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RESEARCH ARTICLE

Morphological fruit types of basal angiosperms in the flora of Ukraine

Anastasiya Odintsova

Ivan Franko National University of Lviv, Hrushevskyi str. 4, 79005 Lviv, Ukraine; anastasiya.odintsova@lnu.edu.ua

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Abstract

Basal angiosperms is a paraphyletic group of plants before branching eudicots and monocots. This group of angiosperms is of great scientific interest because it is the most ancient representative of the flowering plants retained for today. In Ukraine, both ANA-grade and magnoliids are presented. The species diversity of basal angiosperms is about half a percent of the flora of vascular plants of Ukraine, which caused a low research activity on this subject. The objectives of the present study were to elucidate the morphological diversity of fruits within basal angiosperms inhabiting Ukraine and estimate their evolutionary level and adaptations. The morphological diversity of fruit, according to our concept, comprises the structure of the gynoecium, ovary insertion, placentation, ovule number (pre-anthetic features), as well as principal fruit type and morphological adaptations for dispersal (post-anthetic features). The principal fruit types were distinguished according to the principles established previously for classifying fruits of monocots and rosids of the flora of Ukraine. Within the basal angiosperms of the flora of Ukraine, four principal fruit types were established: aggregate fruit, capsule, berry, and one-seeded fruit. Among them, the aggregate fruits are the most numerous. In Nymphaeaceae and Aristolochiaceae, which belong to the native flora of Ukraine, fruits are syncarpous, multi-seeded and inferior, while in the families cultivated in Ukraine (Annonaceae, Magnoliaceae, Calycanthaceae, Schisandraceae, and Lauraceae) fruits are apocarpous, superior and often have low seed number in a carpel. Each family has peculiar gynoecium and fruit features, which can be advanced as well as ancestral. In this article, the carpological spectrum was created to reveal the distribution of principal fruit types in families, genera, and species of the basal angiosperms of the flora of Ukraine. In these spectra, aggregate fruits are the most numerous; however, they occur in families of cultivated flora only. Most species have adaptation for dispersal by animals (birds or ants). The conclusion was made that in the native flora of Ukraine, the most derived members of basal angiosperms are retained.

Keywords: Magnoliidae, Nymphaeideae, evolution, aggregate fruit, gynoecium, fruiting ovary, seed

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Introduction

Basal angiosperms is a paraphyletic group of plants before branching eudicots and monocots (APG, 2016). Within this group, ANA-grade and magnoliids clade are recognized. The basal angiosperms in the flora of Ukraine include seven families belonging to two subclasses – Nymphaeidae J.W.Walker ex Takht. and Magnoliidae Novak ex Takht. (Mosyakin, 2013). According to the checklist of the flora of Ukraine (Mosyakin

& Fedoronchuk, 1999), 13 genera and about 33 species are presented within basal angiosperms. In the native flora of Ukraine, only members of the families Nymphaeaceae Salisb. and Aristolochiaceae Juss. occur, while the cultivated *Laurus nobilis* L. (Lauraceae) sometimes escaped and naturalized in the Crimea (Mosyakin, 2013). The part of the species diversity is about 0.55% of the flora of vascular plants of Ukraine. This is the lowest number of species diversity within the main clades of angiosperms (along with monocots and eudicots), which caused a low research activity on this subject; however, this group has great scientific value as the most ancient representatives of the flowering plants inhabiting the territory of the study. The objectives of the study were to elucidate the morphological diversity of fruits within basal angiosperms inhabiting Ukraine and estimate their evolutionary level and adaptations.

Material and methods

The morphological analysis of fruits in early angiosperms was carried out to compile a spectrum of principal types of fruits and to identify their features in comparison with monocots and eudicots. The morphological diversity of fruit, according to our concept (Odintsova, 2022), comprises the pre-anthetic features (structure of the gynoecium, ovary insertion, placentation, ovule number) as well as post-anthetic features (fruit type, dehiscence and morphological adaptations for dispersal). The annotated list of fruit characteristics was compiled using the sources which are provided in the results section. The number or genera and species within families of early angiosperms are given according to the taxonomic synopses (Mosyakin & Fedoronchuk, 1999; Kokhno & Parkhomenko, 2002).

