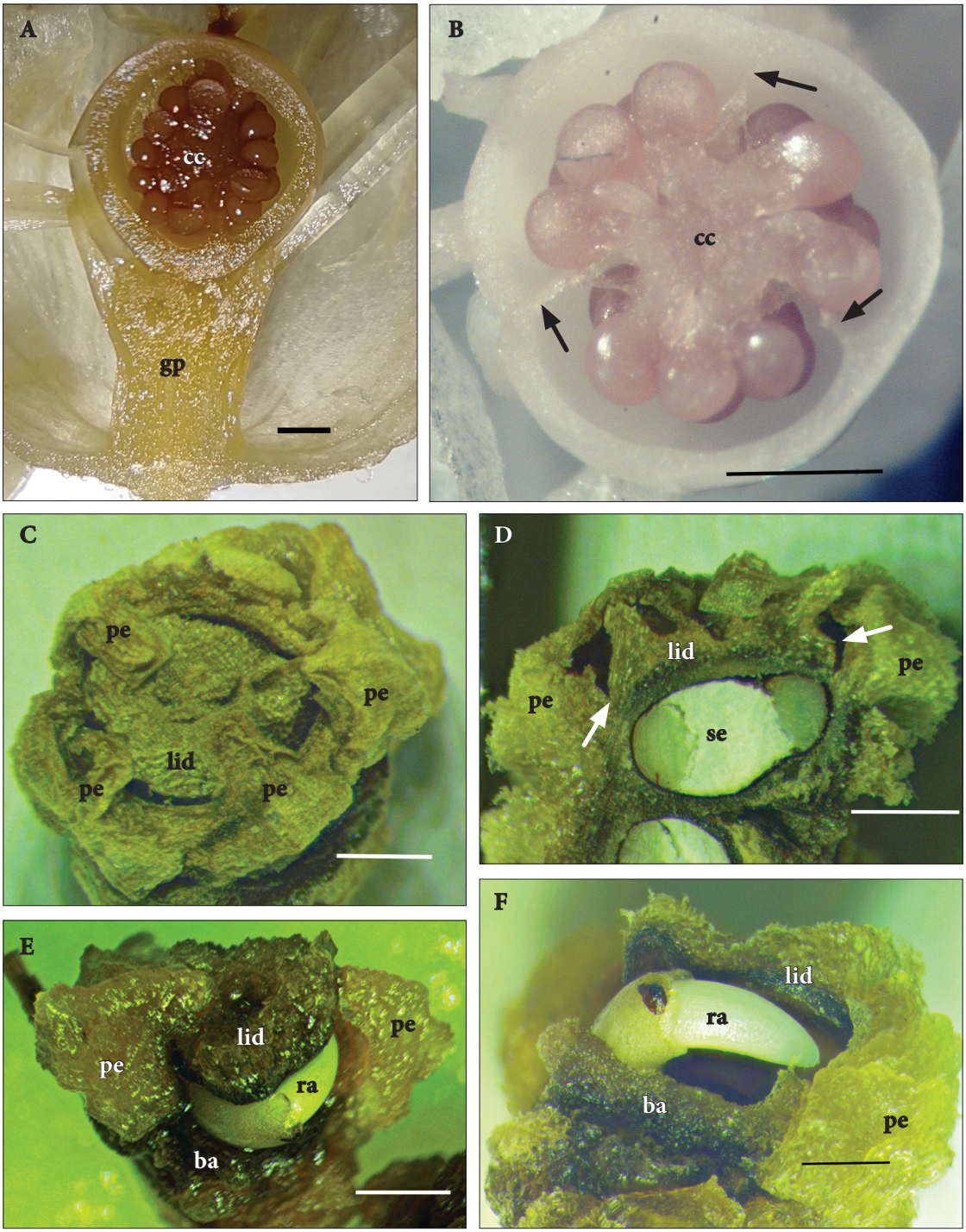

Fig. 2. Dissected fruits of *Cucubalus baccifer* [now mainly accepted as *Silene baccifera* (L.) Durande] (*Caryophyllaceae*) (A, B) and *Beta vulgaris* (*Chenopodiaceae*) (C–F). A: fruit in longitudinal section; B: fruit in transversal section, black arrows mark remnants of septas; C: indehiscent ripe fruit from the above; D: fruit in longitudinal section; note the inferior ovary and curved embryo in seeds, circumscissile slit is marked with white arrows; E, F: dehiscing fruit with radicle enforcing the lid to detach the base; ba — fruit base, cc — central column; gp — gynophore, lid — fruit lid; pe — perigonium members; ra — radicle; se — seed. Scale bars 1.0 mm

***Chenopodiaceae* Vent.** [included in *Amaranthaceae* Juss. sensu APG IV (2016)] (20/124) — fruit is a superior lysicarpous utricle (Kaden, 1965). The fruit is a nut, utricle or achene, sometimes dehiscent, the pericarp is membranous. The fruit is covered by persistent perianth, bracts, and bracteoles (the latter are accrescent and modified), often dispersed in infructescences (Kühn, 1993). Spjut (1994: 29) treated the fruit in *Chenopodium* L. as a typical achene, a uni-seeded indehiscent fruit with a pericarp contiguous to the seed. In *Atriplex* L. and *Salsola* L., the fruit is interpreted as a diclesium, a simple dry or fleshy achene-like or utricular fruit covered with a dry accrescent fruiting perianthium (Spjut, 1994). The ovary is unilocular, uni-ovulate, with a basal ovule (Eichler, 1878).

According to Kaden (1965), fruits are classified as follows.

A. Fruit tetramerous, covered with bracts — *Spinacia* L.

B. Fruit dimerous.

1. Pyxidium covered with perigonium, dehiscing with a circumscissile lid — *Beta* L. In *Beta*, the ovary is almost inferior (Eichler, 1878; Volkens, 1893); the fruit opens with a lid being forced to detach by a germinating embryo (Volkens, 1893). The fruit in *Beta vulgaris* L. was called by Spjut (1994: 53) a **catoclesium**, a compound unit of indehiscent fruitlets enclosed by leaves, bracts or fused perigonium parts. As it has been found earlier, the fruit in *B. vulgaris* dispersed as a diaspore with a seed inside (Fig. 2C–D); it dehisces during the germination of the embryo (Fig. 2E, F). Therefore, we consider the fruit of *Beta vulgaris* to be of a one-seeded basic fruit type.

2. Fruit indehiscent, dry.

1) enveloped with perigonium — most genera (*Chenopodium*, *Kochia* Roth (now included in *Bassia* All.), *Salsola* s. l., *Suaeda* Forssk. ex J.F. Gmel., etc.);

2) covered — *Corispermum* L.;

3) enveloped by bracts — *Atriplex*, *Ceratocarpus* L., *Krascheninnikovia* Gueldenst.;

4) semi-inferior, enveloped with a perigonium — *Halocnemum* M. Bieb., *Salicornia* L.

Heteromorphy of fruits and seeds is widespread in the family; it was reported in *Atriplex*, *Chenopodium*, *Suaeda*, *Salsola*, *Salicornia*, and other genera (Levina, 1957; Pijl, 1982; Kühn, 1993).

***Droseraceae* Salisb.** (2/5) — Fruit is a paracarpous superior 3–5-merous, covered, dorsally dehiscent capsule (Kaden, 1965). Fruit is a loculicidal capsule (Spjut, 1994; Kubitzki, 2003a). Placentation is parietal, ovules are numerous. *Aldrovanda vesiculosa* L. has 5-merous ovary, with 1–4-ovulate placentas (Eichler, 1878); seeds are released underwater after fruit rotting (Kubitzki, 2003a).

***Frankeniaceae* Desv.** (*Frankenia hirsuta* L., *F. pulverulenta* L.) — a paracarpous superior 3-merous enveloped capsule, dorsally dehiscent (Kaden 1965). The fruit is a loculicidal capsule (Spjut, 1994; Kubitzki, 2003b). Placentation is parietal, ovules are numerous (Eichler, 1878).

***Molluginaceae* Bartl.** (*Glinus lotoides* L., *Mollugo cerviana* (L.) Ser.) — superior trimerous syncarpous enveloped capsule, dorsiventrally dehiscent (Kaden, 1965). The fruit is a loculicidal capsule, placentation axile (Endress, Bittrich, 1993). Spjut (1994) suggested that the fruit in *Molluginaceae* is a septifragal capsule — capsular fruit, opened incompletely along the dorsal sutures and breaking the septas near the persistent central columella. In *Mollugo cerviana* the ovary is 3-locular with 3 sessile stigmas, ovules numerous, arranged in two rows in each locule; the fruit is a loculicidal 3-valved capsule with persistent stamens and stigmas, enveloped by tepals (Maddala, Aluri, 2019). In *Glinus lotoides*, the ovary is 5-locular with 5 sessile stigmas, containing about 200 (182–242) ovules, arranged in two rows in each locule; fruit is a loculicidal 5-valved capsule with persistent stamens and stigmas, enveloped by tepals. In both species, the capsule opens when moistures; seed dispersal is anemochorous, ombrohydrochorous, and hydrochorous (Endress, Bittrich, 1993; Sulakshana, Raju, 2018; Maddala, Aluri, 2019).