The principal fruit types were distinguished according to the principles established for the classification of fruits of monocots (Odintsova et al., 2021, 2022) and rosids of the flora of Ukraine (Odintsova, 2023). Four principal fruit types were established for this group in the flora of Ukraine:

Aggregate fruit – polymerous apocarpous fruit composed of numerous or several free carpels with one to few seeds inside each carpel. Fruiting carpels can be follicles, berries or achenes.

Capsule – syncarpous multi-seeded dehiscent fruit. In early angiosperms, the capsule is found to be inferior and hexamerous.

Berry-like fruit – indehiscent syncarpous fruit with fleshy fruit wall.

One-seeded fruit – unilocular indehiscent fruit with a solitary seed. It can be berry-like or drupaceous and monomerous in the studied material.

Results

Subclassis Nymphaeidae

Nymphaeaceae (2 genera / 3 species) – fruit is a polymerous multi-seeded spongy berry, carpels are numerous; placentation is laminar (Fig. 1 A) (Schneider & Williamson, 1993). In *Nymphaea* L., ovary is partly inferior (petal and stamens are adnated to the fruit wall at different levels); carpels are free above the syncarpous ovary, forming carpel appendages encircling a stigmatic disc; floral axis is projected between carpels. Fruits of *Nymphaea* rupture irregularly underwater due to the enlargement of seeds and the volume of mucilage. Seeds are arillate, with mucilaginous arillus.

In *Nuphar* Sm., the ovary is superior, apically constricted and bear concave disc with stigmatic rays, carpels 5–30, fused. Fruit is ovoid, dehisces irregularly (or from the base to tip) releasing floating aerenchymatous white floating packets of seeds and filled by mucilage. Seeds are nonarillate, dispersed by water after the decay of aerenchyma (Smits et al., 1989; Hart & Cox, 1995; Padgett, 2007; Shiga, 2007).

According to Spjut (1994, p. 84), fruit in *Nymphaea* is hesperidium, "a simple indehiscent fruit with axile placentae and a pericarp that is internally fleshy and externally of a leathery rind". The fruit in *Nuphar* is ceratium, "fruit ... like a berry but is distinguished from it by the bursting of the outer stout layer of the pericarp; the inner lining of each locule detaches, and floats on the water like a sac containing the seeds" (Spjut, 1994, p. 57). Ceratium is a capsular fruit which opens by separation of pericarpium layers, with persistent placentas.

Figure 1. Peculiarities of fruits of early angiosperms in the flora of Ukraine: **A** – syncarpous polymerous berry with laminar placentation in *Nuphar lutea*, preanthetic stage; **B** – apocarpous polymerous berry in *Schisandra chinensis*; **C & D** – fleshy capsule in *Asarum europaeum*, general view (**C**) and longitudinally dissected one (**D**). **cc** – central column; **ov** – ovule. Scale bars: 1 mm.

In Nymphaeaceae, the carpels are united without forming an internal compitum, by the deformation of the basically ascidiate carpels. The floral axis expands between carpels which appear to be plicate. Stigma is sessile, in the stigma center there is a protrusion formed by the alongated floral apex; ovules numerous (up to 400 per carpel in *Nymphaea*) (Igersheim & Endress, 1998).

Both genera have unlignified fruit wall which dehisces to release seeds. In this reason, the definition of the fruit as berry is debatable,

like this: "The fruit of *Nuphar lutea* (L.) Sm. is a fleshy capsule (or dehiscent berry)..." (Hart & Cox, 1995). Sometimes, fruit in Nymphaeaceae is regadred as a coenocarpous fleshy berry-like multi-follicle, dispersed by water or endozoochorously (Didukh et al., 2004).

Schisandraceae (1 genus / 1 species – *Schisandra chinensis* (Turcz.) Baill.) – fruit is aggregate, composed of numerous globose 1–5-seeded carpels arranged spirally on elongated receptacle, a torus (Keng, 1993). Fruit is baccetum – apocarpous berry (Spjut, 1994). Carpels are ascidiate, ovules 2–5 (Igersheim & Endress, 1997). The receptacle elongates after flowering, resulting in raceme-like aggregate fruit, with small individual carpels, red at maturity, widely separated on the torus, and contain 1–2(–3) seeds (Saunders, 2000). Carpels 14–40 per flower, however, Saunders (2000) in the fig. 37 F just as in the studied material (Lviv city, Olena Pchilka str., cultivated), indicated some carpels as underdeveloped in the pendent fruit (Fig. 1 B). In the conditions of Kyiv, *S. chinensis* pruduces 13 to 34 red fruiting carpels per fruit with 1–2 seeds inside (Skrypchenko & Slyusar, 2020); ovules two per carpel (Sliusar, 2018).