***Montiaceae* Raf.** (*Montia fontana* L.) — a lysicarpous, trimerous, superior, covered, disjunctively dehiscent capsule (Kaden, 1965). Placentation is free-central or basal; the capsule dehisces with three involute reflexed valves, thus forcibly ejecting the seeds (Carolin, 1993). The ovary is trilocular, with a solitary ovule in each locule, attached to the central axis; the fruit is a trivalvate capsule (Eichler, 1878).

******Nyctaginaceae* Juss.** (1/3; ******Mirabilis* L. s. l., incl. *Oxybaphus*, 3 spp., *Mirabilis nyctaginea* (= *Oxybaphus nyctagyneus*) is locally naturalized) — The fruit is an achene or thin-walled nutlet enveloped by persistent perianthium base (anthocarp) (Bittrich, Kühn, 1993). An anthocarp is treated as a lower portion of a corolla-like calyx (Vanvinckenroye et al., 1993). The fruit is a typical diclesium,

like in *Basellaceae*, according to Spjut (1994). The gynoecium is monomerous, ovule one, basal, fruit is achen-like, covered with the lower portion of corolla forming "induvium" (anthocarpium) (Eichler, 1878). The researchers who studied flower development suggested that an ovule in *Nyctaginaceae* is of cauline origin (Sattler, Perlin, 1982) or, from another viewpoint, of carpellate origin (Vanvinckenroye et al., 1993).

****Phytolaccaceae* R. Br.** (*Phytolacca acinosa* Roxb., *P. americana* L.). The fruit is a berry, aggregate or syncarpous, depending on the degree of connation between carpels. Carpels are more or less united, styles free, ovary superior, ovule one per carpel, fruits indehiscent (Rohwer, 1993). Apocarpy is considered to be a secondary condition in *Phytolacca*, a kind of secondary "apocarpy" or "pseudoapocarpy" (Rohweder, 1965; Eckardt, 1976). Spjut (1994) identified the fruit in *Phytolacca* as a baccarium — a berry derived from the schizocarpic gynoecium consisting of fleshy-indehiscent fruitlets. In *P. acinosa*, carpels are almost free, 7–8 in number, with persistent stylodia (Fig. 3A, B), while in *P. americana* there are 10 carpels; in both species carpels are fused laterally during the early flower development (Ronse De Craene et al., 1997). There is no difference between apocarpous and syncarpous gynoecium at the initiation stage in this genus, but later during the flower development, septas develop differently in different species, forming more or less united carpels; so there is no true apocarpy in the genus (Zheng et al., 2015). According to Endress (2011, 2019), the gynoecium of *Phytolacca* with bulged ovaries is often misinterpreted as apocarpous, but really is a syncarpous gynoecium with common transmitting tract to ovules. The ovule in *Phytolacca* develops separately from carpellary tissue on the floral apex, thus the placentation as axile; the synascidiate zone is small compared to the symplicate and asymplicate zones (Ronse De Craene, 2021). The increasing size of the floral apex may be responsible for the spatial separation and loosening of the connections between carpels, which appear almost free.

***Plumbaginaceae* Juss.** (5/26; including *Armeriaceae* Horan. and *Limoniaceae* Ser.) — The fruit is a dry membranous one-seeded achene, enclosed in persistent calyx, dispersed by wind (Kubitzki, 1993). Sometimes the fruit is a capsule with circumscisisle or valvate dehiscence (Kubitzki, 1993). The fruit is lysicarpous, superior, pentamerous, pseudomonomerous (Kaden, 1965). According to Spjut (1994), the fruit is a diclesium. The ovary is unilocular, uni-ovular, with five antesepalous stylodia; the ovule is basal, on a long funiculus curved around the ovule (Eichler, 1875); it has been called circinotropous ovule (De Laet et al., 1995). The gynoecium is always pentamerous, ovule solitary, basal (Kubitzki, 1993). The ovule is born on the floral apex (with no touching to the carpel blades) (De Laet et al., 1995), thus, the gynoecium was treated as acarpellate sensu Sattler and Perlin (1982) and Sattler and Lacroix (1988). The prominent obturator is formed on the base of the style downwards into the ovary by meristematic activity of the inner epidermis (Roth, 1977; De Laet et al., 1995).

A. The fruit is an indehiscent achene in **Ceratostigma plumbaginoides* Bunge and most species of *Limonium* Mill.

B. The fruit is a capsule which dehisces by an apical lid in *Goniolimon* Boiss. or by basal circumscissile slit in *Armeria* (DC.) Willd. (Pax, 1889). In *Psylliostachys spicatus* (Willd.) Nevski capsule is irregularly dehiscent (Kubitzki, 1993).

***Polygonaceae* Juss.** (11/101). The fruit is a lysicarpous superior nutlet, enclosed by fruiting perigonium (Kaden, 1965). The fruit is an achene, trigonal in shape, achene is winged in *Fagopyrum* Mill., *Oxyria* Hill, *Rheum* L.; the perigonium is persistent and enlarged serving for dispersal in *Fallopia* Adans. and members of the tribe *Polygoneae* Eaton (Brandbyge, 1993). According to Spjut (1994), the fruit is a diclesium**.** The ovary is unilocular, uni-ovular, with 2–3 carpels, ovule is basal. The fruit is an achene, wings are formed by the fruiting ovary (Eichler, 1878).

Below, fruits of *Polygonaceae* are classified according to Kaden (1965).

A. Fruit trimerous, covered with a perigonium — *Fagopyrum.*

B. Fruit trimerous, enveloped — *Atraphaxis frutescens* (L.) K. Koch, *Bistorta officinalis* Delarbre, *Bistorta vivipara* (L.) Delarbre, *Fallopia convolvulus* (L.) Á. Löve, *Fallopia dumetorum* (L.) Holub, *Koenigia alpina* (All.) T.M. Schust. & Reveal, *Polygonum arenarium* Waldst. & Kit., *P. aviculare* L., *P. neglectum* Besser (=*Polygonum aviculare* L. subsp. *neglectum* (Besser) Arcang.), *P. patulum* M. Bieb., *P. salsugineum* M. Bieb., *Rumex* L., *Rheum.*

C. Fruit dimerous, enveloped — rest of species: *Atraphaxis replicata* Lam., *Oxyria digyna* (L.) Hill, *Persicaria* Mill. (*P. orientalis* (L.) Spach, *P.*

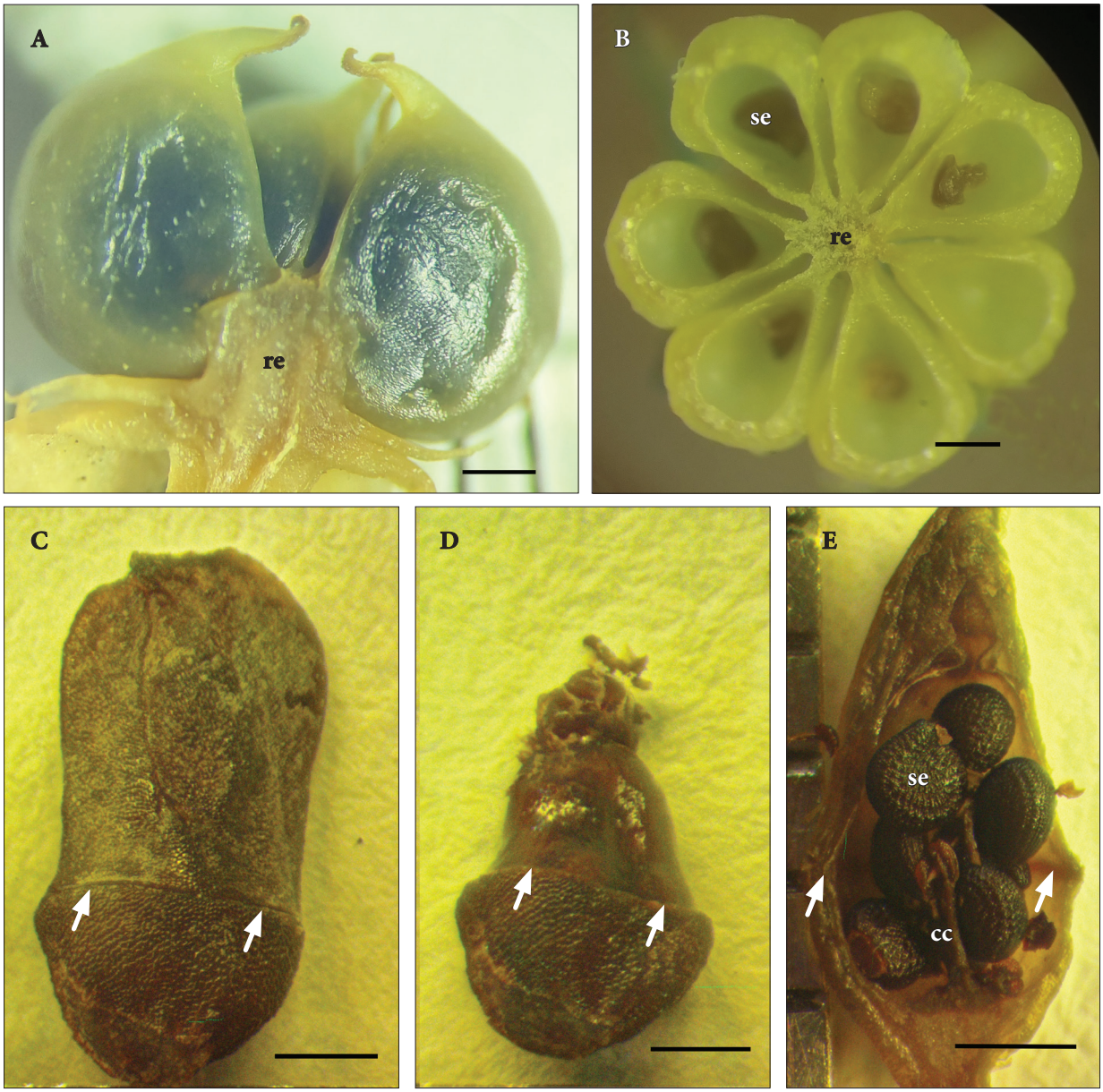

Fig. 3. Dissected fruits of *Phytolacca acinosa* (*Phytolaccaceae*) (A, B) and cleistogamous fruit of *Portulaca oleracea* (*Portulacaceae*) (C–E). A: fruit in longitudinal section; B: fruit in transversal section; C: fruit covered with sepals; D: fruiting ovary with deleted sepals; E: longitudinal section of the fruiting ovary; the circumscissile slit (and sepal bases) is marked with white arrows; cc — central column; re — receptacle; se — seed. Scale bars 1 mm

lapathifolia (L.) Delarbre, *P. amphibia* (L.) Delarbre, *P. diospirifolia* (Cham. & Schltdl.) Funez & Hassemer, etc.).

***Portulacaceae* Juss.** (*Portulaca oleracea* L., **P. grandiflora* Hook.) — capsule lysicarpous trimerous semi-inferior, unilocular, many-seeded, enveloped by calyx, circumscissile dehiscent (Kaden, 1965). Placentation is free-central or basal (Carolin, 1993). Fruit is a pyxidium (Roth, 1977; Spjut, 1994). Eichler (1878) reported 4- or 5-carpellate ovaries in *P. oleracea* and the polymerous (with 8 carpels) ovary in *P. grandiflora*. Roth (1977) described the anatomy of the dehiscence line in *P. oleracea*. She revealed that basal portion of capsule

(sunken into hypanthium) is rigid and lignified while the lid is relatively thin. The dehiscence zone occurs along the line of mechanical weakness composed of thin-walled parenchyma. The lid separates from the capsule base due to the pressure caused by growing seeds (Roth, 1977). According to our personal observations, flowers of *P. oleracea* found in Lviv City are often cleistogamous, dehiscing with a lid being covered by a closed perianthium (Fig. 3C–E). The sepals are attached to the ovary at the level of dehiscing.

***Tamaricaceae* Link** (2/8, including a new species in the flora of Ukraine *Tamarix laxa* Willd.: see Bronskov, Bronskova, 2024). The fruit is a paracarpous superior 3–4-locular covered capsule, dorsally dehiscent (Kaden, 1965). The fruit is a loculicidal capsule (Eichler, 1878; Spjut, 1994; Gaskin, 2003). Carpels (2)3–4(5), ovary unilocular, sometimes almost plurilocular; placentation parietal, basal or parietal-basal; calyx persistent in fruit (Gaskin, 2003). In *Myricaria* Desv., there are three carpels, in *Tamarix* L., the ovary can also be 4-, 2- or 5-carpellate, ovules are numerous, arranged basally on parietal placentas; in *Tamarix*, placentas are fused together at the bottom of the ovary (Eichler, 1878).

Order *SANTALALES*

***Loranthaceae* Juss.** (*Loranthus europaeus* Jacq.). The fruit is an inferior one-seeded berry, crowned with a calyx which is reduced to the calyculus (Kuijt, Hansen, 2015a, 2015b). The ovary is inferior, tricarpellare, solid, with 1–6 embryo sacs inside (Eichler, 1878). Carpels 3–4; ovary is unilocular, with 4–12 ovules embedded in the basal tissue of the ovary (Takhtajan, 2009). The placenta is missing, archesporial cells develop in the subepidermal layer of the ovary bottom (Eames, 1961). The viscid layer is located outside the vascular bundles of the fruit wall (Teryokhin, 1977).

***Santalaceae* R. Br.** (3/11) — fruits inferior, one-seeded (Kuijt, Hansen, 2015a, 2015c). Ovary inferior, bicarpellate, solid, with one central orthotrop ovule inside (Eichler, 1878). Gynoecium is supposed to be lysicarpous, with free-central or reduced placentas (Teryokhin, 1977).

A. Inferior paracarpous (pseudomonomerous) dry drupe — *Thesium* L. (Kaden, 1965). The fruit is a small nutlet with conspicuous surface venation, petals persistent, calyculus absent, the ovule is attached to the tip of the convoluted funiculus (Kuijt, Hansen, 2015c). In many *Thesium* species, the elaiosome is formed from the pedicel and the base of the ovary adapting fruit for myrmecochory; fruit is a nutlike achene or fleshy drupe (García et al., 2024). The gynoecium is composed of (2)3(5) carpels, the ovary is superior to inferior, completely uni-locular or with basal septa, with straight or spirally coiled free-central placenta bearing 1–4, less often 4–5 pendulous ovules. Ovules are well-developed (Eames, 1961).

B. Inferior paracarpous (pseudomonomerous) fleshy fruit, bacca (inferior berry) — *Arceutobium oxycedri* (DC) M. Bieb. and *Viscum* L. (Kaden, 1965; Spjut, 1994). Carpels 3–4, fruit is 1–2 seeded berry (Takhtajan, 2009). Since fleshy fruit of *Viscaceae* does not consist only of carpel tissue (ovary is inferior), it is not a true bacca, but rather a pomaceous fruit (pyrenarium with several stones), or, alternatively, it was proposed to denominate such fruit a "viscidio" in allusion to the presence of the viscin layer, which is exclusive for this group of plants (Polli et al., 2016). The fruit contains a seed lacking testa, surrounded by endosperm and viscid layer, which is located inside the vascular bundles of the fruit wall (Fig. 4A) (Teryokhin, 1977).

In *Arceutobium* M. Bieb., the placenta is reduced to a central massive bulge, with two or more ategmic ovules inside (nucellus undifferentiated) (Eames, 1961). In the *Arceuthobium* fruit, perianth members are two; the remarkable explosive dehiscence of fruits occurs, in which the minute, bullet-shaped seed may be shot away for 20 m or more. In nature, the *Arceuthobium* fruit recurves when mature and the seed is expelled upwards through its base (Kuijt, Hansen, 2015d). In *Arceuthobium oxycedri*, the proximal part of the fruit is light-green, and the distal part is dark-green; the dispersed seeds are ballistic and ornitochorous (Krasylenko et al., 2017).

In *Viscum album* L., the placenta is missing, archesporial cells develop in the subepidermal layer of the ovary bottom (Eames, 1961). The fruit a 1(2)-seeded berry, predominantly white, with green endosperm; the seed is surrounded by a massive layer of viscin (Kuijt, Hansen, 2015d). According to our own observations, the fruit in *V. album* is spherical, inferior, and white, with green endosperm and embryo inside (Fig. 4B–D). In the fruit treated with phloroglucinol and chloride acid, a positive reaction for lignin in the inner zone of the fruit wall was revealed (Fig. 4D). This test indicates that the fruit