Subclassis Magnoliidae

Annonaceae (1 genus / 1 species – *Asimina triloba* (L.) Dun.) – fruit is an apocarpous polymerous berry composed of 3–15 carpels; ovules numerous, biseriate; fruits dispersed by birds or bats (Kessler, 1993). Fruit is a baccetum, with fleshy indehiscent fruit wall, a sarcocarp (Spjut, 1994). Carpels are plicate (Igersheim & Endress, 1997).

Aristolochiaceae (2 genera / 2 species) – syncarpous hexamerous capsule. It is semi-inferior, fleshy, rupturing irregularly at ripening (*Asarum europaeum* L.). In *Aristolochia clematitis* L. the capsule is fully inferior, dry, dehisces septicidal-ventrally. Capsule septicidal or rupturing, placentation is axile (Huber, 1993). Spjut (1994) designated the fruit in *Aristolochia* L. species as ceratium or septicidal capsule. Ovary has synascidiate and symplicate zones in *Asarum*, and almost completely symplicate in *Aristolochia* (Igersheim & Endress, 1998). In *Aristolochia* stamens are adnated to the style forming a gynostemium. Ovules 2–10 per carpel, placentation partly axile in *Asarum* L.; and more that 12 ovules per carpel, placentation parietal in *Aristolochia* (Igersheim & Endress, 1998). In the studied material (Lviv city, Holosko forest), fruits of *Asarum europaeum* are crowned with three tepals, ovary is inferior, and seeds are not numerous, bear elaiosoma (Fig. 1 C, D).

Seeds are dispersed by ants in *Asarum* and by wind in *Aristolochia* (Didukh et al., 2004). The research of seed dispersal of *Asarum europaeum* and other spring geophytes in beech-dominated forests in Central Europe demonstrated that slugs *Arion rufus* L. (red slug) and *Limax cinereo-niger* Wolf (ash-grey slug) are common consumers of elaiosomes or entire seeds of ant-dispersed plants (Türke et al., 2010). The terrestrial gastropods can generally act as seed dispersers of myrmecochorous plants and even substitute myrmecochory, especially where ants are absent or uncommon (Türke et al., 2012). It was also revealed that diaspore removal rates in *Asarum europaeum* are low probably due to the small size of ants relative to heavy diaspores. Ant-plant relationships in that case are not mutualistic but rather neutral/slightly negative, because the plants do not obtain any benefits from their interactions with ants (Prokop et al., 2022).

Calycanthaceae (2 genera / 5 species – *Calycanthus* L. with 3 species and *Chimonanthus* Lindl. with 2 species) – fruit is indehiscent, dry, the carpels few to many, free, spirally arranged, uni-ovulate, enclosed in a cup-shaped receptacle (a pseudocarp); ovule basal (Kubitzki, 1993). In *Calycanthus*, achenes 15–35; in *Chimonanthus* achenes 5–15. In the conditions of the North Ukraine, *Calycanthus* species have fruits with 3–13 carpels / seeds inside (Gavrylyuk, 2015).

Seeds are toxic for mammals, so they germinate after dacay of external fruit coverings in the fallen fruits. Spjut (1994) designated the fruit as pometum – an apocarpous fruit of carpels embedded in a hypanthium with one cavity (like in *Rosa* L.). Carpels numerous (up to 35), free, spirally arranged, ovary plicate; ovules two, but only one of them (the lowest) develop seed (Endress & Igersheim, 1997). Carpellodes are situated on the upper rim of the floral cup, and persistent in fruit forming a woody crown around the orifice that includes the fruitlets.

Table 1. Principal fruit types in the families of basal angiosperms of the flora of Ukraine.

Basic fruit type	Subclasses and families
Aggregate fruit	**Magnoliidae**: Annonaceae *, Magnoliaceae *, Calycanthaceae * **Nymphaeidae**: Schisandraceae *
Capsule	**Magnoliidae**: Aristolochiaceae
Berry	**Nymphaeidae**: Nymphaeaceae
One-seeded fruit	**Magnoliidae**: Lauraceae*

Note. * – cultivated taxa.