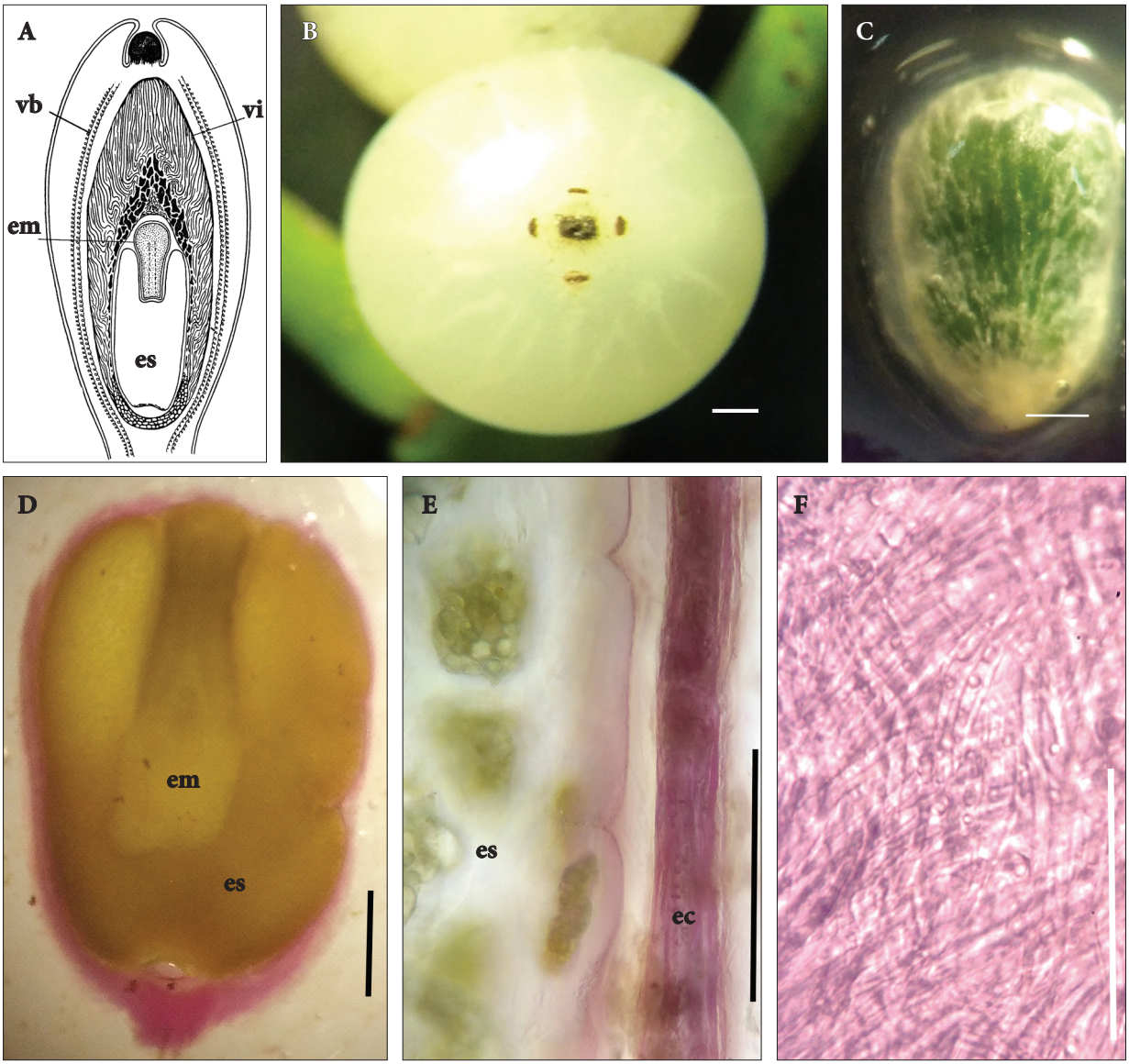

Fig. 4. Fruit structure in *Santalaceae* (A–F). A: fruit inner structure in *Arceuthobium oxycedri* (from Teryokhin, 1977: 151); B–F: fruit in *Viscum album*; B: berry-like one-seeded inferior fruit with scars of four perianth members, viewed from above; C: fruit central part released from viscid layer, green endosperm is visible, covered with whitish "endocarp"; D: longitudinally sectioned fruit treated with phloroglucinol and chloride acid, positive reaction for lignin in thin "endocarp" zone is evident; E: lignified cells on the sectioned endocarp and endosperm; F: lignified endocarp; ec — endocarp; em — embryo, es — endosperm, vb — vascular bundle, vi — viscid layer. Scale bar 1 mm (B–D); 100 mkm (E), 50 mkm (F)

has a thin lignified "endocarp" composed of a few layers of elongated cells arranged in different dimentions (Fig. 4E, F). The external cell walls of endosperm are also lignified (Fig. 4E). Therefore, we suggested that the fruit in *V. album* is a one-seeded berry-like pyrenarium (one-seeded basic fruit type), not a true berry.

Discussion

Morphogenetic characteristics of fruits

According to the concept of morphogenesis of the fruit (Odintsova, 2022), we distinguish pre-anthetic and post-anthetic stages in the morphogenesis of the fruit. From this viewpoint, characteristics of

the gynoecium of an anthetic flower are regarded as characteristics of the fruit at the pre-anthetic stage. The gynoecium in members of *Caryophyllidae* in the flora of Ukraine can be 2-, 3-, 4-, 5-merous, or polymerous. The most common condition is a trimerous syncarpous gynoecium, found in 11 families. The pentamerous condition of the gynoecium (isomerous to the perianthium) is found in *Aizoaceae*, *Caryophyllaceae*, *Droseraceae*, *Plumbaginaceae*, and *Tamaricaceae*, while the polymerous gynoecium (with 8–10 carpels) appears only in taxa of *Phytolaccaceae*. The true monomerous gynoecium is found in *Nyctaginaceae*; it develops into a monocarpous fruit *sensu* Leins and Erbar (2010). Pseudomonomerous one-seeded fruits developing from the oligomerous gynoecium are typical for *Amaranthaceae* s. str., *Chenopodiaceae*, *Polygonaceae*, *Plumbaginaceae*, *Basellaceae*, and some *Caryophyllaceae*. Most taxa of *Loranthaceae* and *Santalaceae* also have the uni-ovulate gynoecium; however, their structure is not typical because of the absence of discrete ovules. The number of ovules varies from many (*Cactaceae*, *Caryophyllaceae*) to one per carpel (*Montia*, *Phytolacca*) or one per ovary (*Amaranthaceae*, *Basellaceae, Chenopodiaceae*, *Plumbaginaceae*, *Polygonaceae*).

Within *Caryophyllaceae*, members of the earliest-diverging clade reconstructed from molecular phylogeny (Greenberg, Donoghue, 2011) are inferred to have had one-seeded, indehiscent or irregularly dehiscent fruit (utricle), like those found in *Amaranthaceae*. The evolution of capsular fruits is inferred to have taken place along the branch subtending a clade that includes *Sperguleae* (mostly containing former members of *Paronychioideae*) and the remainder of *Caryophyllaceae*. This part of the family having capsular fruits and some other morphological synapomorphies was referred to as *Plurcaryophyllaceae* A.K. Greenberg and M.J. Donoghue (2011).

Apocarpous aggregate gynoecia and fruits have not been found in the representatives of subclass *Caryophyllidae* in the flora of Ukraine. However, in *Phytolacca acinosa* the gynoecium is considered to be secondary apocarpous (a syncarpous gynoecium with reversal to the mininized carpel fusion). The reduced connection between carpels may also have facilitated the transition to a single carpel in close relatives, as it has evolved in *Petiveriaceae* C. Agardh and *Nyctaginaceae* (Ronse De Craene, 2021).

The inferior ovary occurs in the taxa of *Aizoaceae* and *Cactaceae* cultivated and escaped in Ukraine, as also in parasitic *Loranthaceae* and *Santalaceae*. In *Beta* (*Chenopodiaceae*) the ovary is almost inferior, too (Eichler, 1878); it is weaky inferior in *Paronychia* (*Caryophyllaceae*) or semi-inferior in *Portulaca* (*Portulacaceae*). These families are not closely related, and for that reason we suppose the inferior ovary in these families could have evolved independently.

The syncarpous multi-locular gynoecium with an axile placenta is characteristic for *Aizoaceae*, *Molluginaceae*, and *Phytolaccaceae*. The gynoecium is paracarpous and unilocular with parietal placentation (or derived placentation) in *Cactaceae*, *Droseraceae*, *Frankeniaceae*, and *Tamaricaceae*. The lysicarpous multi-ovulate gynoecium with free-central or basal placentation is found in *Caryophyllaceae*, *Montiaceae*, and *Portulacaceae*. The unilocular pseudomonomerous gynoecia of *Caryophyllales* are often regarded as lysicarpous, with a basal placenta and reduced ovule number. Basal placentation is regarded to be a derived state from axile placentation in the gynoecia with reduced ovule number.

One of the synapomorphic characters of *Caryophyllales* is the absence of septas in the pluricarpellate gynoecium (Bittrich, 1993a; Takhtajan, 2009). Septas can be partly reduced in the upper portion of the ovary or totally reduced from the ovary base to the top. The placentation is transformed from the axile (if septas are present) to free-central or (sub) basal (if septas are missing and the ovule number is low or reduced to one). This condition appears, for example, in *Cucubalus baccifer* and other *Caryophyllaceae*. The free-central placentation almost exclusively occurred in the superasterid clade, while in basal clades of angiosperms, and in rosid and monocots, it is rare (Shivaprakash, Bawa, 2022).

Fruits in *Santalaceae* and *Lorantaceae* are one-seeded and the fruit wall is presumably fleshy, so most researchers consider them berry-like. If the lignified cell layers are considered to be the endocarp, the fruit should be named a pyrenarium. The lignified thin endocarp was found in *Viscum* fruits previously, for the first time, probably by Gjokic (1896), later also by Von Grazi and Urech (1981), Godschalk (1983), and de Almeida et al. (2023); the authors of the two latter publications insisted that the seed coat is absent. Consequently, it is most evident the origin of lignified tissue from the fruit wall (endocarp) but not from the rudiments of the seed coat.

There is a great diversity of dehiscence of capsular fruits in *Caryophyllales*. It can be dorsal

Table 1. **Distribution of the basic fruit types in the families of *Caryophyllidae* in the flora of Ukraine**

Basic fruit type	Families representing this fruit type
Capsule	*Aizoaceae*, *Amaranthaceae* (most species), *Caryophyllaceae* (most species), *Droseraceae*, *Frankeniaceae*, *Molluginaceae*, *Montiaceae*, *Plumbaginaceae* (*Armeria, Goniolimon, Psylliostachys*), *Portulacaceae*, *Tamaricaceae*
Berry-like fruit	*Cactaceae*, *Caryophyllaceae* (*Cucubalus baccifer*), *Phytolaccaceae*
One-seeded fruit	*Amaranthaceae* (*Amaranthus*), *Basellaceae*, *Caryophyllaceae* (*Herniaria*, *Paronychia*, *Queria*, *Scleranthus*), *Chenopodiaceae*, *Nyctaginaceae*, *Plumbaginaceae (Ceratostigma, Limonium), Polygonaceae*; *Loranthaceae*, *Santalaceae*

(loculicidal), dorsi-ventral, dorsi-lateral, disjunctive (*i.e.* septicidal in the unilocular gynoecium without septas), disjunctive-dorsal, transversal (circumscissile), or irregular (rupturing). The longitudinal slits can be short (denticidal capsule in many *Caryophyllaceae*) or as long as the fruiting ovary. The capsular inferior and semi-inferior fruits are found in *Aizoaceae* and *Portulacaceae*, with dehisce above the bases of sepals. In *Aizoaceae*, the longitudinal dehiscence occurs, while in *Portulacaceae* the transversal slit is formed at the level of sepal bases. The same condition appears in *Beta vulgaris* with one seed inside. According to our classification of variants of the location of dehiscence slits in the inferior fruits (Odintsova, 2016), we can call this variant a suprasepalous dehiscence. The opposite condition was found in *Onagraceae*, where dorsal slits are formed along the fruiting ovary beneath sepal bases (*i.e.* infrasepalous) (Odintsova, 2016). Suprasepalous dehiscence occurs in the carpellary tissues, without engagement of the complex tissue of the inferior ovary wall; and it is regarded to be an ancestral condition compared to the infrasepalous one.

Functional characteristics of fruits

Among *Caryophyllidae* of the flora of Ukraine, several functional fruit types have been found. Berries and one-seeded fruits are indehiscent diaspores, developing adaptations for dispersal as a whole unite, while capsular fruits release naked seeds which demonstrated dispersal adaptations as separate units.

Most capsular fruits of *Caryophyllales* have a xerochastic trigger for opening the fruit during desiccation. *Aizoaceae* and *Molluginaceae* are known to have a hygrochastic dehiscence, and their capsules open suddenly, which is very characteristic of plants in arid conditions (Roth, 1977). Many *Caryophyllaceae* have fruits that open incompletely, which is characteristic of ballistochores, keeping the seed container almost intact (Pijl, 1982).

According to Fedoronchuk and Didukh (2002), most *Caryophyllaceae* have small seeds dispersed by wind; the second most common dispersal mode is barochory, while endozoochory, mirmecochory, epizoochory, and other modes are rare. In that study, ballistochory was obviously regarded in the category of anemochory, as well as tumbleweeds (*Gypsophila*, some *Silene* species). Ballistochorous plants can disperse by seeds or by one-seeded fruits (*Polygonum*). The first variant is known as the *Caryophyllaceae*-type of dispersal of ballistochores and the second variant as the *Apiaceae*-type (Levina, 1957).

One-seeded fruits of *Caryophyllales* are mostly autochorous and anemochorous, and small. Anemochores have fruits winged with attached wings derived from bracts (*Atriplex*, *Ceratostigma*), perianth (*Anredera*), or pericarp (*Polygonaceae*). There are no anemochorous one-seeded fruits with hairy diaspores. Anthocarps of *Nyctaginaceae* can be dispersed by various agents: animals, wind, or water (Bittrich, Kühn, 1993).

Berry-like fruits of *Caryophyllales* and *Santalales* are dispersed by birds (Pijl, 1982). The fruits are usually red, black, purple, green, yellow, or white. Among representatives of *Santalales*, it is related with parasitism on tree branches (Krasylenko et al., 2019). There are no parasites with small seeds among woody plants of *Santalales*, while fruits in herbaceous *Thesium* species are dispersed mostly by ants (García et al., 2024), and in *Arceuthobium oxycedri* they are dispersed ballistically.

Distribution of basic fruit types among *Caryophyllidae*

Only limited morphological diversity of fruit types in the representatives of *Caryophyllidae* was found in Ukraine (Table 1), compared with monocots and rosids, where five and seven basic fruit types were revealed (Odintsova et al., 2021; Odintsova, 2023a).

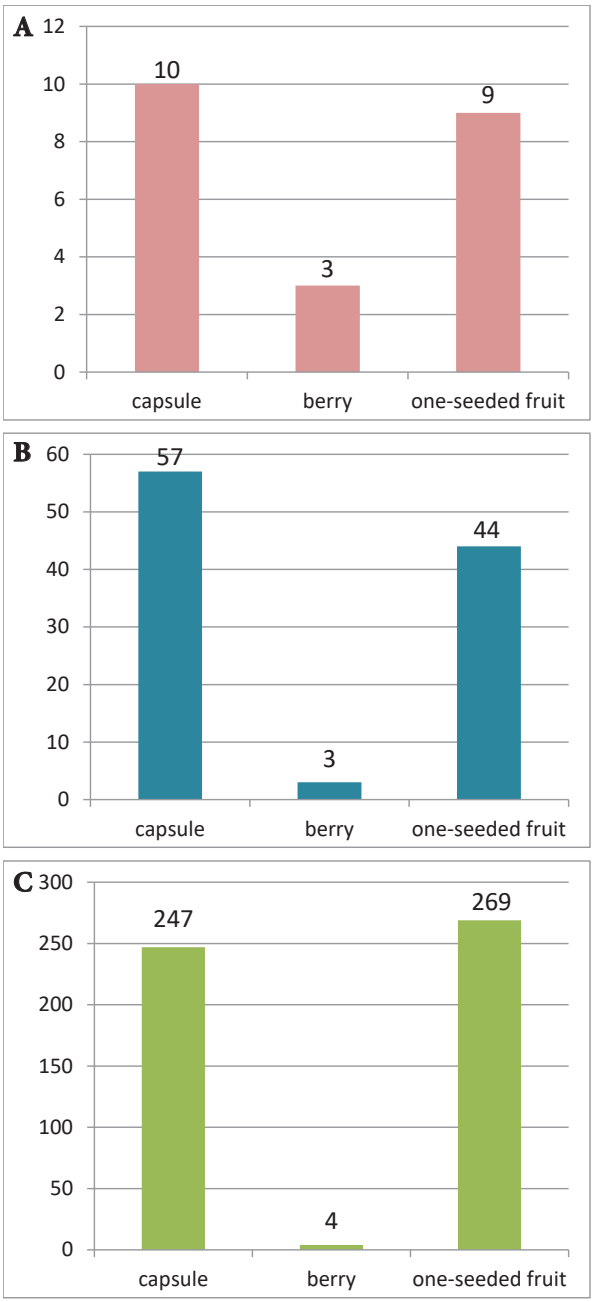

Fig. 5. Number of taxa of the subclass *Caryophyllidae* of the flora of Ukraine having basic fruit types, a capsule, berry, and one-seeded fruit. A: families; B: genera; C: species

Within *Caryophyllidae*, there was no gynoecium with postgenital carpel fusion found, and the merosity of the gynoecium is various; the condition is quite different from the monocot's gynoecium with a widespread intermediate degree of carpel fusion and trimerous condition (Odintsova et al., 2022). Comparing to *Rosidae* (Odintsova, 2023a), there were no multi-follicles, multi-seeded monocarps, multi-seeded pyrenaria, schizocarps, and articulate fruits found.