Lauraceae (3 genera / 3 species – *Lindera* Thunb., *Cinnamomum* Schaeff., *Laurus* L.) – fruit is a one-seeded berry or a drupe with a weaky developed endocarp; carpel one, uni-ovulate, ovule pendulous; receptacle and peduncle of fruit enlarged and forming a cupule at the base of fruit (Rohwer, 1993). Fruits are dispersed by frugivorous birds. In *Laurus nobilis* L., endocarp is lignified, with "wavy walls" (Roth, 1977). For *Cinnamomum litsaeifolium* Thwaites, Spjut (1994) used the name of fruit – glans (ukr. – zholud) due to the cupule, a woody floral cup; and for *C. macrocarpum* Hook. fil., he uses the name amphisarcum, a berry-like indehiscent fruit with dry crust exocarp. Carpel one, ovary is ascidiate; ovule one, median, pendent (Endress & Igersheim, 1997).

Magnoliaceae (2 genera / 17 species) – fruits apocarpous, dry, woody; carpels are numerous, free, arranged spirally on the elongated receptacle; ovules two per carpel; fruiting carpels dehisce dorsally (in *Magnolia* Plum. ex L.) or indehiscent caducous samaroids (ukr. – krylatyj bahatohorishok) in *Liriodendron* L. In *Magnolia*, seeds are 1–2 per carpel, hanged on the elongated vessels of funiculi from the dehiscent, or opened fruit; testa has arilloid (Nooteboom, 1993). Carpels are plicate with short ascidiate zone; ovules mostly two in a carpel (Igersheim & Endress, 1997). According to Spjut (1994, p. 61), fruit in *Magnolia* is a coccetum, "a multiple fruit with dehiscent fruitlets opening along the dorsal and ventral sutures". In *M. tripetala* (L.) L., instead, Spjut (1994, p. 76) adopted the name fruit-follicetum, "a multiple fruit of dehiscing apocarps that open only along one suture, dorsally or ventrally". For *Liriodendron*, Spjut (1994, p. 108) recognized a samaretum, "a multiple fruit of winged indehiscent apocarps, the wing of each apocarp exceeding the length of the seed". The German botanists have a tradition to designate the fruit in *Magnolia* as legumes-fruit (germ. – die Hülse; die Hülsenfrucht; ukr. – bib). In this fruit, the fruiting carpels are legumes, they open by both ventral and dorsal dehiscense lines (Leins & Erbar, 2010; Kadereit et al., 2014).

Discussion

In basal angiosperms of the flora of Ukraine, both aggregate and simple fruits were found to be superior or inferior, syncarpous or monomerous apocarpous. Aggregate fruits occur in Schisandraceae, Annonaceae, Magnoliaceae, Calycanthaceae (Table 1). All these families are cultivated in Ukraine and have woody habits (Kokhno & Parkhomenko, 2002). Aggregate fruits are fleshy, berry-like (*Schisandra chinensis*, *Asimina triloba*), dry follicles with sarcotestal seeds (*Magnolia*), or multi-achene born on the conical receptacle (*Liriodendron*) or the invaginated receptacle (*Calycanthaceae*). Carpels are numerous and arranged spirally (Endress & Igersheim, 1997; Igersheim & Endress, 1997). In Nymphaeaceae and Aristolochiaceae the gynoecium is congenitally syncarpous, with a tendency to inferiority of the ovary. Fruits are fleshy untypical berries (Nymphaeaceae) or fleshy capsules (*Asarum*), or dry capsules (*Aristolochia*). These two families represent a high level of morphological progress in the female reproductive sphere. The high number of carpels in Nymphaeaceae may be equivocally a result of a secondary increase as well as a plesiomorphic condition (De Craene et al., 2003). In Aristolochiaceae, two trimerous condensed carpel whorls are presented. In Lauraceae the gynoecium is apocarpous and

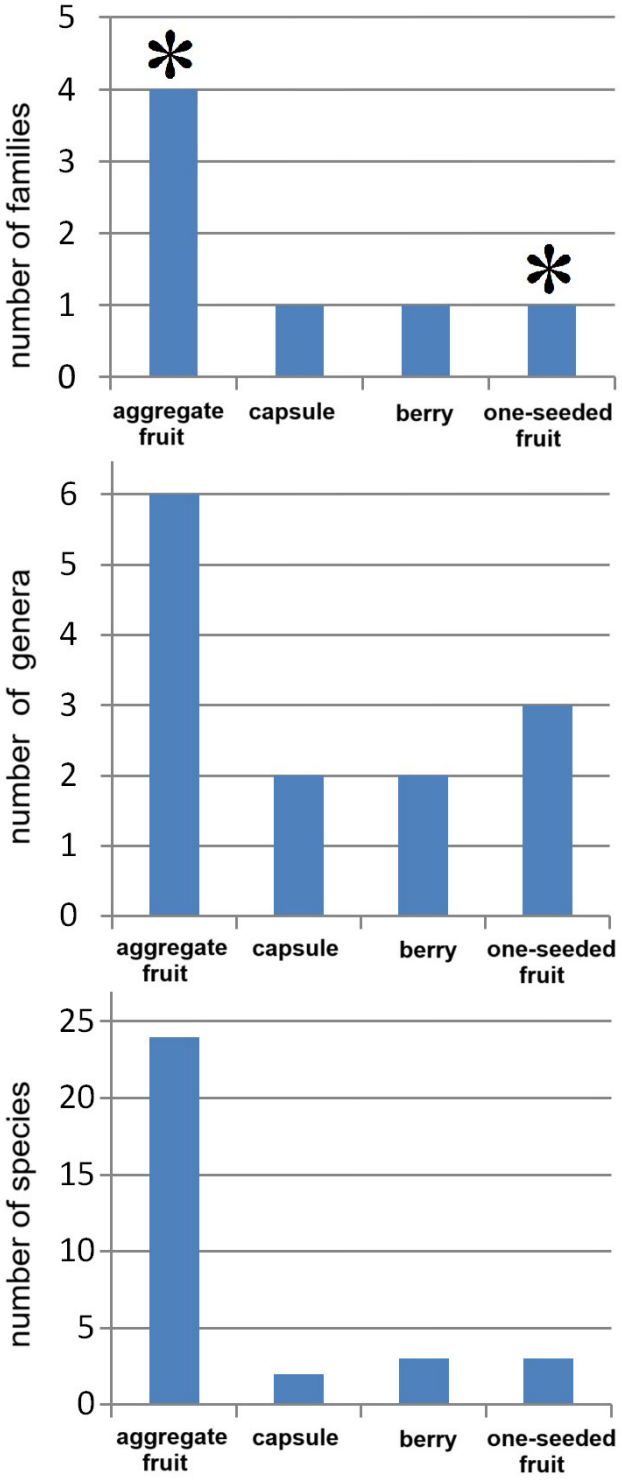

Figure 2. Distribution of principal fruit types in the families (**A**), genera (**B**), and species (**C**) of basal angiosperms in the flora of Ukraine. * – cultivated taxa.

monomerous; ovule solitary. In this family, the terminal stage of the gynoecium and fruit evolution is observed resulting in extremely reduced carpels' and ovules' number (De Craene et al., 2003).

Seed number in a carpel varies from many (Nymphaeaceae, Annonaceae) to few (Schisandraceae, Aristolochiaceae, Magnoliaceae) and one (Calycanthaceae, Lauraceae). In Nymphaeaceae, the highest number of ovules within basal angiosperms is regarded as a derived character (Endress & Igersheim, 2000). Placentation is axile, parietal or laminar in the gynoecium with numerous ovules, and basal or apical in monovulate carpels. Laminar placentation is very uncommon for angiosperms; it is regarded as a derived condition from marginal placentation (Shivaprakash & Bawa, 2022).

Within studied families, somewhat different adaptations to dispersal are evident which cause different fruit names of the representatives given by Spjut (1994). Namely, in Nymphaeaceae, fruit in *Nymphaea* is defined as hesperidium, and fruit in Nuphar – as ceratium. Fruit in *Magnolia* is defined as a coccetum, and fruit in *Liriodendron*, as a samaretum. In *Asarum europaeum* and *Aristolochia clematitis* capsules open by different lines and seeds are dispersed by different agents (wind or animals).