The three largest (in terms of species numbers) families of *Caryophyllidae* in the flora of Ukraine, *Caryophyllaceae*, *Chenopodiaceae,* and *Polygonaceae*, together compose 77 genera and ca. 434 species that is 75% and 83% of genera and species richness, correspondingly. Among them, *Caryophyllaceae* have mostly capsular fruits, while *Chenopodiaceae* and *Polygonaceae* have one-seeded dry fruits. Several basic types of fruits were found in *Amaranthaceae, Plumbaginaceae* (capsular and one-seeded indehiscent fruit), and *Caryophyllaceae* (capsule, berry, and one-seeded indehiscent fruits).

Several fruits within *Caryophyllidae* could be equivocally classified. In the first case, the fruits in *Amaranthaceae, Chenopodiaceae* (*Beta*) and *Plumbaginaceae* are one-seeded and sometimes dehisce regularly or irregularly (utricle), or are indehiscent. Thus, transitional stages from capsular to dry indehiscent one-seeded fruits (achene or nut) appear, which can be found even in a single genus. The second case is the syncarpous fruit in *Phytolacca acinosa* with a reversion to minimal carpel fusion. This fruit can be alternatively treated as an aggregate berry-like fruit; however, the derived character of apocarpy is confirmed. In the third case, fruits in *Santalaceae* and *Lorantaceae* are usually classified as berries or, according to our viewpoint, as a one-seeded pyrenarium because of the presence of the reduced stone in *Viscum album*.

The capsular fruits occur in the representatives of ten families, and the one-seeded fruits in nine families of *Caryophyllidae* (Fig. 5A). At the level of generic diversity, capsular fruits are the most numerous (57 genera *versus* 44 genera with one-seeded fruits) (Fig. 5B). In contrast, at the species level, one-seeded fruits are most numerous, but the number of species with capsular fruits is also very high (Fig. 5C). The carpological spectrum of the *Caryophyllidae* in the flora of Ukraine is pointed out by the predominance of two basic types of fruits — capsular and one-seeded, with some taxa equivocally classified as having one or another type of fruit.

Berry-like fruits of the *Caryophyllidae* in the flora of Ukraine are uncommon; they were found only in four species of three families. According to the resent comprehensive research (Lorts et al., 2008), plants of

tropical forests mostly have fleshy fruits dispersed by animals, while plants inhabiting plains and prairies (open arid habitats) often have capsules and achens dispersed by wind. This is actualized by the prevalence of dry fruits in *Caryophyllidae*. The prevalence of capsular and one-seeded fruits within *Caryophyllales* and *Santalales* has support from the nuclear phylogeny as a realization of the most frequent ovary-fruit "modules" — syncarpous multi-ovuled and syncarpous one-ovuled ones (Xiang et al., 2024). In xerophytic *Caryophyllidae*, both modules are implemented in dry fruit variants, capsule and achene.

Summarizing the data on fruit morphological diversity patterns in *Caryophyllidae* (present study), *Rosidae* (Odintsova, 2023a), and monocots (Odintsova et al., 2021; Odintsova, 2023b), we revealed quite different carpological spectra for all these groups. In monocots, one-seeded fruits are most numerous at the species level, too (Odintsova, 2023b), while in *Rosidae*, the capsular fruits are the most numerous (Odintsova, 2023a). In *Rosidae*, the prevalence of capsular fruits is twice more over one-seeded fruits, and in monocots one-seeded fruits prevail two times over the capsular fruits.

Conclusions

Poor morphological diversity of basic fruit types within the subclass *Caryophyllidae* is related with the low species richness of this subclass in the Ukrainian flora (about 520 species). The most species-rich family *Caryophyllaceae* has capsular fruits developed mostly from the superior lysicarpous ovary. Two other large families, *Chenopodiaceae* and *Polygonaceae*, have one-seeded fruits developed from one-ovuled ovaries composed of 2–3 united carpels. The phylogenetic, ecological and evolutionary analysis supplied arguments for the bifid carpological spectrum of the *Caryophyllidae*. These arguments came from the evolutionary history of the group, which most probably emerged under arid conditions. Within this group, two main ovary-fruit "modules" were evolutionarily implemented: with multi-ovuled and one-ovuled ovaries. In both variants, dry one-seeded diaspores are often developed that are well adapted to the wind dispersal. The method of carpological spectra may be conceived as a tool for the ecological treatment of the flora.

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ETHICS DECLARATION

The author declares no conflict of interest.

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REFERENCES

Almeida de V.P., Monchak I.T., da Costa Batista J.V., Grazi M., Ramm H., Raman V., Baumgartner S., Holandino C., Manfron J. 2023. Investigations on the morpho-anatomy and histochemistry of the European mistletoe: *Viscum album* L. subsp. *album*. *Scientific Reports*, 13: 4604. https://doi.org/10.1038/s41598-023-29799-z

APG IV. 2016. 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): 1–20. https://doi.org/10.1111/boj.12385

Barthlott W., Hunt D.R. 1993. *Cactaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid*, *Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin, Heidelberg: Springer, pp. 161–196.

Bittrich V. 1993a. Introduction to Centrospermae. In: *The families and genera of vascular plants*. Vol. 2. *Flowering plants. Dicotyledons. Magnoliid*, *Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin, Heidelberg: Springer, pp. 13–19.

Bittrich V. 1993b. *Caryophyllaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid*, *Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin, Heidelberg: Springer, pp. 206–236.

Bittrich V., Kühn U. 1993. *Nyctaginaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid*, *Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin, Heidelberg: Springer, pp. 473–485.

Brandbyge J. 1993. *Polygonaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 531–543.

Bronskov O.I., Bronskova O.M. 2024. *Tamarix laxa* (*Tamaricaceae*), a new species in the flora of Ukraine. *Ukrainian Botanical Journal*, 81(3): 229–241. [Бронсков О.І., Бронскова О.М. 2024. *Tamarix laxa* (*Tamaricaceae*) — новий вид флори України. *Український ботанічний журнал*, 81(3): 229–241.] https://doi.org/10.15407/ukrbotj81.03.229

Carolin R.C. 1993. *Portulacaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 544–555.

Costea M., Waines G., Sanders A. 2001. Structure of the pericarp in some *Amaranthus* L. (*Amaranthaceae*) species and its taxonomic significance. *Aliso*, 20(2): 51–60. https://doi.org/10.5642/aliso.20012002.02

Cronquist A. 1981. *An integrated system of classification of flowering plants*. New York: Columbia University Press, 1262 pp.

Cuénoud Ph. 2003. Introduction to expanded *Caryophyllales*. In: *The families and genera of vascular plants.* Vol. 5. *Flowering plants. Dicotyledons: Malvales, Capparales and non-betalain Caryophyllales*. Eds K. Kubitzki, C. Bayer. Berlin; Heidelberg: Springer, pp. 1–4.

De Laet J., Clinckemaillie D., Jansen S., Smets E. 1995. Floral ontogeny in the *Plumbaginaceae. Journal of Plant Research*, 108(3): 289–304. https://doi.org/10.1007/BF02344355

Eames A.J. 1961. *Morphology of the angiosperms.* New York, Toronto: McGraw-Hill, 498 pp. https://doi.org/10.5962/bhl.title.5986

Eckardt Th. 1976. Classical morphological features of Centrospermous families. *Plant Systematics and Evolution*, 126(1): 5–25.

Eichler A.W. 1875. *Bluethendiagramme*. Bd 1. Leipzig: Engelmann, 348 pp. https://doi.org/10.5962/bhl.title.12323

Eichler A.W. 1878. *Bluethendiagramme*. Bd 2. Leipzig: Engelmann, 575 pp. https://doi.org/10.5962/bhl.title.12323

Endress M.E., Bittrich V. 1993. *Molluginaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 419–425.

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

Endress P.K. 2019. The morphological relationship between carpels and ovules in angiosperms: pitfalls of morphological interpretation. *Botanical Journal of the Linnean Society*, 189(3): 201–227. https://doi.org/10.1093/botlinnean/boy083

Fedoronchuk M.M. 2023. Ukrainian flora checklist. 5: family *Caryophyllaceae* (incl. *Illecebraceae*) (*Caryophyllales*, Angiosperms). *Chornomorski Botanical Journal*, 19(1): 5–57. [Федорончук М.М. 2023. Чекліст флори України. 5: родина *Caryophyllaceae* s. l. (incl. *Illecebraceae*) (*Caryophyllales*, Angiosperms). *Чорноморський ботанічний журнал*, 19(1): 5–57.] https://doi.org/10.32999/ksu1990-553X/2023-19-1-1

Fedoronchuk M.M., Didukh Ya.P. 2002. *Ecoflora of Ukraine*. Vol. 3. Ed. Ya.P. Didukh. Kyiv: Phytosociocentre, 496 pp. [Федорончук М.М., Дідух Я.П. 2002. *Екофлора України*. Т. 3. Відпов. ред. Я.П. Дідух. Київ: Фітосоціоцентр, 496 с.]