Within basal angiosperms of the flora of Ukraine, there were no monomerous multi-seeded fruits, nor schizocarps and multi-seeded pyrenaria found. Contrary to the monocots and rosids of the flora of Ukraine (Odintsova et al., 2021; Odintsova, 2023), there were no fruit with ambiguous gynoecium type found (syncarpous or apocarpous; monomerous or pseudomonomerous).

All studied families of basal angiosperns have peculiar and unique features of the fruit. In Nymphaeaceae, fruit has deformation of the gynoecium structure during the development and laminar placentation. In Schisandraceae, the fruit turn to be raceme-like inflorescence due to the elongation of the fruiting receptacle. In Schisandraceae, like in Annonaceae, a rare fruit type occurs, a polymerous apocarpous berry. In *Aristolochia*, the gynostemium is formed. In Calycanthaceae and Lauraceae, a hypanthium is formed enclosing whole carpels or only base of carpel. In *Magnolia*, the fruit is polymerous legume-like (ukr. – bahatobib).

Despite the fact that basal angiosperms are the most ancient group of flowering plants, not only the most primitive apocarpous fruits, but also a syncarpous inferior fruits have been described in its members. It is an evidence for early diversification of the morphological structure of the gynoecium in angiosperms. The polymerous gynoecium in some basal angiosperms may be a reversal derived from a whorled arrangement of several carpels. The cyclization and reduction of the gynoecium are common trends of the gynoecium evolution in basal angiosperms (De Craene et al., 2003).

In Schisandraceae, Nymphaeaceae, Annonaceae and Lauraceae fruit wall is fleshy or partly fleshy that is an adaptation to dispersal by birds or water (Nymphaeaceae).

The spectra of the distribution of principal fruit types in families, genera and species of basal angiosperms in the flora of Ukraine demonstrated, that the aggregate fruits are the most numerous (Fig. 2). Capsules, berries and one-seeded fruits are almost equally presented. In is notable that the most derived syncarpous and inferior fruits are revealed only in the taxa of the native flora of Ukraine, while aggregate and one-seeded superior fruits available only in cultivated taxa.

Conclusions

The present research revealed four principal fruit types within basal angiosperms of the flora of Ukraine. The most common are the aggregate fruits of numerous spirally arranged berries, follicles or achenes. In Lauraceae, the fruit is one-seeded and one-carpellate (monomerous apocarp). In the families of the native flora of Ukraine, Nymphaeaceae and Aristolochiaceae, the most derived characters of fruit occur (syncarpous gynoecium and inferior ovary). It could be evidence that only the most derived representatives of the ancient group spread on the moderate climate of Central Europe by natural ways. The adaptation for dispersal as well as morphological and morphogenetic features of fruits in basal angiosperms are revealed to be very diverse and should be more precisely examined in the Ukrainian flora.

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References

APG. (2016). 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

De Craene, R.L.P., Soltis, P.S., & Soltis, D.E. (2003). Evolution of floral structures in basal angiosperms. *International Journal of Plant Sciences, 164*(Suppl. 5), S329–S363. https://doi.org/10.1086/377063

Didukh, Y.P., Burda, R.I., Ziman, S.M., Korotchenko, I.A, Fedoronchuk, M.M., & Fitsaylo, T.V. (2004). *Ecoflora of Ukraine. Vol. 2.* Phytosociocenter, Kyiv. (In Ukrainian)

Endress, P.K., & Igersheim, A. (1997). Gynoecium diversity and systematics of the Laurales. Botanical *Journal of the Linnean Society, 125*(2), 93–168. https://doi.org/10.1111/j.1095-8339.1997.tb02250.x

Endress, P.K., & Igersheim, A. (2000). Gynoecium structure and evolution in basal angiosperms. *International Journal of Plant Sciences, 161*(S6), S211–S213. https://doi.org/10.1086/317572

Gavrylyuk, O. (2015). Peculiarities of ontogenesis of the genus *Calycanthus* L. species under conditions of Volyn Upland. *Plant Introduction, 67*, 64–68. (in Ukrainian). https://doi.org/10.5281/zenodo.2527002

Hart, K.H., & Cox, P.A. (1995). Dispersal ecology of *Nuphar luteum* (L.) Sibthorp & Smith: abiotic seed dispersal mechanisms. *Botanical Journal of the Linnean Society, 119*(1), 87–100. https://doi.org/10.1111/j.1095-8339.1995.tb00732.x

Huber, H. (1993). Aristolochiaceae. In K. Kubitzki, J.G. Rohwer, & V. Bittrich (Eds.), *The families and genera of vascular plants. Vol. 2. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families* (pp. 129–137). Springer, Berlin, Heidelberg.

Igersheim, A., & Endress, P.K. (1997). Gynoecium diversity and systematics of the Magnoliales and winteroids. *Botanical Journal of the Linnean Society, 124*, 213–271. https://doi.org/10.1111/J.1095-8339.1997.TB01792.X

Igersheim, A., & Endress, P.K. (1998). Gynoecium diversity and systematics of the paleoherbs. *Botanical Journal of the Linnean Society, 127*(4), 289–370. https://doi.org/10.1111/j.1095-8339.1998.tb02102.x

Kadereit, J.W., Körner, C., Kost, B., & Sonnewald, U. (2014). *Strasburger Lehrbuch der Pflanzenwissenschaften, 37 Auflage.* Springer, https://doi.org/10.1007/978-3-642-54435-4

Keng, H. (1993). Schisandraceae. In K. Kubitzki, J.G. Rohwer, & V. Bittrich (Eds.), *The families and genera of vascular plants. Vol. 2. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families* (pp. 589–591). Springer, Berlin, Heidelberg.

Kessler, P.J.A. (1993). Annonaceae. In K. Kubitzki, J.G. Rohwer, & V. Bittrich (Eds.), *The families and genera of vascular plants. Vol. 2. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families* (pp. 93–129). Springer, Berlin, Heidelberg.

Kokhno, M.A., & Parkhomenko, L.I. (Eds.). (2002). *Dendroflora of Ukraine. Wild and cultivated trees and shrubs. Angiosperms. Catalogue. Part. 1.* Phytosociocenter, Kyiv. (In Ukrainian)

Kubitzki, K. (1993). Calycanthaceae. In K. Kubitzki, J.G. Rohwer, & V. Bittrich (Eds.), *The families and genera of vascular plants. Vol. 2. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families* (pp. 197–199). Springer, Berlin, Heidelberg.

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

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. (in Ukrainian)

Mosyakin, S.L., & Fedoronchuk, M.M. (1999). *Vascular plants of Ukraine. A nomenclatural checklist.* M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv.

Nooteboom, H.P. (1993). Magnoliaceae. In K. Kubitzki, J.G. Rohwer, & V. Bittrich (Eds.), *The families and genera of vascular plants. Vol. 2. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families* (pp. 391–401). Springer, Berlin, Heidelberg.

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. (In Ukrainian). https://doi.org/10.30970/sbi.1603.688

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

Odintsova, A.V. (2023). 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.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

Padgett, D.J. (2007). A monograph of *Nuphar* (Nymphaeaceae). *Rhodora, 109*(937), 1–95. https://doi.org/10.3119/0035-4902(2007)109[1:AMONN]2.0.CO;2

Prokop, P., Fančovičová, J., & Hlúšková, Z. (2022). Seed dispersal by ants in three early-flowering plants. *Insects, 13*, Article 386. https://doi.org/10.3390/insects13040386

Rohwer, J.G. (1993). Lauraceae. In K. Kubitzki, J.G. Rohwer, & V. Bittrich (Eds.), *The families and genera of vascular plants. Vol. 2. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families* (pp. 366–390). Springer, Berlin, Heidelberg.

Roth, I. (1977). Fruits of angiosperms. In: W. Zimmermann, S. Carlquist, P. Ozenda, & H.D. Wulff (Eds.), *Encyclopedia of plant anatomy. Bd. 10. Teil 1* (pp. 1–675). G. Borntraeger.

Saunders, R.M.K. (2000). Monograph of *Schisandra* (Schisandraceae). *Systematic Botany Monographs, 58*, 1–146.

Schneider, E.L., & Williamson, P.S. (1993). Nymphaeaceae. In K. Kubitzki, J.G. Rohwer, V. Bittrich (Eds.), *The families and genera of vascular plants. Vol. 2. Flowering plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid families* (pp. 486–493). Springer, Berlin, Heidelberg.