García M.A., Mucina L., Nickrent D. 2024. A tough nutlet to crack: Resolving the phylogeny of *Thesium* (*Thesiaceae*), the largest genus in *Santalales*. *Taxon*, 73: 190–236. https://doi.org/10.1002/tax.13123

Gaskin J.F. 2003. *Tamaricaceae*. In: *The families and genera of vascular plants.* Vol. 5. *Flowering plants. Dicotyledons: Malvales, Capparales and non-betalain Caryophyllales*. Eds K. Kubitzki, C. Bayer. Berlin; Heidelberg: Springer, pp. 363–368.

Gjokić G. 1896. Zur Anatomie der Früchte und des Samens von *Viscum*. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*. K1., Abt. 1. 105: 447–464. Available at: https://parasiticplants.siu.edu/Viscaceae/Gjokic1896German.pdf

Godschalk S.K.B. 1983. The morphology of some South African mistletoe fruits. *South African Journal of Botany*, 2(1): 52–56. https://doi.org/10.1016/S0022-4618(16)30145-0

Grazi Von G., Urech K. 1981. Einige morphologische Merkmale der Mistelheere (*Viscum album* L.) und deren taxonomische Bedeutung. *Beiträge zur Biologie der Pflanzen*, 56: 293–306.

Greenberg A.K., Donoghue M.J. 2011. Molecular systematics and character evolution in *Caryophyllaceae*. *Taxon*, 60(6): 1637–1652. https://doi.org/10.1002/tax.606009

Hartmann H.E.K. 1993. *Aizoaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 37–69.

Kaden N.N. 1965. The fruit types of plants inhabiting the middle zone of the European part of the USSR. *Botanicheskii Zhurnal*, 50(6): 775–787. [Каден Н.Н. 1965. Типы плодов растений средней полосы европейской части СССР. *Ботанический журнал*, 50(6): 775–787.]

Krasylenko Y.A., Janošíková K., Kukushkin O.V. 2017. Juniper dwarf mistletoe (*Arceuthobium oxycedri*) in the Crimean Peninsula: novel insights into its morphology, hosts, and distribution. *Botany*, 95: 897–911. http://dx.doi.org/10.1139/cjb-2016-0289

Krasylenko Yu.A., Gleb R.Yu., Volutsa O.D. 2019. *Loranthus europaeus* (*Loranthaceae*) in Ukraine: an overview of distribution patterns and hosts. *Ukrainian Botanical Journal*, 76(5): 406–417. https://doi.org/10.15407/ukrbotj76.05.406

Kubitzki K. 1993. *Plumbaginaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid*, *Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 523–530.

Kubitzki K. 2003a. *Droseraceae.* In: *The families and genera of vascular plants.* Vol. 5. *Flowering plants. Dicotyledons: Malvales*, *Capparales and non-betalain Caryophyllales*. Eds K. Kubitzki, C. Bayer. Berlin; Heidelberg: Springer, pp. 198–202.

Kubitzki K. 2003b. *Frankeniaceae.* In: *The families and genera of vascular plants.* Vol. 5. *Flowering plants. Dicotyledons: Malvales*, *Capparales and non-betalain Caryophyllales*. Eds K. Kubitzki, C. Bayer. Berlin; Heidelberg: Springer, pp. 209–212.

Kühn U. 1993. *Chenopodiaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid*, *Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 253–280.

Kuijt J., Hansen B. 2015a. Fruits, seeds and seedlings. In: *The Families and Genera of Vascular Plants.* Vol. 12. *Flowering Plants. Eudicots. Santalales*, *Balanophorales*. Eds J. Kuijt, B. Hansen. Cham; Heidelberg: Springer. pp. 21–23. https://doi.org/10.1007/978-3-319-09296-6_4

Kuijt J., Hansen B. 2015b. *Loranthaceae*. In: *The Families and Genera of Vascular Plants.* Vol. 12. *Flowering Plants. Eudicots. Santalales*, *Balanophorales*. Eds J. Kuijt, B. Hansen. Cham; Heidelberg: Springer, pp. 73–119. https://doi.org/10.1007/978-3-319-09296-6_14

Kuijt J., Hansen B. 2015c. *Santalaceae*. In: *The Families and Genera of Vascular Plants.* Vol. 12. *Flowering Plants. Eudicots. Santalales*, *Balanophorales*. Eds J. Kuijt, B. Hansen. Cham; Heidelberg: Springer, pp. 143–165. https://doi.org/10.1007/978-3-319-09296-6_19

Kuijt J., Hansen B. 2015d. *Viscaceae*. In: *The Families and Genera of Vascular Plants.* Vol. 12. *Flowering Plants. Eudicots. Santalales*, *Balanophorales*. Eds J. Kuijt, B. Hansen. Cham; Heidelberg: Springer, pp. 169–185. https://doi.org/10.1007/978-3-319-09296-6_21

Leins P., Erbar C. 2010. *Flower and fruit: Morphology*, *ontogeny*, *phylogeny*, *function and ecology.* Stuttgart: Schweizerbart, 439 pp.

Levina R.E. 1957. *Modes of dispersal of fruits and seeds*. Moscow: Moscow State University, 358 pp. [Левина Р.Е. 1957. *Способы распространения плодов и семян*. Москва: Издательство Московского университета, 358 с.].

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. https://doi.org/10.3724/SP.J.1002.2008.08039

Maddala S., Aluri J.S.R. 2019. Pollination ecology of the species *Mollugo cerviana* (L.) Ser. (*Molluginaceae*). *Transylvanian Review of Systematical and Ecological Research*, 21(2): 13–22. https://doi.org/10.2478/trser-2019-0009

Morales-Briones D.F., Kadereit G., Tefarikis D.T., Moore M.J., Smith S.A., Brockington S.F., Timoneda A., Yim W.C., Cushman J.C., Yang Y. 2021. Disentangling sources of gene tree discordance in phylogenomic data sets: testing ancient hybridizations in *Amaranthaceae* s. l. *Systematic Biology*, 70(2): 219–235. http://doi.org/10.1093/sysbio/syaa066

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. [Мосякін С.Л. 2013. Родини і порядки квіткових рослин флори України: прагматична класифікація та положення у філогенетичній системі. *Український ботанічний журнал*, 70(3): 289–307.] https://doi.org/10.15407/ukrbotj70.03.289

Mosyakin S.L., Fedoronchuk M.M. 1999. *Vascular plants of Ukraine. A nomenclatural checklist*. Kyiv, M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, xxiii + 345 pp.

Mosyakin S.L., Mosyakin A.S. 2021. Lockdown botany 2020: some noteworthy records of alien plants in Kyiv City and Kyiv Region. *Ukrainian Botanical Journal*, 78(2): 96–111. https://doi.org/10.15407/ukrbotj78.02.096

Odintsova A. 2016. Loculicidal dehiscence of superior and inferior capsular fruits in *Myrtales*. *Studia Biologica*, 10(3–4): 129–140. [Одінцова А.В. 2016. Локуліцидне розкривання верхніх і нижніх коробчастих плодів у порядку Myrtales. *Studia Biologica*, 10(3–4): 129–140.] https://doi.org/10.30970/sbi.1003.504

Odintsova A.V. 2022. Morphogenesis of fruit as a subject matter for the carpological studies. *Ukrainian Botanical Journal*, 79(3): 169–183. [Одінцова А.В. 2022. Морфогенез плоду як предмет карпологічних досліджень. *Український ботанічний журнал*, 79(3): 169–183.] https://doi.org/10.15407/ukrbotj79.03.169

Odintsova A.V. 2023a. Morphological and taxonomical treatments of fruits in the subclass *Rosidae* Takht. of the flora of Ukraine. *Studia Biologica*, 17(2): 123–152. https://doi.org/10.30970/sbi.1702.715

Odintsova A. 2023b. Morphological fruit types in the monocots of the flora of Ukraine. In: *Status and biodiversity of the ecosystems of Shatskyi National Nature Park and other protected areas*: *Proceedings of the all-Ukrainian scientific conference (Lviv-Shatsk, 7–10 September, 2023)*. Eds Y.V. Tsaryk et al., Lviv: SPOLOM, pp. 56–59. [Одінцова А. 2023b. Морфологічні типи плодів однодольних рослин флори України. В зб.: *Стан і біорізноманіття екосистем Шацького національного природного парку та інших природоохоронних територій: матеріали всеукраїнської наукової конференції (Львів-Шацьк, 7–10 вересня 2023 р.)*. Ред. Й.В. Царик та ін. Львів: СПОЛОМ, с. 56–59.]