Shiga, T. (2007). A systematic study of Nuphar (Nymphaeaceae) in Japan with special reference to the role of hybridization. Doctoral Dissertation. Kobe University. https://www.researchgate.net/publication/322300458_A_systematic_study_of_Nuphar_Nymphaeaceae_in_Japan_with_specieal_reference_to_the_role_of_hybridization

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*, Article 784077. https://doi.org/10.3389/fevo.2022.784077

Skrypchenko, N., & Slyusar, G. (2020). Seed productivity and reproduction features of *Schisandra chinensis* under conditions of the M.M. Gryshko National Botanical Garden. *Plant Introduction, 87/88,* 39–46. https://doi.org/10.46341/PI2020018

Sliusar, G. (2018). Peculiarities of *Schisandra chinensis* (Turcz.) Baill. flowering and fruiting under conditions of inroduction in the Right-Bank of Forest-Steppe of Ukraine. *Plant Introduction, 79*, 9–16. (in Ukrainian). https://doi.org/10.5281/zenodo.2277380

Smits, A.J.M., van Ruremonde, R., & van der Velde, G. (1989). Seed dispersal of three nymphaeid macrophytes. *Aquatic Botany, 35*(2), 167–180. https://doi.org/10.1016/0304-3770(89)90103-4

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

Türke, M., Andreas, K., Gossner, M.M., Kowalski, E., Lange, M., Boch, S., Socher, S.A., Müller, J., Prati, D., Fischer, M., Meyhöfer, R., & Weisser, W.W. (2012). Are gastropods, rather than ants, important dispersers of seeds of myrmecochorous forest herbs? *The American Naturalist, 179*(1), 124–131. https://doi.org/10.5061/dryad.p3p0621d

Türke, M., Heinze, E., Andreas, K., Svendsen S.M., Gossner M.M., & Weisser W.W. (2010). Seed consumption and dispersal of ant-dispersed plants by slugs. *Oecologia, 163*, 681–693. https://doi.org/10.1007/s00442-010-1612-6

Морфологічні типи плодів у базальних покритонасінних рослин флори України

Анастасія Одінцова

Львівський національний університет імені Івана Франка, вул. Грушевського, 4, Львів, 79005, Україна; anastasiya.odintsova@lnu.edu.ua

Базальні покритонасінні – це парафілетична група рослин до відокремлення еудікотів та монокотів. Ця група має велике наукове значення, оскільки охоплює найбільш давніх представників квіткових рослин, які збереглися до сьогодні. В Україні представлені як ANA-града, так і клада магноліїд. Видове різноманіття базальних покритонасінних становить лише приблизно півпроцента від усіх судинних рослин України, що зумовлює незначну кількість досліджень цієї групи. Метою цього дослідження є висвітлення морфологічної різноманітності плодів серед базальних покритонасінних флори України та оцінка їхнього еволюційного рівня і адаптацій. Згідно з нашою концепцією, морфологічна різноманітність плодів охоплює структуру гінецею, положення зав'язі, плацентацію, кількість насінних зачатків (пре-антетичні ознаки) та тип плоду і морфологічні адаптації до рознесення (пост-антетичні ознаки). Основні типи плодів виділялися згідно з попередньо встановленими принципами, застосованими для однодольних рослин та розидів флори України. У межах базальних покритонасінних флори України було виділено чотири основні типи плодів: збірний плід, коробочка, ягода, однонасінний плід. Серед них збірні плоди були найбільш поширені. У Nymphaeaceae та Aristolochiaceae, які належать до природної флори України, плоди синкарпні, нижні, багатонасінні, позаяк у родинах з культурної флори України (Annonaceae, Magnoliaceae, Calycanthaceae, Schisandraceae та Lauraceae) плоди апокарпні, верхні та з малонасінними плодиками. У кожній родині були виявлені особливі риси гінецею і плоду, серед них були і просунуті, і примітивні ознаки. У статті представлені карпологічні спектри розподілу основних типів плодів серед родин, родів і видів базальних покритонасінних флори України. У цих спектрах збірні плоди переважають, однак, вони виявлені виключно в родинах культурної флори. Більшість видів мають адаптації до рознесення тваринами (птахами або мурахами). Зроблений висновок про переважання в природній флорі України найбільш просунутих представників базальних покритонасінних.

Ключові слова: Magnoliidae, Nymphaeideae, еволюція, збірний плід, гінецей, зав'язь, насінина