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. https://doi.org//10.15421/022151

Odintsova A., Fishchuk O., Danylyk I. 2022. Evolutionary and ecological estimation of fruit structure in monocotyledonous plants of the flora of Ukraine. *Studia Biologica*, 16(3): 83–100. [Одінцова А., Фіщук О., Данилик І. 2022. Еволюційна та екологічна інтерпретація структури плодів однодольних рослин флори України. *Studia Biologica*, 16(3): 83–100.] https://doi.org/10.30970/sbi.1603.688

Oyama S.O., Souza L.A., Muneratto J.C., Albiero A.L.M. 2010. Morphological and anatomical features of the flowers and fruits during the development of *Chamissoa altissima* (Jacq.) Kunth (*Amaranthaceae*). *Brazilian Archives of Biology and Technology*, 53(6): 1425–1432. https://doi.org/10.1590/S1516-89132010000600019

Pax F. 1889. *Plumbaginaceae***.** In: *Die natürlichen Pflanzenfamilien*. T. 4, Abt. 1. Eds H.G.A. Engler, K.A.E. Prantl. Leipzig: Engelman, pp. 116–125. https://doi.org/10.5962/bhl.title.4635

Pijl L. van der. 1982. *Principles of dispersal in higher plants*. 3nd ed., Berlin, Heidelberg; New York: Springer, 215 pp. https://doi.org/10.1007/978-3-642-87925-8

Polli A., Souza L.A., Almeida O.J.G. 2016. Structural development of the fruits and seeds in three mistletoe species of *Phoradendron* (*Visceae: Santalaceae*). *Rodriguesia*, 67(3): 649–659. https://doi.org/10.1590/2175-7860201667309

Rohweder O. 1965. Centrospermen-Studien 2. Entwicklung und morphologische Deutung Gynoeciums bei *Phytolacca*. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 84: 509–526.

Rohwer J.G. 1993. *Phytolaccaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 506–515.

Ronse De Craene L.P. 2013. Reevaluation of the perianth and androecium in *Caryophyllales*: implications for flower evolution. *Plant Systematics and Evolution*, 299: 1599–1636. https://doi.org/10.1007/s00606-013-0910-y

Ronse De Craene L.P. 2021. Gynoecium structure and development in core *Caryophyllales*: a matter of proportions. *Botanical Journal of the Linnean Society*, 195(3): 437–466. https://doi.org/10.1093/botlinnean/boaa048

Ronse De Craene L.P., Vanvinckenroye P., Smets E.F. 1997. A study of floral morphological diversity in *Phytolacca* (*Phytolaccaceae*) based on early floral ontogeny. *International Journal of Plant Sciences*, 158(1): 57–72. https://doi.org/10.1086/297414

Rosas-Reinhold I., Piñeyro-Nelson A., Rosas U., Arias S. 2021. Blurring the boundaries between a branch and a flower: Potential developmental venues in *Cactaceae*. *Plants*, 10: 1134. https://doi.org/10.3390/plants10061134

Roth I. 1977. Fruits of Angiosperms. In: *Encyclopedia of Plant Anatomy.* Vol. 10, part 1. Eds W. Zimmermann, S. Carlquist, P. Ozenda, H.D. Wulff. Berlin: Borntraeger, xvi + 675 pp.

Sattler R., Lacroix C. 1988. Development and evolution of basal cauline placentation: *Basella rubra*. *American Journal of Botany*, 75(6): 918–927. https://doi.org/10.2307/2444012

Sattler R., Perlin L. 1982. Floral development of *Bougainvillea spectabilis* Willd., *Boerhaavia diffusa* L. and *Mirabilis jalapa* L. (*Nyctaginaceae*). *Botanical Journal of the Linnean Society*, 84(3): 161–182. https://doi.org/10.1111/j.1095-8339.1982.tb00532.x

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. https://doi.org/10.3389/fevo.2022.784077

Sperling C.R., Bittrich V. 1993. *Basellaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 143–146.

Spjut R.W. 1994. A systematic treatment of fruit types. *Memoirs of the New York Botanical Garden*, 70: 1–182. Available at: http://www.worldbotanical.com/fruit_types.htm

Stevens P.F. (2001–onwards). *Angiosperm phylogeny website*. Version 14, July 2017 [and more or less continuously updated since]. Available at: http://www.mobot.org/MOBOT/research/APweb/ (Accessed 8 July 2024).

Sulakshana M., Raju A.J.S. 2018. Floral biology and pollination of carpet weeds, *Glinus lotoides* L. and *Glinus oppositifolius* (L.) Aug. DC. (*Molluginaceae*). *Anales de Biologia*, 40: 103–114. https://doi.org/10.6018/analesbio.40.12

Takhtajan A. 2009. *Flowering Plants*. 2nd ed. Dordrecht: Springer, 871 pp. https://doi.org/10.1007/978-1-4020-9609-9

Teryokhin E.S. 1977. *Parasitic flowering plants: evolution of ontogenesis and way of life*. Leningrad: Nauka, 220 pp. [Терехин Э.С. 1977. *Паразитные цветковые растения: эволюция онтогенеза и образа жизни.* Ленинград: Наука, 220 с.].

Townsend C. C. 1993. *Amaranthaceae*. In: *The families and genera of vascular plants.* Vol. 2. *Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Eds K. Kubitzki, J.G. Rohwer, V. Bittrich. Berlin; Heidelberg: Springer, pp. 70–91.

Vanvinckenroye P., Cresens E., Ronse De Craene L.P., Smets E. 1993. A comparative floral developmental study in *Pisonia*, *Bougainvillea* and *Mirabilis* (*Nyctaginaceae*) with special emphasis on the gynoecium and floral nectaries. *Bulletin du Jardin Botanique National de Belgique*, 62(1/4): 69–96. https://doi.org/10.2307/3668267

Volkens G. 1893. *Chenopodiaceae*. In: *Die natürlichen Pflanzenfamilien*. T. 3, Abt. 1a. Eds H.G.A. Engler, K.A.E. Prantl. Leipzig: Engelman, pp. 36–91. https://doi.org/10.5962/bhl.title.4635

Walker J.F., Yang Y., Feng T., Timoneda A., Mikenas J., Hutchison V., Edwards C., Wang N., Ahluwalia S., Olivieri J., Walker-Hale N., Majure L.C., Puente R., Kadereit G., Lauterbach M., Eggli U., Flores-Olvera H., Ochoterena H., Brockington S.F., Moore M.J., Smith S.A. 2018. From cacti to carnivores: Improved phylotranscriptomic sampling and hierarchical

homology inference provide further insight into the evolution of *Caryophyllales*. *American Journal of Botany*, 105(3): 446–462. https://doi.org/10.1002/ajb2.1069

Xiang Y., Zhang T., Zhao Y., Dong H., Chen H., Hu Y., Huang C.-H., Xiang J., Ma H. 2024. Angiosperm-wide analysis of fruit and ovary evolution aided by a newnuclear phylogeny supports association of the same ovarytype with both dry and fleshy fruits. *Journal of Integrative Plant Biology*, 66(2): 228–251. https://doi.org/10.1111/jipb.13618

Yao G., Jin J.-J., Li H.-T., Yang J.-B., Mandala V.S., Croley M., Mostow R., Douglas N.A., Chase M.W., Christenhuszh M. J.M., Soltis D.E., Soltis P.S., Smith S.A., Brockington S.F., Moore M.J., Yi T.-S., Li D.-Z. 2019. Plastid phylogenomic insights into the evolution of *Caryophyllales. Molecular Phylogenetics and Evolution*, 134: 74–86. https://doi.org/10.1016/j.ympev.2018.12.023

Zeng L., Zhang N., Zhang Q., Endress P.K., Huang J., Ma H. 2017. Resolution of deep eudicot phylogeny and their temporal diversification using nuclear genes from transcriptomic and genomic datasets. *New Phytologist*, 214: 1338–1354. https://doi.org/10.1111/nph.14503

Zheng H.C., Lu A.M., Hu Z.H. 2015. Floral organogenesis and ring meristem in *Phytolacca*. *American Journal of Plant Sciences*, 6(3): 445–455. Article ID: 54218. https://doi.org/10.4236/ajps.2015.63050

Морфологічний і таксономічний аналіз плодів у представників підкласу *Caryophyllidae* флори України

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Реферат. Підклас *Caryophyllidae* є парафілетичною групою у складі суперастерид, чий таксономічний склад був суттєво змінений за молекулярно-філогенетичними даними. У статті проаналізовано інформацію про морфологічне різноманіття плодів та структуру гінецею у представників *Caryophyllidae* у флорі України. Серед *Caryophyllidae* розпізнано три базові типи плодів: коробчасті, ягодоподібні та однонасінні. В анотованому переліку морфологічних типів плодів для кожної родини зазначено характеристики та морфологічну різноманітність плодів згідно з різними джерелами. Проаналізовано наявність апокарпних плодів, нижніх плодів, типи плацентації, а також функціональні типи плодів, пристосованих до автохорії, балістохорії, анемохорії, орнітохорії. Карпологічний спектр базових типів плодів на рівні родини, роду та виду свідчить про значне поширення коробчастих та однонасінних плодів (з невеликим переважанням однонасінних плодів на видовому рівні), при цьому ягодоподібні плоди виявлені лише у чотирьох видів.

Ключові слова: *Caryophyllales*, *Santalales*, верхня зав'язь, гінецей, морфологія, однонасінний плід, поперечно-розкривна коробочка, центрально-колончаста плацентація